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[Article]

Comparisons between Consumption Estimates from Bioenergetics Simulations and Field Measurements for Walleyes from Oneida Lake, New York

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Abstract.—Daily consumption was estimated from the stomach contents of walleyes *Sander vitreus* collected weekly from Oneida Lake, New York, during June–October 1975, 1992, 1993, and 1994 for one to four age-groups per year. Field rations were highly variable between weeks, and trends in ration size varied both seasonally and annually. The coefficient of variation for weekly field rations within years and ages ranged from 45% to 97%. Field estimates were compared with simulated consumption from a bioenergetics model. The simulation averages of daily ration deviated from those of the field estimates by −20.1% to +70.3%, with a mean across all simulations of +14.3%. The deviations for each time step were much greater than those for the simulation averages, ranging from −92.8% to +363.6%. A systematic trend in the deviations was observed, the model producing overpredictions at rations less than 3.7% of body weight. Analysis of variance indicated that the deviations were affected by sample year and week but not age. Multiple linear regression using backwards selection procedures and Akaike's information criterion indicated that walleye weight, walleye growth, lake temperature, prey energy density, and the proportion of gizzard shad *Dorosoma cepedianum* in the diet significantly affected the deviations between simulated and field rations and explained 32% of the variance.

Bioenergetics models (BEMs) have been used to address a variety of ecological and management questions for at least half a century (Kitchell 1983; Hansen et al. 1993; Ney 1993). A balanced energy equation accounting for energy intake, metabolism, growth, and activity is used in BEMs to derive consumption, which is hard to measure, from growth, which can be measured relatively easily. Bioenergetics equations are also integral to individual-based and multispecies models (Madenjian and Carpenter 1991; Kershner et al. 1999; Rose et al. 1999; Cyterski and Ney 2005). The Wisconsin approach (Ney 1993) has been particularly popular, with user-friendly software (Hanson et al. 1997) listing parameters for over 40 species of fish, and is well suited for a wide range of applications, including small lakes (Kitchell et al. 1977; Cyterski and Ney 2005), large lakes (Stewart et al. 1983; Lantry and Stewart 1993), marine systems (Rudstam et al. 1992; Hansson et al. 1996), and invertebrates (Schneider 1992; Johannsson et al. 1994).

One of the first Wisconsin BEMs (Kitchell et al. 1977) was developed for yellow perch *Perca flavescens* and walleye *Sander vitreus* and was cited in more than 387 articles from 1985 to 2006. The model used consumption and respiration data from Eurasian perch *P. fluviatilis* (Solomon and Brafield 1972), excretion and egestion functions developed for brown trout *Salmo trutta* (Elliott 1976), and specific dynamic action measured from largemouth bass *Micropterus salmoides* (Beamish 1974) and bluegill *Lepomis macrochirus* (Schalles and Wissing 1976). Where corroboration was undertaken, model predictions often

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deviated substantially from field observations for growth and consumption for walleye (Hurley 1986; Fox 1991; Johnston 1999), yellow perch (Boisclair and Leggett 1989; Post 1990; Haas and Schaeffer 1992; Schaeffer et al. 1999), and Eurasian perch (Karås and Thoresson 1992; Bajer et al. 2003). Disagreements about the use of this particular model led to a spirited exchange in the literature (Boisclair and Leggett 1990, 1991; Hayward 1990; Hewett et al. 1991). Extensive application of the Kitchell et al. (1977) model to examine consumption and growth of percids and questions about the accuracy of model predictions warranted further corroboration with field data.

Several laboratory studies have detected an effect of ration size on the error between bioenergetics model predictions and observed ration levels (Madenjian and O'Connor 1999; Chipps et al. 2000; Bajer et al. 2003; Whitledge et al. 2003; Chipps and Wahl 2004; Madenjian et al. 2006). Recently, Bajer et al. (2004b) reexamined laboratory studies for lake trout *Salvelinus namaycush* (Madenjian and O'Connor 1999), yellow and Eurasian perch (Bajer et al. 2003), and white crappie *Pomoxis annularis* (Bajer et al. 2004a) and found that those bioenergetics simulations exhibited a systematic error in predictions for growth at high and low rations. Although the magnitude of the error varied among the BEMs, they all had the same trend, underpredicting growth at low rations and overpredicting growth at high rations. These analyses need to be extended to field evaluations, but few data sets exist with enough measurements of growth, condition, diet, and daily ration to evaluate model predictions with field measurements.

The walleye and yellow perch populations of Oneida Lake, New York, have been studied since 1957 (Mills and Forney 1988; Rudstam et al. 2004), and the long-term data collected on these two species provide an excellent opportunity to use field measurements of daily ration to corroborate bioenergetics simulations. A bioenergetics approach was applied in the 1970s (Tarby 1977; Mills and Forney 1981) and data from Oneida Lake were used in the original Kitchell et al. (1977) model. Detailed analyses of walleye daily ration were performed in the 1970s (Forney 1977) and again in the 1990s (Lantry 1997). In 1975 and in 1992–1994, data were also collected on the seasonal energy density of age-0 yellow perch and age-0 gizzard shad *Dorosoma cepedianum*, both major prey of walleye. These data combined with annual measurements of growth and lake temperature, provided all site specific information necessary to apply the Kitchell et al. (1977) walleye BEM to the Oneida Lake population.

