Widespread consumption-dependent systematic error in fish bioenergetics models and its implications

Przemyslaw G. Bajer, Gregory W. Whitledge, and Robert S. Hayward

Abstract: Data from laboratory evaluations of seven fish bioenergetics models (BEMs) were used to investigate possible associations between BEM prediction error in relative growth rate (RGR_{error}) and levels of model input variables: mean daily food-consumption rate and fish body weight. Correlation between RGR_{error} and fish body weight was found in three BEMs applied under submaintenance feeding conditions. A strong correlation between RGR_{error} and mean daily consumption level was observed in all models over full consumption ranges; consumption level explained 70%–96% of variation in RGR_{error}. All BEMs underestimated (by 2- to 5-fold) growth at lower consumption levels and overestimated (by 2- to 3-fold) growth at higher consumption levels. RGR_{error} values associated with higher consumption levels were greater (up to 22 $cal \cdot g^{-1} \cdot day^{-1}$) than those at lower consumption levels (up to 10 $cal \cdot g^{-1} \cdot day^{-1}$). Correlation between consumption rate and RGR_{error} in all seven models indicates widespread systematic error among BEMs that likely arises from deficiencies in consumption-dependent model parameters. Results indicate that many BEMs are substantially inaccurate when predicting fish growth from higher feeding rates or estimating consumption from higher growth rates, even when higher consumption levels or growth episodes are of short duration. Findings obtained under submaintenance feeding conditions indicate that additional body-weight- and consumption-dependent terms should be added to BEM subequations for routine metabolism to account for metabolic reduction.

Résumé : Les données des évaluations en laboratoire de sept modèles bioénergétiques (BEM) de poissons nous ont servi à étudier les associations possibles entre l'erreur de prédiction par les BEM du taux relatif de croissance (RGR_{erreur}), d'une part, et la valeur des variables d'entrée des modèles, soit le taux journalier moyen de consommation de nourriture et la masse corporelle des poissons, d'autre part. Il existe une corrélation entre RGR_{erreur} et la masse corporelle des poissons dans trois des BEM utilisés dans des conditions d'alimentation inférieures au niveau de maintien (SMFC). Il y a aussi une forte corrélation entre RGR_{erreur} et le taux journalier moyen de consommation dans tous les modèles sur toute l'étendue des taux de consommation; le taux de consommation explique 70–96 % de la variation de RGR_{erreur}. Tous les BEM sous-estiment la croissance (par un facteur de 2–5) aux faibles taux de consommation et la surestiment (par un facteur de 2–3) aux taux de consommation plus élevés. Les RGR_{erreur} associées aux taux plus élevés de consommation sont plus grandes (pouvant atteindre 22 $cal \cdot g^{-1} \cdot jour^{-1}$) que celles liées aux taux de consommation plus faibles (atteignant 10 $cal \cdot g^{-1} \cdot jour^{-1}$). La corrélation entre le taux de consommation et RGR_{erreur} dans les sept modèles indique qu'il y a une erreur systématique générale dans les BEM qui provient vraisemblablement d'imprécisions des paramètres des modèles reliés à la consommation. Nos résultats montrent que plusieurs BEM sont erronés dans la prédiction de la croissance des poissons à partir des taux d'alimentation élevés et dans l'estimation de la consommation à partir de taux de croissance élevés, même lorsque les épisodes de forte consommation ou de forte croissance sont de courte durée. Dans les conditions SMFC, nos résultats indiquent qu'on doit ajouter aux sous-équations du métabolisme ordinaire des BEM des termes additionnels pour la masse corporelle et la consommation, afin de tenir compte de la réduction du métabolisme.

[Traduit par la Rédaction]

Introduction

Construction and application of fish bioenergetics models (BEMs) have increased substantially in the last decade (Hewett and Johnson 1987; Hanson et al. 1997; Bajer et al. 2004). Models for almost 40 fish species are now readily available through user-friendly software (Hanson et al. 1997) while many others exist in various formats. BEMs are appealing because they are based on balanced, energy-fate equations that have been thought to promote reasonable predictive behavior. These models have been widely used to evaluate factors that constrain fish growth (Hayward and

Received 6 August 2003. Accepted 27 July 2004. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 26 January 2005.
J17692

P.G. Bajer, G.W. Whitledge, and R.S. Hayward.[1] Department of Fisheries and Wildlife Sciences, 302 Anheuser–Busch Natural Resources Building, University of Missouri–Columbia, Columbia, MO 65211-7240, USA.

[1] Corresponding author (e-mail: HaywardR@missouri.edu).

doi: 10.1139/F04-159

Margraf 1987; Hill and Magnuson 1990), impacts of fish predation on prey populations (Jones et al. 1993; Rand et al. 1995; Kershner et al. 1999), contaminant bioaccumulation in fishes (Jackson 1996), and waste loads from aquaculture (Axler et al. 1994). They have also been applied to enhance understanding of basic ecological processes such as the role of fish in lake nutrient cycling (Schindler and Eby 1997), and commonly serve as subcomponents of individual-based models of fish life history and population dynamics (Trebitz 1991; Rose and Cowan 1993) and other model types (Hayes et al. 2000; Burke and Rice 2002). Unquestionably, BEMs are contributing significantly to current perceptions of what is true in many of the less directly observable aspects of aquatic ecology, fisheries management, and aquaculture.

In fact, however, most BEMs have not been well evaluated over the ranges of conditions to which they have been applied. Rigorous, independent evaluations of BEMs under controlled laboratory conditions are disproportionately rare relative to the high and increasing number of times they have been applied. Laboratory-based tests of BEMs can greatly reduce the uncertainty inherent in field-based evaluations, because model input and output variables, including daily food consumption, growth rate, diet composition, predator and prey caloric densities, and fish thermal experience can be determined with much greater accuracy. Because laboratory evaluations are more likely to correctly identify errors in BEMs, they are essential for assuring model accuracy and for facilitating model improvement (Ney 1993; Bajer et al. 2003). Despite their limited number relative to field-based evaluations, laboratory evaluations of fish BEMs have provided valuable insights into model strengths and weaknesses. Such evaluations have indicated that BEM predictions may not be equally accurate over the ranges of conditions to which they are applied. For example, BEMs have exhibited varying degrees of performance associated with different ration levels (Cui and Wootton 1989; Whitledge and Hayward 1997), fish body weights (Bajer et al. 2004), and temperatures (Hartman and Brandt 1993; Chipps et al. 2000). However, experimental designs and analytical approaches used in laboratory evaluations have tended not to facilitate identification of error sources in BEMs, so model-improvement efforts have been rare.