The use of field measurements of daily ration to corroborate bioenergetics simulations presents several challenges. Daily rations are affected by many factors (e.g., fish age and size, seasonal prey availability, and digestion rates) and sample size and frequency must be adjusted to accommodate variation between individual predators and seasonal cycles linked to temperature and prey availability. Methods developed previously to produce daily ration estimates for Oneida Lake walleye have been critically examined (Forney 1977). Forney reconstructed daily rations from the stomach contents of walleyes collected in bottom trawls at sunrise during June through September 1971–1973. He observed that walleyes sampled at 2–3-h intervals over a 24-h period showed a consistent decline in stomach contents after sunrise and concluded that walleye fed almost exclusively at night because stomachs contents became increasingly unidentifiable in the hours between sunrise and sunset. He also determined that evacuation rate during the June–September sampling period was dependent on prey size and was not related to temperature (range, 16.8–23.5°C) or meal size. Weekly ration estimates for Oneida Lake walleye produced during the 1970s and 1990s using Forney's (1977) methods provided an exceptional opportunity for testing the Kitchell et al. (1977) model and for providing focused insight into the accuracy of field applications of BEMs in general.

The objective of this study was to test the ability of the Kitchell et al. (1977) model to predict in situ estimates of walleye daily ration in years when prey composition and consumption differed. We used growth and daily ration estimates from walleyes collected weekly from June to October to compare with model results. Simulations were run for 2 years when walleye diets were dominated by age-0 yellow perch (1975 and 1994), and for 2 years when substantial amounts of gizzard shad were consumed (1992 and 1993). The 1975 pre–gizzard shad simulation was characterized by higher age-specific walleye growth and ration than during 1992–1994. The later years represent high (1992), moderate (1993), and low (1994) abundance of gizzard shad. We used differences between simulated years and ages to examine factors influencing the accuracy of model predictions. In addition, our analysis extends observations from previous laboratory studies of ration-dependent effects on simulation results to a field test for BEMs. Because we are simulating consumption from observed growth, a similar trend in deviations between simulated and field estimates would exhibit an overprediction of field ration at low growth and an underprediction at high growth.

Methods

Site description.—Oneida Lake is a shallow, moderately eutrophic, well-studied percid lake (Mills and

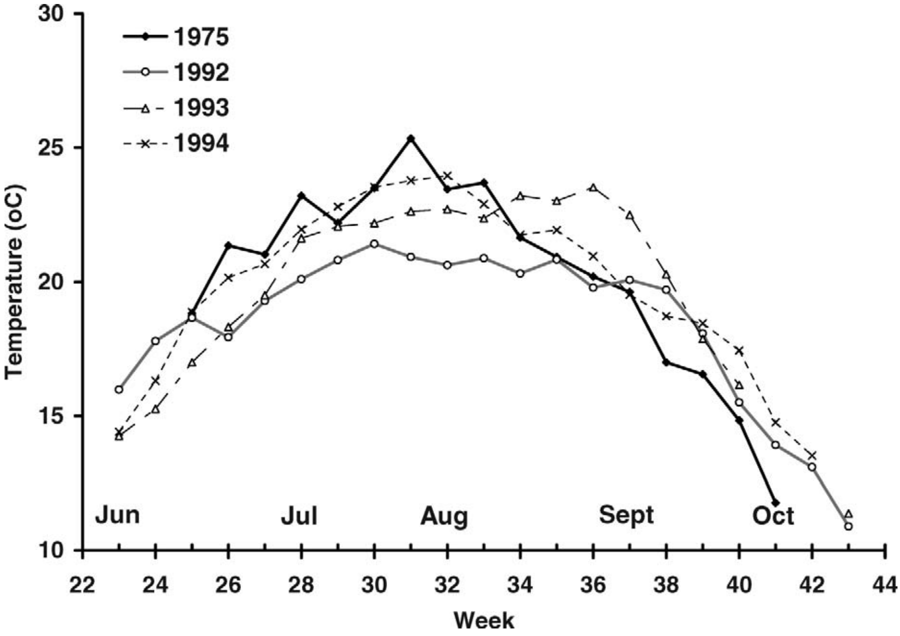

FIGURE 1.—Weekly temperatures from measurements in Oneida Lake, New York. The month labels above the x-axis refer to the first week of each month.

Forney 1988; Rose et al. 1999; Rudstam et al. 2004) with a surface area of 20,700 ha (Mills et al. 1978). The lake is polymictic and generally homothermal with a mean depth of 6.8 m. Although over 60 species of fish have been reported from Oneida Lake (Clady 1976), 78% of the fish caught in variable mesh gill nets between 1958 and 2002 were yearling and older walleyes and yellow perch. During the 1970s, walleyes and yellow perch formed a simple predator–prey association, walleyes feeding mainly on age-0 and yearling yellow perch (Forney 1980; Rose et al. 1999) and less frequently on white perch *Morone americana*. In the 1990s, however, walleyes had a more diverse diet that included yellow perch, gizzard shad, emerald shiner *Notropis atherinoides*, and white perch (Fitzgerald et al. 2006).

Walleye bioenergetics.—Walleye consumption was estimated using the equations and parameters from Kitchell et al. (1977). The model was based on an energy-balance equation,

$$\text{consumption}\,(C) = \text{growth}\,(G) + \text{respiration}\,(R) + \text{egestion}\,(F) + \text{excretion}\,(U),$$

where G is from field observations; R is a function of fish weight, temperature, meal size, and activity; and F and U are functions of temperature and meal size. The original Kitchell et al. (1977) model used biomass units and the intercept of the allometric function for respiration was in grams of O_2 per gram of body weight per day. Following Stewart et al. (1983) and Hanson et al. (1997), we converted the intercept of the allometric function for respiration to joules per gram per day to allow explicit input of differential energy densities of predator and prey. In this study, we use the BEM to predict food consumption for Oneida Lake walleyes given the observed growth rates, diet composition, temperature, and energy density of predator and prey. Simulations were based on the average individual from one age-class, predicting daily ration and recalculating P_{cmax}, the proportion of maximum consumption, for the same June through October dates for which field rations were estimated. In this model formulation, F, U, and specific dynamic action (SDA) are dependent on P_{cmax}. Negative values for predicted consumption on 3 of 192 dates occurred because model inputs for observed growth yielded weight losses exceeding weight and temperature-specific metabolism costs for starving fish. Those dates were not included in the analysis.

Temperature.—The temperatures used in the 1975 simulation (Figure 1) were the averages of weekly measurements made at five standard locations in Oneida Lake (Mills and Forney 1988). Thermal profiles were recorded at each site from late April through October. Each temperature was the weekly mean of all measurements within a profile averaged

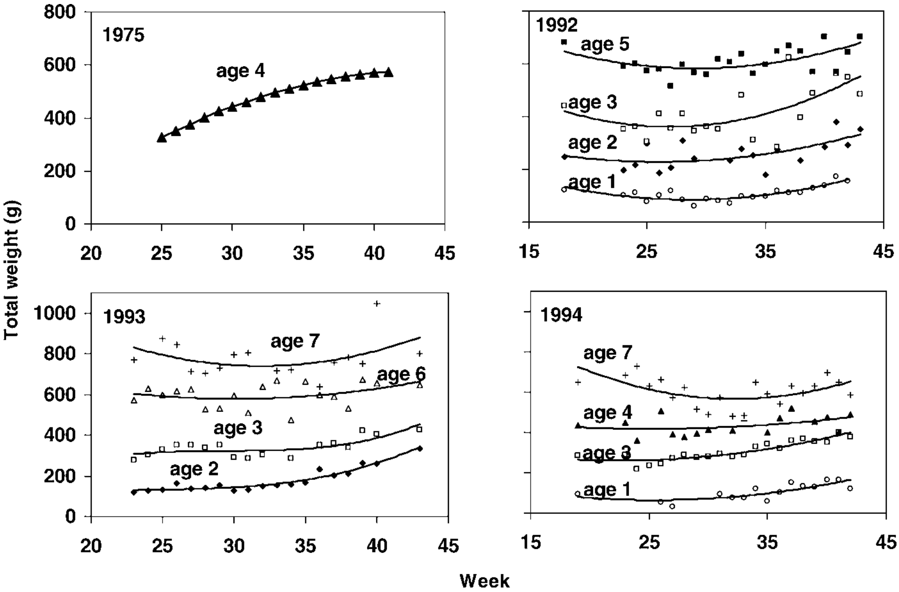

FIGURE 2.—Age- and year-specific walleye growth in Oneida Lake by week. Week 23 is the first week of June and week 41 is the first week of October. The symbols represent weight measurements for walleyes captured in weekly index sampling in 1975 and during sampling for diet analysis in 1992–1994. The lines represent interpolations between weight measurements for 1975, third-order polynomial fits for ages 2 and 3 in 1993, and second-order polynomial fits for all other ages from 1992 to 1994.

across the five stations. Temperatures for the 1990s simulations (Figure 1) were measured with two Ryan continuous temperature recorders suspended at 2 and 10 m beneath the surface near Shackelton Point, Bridgeport. Temperature readings from both depths were averaged to give a water column temperature. Mean water column temperatures were used because Oneida Lake's orientation from west–northwest to east–southeast is fully exposed to prevailing winds, which, combined with its long axis, results in homothermal conditions throughout most of the summer (Jackson et al. 2008). Even when thermal stratification developed during prolonged calm periods, the temperature range in a profile seldom exceeds 4°C.