A recent evaluation of two BEMs based on laboratory-derived consumption and growth data for yellow perch (*Perca flavescens*) (Bajer et al. 2003) showed that growth-prediction error was strongly correlated with mean daily food consumption (a BEM input variable) in both models. Both BEMs underestimated growth rate at lower consumption levels and overestimated growth rate at higher consumption levels, albeit to differing degrees. Madenjian and O'Connor (1999) found similar error in a lake trout (*Salvelinus namaycush*) BEM. Identification of consumption-dependent prediction error in these three BEMs suggests that their internal subequations for calculating energy costs of egestion, excretion, and specific dynamic action are likely error sources, because each involves consumption dependence (Bajer et al. 2003). In a yet more recent laboratory evaluation (Bajer et al. 2004), mean daily consumption level was again found to be correlated with growth-prediction error in a white crappie (*Pomoxis annularis*) BEM, explaining approximately 80% of total model prediction error. In this BEM, fish body weight was also found to be correlated with growth-prediction error, particularly for fish feeding at submaintenance levels.

Finding a similar correlation between growth-prediction error and consumption level in four BEMs suggested that consumption-dependent systematic error may be widespread among BEMs. To further substantiate this, we reevaluated data from published laboratory evaluations of three additional BEMs for the presence of consumption-dependent error. The presence of body-weight-dependent error, as was observed in the white crappie model, was also further explored in six BEMs. We show the frequency of occurrence of consumption- and body-weight-dependent error across a total of seven BEMs, and portray the range of magnitude of consumption-dependent error that exists among these models. Through modeling we also demonstrate the importance of consumption-dependent error in BEMs and show why its presence may often be overlooked in model evaluations. Types of BEM applications that may be most prone to this error are suggested, and insights are given into potential error sources within BEMs. Our findings demonstrate a critical need to evaluate and improve predictive accuracies of fish BEMs.

Materials and methods

We reevaluated data from published laboratory evaluations of three BEMs that provided sufficient information to explore possible consumption-dependent growth-prediction error. These include evaluations of BEMs for largemouth bass (*Micropterus salmoides*) (Whitledge and Hayward 1997), smallmouth bass (*Micropterus dolomieu*) (Whitledge et al. 2003), and bluegill (*Lepomis macrochirus*) (Whitledge et al. 1998). Data from laboratory evaluations of four additional BEMs for which consumption-dependent growth-prediction error has previously been identified were included so that the nature of this type of error could be broadly portrayed across a total of seven BEMs. These four evaluations involved BEMs for lake trout (Madenjian and O'Connor 1999), yellow perch and Eurasian perch (*Perca fluviatilis*) (Bajer et al. 2003), and white crappie (Bajer et al. (2004) this issue). Body-weight dependence of growth-prediction error, previously detected only in the white crappie BEM (Bajer et al. 2004), was explored in the six other BEMs identified above. We did not assess temperature influences (another primary BEM input variable) on prediction errors in the seven BEMs because, for the most part, laboratory evaluations of these models were performed over narrow temperature ranges (but see Bajer et al. 2004).

For each model, observed ($\mathrm{RGR_O}$; $\mathrm{cal\cdot g^{-1}\cdot day^{-1}}$, 1 cal = 4.184 J) and predicted ($\mathrm{RGR_P}$; $\mathrm{cal\cdot g^{-1}\cdot day^{-1}}$) relative growth rates were determined as

$$(1)\qquad \mathrm{RGR_O} = \frac{O_\mathrm{f} - O_\mathrm{i}}{n\,\overline{O}} \cdot \mathrm{ED_{predator}}$$

and

$$(2)\qquad \mathrm{RGR_P} = \frac{P_\mathrm{f} - O_\mathrm{i}}{n\,\overline{O}} \cdot \mathrm{ED_{predator}}$$

where O_f, P_f, and O_i are the observed and predicted final weights and observed initial fish weight for each modeling interval, respectively; $\overline{O}$ is the mean observed fish weight

Table 1. Experiment durations, total number of modeling intervals (number of fish × number of experimental intervals), and ranges of fish body weight, daily consumption level, and temperature for laboratory evaluations of bioenergetics models (BEMs).

BEM	Duration of exp. (days)	Total modeling interval	Fish body weight (g)	Daily consumption (% body weight·day^{-1}; cal·g^{-1}·day^{-1})[†]	Temp. (°C)	Model source
Largemouth bass	63*	24	141–292	1.4 –3.8 (17–46)	22, 27	Hanson et al. 1997
Smallmouth bass	63*	21	121–262	1.7–5.2 (16–48)	22, 27	Whitledge et al. 2003
Bluegill	105–112	42	9–52	0.6–2.2 (15–56)	24	Hanson et al. 1997
Lake trout	320–407	12	713–3240	0.2–1.2 (3.5–18)	3.1–10.2	Hanson et al. 1997
Yellow perch	125–144*	347	18–35	0–3.5 (0–77)	21	Hanson et al. 1997
Eurasian perch	125–144*	347	18–35	0–3.5 (0–77)	21	Karås and Thoresson 1992
White crappie	63–70*	39	72–341	0.5–7.3 (4.3–91)	23–30	Bajer et al. 2004

*Study for which values of relative growth rate error (RGR$_{error}$; cal·g^{-1}·day^{-1}) were determined separately over multiple 10- to 21-day experiment subintervals for which temperature and applied ration levels were constant. For other studies RGR$_{error}$ values were determined over the full modeled growth trajectories. In such cases the number of modeled intervals equals the number of fish used in experiments. References containing details on each BEM are provided.

[†] 1 cal = 4.184 J.

during the interval; n is the number of days in the modeling interval; and ED$_{predator}$ is fish energy density (cal·g^{-1}). The relative growth-rate-prediction error (RGR$_{error}$; cal·g^{-1}·day^{-1}) was calculated as the difference between predicted and observed relative growth rates (RGR$_{error}$ = RGR$_P$ – RGR$_O$) for each model.

For all but the lake trout model, values of RGR$_O$, RGR$_P$, and RGR$_{error}$ were determined from multiple model-predicted and laboratory-observed growth trajectories of individual fish. For the lake trout model these values were calculated from group means of initial and final fish body weights reported in Madenjian and O'Connor (1999, their tables 3 and 4). Durations of modeling intervals used for calculating RGR$_O$, RGR$_P$, and RGR$_{error}$ were the same as those used in the original evaluation studies (Table 1); some studies (lake trout, Madenjian and O'Connor 1999; hybrid bluegill, Whitledge et al. 1998) used single modeling intervals that spanned the full durations of experiments, while others involved multiple subintervals for which temperature and fish feeding levels were consistent (Table 1).

To permit direct comparisons of error among models, RGR$_{error}$ values were expressed in cal·g^{-1}·day^{-1} (converted from g·g^{-1}·day^{-1}) to standardize for differences in fish energy densities across the seven model-evaluation data sets. Values of fish energy density were determined as in the original BEM-evaluation studies. Fish energy densities were modeled as constant values in published laboratory evaluations of the bluegill, largemouth bass, and smallmouth bass BEMs. Various values of fish energy density were used in the published evaluations of BEMs for lake trout, yellow perch, Eurasian perch, and white crappie.

For each BEM, RGR$_{error}$ values were regressed against corresponding mean observed daily consumption rates (cal·g^{-1}·day^{-1}) across all modeling intervals. Regressions of RGR$_O$ and RGR$_P$ values against corresponding mean observed daily consumption rates were also performed for each BEM so that both proportional and absolute BEM prediction error could be determined across consumption levels. A third set of regressions was performed to explore possible relationships between RGR$_{error}$ values and corresponding mean observed fish body weights for each model. For each BEM, regressions involving fish body weight were run over full ranges of consumption level and separately over submaintenance feeding conditions when these were present.

Errors for BEM estimates of consumption were not evaluated because these have consistently been of similar magnitude as RGR$_{error}$ values over broad ranges of conditions, but in the opposite direction (Bajer et al. 2003; Bajer et al. 2004). When significant relationships have been observed between RGR$_{error}$ and consumption level or fish body weight, corresponding relationships between consumption-prediction error and these two input variables have been likewise significant but with slopes of opposite sign (Bajer et al. 2004).

We demonstrate the effect that even short periods of relatively high consumption level can have on growth-prediction error when a BEM containing consumption-dependent error is used. We used the bluegill BEM (Hanson et al. 1997) to predict observed 22-day growth trajectories for two groups of hybrid bluegill (F$_1$ female *Lepomis cyanellus* × male *L. macrochirus*), one in which fish fed consistently at low to moderate rates (control group) and a second in which fish fed at relatively high rates over an early portion of the 22-day interval (treatment group). Daily food-consumption and growth data for the hybrid bluegill were obtained from a selected 22-day segment of a 105-day laboratory experiment (Whitledge et al. 1998). Control fish that had been fed continually ad libitum before and during the 22-day period consumed only 1.0%–1.9% body weight·day^{-1}, on average, throughout the 22 days. In contrast, the treatment group that was food-deprived for 14 days just prior to the 22-day period consumed, on average, 8.0% body weight·day^{-1} on the first day of refeeding, whereupon consumption rates declined to 3.5% and 1.6% (moderate feeding levels) by days 12 and 22, respectively. Mean body weights of control and treatment fish were similar (15.9 and 17.3 g, respectively), and both groups experienced a constant temperature of 24 °C. A mean body weight trajectory (g) was predicted by the bluegill BEM for each group based on known temperature and directly determined group-specific mean daily food consumption (g). The accuracy of growth predictions was evaluated by comparing predicted and observed mean growth trajectories for each group. Predictive error was presented as the percent difference between predicted and observed mean

Table 2. Coefficients and statistics for regression relationships between $\text{RGR}_{\text{error}}$ ($\text{cal}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$; 1 cal = 4.184 J) and mean daily consumption rate (MCON; $\text{cal}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$) for each of the seven BEMs evaluated.

BEM	β_0	β_1	F	df	r^2
Largemouth bass	–7.58	0.42	104.9	1, 22	0.82
Smallmouth bass	–6.87	0.28	56.2	1, 19	0.74
Bluegill	–21.1 (–5.65)	6.11 (0.17)	561.5	1, 40	0.93
Lake trout	–3.43 (–1.60)	1.76 (0.19)	235.1	1, 10	0.96
Yellow perch	–11.5	0.45	1808.9	1, 345	0.83
Eurasian perch	–8.32	0.26	815.2	1, 345	0.70
White crappie	–5.99	0.32	180.3	1, 37	0.83

Note: All regression relationships were highly significant ($p < 0.0001$). Regression relationships for all BEMs were linear ($\text{RGR}_{\text{error}} = \beta_0 + \beta_1 \cdot \text{MCON}$), except for the lake trout and bluegill models, which were of the form $\text{RGR}_{\text{error}} = \beta_0 + \beta_1 \cdot \ln(\text{MCON})$. To facilitate comparisons of coefficient values among all seven models, β_0 and β_1 values for linear regression models are also shown parenthetically for the bluegill and lake trout models (linear models fit the data reasonably well for these two BEMs).

body weights (g) on each day of the 22-day modeling interval for both groups.

Results

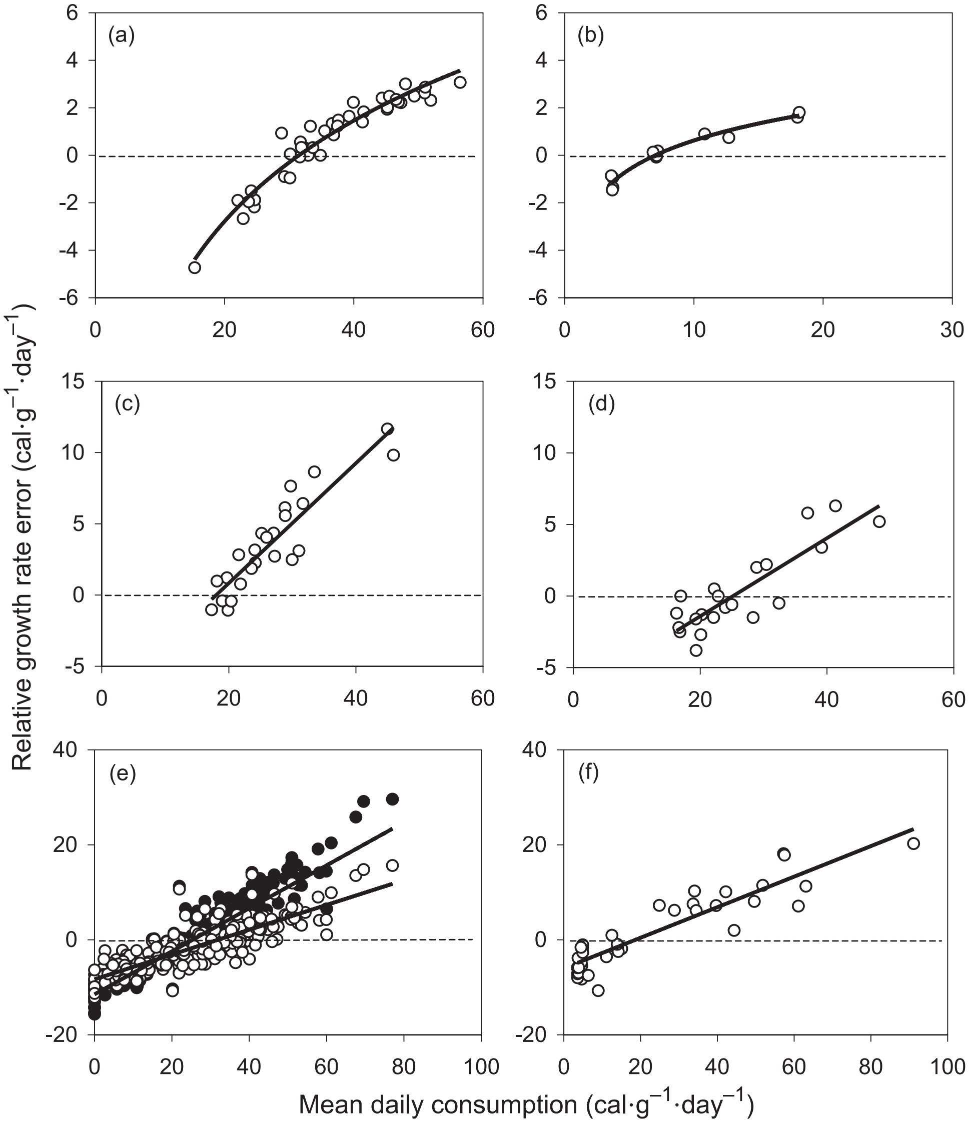
Significant positive regression relationships were observed between $\text{RGR}_{\text{error}}$ values and corresponding mean daily consumption levels for all seven BEMs (Table 2). Mean daily consumption level accounted for between 70% (Eurasian perch BEM) and 96% (lake trout BEM) of the total variation in $\text{RGR}_{\text{error}}$ across all models. All BEMs underestimated growth rates at lower ration levels and overestimated growth at higher ration levels (Fig. 1), clearly demonstrating the widespread presence of systematic model error. Models exhibited zero $\text{RGR}_{\text{error}}$ at intermediate consumption levels, which varied among the models for different species, and ranged from 8 $\text{cal}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ for the lake trout model to about 35 $\text{cal}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ for the bluegill and yellow perch models. Slopes of regression models relating $\text{RGR}_{\text{error}}$ to mean daily consumption level varied more than 2-fold across the seven BEMs (Table 2); higher slope values indicated a greater tendency for a BEM to over- and under-estimate growth rates at higher and lower consumption levels, respectively. Regression slopes were lowest for the bluegill (0.17) and lake trout (0.19) models and highest for the yellow perch (0.45) and largemouth bass (0.42) models.