Walleye growth.—Walleye size and age were determined weekly for fish collected in assessment netting during 1975 by Cornell University (Tarby 1977). Walleye size and age for the 1990s simulations were determined from fish collected for diet analyses. For all years, ages were determined from scales. In 1975, age-4 walleyes grew throughout the simulation period and walleye size was interpolated between sample days for input into the model. During 1992–1994, growth was erratic and often negative. To smooth the data, we calculated walleye growth for these years by fitting second- or third-order polynomial regression lines to age-specific May through October weight measurements (Figure 2; Table A.1 in the appendix). Although both moving averages and curves were initially fit to the data, polynomial curves were chosen for several reasons: weekly size-at-age measurements are autocorrelated; differences between weeks were often excessive, unrealistic, and related to sample size; a three- or four-point moving average gave excessive weight to data that were highly divergent from the other points used in moving averages; and a curve used all of the data to model seasonal growth whereas a moving average used shorter segments. Daily growth was then calculated as the change in weight of an age-class over the 2-week period surrounding the sampling date divided by 14 d. For the first and last simulated time step, growth was calculated as the average daily weight change over the two following or preceding intervals, respectively. This technique effectively linearized the curve for the 2-week period surrounding the current weight measurement and yielded the same growth value as the slope of that line. After maturity is reached, walleye size can differ between males and females, but because most walleyes used in field estimates of size or ration were not sacrificed we were not able to determine their sex. Preliminary graphical examination for walleyes that were sacrificed and sexed indicated that while size was slightly lower for males, there was no sex-related pattern in ration size. For comparison between years, prey fish weight was converted to energy units (joules)

TABLE 1.—Year- and age-specific simulation inputs for Oneida Lake walleye diets. The first column shows the calendar year and walleye age; asterisks denote strong year-classes. Growth is the increment from mid-June through September (i.e., the product of the week 26 mass and energy density subtracted from the product of the week 40 mass and energy density) divided by the initial walleye mass. Predator and prey energy density are averages for the dates simulated, with the ranges in parentheses. The last eight columns show the proportions of various diet items in walleye stomachs averaged over all simulation dates. Abbreviations are as follows: INV = invertebrates, YP = age-0 yellow perch, GS = gizzard shad, WP = white perch, ES = emerald shiner, 1+YP = yearling and older yellow perch, Other = all other identifiable fish prey, and UFR = unidentifiable fish remains. A total of 2,653 walleye stomachs were sampled across all simulations. The proportion of the walleye diet consisting of invertebrates was not determined for the 1975 samples; in that year, the walleye diet was predominantly age-0 yellow perch (all other fish prey are in the Other category).

				Diet item							
Year–age	Growth (J/g)	Predator energy density (J/g)	Prey energy density (J/g)	INV	YP	GS	WP	ES	1+YP	Other	UFR
1975–4*	4,982.2	6,462 (6,747–5,797)	3,597 (4,116–3,231)		0.825					0.175	
1992–1*	1,941.3	4,893 (5,262–4,204)	3,653 (4,270–3,138)	0.137	0.137	0.330	0.000	0.014	0.000	0.013	0.308
1992–2	614.6	5,647 (6,393–5,012)	3,756 (4,202–3,138)	0.089	0.083	0.279	0.012	0.041	0.018	0.057	0.309
1992–3	2,789.4	6,886 (constant)	3,787 (4,438–3,212)	0.077	0.068	0.233	0.001	0.051	0.032	0.001	0.431
1992–5*	492.5	6,971 (7,079–6,698)	3,766 (4,394–3,255)	0.098	0.083	0.279	0.001	0.017	0.096	0.044	0.381
1993–2*	5,502.9	5,146 (5,389–4,945)	3,753 (4,436–3,241)	0.057	0.256	0.181	0.014	0.035	0.000	0.200	0.271
1993–3	1,213.2	5,670 (5,864–5,552)	3,608 (4,272–3,181)	0.129	0.278	0.144	0.038	0.007	0.000	0.124	0.263
1993–6*	414.3	5,633 (5,864–5,525)	3,738 (4,381–3,220)	0.077	0.318	0.138	0.011	0.016	0.023	0.113	0.315
1993–7	268.8	5,621 (5,864–5,529)	3,800 (4,459–3,226)	0.093	0.153	0.255	0.057	0.014	0.021	0.160	0.305
1994–1	5,382.6	4,366 (4,372–4,357)	3,987 (4,676–3,406)	0.010	0.277	0.011	0.044	0.013	0.000	0.205	0.484
1994–3*	2,170.7	5,485 (5,531–5,440)	3,750 (4,751–3,186)	0.064	0.283	0.113	0.007	0.004	0.025	0.100	0.412
1994–4	593.4	5,587 (constant)	3,682 (4,028–3,285)	0.018	0.179	0.000	0.000	0.027	0.000	0.049	0.727
1994–7*	182.9	5,587 (constant)	3,802 (4,863–3,138)	0.096	0.160	0.145	0.000	0.003	0.063	0.076	0.457

and growth expressed as joules per gram from June to September (Table 1).

Walleye diet.—Diet composition and daily ration were determined from stomach contents, adjusted for evacuation rates, of walleyes caught in 12.2-m bottom trawls at dawn. Two or three sites were fished on successive days for each weekly sample. The average number of walleye stomachs examined per week in 1975 was 30 (range, 11–65; Table 2). During 1992–1994, the average number of walleyes examined was more than 10 for strong year-classes and less than 10 for weak year-classes (range, 4–46). For a more thorough description of methods and assumptions, see Forney (1977).