Over- and under-estimation of growth rates at high and low ration levels were substantial. At higher consumption levels (35–80 $\text{cal}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$) the most-error-prone yellow perch model overestimated observed relative growth rates by 2- to 3-fold (5–21 $\text{cal}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$), while the least-error-prone bluegill model overestimated growth rates by 15%–50% (0.7–5 $\text{cal}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$; Fig. 2). At lower consumption levels (<12 $\text{cal}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$) $\text{RGR}_{\text{error}}$ values expressed on proportional bases were even greater; the yellow perch and bluegill BEMs underestimated observed growth rates by 5- and 2.5-fold, respectively. However, these higher proportional errors at low consumption levels arose mainly from the effect of lower observed growth rates in denominators; absolute errors associated with low consumption levels were generally lower (approximately 6 $\text{cal}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$) than those associated with higher consumption levels (Fig. 2). $\text{RGR}_{\text{error}}$ values observed for the other five models were intermediate to those determined for the yellow perch and bluegill models.

The white crappie BEM had exhibited a significant positive relationship ($p \leq 0.0001$) between $\text{RGR}_{\text{error}}$ and observed mean body weight, but only under conditions where fish were feeding at submaintenance levels (see Bajer et al. 2004). Likewise, no significant body-weight dependence of $\text{RGR}_{\text{error}}$ was found for any of the six other BEMs ($p > 0.05$) when evaluation data sets included broad ranges of consumption levels. However, the yellow perch and Eurasian perch models, whose evaluations also included fish fed at submaintenance levels, both also showed significant positive linear relationships ($p < 0.05$) between $\text{RGR}_{\text{error}}$ and mean body weight under submaintenance feeding conditions. For both models, as for the white crappie model, weight loss was more substantially overpredicted for smaller fish than for larger fish. Hence, all three of the BEMs whose evaluations included submaintenance feeding showed similar body-weight dependencies under these conditions.

When applied to the control hybrid bluegill group that fed continually at low to moderate levels (1.0%–1.9% body $\text{weight}\cdot\text{day}^{-1}$), the least-error-prone bluegill BEM accurately predicted mean growth rate over the 22-day period. The growth prediction error remained below 2.5% of observed mean body weight (Fig. 3*a*). However, the same model severely overestimated growth of the treatment hybrid bluegills, whose consumption level was initially high (8% body $\text{weight}\cdot\text{day}^{-1}$) but then declined over the 22-day period to levels similar to those of control fish. The growth prediction error for this group reached 29% of observed mean body weight by the end of the 22-day simulation (Fig. 3*b*). Of the total growth-prediction error that had accumulated by the end of the 22-day model run for treatment fish, 66% and 93% developed within the first 7 and 14 days of the simulation, when daily consumption levels averaged 5.75% and 3.39% body $\text{weight}\cdot\text{day}^{-1}$, respectively (Fig. 4). Relatively little additional error accumulated during the final 8 days of simulation, when consumption levels were mostly moderate (between 1.64% and 2.77% body $\text{weight}\cdot\text{day}^{-1}$), indicating that model predictions were essentially in agreement with the observed growth pattern during this time. The substantial error that accumulated during simulation days 1–14 under higher consumption levels was not diminished by the lower

Fig. 1. Relationships between relative growth rate prediction error (RGR_{error}; the difference between predicted and observed relative growth rates ($cal·g^{-1}·day^{-1}$; 1 cal = 4.184 J)) and mean daily consumption rate (also $cal·g^{-1}·day^{-1}$) determined from laboratory evaluations of seven bioenergetics models (BEMs). (*a*) Bluegill, *Lepomis macrochirus* (Whitledge et al. 1998). (*b*) Lake trout, *Salvelinus namaycush* (Madenjian and O'Connor 1999). (*c*) Largemouth bass, *Micropterus salmoides* (Whitledge and Hayward 1997). (*d*) Smallmouth bass, *Micropterus dolomieu* (Whitledge et al. 2003). (*e*) Yellow perch, *Perca flavescens* (●), and Eurasian perch, *Perca fluviatilis* (○) (Bajer et al. 2003). (*f*) White crappie, *Pomoxis annularis* (Bajer et al. 2004).



consumption levels that followed in the final 8 days of the modeling interval.

Discussion

Results showed that all seven of the examined BEMs contained systematic error that was associated with consumption rate. Finding significant positive relationships between food-consumption level and RGR_{error} that transected zero-error reference lines in all seven models indicates that consumption-dependent error is common among BEMs. This apparently widespread error can be substantial, resulting in over- or under-estimation of growth rates by as much as 2- to 5-fold when these models are applied under conditions involving relatively high or low consumption levels. Less, but potentially important error can occur at intermediate consumption levels as well. We expect that the errors in predicting fish growth rates that we observed will be of similar magnitude when BEMs are used to estimate consumption levels from high or low growth rates, except in the opposite direction, as demonstrated for the white crappie model by Bajer et al. (2004). Symmetry of consumption- and growth-prediction error (relative to the zero-error axis) tends to result under a given set of growth conditions because growth and consumption variables occur on opposite sides of the energy-balance equation at the core of BEMs; for example, underestimation of a fish's energy costs by a BEM will lead to overestimation of its growth and underestimation of its energy consumption.

Although our findings showed that BEM predictions of growth rate became substantially inaccurate at both high and low consumption levels, predictive inaccuracy was greatest

Fig. 2. Comparisons of observed (●) and BEM-predicted (○) relative growth rates (cal·g^{-1}·day^{-1}; 1 cal = 4.184 J) in relation to mean daily consumption rates (also cal·g^{-1}·day^{-1}) determined from laboratory evaluations of BEMs for bluegill, *Lepomis macrochirus* (Whitledge et al. 1998) (*a*), and yellow perch (Bajer et al. 2003) (*b*). Among all seven BEMs considered, the accuracy of growth predictions versus consumption level was greatest (the least difference between observed and predicted regression lines) for the bluegill model and lowest for the yellow perch model.

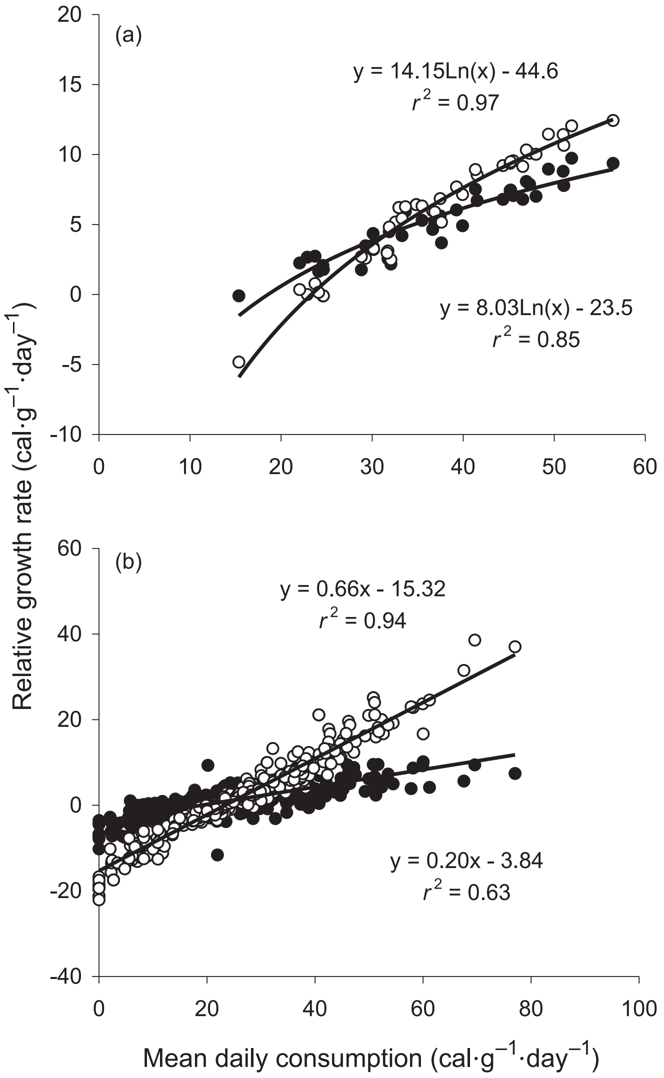
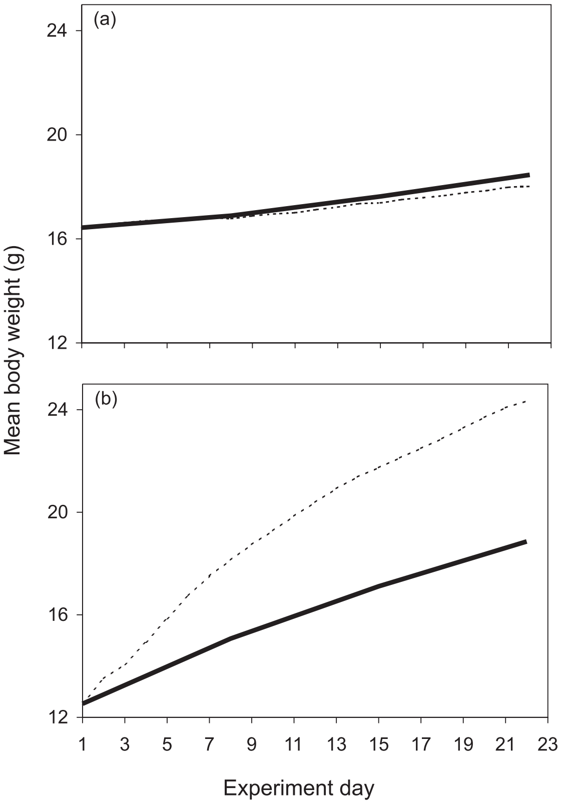


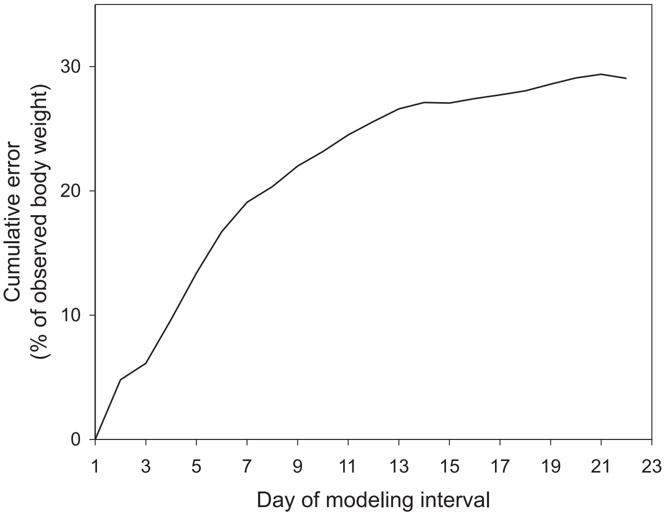
Fig. 3. Observed 22-day mean body weight trajectories for hybrid bluegill (F_1; female *Lepomis cyanellus* × male *L. macrochirus*) (solid lines) and corresponding predicted trajectories from a bluegill (*L. macrochirus*) BEM (broken lines) for the control group (*a*) and treatment group (*b*). Control fish consumed food at uniform low to moderate rates (1.0%–1.9% body weight·day^{-1}) over the 22 days; treatment fish were caused to become hyperphagic and initially consumed food at high rates over days 1–7 (8.0%–3.8% body weight·day^{-1}), after which their consumption rates gradually declined to those of the control fish.



under conditions of higher consumption because here, absolute error rates were highest even though relative error was often greater under low-consumption conditions. For example, the yellow perch BEM under- and over-estimated observed growth rates by the same relative magnitude (2.9-fold) at consumption levels of 21 and 60 cal·g^{-1}·day^{-1}, respectively. However, in absolute terms (in cal·g^{-1}·day^{-1}), predictive error was nearly 20 times greater at the higher versus the lower consumption level (16 and 0.9 cal·g^{-1}·day^{-1}, respectively). Likewise, we expect that predictions of consumption will be most severely underestimated when high growth rates are entered into BEMs.