Walleyes collected for diet analyses were measured for total length (TL; mm) and weight (g), and stomach contents were removed. Fish prey were identified to species when possible and enumerated. Prey fish found in stomachs were considered representative of all consumed in the previous night of feeding. In earlier studies, between about one-half (June) and 90% (September–October) of the fish in stomachs of walleyes collected at dawn were identifiable to species (Forney 1977). Unidentified remains were assigned to species based on the composition of the identifiable portion. Intact prey fish were measured for TL and weight was estimated from length–weight regressions determined for Oneida Lake fishes. Prey fish that were not measurable were assigned the average weight of that species consumed that day. Diet composition was calculated after daily fish rations were reconstructed and added to the daily ration of invertebrates.

Ration due to invertebrates was only calculated for the 1990s data. Invertebrates found in walleye stomachs were predominantly from three groups: amphipods, chironomids, and cladoceran zooplankton. Preliminary plots indicated no trend between the proportion of invertebrates in the dawn diet samples and walleye size. Daily ration consisting of invertebrates was calculated as the total weight of all invertebrates in the stomachs divided by the total weight of predators examined. All invertebrate rations were averaged for each sample date and added to the fish ration. Because we had no data on the diel periodicity of Oneida Lake walleyes feeding on invertebrates, evacuation rates were not used to calculate the proportion of this diet item. This strategy may have underestimated the invertebrate portion of walleye rations; however, the ration size due to invertebrates was always low (annual mean percentage of predator body weight: 1992 = 0.127%, 1993 = 0.044%, 1994 = 0.035%) and only exceeded 0.5% of predator body weight (0.62–1.1%) in three ration estimates for age-1 and age-2 walleyes in 1992.

Based on earlier investigations (Forney 1977), we assumed that walleyes fed exclusively at night. Substantial increases in light penetration in Oneida Lake after the colonization of dreissenid mussels in 1991 (Idrisi et al. 2001) probably further confined walleyes to night feeding during 1992 to 1994. Rate of

TABLE 2.—Comparisons of model and field ration estimates for Oneida Lake walleyes. Rations (100• [grams of prey per gram of predator per day]) are averaged across sampling dates for similar seasonal periods; the average weekly sample size (n) for field rations is given in parentheses. The coefficients of variation (CVs) are from the ANOVAs of field ration estimates; RCD is the average of the deviations between the weekly simulated rations and the corresponding values running averages over three measurement intervals within years and ages, and SRCD is the measure of the deviations between the averages of the simulated and field estimates. See text for more details.

Year–age	Weeks simulated	Model ration	Field ration (n)	CV	RCD	SRCD
1975–4*	17 (Jun–Oct)	3.54	2.90 (30.1)	60.7	31.0	22.2
1992–1*	19 (Jun–Oct)	2.45	2.48 (12.3)	45.9	−0.1	−1.3
1992–2	10 (Jun–Oct)	1.46	1.62 (8.8)	77.6	26.6	−10.0
1992–3	9 (Jun–Oct)	1.81	1.36 (6.2)	66.4	46.6	33.5
1992–5*	21 (Jun–Oct)	1.43	1.11 (19.1)	75.0	58.4	28.4
1993–2*	18 (Jun–Oct)	3.49	2.70 (21.3)	75.5	57.9	29.2
1993–3	10 (Jun–Oct)	2.08	1.58 (6.6)	77.0	57.3	31.5
1993–6*	19 (Jun–Oct)	1.42	1.08 (13.9)	97.4	73.8	30.9
1993–7	13 (Jun–Oct)	1.48	0.87 (6.4)	87.4	106.5	70.3
1994–1	10 (Jun–Oct)	3.51	3.80 (6.6)	62.7	6.3	−7.5
1994–3*	20 (Jun–Oct)	2.35	2.48 (16.2)	49.4	3.6	−5.4
1994–4	6 (Jun–Oct)	1.75	2.07 (4.7)	55.4	−9.5	−15.5
1994–7*	17 (Jun–Oct)	1.38	1.72 (7.0)	66.4	−14.1	−20.1
Mean values						14.3

stomach evacuation was determined from three to five samples collected on 34 d between 1971 and 1973 (Forney 1977). In these years, age-0 yellow perch constituted over 90% of the diet, and the initial weight of individual yellow perch eaten increased from 0.1 g in June to 2–7 g by the fall. Weight of the stomach contents at dawn ranged from 0.35% to 3.32% of walleye body weight, and temperatures ranged from 16.8°C to 23.5°C. Mean weight of the meal and temperature did not improve predictions. The prey-weight-dependent evacuation function (Forney 1977) used to reconstruct walleye rations was

$$B = -0.6590 + 0.5554 \times X^{1/3} - 0.1474 \times X^{2/3},$$

where B is the instantaneous rate of food depletion and X is prey weight. The time t to 95% digestion of the meal was calculated from

$$S_t = S_0 \cdot \exp(-Bt),$$

where S_0 is the original weight of the meal, S_t is the weight of the meal remaining in the stomach at time t, and S_t is set to $0.05 \times S_0$ for calculations of time to 95% digestion. Stomach evacuation rates for yellow perch were similar to those obtained by Swenson and Smith (1973) for walleyes fed fathead minnow *Pimephales promelas*. On days when predicted evacuation times were greater than the sunset-to-sunrise feeding period, but less than 24 h, the number of fish remains observed in stomachs of walleyes captured at sunrise represented the daily meal. When young yellow perch were large and evacuation times exceeded 24 h, inclusion of fish ingested during earlier feeding periods was avoided by ignoring highly digested particles. Conversely on days when estimated evacuation times were less than the nocturnal feeding period (weeks 22–25) the weight of fish observed in stomachs was increased by the ratio of feeding period to evacuation time. On days when ration reconstruction was necessary some empty stomachs may have been the result of feeding bouts early in the night being completely evacuated by the time our dawn samples were collected; however, this source of error probably would have been offset by some of the fish only capturing prey late in the nighttime interval. Ration was expressed as a percentage of walleye wet weight.

Predator and prey energy density.—Simulated predator energy densities were measured from walleyes collected in Oneida Lake during each model year. The energy densities for the predominant prey fish in walleye diets, yellow perch and gizzard shad, also came from samples collected from Oneida Lake. Tarby (1977) determined seasonal energy density for age-4 walleyes collected in 1975 using bomb calorimetry. Energy densities of walleye for the 1990s simulations, and energy densities of yellow perch and gizzard shad for all simulations, were calculated from regressions of energy density as a function of percent dry weight (Lantry 1997). Regressions were derived from published values and Lantry's (1997) calorimetric measurements. To determine seasonal energy density for walleye, regressions were applied to year- and age-specific monthly determinations of percent dry weight from walleyes collected during 1992–1994 (Lantry 1997). To determine the energy density of prey, regressions were applied to measurements of percent dry weight of age-0 yellow perch collected monthly from Oneida Lake in 1992–1994 and age-0 gizzard shad collected monthly in 1992 and in August and

October 1995. Age-specific seasonal trends in walleye energy density were modeled using linear or second-order polynomial regressions of energy density as a function of simulation week.

The energy density of the walleye ration was determined for the proportion in the diet by weight of each fish group. Energy density for age-0 yellow perch (also white perch) was modeled with a second-order polynomial regression of energy density (E; J/g) on weight (W; g):

$$E = -18.1 \times W^2 + 307 \times W + 3103$$
$$(R^2 = 0.67, n = 21).$$

The energy densities of gizzard shad and emerald shiners were modeled with a linear regression on TL; mm):

$$E = 21.9 \times \text{TL} + 2562 \qquad (r^2 = 0.76, n = 6).$$

The energy density of age-1 yellow perch was set to 4,500 J/g (the approximate value for a 110-mm perch; Lantry 1997). The energy density of invertebrates was set at 3,138 J/g, which represents the mean of values reported for the three invertebrate taxa (Wissing and Hasler 1968; Cummings and Wuycheck 1971). Finally, we calculated the energy density of the prey consumed as the average energy density of the individual prey groups weighted by their proportion by weight in the diet.

Evaluation of ration estimates.—For comparisons of ration estimates, all values are presented as the percentage of the predator's body weight consumed per day, that is, $(\text{g}_{\text{prey}} \cdot \text{g}_{\text{predator}}{}^{-1} \cdot \text{d}^{-1}) \times 100$. Field ration estimates from sample sizes of fewer than four walleyes were too variable to yield reliable results and were not used. Comparisons of simulated rations and field estimates were complicated by the high variability in field estimates, both among individuals and among sample groups collected through the season. Unlike growth, ration estimates were not necessarily autocorrelated, but were dependent on seasonal prey availability and on individual fish-to-fish variability. Rather than fitting a curve to field ration estimates to smooth variability, we calculated a running average of field rations over three measurement intervals (f_3). The measurement intervals matched the intervals used to interpolate growth and approximated monthly averages often used to analyze bioenergetics simulations.

Analysis of variance (ANOVA) was performed with the general linear model [GLM] procedure in SAS to examine the effects of the class variables—year, week, and walleye age—on field rations, and the coefficient of variation ($\text{CV} = 100 \cdot \text{SD/mean}$) was used to describe the variation in field ration within years and ages. To compare the f_3 and simulated (predicted) rations, we used major axis regression. Major axis regression defines a line that minimizes the perpendicular distances from the line to the points (Warton et al. 2006), unlike linear regression, which only minimizes the vertical distances (the variability in the y variable). In this case it is appropriate to use major axis regression because of the variability in both the field and predicted rations. Both variables were square-root transformed to stabilize variance. To test for a one-to-one relation, major axis regression was fit to the data. If the slope was significantly different from one or the intercept was significantly different from zero, the null hypothesis of a one-to-one relation was rejected, indicating a systematic deviation between model predictions and field estimates. To calculate 95% confidence intervals ($\hat{y} \pm t_{\alpha,\text{df}}\hat{s}(\hat{y}\,|\,x)$; $\alpha = 0.05$, df = 188, $t = 1.973$), simple linear regression was carried out using a coordinate system with the major axis line as the x-axis, so that the confidence intervals (CIs) would be symmetric about the major axis. The resulting CIs were plotted to determine where the relation significantly differed from the one-to-one line.