Because of the high magnitude of BEM prediction errors under conditions of high growth or consumption rates, even relatively short episodes of these conditions within a modeling interval can result in substantial overall predictive inaccuracy. Moreover, such error effects of high growth or consumption conditions, once incurred, are not likely to diminish even if lower growth rates and consumption levels follow in the modeling interval, because of their lesser opposing effects. When the bluegill BEM was applied to the treatment-group hybrid bluegill, growth of these fish, which fed at high rates (4.0%–8.0% body weight·day^{-1}) over the initial 7 days of the 22-day modeling interval, was substantially overestimated. Despite subsequent declining consumption rates that ultimately reached lower levels over the remaining 15 days, the prediction error that had mostly accumulated early on, persisted throughout the entire modeling interval. Hence, initially accumulated error was not offset by the subsequent improvement of model performance. In contrast, model predictions for the control group of hybrid bluegills that did not experience initially high consumption rates were very accurate. These results also demonstrate that a restricted period of high consumption can lead to substantial and sustained inaccuracy of BEM predictions, even for models that are otherwise capable of producing accurate growth

Fig. 4. Cumulative error (percentage of observed body weight) for bluegill (*Lepomis macrochirus*) BEM predictions of the observed 22-day mean weight trajectory of treatment-group hybrid bluegill (F_1; female *Lepomis cyanellus* × male *L. macrochirus*). Hybrid bluegill were fed at high levels (8.0%–3.8% body weight·day^{-1}) during days 1–7, moderate levels (4.25%–2.11%) during days 8–14, and lower levels (2.77%–1.64%) throughout the remaining 8 days.



predictions under more moderate consumption levels. The same would be expected for estimates of a fish's cumulative consumption over modeling intervals that include short episodes of rapid growth. The observations highlight the importance of evaluating BEMs over the full ranges of growth conditions under which they may be applied, to avoid the misperceptions of overall BEM predictive accuracy that can result if models are tested only under conditions of moderate growth and consumption.

Modeling of hybrid bluegill growth also demonstrated that even the BEM containing the least systematic error among the seven evaluated, the bluegill BEM, was capable of producing substantially erroneous predictions when applied to a relatively short episode of high consumption rate. Prediction errors from the six other BEMs would have been greater if they had been applied under comparable conditions. In general, users should not assume that BEMs will yield equally accurate predictions across all consumption levels and should be cautious about applying them beyond the ranges of conditions under which their performance has been rigorously evaluated.

That many BEMs may be substantially inaccurate, particularly when applied under high or low consumption and growth conditions, suggests a number of common application settings where important predictive error would be expected. First, however, in-situ estimates of the consumption rates of fish (i.e., not from BEMs) indicate that episodes of both high and low consumption levels may commonly occur in a variety of natural aquatic environments (e.g., Hayward and Margraf 1987; Weiland and Hayward 1997; Whitledge and Hayward 2000). Consequently, applications of BEMs to natural fish populations in general are likely to involve episodes of high and low consumption levels, particularly during growing seasons, when water temperatures permit fish consumption levels to range broadly.

BEMs used to estimate the predatory demand of fish populations would appear to be particularly vulnerable to substantial inaccuracy. Predatory demand is the amount of food required by individual fish, and ultimately whole populations, to achieve maximum growth rates. This metric is used to estimate the prey biomass that a population would consume over a time period if sufficient prey were available (Ney 1993). The inference from our results is that BEMs could yield substantial underestimates of predatory demand because when growth rates are high, corresponding consumption rates would be severely underestimated. Consequently, BEM-based estimates of predator population biomasses that could be supported by local prey populations would be substantially overestimated. Management policies based on such results could pose a serious risk of overexploiting local prey populations and destabilizing existing predator–prey balances. The ecological and economic implications of such modeling errors could be serious, particularly for large systems such as the Great Lakes, where large-scale BEM-based predictions of predatory demand have been applied to ecologically and commercially important fish species.

The accuracy of spatially explicit modeling of fish growth rate potentials could also be impacted by BEM error trends observed in our evaluations. Such modeling combines the results of BEMs and foraging models implemented with spatially (the environment is divided into grid cells) and temporally varying inputs of temperature, prey abundance, and prey size to produce maps of spatial growth potentials. Our results indicate that modeled growth potentials for environmental cells offering very good and poor consumption conditions could be substantially over- and under-estimated, respectively, leading to overrepresentation of the extent to which growth conditions vary over space and time.

Applications of BEMs in aquaculture settings, where fish are typically fed and grown at high rates, may also be particularly error-prone. Uses of BEMs not only to predict fish growth and consumption rates but also to assess the impacts of aquaculture on, for example, water quality according to modeled fish egestion and excretion rates may be affected. Also, BEMs are being used increasingly as components of broader models relating to fisheries management, aquatic ecology, and aquaculture. The impacts of the systematic error that we have observed in BEMs on the accuracy of predictions and the insights generated by models that incorporate BEMs are likely variable and currently unknown. Potential effects of widespread systematic error in BEMs should be carefully considered when either constructing or applying models that contain BEMs as subcomponents.

If the subequation that calculates energy cost or loss for a given parameter within a BEM is erroneous, the overall prediction error of the BEM will tend to be correlated with the input variable that drives the erroneous subequation. Consequently, the consumption-dependent prediction error observed in the seven BEMs likely emanates from inaccuracies in subequations for calculating egestion (F), excretion (U), or specific dynamic action (SDA), because these are consumption-dependent parameters in the seven models, and in most other BEMs. Brett and Groves (1979) provided laboratory evidence that fish fed at near-maximum rates have SDA costs that approach those of resting routine metabolism. That such levels of SDA were observed under high-consumption conditions in the seven models that we evaluated, including the most-error-prone yellow perch model (Bajer et al. 2003, their Figs. 4*b* and 4*d*), suggests that SDA was appropriately calculated under conditions where BEM errors were greatest. However, Beamish and Trippel (1990) advised that SDA could represent substantial portions of fish energy budgets and vary widely (3%– 41%) in response to a number of variables including energy intake, fish body weight, composition of the diet, and environmental factors such as temperature. They suggested that the practice of calculating SDA costs as constant proportions of gross or digestible energy intake in BEMs may be inappropriate oversimplification. Given the substantial role that SDA can play in energy budgets and the uncertainty with which it is accurately determined in BEMs, its potential involvement in the consumption-dependent error in BEMs cannot be dismissed.