To compare the averages of the predicted and field rations for an entire simulation, the simulation-relative-consumption deviation (SRCD) was calculated as

$$\text{SRCD} = \left(\frac{\text{avgp} - \text{avgf}}{\text{avgf}}\right) \times 100,$$

where avgp is the average of predicted rations and avgf is the average of field rations over the entire simulation. Calculating simulation averages in this manner preserved the sign of the difference, indicating whether consumption was, on average, over- or underpredicted. To evaluate the deviations between predicted p and f_3 for each time step the relative consumption deviation (RCD) was calculated as

$$\text{RCD} = \left(\frac{p - f_3}{f_3}\right) \times 100.$$

Relative consumption deviations, with the field ration value in the denominator, have the advantage of removing the size dependence from model–field comparisons, and past studies have found that ration size was strongly related to relative consumption deviations (Bajer et al. 2003, 2004b).

We used $p - f_3$ uncorrected for field ration size to evaluate the effects of several independent variables on the accuracy of the simulation results. Of the independent variables used in our analysis, walleye age, weight, and growth were most strongly correlated with field ration size ($P < 0.0001$; Pearson correlation coefficients of −0.40, −0.41, and +0.54) and had the

TABLE 3.—Effects of seven independent variables on the deviations between simulated daily rations (p) and running averages of field values over three measurement intervals, as determined by multiple linear regression with backwards stepwise elimination ($\alpha = 0.05$, $N = 189$; final model $R^2 = 0.32$) (f_3). Variables are the number of walleyes in weekly diet samples (#WAE), average walleye weight (Wt), weekly growth increment (G), lake temperature (Temp), average prey energy density (PreyEn), the proportion of invertebrates in the diet (%INV), and the proportion of gizzard shad in the diet (%GS). For the independent variables retained in the model, the βs are the partial regression coefficients, the β_1s are the standardized partial regression coefficients, and the r^2s are the squared partial correlation coefficients.

Variable	Mean (range)	β	β_1	r^2	P-value
Variables retained					
Wt (g)	413.8 (61.5–881.5)	0.001	0.171	0.028	0.0302
G ($\mathrm{J \cdot g^{-1} \cdot d^{-1}}$)	15.2 (−31.1–80.2)	0.014	0.273	0.047	0.0047
Temp (°C)	19.2 (18–31)	0.116	0.385	0.144	<0.0001
PreyEn (J/g)	3,337 (3,138–4,863)	−0.001	−0.384	0.093	<0.0001
%GS	17.9 (0–100)	0.818	0.226	0.050	<0.0036
Variables removed					
#WAE	12 (4–65)			0.003	0.3937
%INV	6.9 (0–100)			0.001	0.7064

most potential to cause heteroscedasticity in $p - f_3$. Plots of those independent variables, however, indicated that they had little effect on deviation size or sign. To test for the effect of the class variables year, week, and walleye age on the deviations between predicted and field rations ($p - f_3$), ANOVA (GLM test; SAS) was used. To test for the possible effects of several factors that affect ration or metabolism on $p - f_3$, we used the GLM (SAS) with two independent variable selection procedures, backwards stepwise elimination ($\alpha = 0.05$) and Akaike's information criterion (AIC). We did not use field ration size (f_3) as an independent variable in these analyses because the probability of a spurious correlation with the consumptions deviations ($p - f_3$) was too high (thus, any detected significance would be uninformative). The AIC values were used to calculate the Akaike weights and evidence ratios were calculated to assess the relative fit of each model in relation to the model the lowest AIC value (Burnham and Anderson 1998). The independent variables included the number of walleyes in weekly diet samples, walleye average weight, walleye weekly growth increment, lake temperature, average prey energy density, diet proportion of invertebrates, and diet proportion of gizzard shad. A total of 189 weekly estimates of consumption were available for this analysis. Pearson correlation coefficients were generated for all independent variables.

Results

Trends in Growth and Field Rations

Field measurements of walleye size at age and growth varied between simulation years (Figure 2). Young walleyes (<age 4; 1992–1994) often lost weight during June (weeks 23–27) but gained weight throughout the remainder of the simulation period (July–October; weeks 28–43). For walleyes ages 4–6, relative seasonal growth was greatest in 1975 (Table 1). Age-4 walleyes in 1975 grew throughout the simulation period (May–September) with growth rate slowing down in August. During the 1990s simulations, age-4 and older walleyes grew little or lost weight from June (week 23) through August (week 33). Young yellow perch abundance was lower during the early 1990s than in the 1970s (Hall and Rudstam 1999) and weight loss occurred in spring to early summer when walleye rations were made up of predominately age-0 yellow perch. Walleyes in all years gained weight from August through October.