BEM outputs have been reported as being relatively insensitive to modest percent changes in parameter values for determining *F* and *U* (Kitchell et al. 1977; Bartell et al. 1986; Adams and Breck 1990). This view has fostered a tendency to not put forth new efforts to develop best possible species-specific estimators of *F* and *U* when new BEMs have been constructed (to a certain extent this applies to SDA as well). Instead, equation forms and even coefficient values for determining *F* and *U* have been liberally “borrowed” (sensu Ney 1993) across BEMs. All of the BEMs that we evaluated, with the exception of the Eurasian perch model (Karås and Thoresson 1992), estimate *F* and *U* largely from equations developed by Elliott (1976) for brown trout (*Salmo trutta*) or from a simplified version of these (Kitchell et al. 1977). We suspect that BEM inaccuracies due to errors in calculating *F* and *U* may not always be negligible as has been suggested. The relatively minor effects of inaccurate determinations of *F* and *U* at low to moderate consumption levels may become more pronounced if these parameters sometimes reach much higher levels. Recently, Bajer et al. (2003) found indirect evidence that energy losses associated with *F* and *U* constituted substantial portions of yellow perch energy budgets (being higher than both routine metabolism and SDA) at higher consumption levels (3% body weight·day^{-1}), indicating a setting for potentially greater impacts when these parameters are inaccurately determined. Perhaps most insightful, however, is an observation from a recent reexamination of the methods of Elliott (1976), the source study for most *F* and *U* calculations in BEMs. It was observed that test fish were food-deprived for up to 3 days prior to feeding, an experimental condition that may have resulted in the determination of anomalously low egestion rates, including at higher consumption levels (James Breck, Michigan Department of Natural Resources, 1109 North University Avenue, Ann Arbor, MI 48109-1084, USA, personal communication).

Unaccounted-for activity costs that may increase with food-consumption level and declining relative prey size (e.g., Kerr 1971; Brett and Groves 1979; Sherwood et al. 2002) cannot be totally dismissed as potential contributors to the consumption-dependent error that we observed in the seven BEMs. However, we consider these unlikely sources of this error. Consumption-dependent prediction error was observed when BEMs were applied to fish consuming evasive (other fish) as well as non-evasive (mealworms) prey types; the magnitudes of model prediction errors were in some cases higher when applied to fish consuming non-evasive prey. We also found no relationship between the magnitude of BEM error (slope of error regressions) and the relative size of prey used in experiments. Such a relationship might be expected if increased feeding-activity cost was incurred as fish were forced to eat prey of progressively smaller relative size, owing to the need to consume more prey items (Sherwood et al. 2002). Moreover, we note that increases in fish activity costs would have had to be very substantial to account for observed growth-prediction errors at high consumption levels. For example, we determined that white crappie metabolic rates would have had to increase substantially (activity multiplier >2) relative to routine resting metabolism to account for the observed growth-prediction errors at high consumption levels. This amount of activity-cost increase seems highly unlikely considering that the fish used to evaluate the white crappie BEM were held individually (without costs of aggression) in relatively small experimental chambers (where movement was limited), and had ready access to their prey. We routinely observed these fish and saw little evidence of substantial activity. Fish used to evaluate five of the six other BEMs (largemouth bass, smallmouth bass, bluegill, yellow perch, and Eurasian perch) were also held individually in chambers that limited their movement during evaluation experiments. Consequently, we believe that efforts to fundamentally improve BEMs should focus first on laboratory studies to develop better estimators of *F* and *U* that are applicable over broad ranges of consumption level, fish body weight, temperature, and prey type.

Growth-rate underestimation by BEMs occurred when fish were provided substantially restricted rations. Under low-consumption conditions, BEM errors associated with *F*, *U*, and SDA should be low because each of these parameters is calculated as a fraction of consumption level. We suspect that model error under these conditions is related to the general inability of BEMs to accommodate the reductions in resting routine metabolism that are known to occur in many fish species during periods of submaintenance feeding in order to conserve energy (Beamish 1964; Glass 1968; Mehner and Wieser 1994). Our finding of consistent body-weight-dependent overprediction of weight loss under submaintenance conditions also indicates that smaller fish reduce their metabolic rates more substantially under weight-loss conditions than do their larger counterparts. Development of consumption- and body-weight-dependent subequations that describe reductions in routine metabolic costs under submaintenance feeding conditions would improve predictions of growth and consumption by BEMs under these conditions.

An efficient approach for reducing systematic error in BEMs that is associated with consumption level or other input variables (e.g., fish body weight and temperature) may be to develop correction equations as was done for the white crappie model (Bajer et al. 2004). Regression-based error-correcting equations were developed for the white crappie BEM from model prediction errors determined from comparisons of predicted and observed growth responses when white crappie of a range of sizes were reared at different feeding levels and temperatures. The correction approach is efficient because (*i*) a model's overall error is reduced without the need to consider specific error sources, and (*ii*) the data set used to initially evaluate a BEM can also provide the information required to develop correction equations. In contrast, efforts to fundamentally improve BEMs will likely require one data set to evaluate a model's prediction error and distinct data sets to improve the subequations for each erroneous parameter.

Finally, we note that the experimental designs in the published laboratory studies used to evaluate most of the BEMs were incomplete, as they did not encompass the full arrays of conditions under which these models may be applied. Most notably, analyses of possible temperature effects on model performance were not possible in most cases. In addition, testing of models under conditions where fish fed at submaintenance levels was restricted to a few models, all of which showed body-weight dependence of growth-prediction error under these conditions. Laboratory evaluations of BEMs should include conditions of weight loss. Also, possible effects of food type on model performance could not be fully evaluated because single prey types were used during each of the model evaluations. Further work is needed to evaluate temperature, submaintenance-feeding, and prey-type effects on the performance of BEMs, as well as possible influences of activity level. More optimal experimental designs for BEM evaluation are described by Bajer et al. (2004).

Acknowledgements

Funding for this work was provided in part by research grants to R.S. Hayward from the Missouri Department of Conservation and the North Central Regional Aquaculture Center. We thank James Breck for helpful insights and suggestions relating to this study, and Marc Trudel for providing a thorough review of the manuscript.

References

Adams, S.M., and Breck, J.E. 1990. Bioenergetics. *In* Methods for fish biology. *Edited by* C.B. Schreck and P.B Moyle. American Fisheries Society, Bethesda, Md. pp. 389–415.

Axler, R., Owe, C., Ameel, J., Ruzycki, E., and Henneck, J. 1994. Water quality issues associated with aquaculture: a case study in Minnesota mine pit lakes. Lake Reservoir Manag. **9**: 53.

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

Bajer, P.G., Hayward, R.S., Whitledge, G.W., and Zweifel, R.D. 2004. Simultaneous evaluation and improvement of a bioenergetics model for white crappie (*Pomoxis annularis*). Can. J. Fish. Aquat. Sci. **61**: xxxx–xxxx. This issue.

Bartell, S.M, Breck, J.E., Gardner, R.H., and Brenkert, A.L. 1986. Individual parameter perturbation and error analysis of fish bioenergetics models. Can. J. Fish. Aquat. Sci. **43**: 160–168.

Beamish, F.W.H. 1964. Influence of starvation on standard and routine oxygen consumption. Trans. Am. Fish. Soc. **93**: 103–107.

Beamish, F.W.H., and Trippel, E.A. 1990. Heat increment: a static or dynamic dimension in bioenergetics models? Trans. Am. Fish. Soc. **119**: 649–661.

Brett, J.R., and Groves, D.D. 1979. Feeding metabolism. *In* Fish physiology. Vol. 8. Bioenergetics and Growth. *Edited by* W.S. Hoar, D.J. Randall, and J.R. Brett. Academic Press, New York. pp. 298–305.

Burke, B.J, and Rice, J.A. 2002. A linked foraging and bioenergetics model for southern flounder. Trans. Am. Fish. Soc. **131**: 120–131.

Chipps, S.R., Einfalt, L.M., and Wahl, D.H. 2000. Growth and food consumption by tiger muskellunge: effects of temperature and ration level on bioenergetic model predictions. Trans. Am. Fish. Soc. **129**: 186–193.

Cui, Y., and Wootton, R.J. 1989. Bioenergetics and growth of a cyprinid, *Phoxinus phoxinus* (L.): development and testing of a growth model. J. Fish Biol. **34**: 47–64.

Elliott, J.M. 1976. Energy losses in waste products of brown trout (*Salmo trutta* L.). J. Anim. Ecol. **45**: 561–580.

Glass, N.R. 1968. The effect of time of food deprivation on the routine oxygen consumption of largemouth black bass (*Micropterus salmoides*). Ecology, **49**: 340–343.

Hanson, P.C., Johnson, T.B., Schindler, D.E., and Kitchell, J.F. 1997. Fish bioenergetics 3.0. University of Wisconsin Sea Grant Institute, Madison.

Hartman, K.J., and Brandt, S.B. 1993. Systematic sources of bias in a bioenergetics model: examples for age-0 striped bass. Trans. Am. Fish. Soc. **122**: 912–926.

Hayes, J.W., Stark, J.D., and Shearer, K.A. 2000. Development and test of a whole-lifetime foraging and bioenergetics growth model for drift-feeding brown trout. Trans. Am. Fish. Soc. **129**: 315–332.

Hayward, R.S., and Margraf, F.J. 1987. Eutrophication effects on prey size and food available to yellow perch in Lake Erie. Trans. Am. Fish. Soc. **116**: 210–223.

Hewett, S.W., and Johnson, B.L. 1987. A generalized bioenergetics model of fish growth for microcomputers. Sea Grant Tech. Rep. No. WISCG-87-245, University of Wisconsin, Madison.

Hill, D.K., and Magnuson, J.J. 1990. Potential effects of global climate warming on the growth and prey consumption of Great Lakes fishes. Trans. Am. Fish. Soc. **119**: 265–275.

Jackson, L.J. 1996. How will decreased alewife growth rates and salmonid stocking affect sport fish PCB concentrations in Lake Ontario. Environ. Sci. Technol. **30**: 701–705.

Jones, M.L., Koonce, J.F., and O'Gorman, R. 1993. Sustainability of hatchery-dependent salmonine fisheries in Lake Ontario: the conflict between predatory demand and prey supply. Trans. Am. Fish. Soc. **122**: 1002–1018.

Karås, P., and Thoresson, G. 1992. An application of a bioenergetics model to Eurasian perch (*Perca fluviatilis* L.). J. Fish Biol. **41**: 217–230.

Kerr, S.R. 1971. Analysis of laboratory experiments on growth efficiency of fishes. J. Fish. Res. Board Can. **28**: 801–808.

Kershner, M.W., Schael, D.M., Knight, R.L., Stein, R.A., and Marschall, E.A. 1999. Modeling sources of variation for growth and predatory demand of Lake Erie walleye (*Stizostedion vitreum*), 1986–1995. Can. J. Fish. Aquat. Sci. **56**: 527–538.

Kitchell, J.F., Stewart, D.J., and Weininger, D. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum*). J. Fish. Res. Board Can. **34**: 1922–1935.

Madenjian, C.P., and O'Connor, D.V. 1999. Laboratory evaluation of a lake trout bioenergetics model. Trans. Am. Fish. Soc. **128**: 802–814.

Mehner, T., and Wieser, W. 1994. Energetics and metabolic correlates of starvation in juvenile perch (*Perca fluviatilis*). J. Fish Biol. **45**: 325–333.

Ney, J.J. 1993. Bioenergetics modeling today: growing pains on the cutting age. Trans. Am. Fish. Soc. **122**: 736–748.

Rand, P.S., Stewart, D.J., Lantry, B.F., Rudstam, L.G., Johannsson, O.E., Goyke, E.P. et al. 1995. Effect of lake-wide planktivory by the pelagic prey fish communities in Lakes Michigan and Ontario. Can. J. Fish. Aquat. Sci. **57**: 1546–1563.

Rose, K.A., and Cowan, J.H., Jr. 1993. Individual-based model of young-of-the-year striped bass population dynamics. I. Model description and baseline simulations. Trans. Am. Fish. Soc. **122**: 415–438.

Schindler, D.E., and Eby, L.A. 1997. Stoichiometry of fishes and their prey: implications for nutrient recycling. Ecology, **78**: 1816–1831.

Sherwood, G.D., Pazzia, I., Moeser, A., Hontela, A., and Rasmussen, J.B. 2002. Shifting gears: enzymatic evidence for the energetic advantage of switching diet in wild-living fish. Can. J. Fish. Aquat. Sci. **59**: 229–241.

Trebitz, A.S. 1991. Timing of spawning in largemouth bass: implications of an individual-based model. Ecol. Modell. **59**: 203–227.

Weiland, M.A., and Hayward, R.S. 1997. Cause for the decline of large rainbow trout in a tailwater fishery: Too much putting or too much taking? Trans. Am. Fish. Soc. **126**: 758–773.

Whitledge, G.W., and Hayward, R.S. 1997. Laboratory evaluation of a bioenergetics model for largemouth bass at two temperatures and feeding levels. Trans. Am. Fish. Soc. **126**: 1030–1035.

Whitledge, G.W., and Hayward, R.S. 2000. Determining sampling date interval for precise in situ estimates of cumulative food consumption by fishes. Can. J. Fish. Aquat. Sci. **57**: 1131–1138.

Whitledge, G.W., Hayward, R.S., Noltie, D.B., and Wang, N. 1998. Testing bioenergetics models under feeding regimes that elicit compensatory growth. Trans. Am. Fish. Soc. **127**: 740–746.

Whitledge, G.W., Hayward, R.S., Zweifel, R.D., and Rabeni, C.F. 2003. Development and laboratory evaluation of a bioenergetics model for sub-adult and adult smallmouth bass. Trans. Am. Fish. Soc. **132**: 316–325.