Field rations were highly variable among weeks, and trends in ration size varied both seasonally and annually (Figure 3). Year, week, and age all affected field ration size ($P = 0.0003$, $P = 0.0070$, $P < 0.0001$, respectively), and the interaction term for year and week was significant ($P = 0.0021$). In general, ration size decreased with increasing age within years and age-specific ration size increased between 1992 and 1994 (Table 2). Based on age 4–6 walleyes, ration size was greatest in 1975. Multiple pairwise comparisons of simulation averages of field rations between years for ages 4–6 (Tukey's honestly significant difference test) indicated that the only significant differences ($P < 0.05$) were between rations of age-4 fish in 1975 and those for age-5 fish in 1992 and age-6 fish in 1993. There were no other significant differences among years among similar ages. The CV from ANOVAs of weekly field rations, within years and ages, ranged between 45% and 97% (Table 2). Three-point running averages smoothed field ration estimates by an average

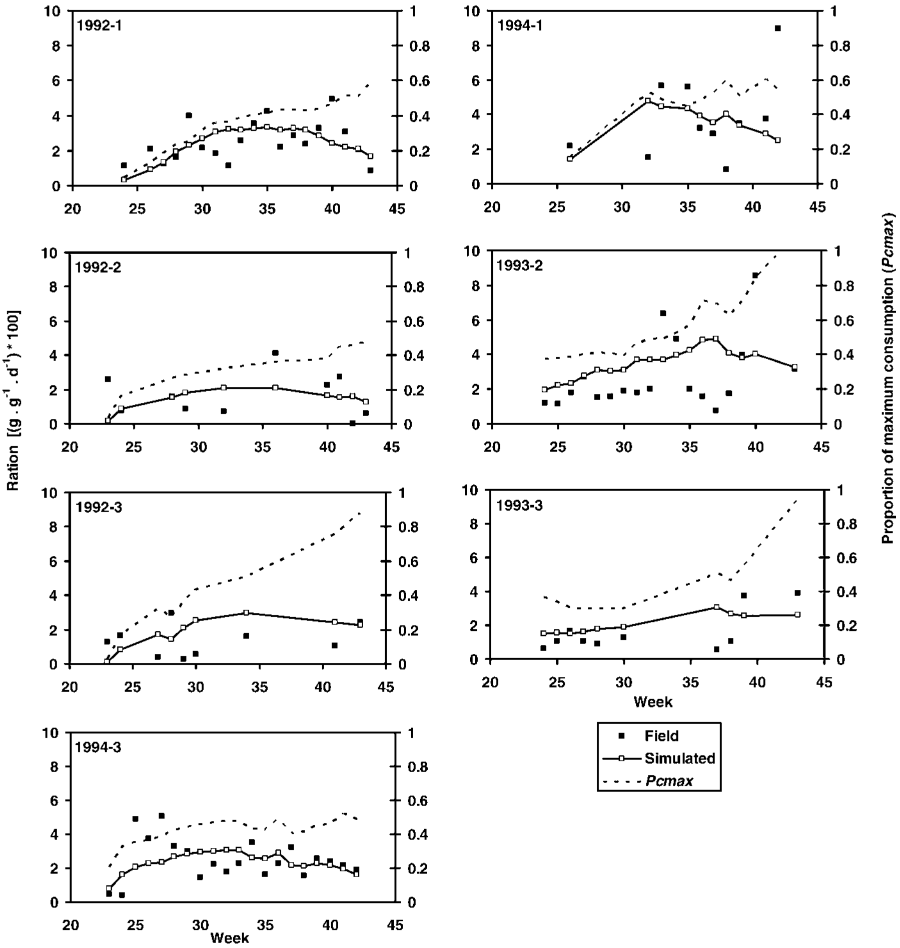

FIGURE 3.—Comparisons of field estimates of walleye daily ration and simulated values for each weekly simulation. The panels are for different age-groups and years (e.g., 1992–1 refers to age-1 fish in 1992); the panels are ordered by age and then year. Week 23 is the first week of June and week 41 is the first week of October.

of 34.4% (relative to the three-point average) across all simulations.

In 1975, field rations declined from mid-June to early October, but in 1992 and 1993 field ration generally increased between mid-May and early October (Figure 3). In 1994, field rations increased from May through July and then decreased (ages 1–4) or remained at higher levels (age 7) through October. For most years and ages, field ration estimates decreased after early October.

Comparisons between Simulated and Field Rations

The analysis of weekly estimates of simulated daily ration, p, and f_3 indicated a systematic deviation between model predictions and field estimates (Figure 4). The major axis regression for the square-root-transformed data had a slope less than one, namely, 0.850 (95% CI = 0.721–0.998) and an intercept greater than zero, namely, 0.288 (95% CI = 0.099–0.477). Simulated rations significantly overestimated field values for rations less than 3.67% of the predator's body weight, which is the ration size at which the lower confidence limit for the major axis regression line intersected the one-to-one line (Figure 4). Examination of separate plots of weekly predicted ration as a function of field ration within years and ages revealed similar trends as for weekly comparisons of all the data grouped. Despite the fact that ration changed with both age and year, the trend of overpredicting consumption for low rations was consistent for all simulations.

The SRCDs were evenly distributed, seven simulations overpredicting field rations and six underpredicting them (Table 2). The SRCDs ranged from −20.1% to +70.3%, with an average of 14.3% for all

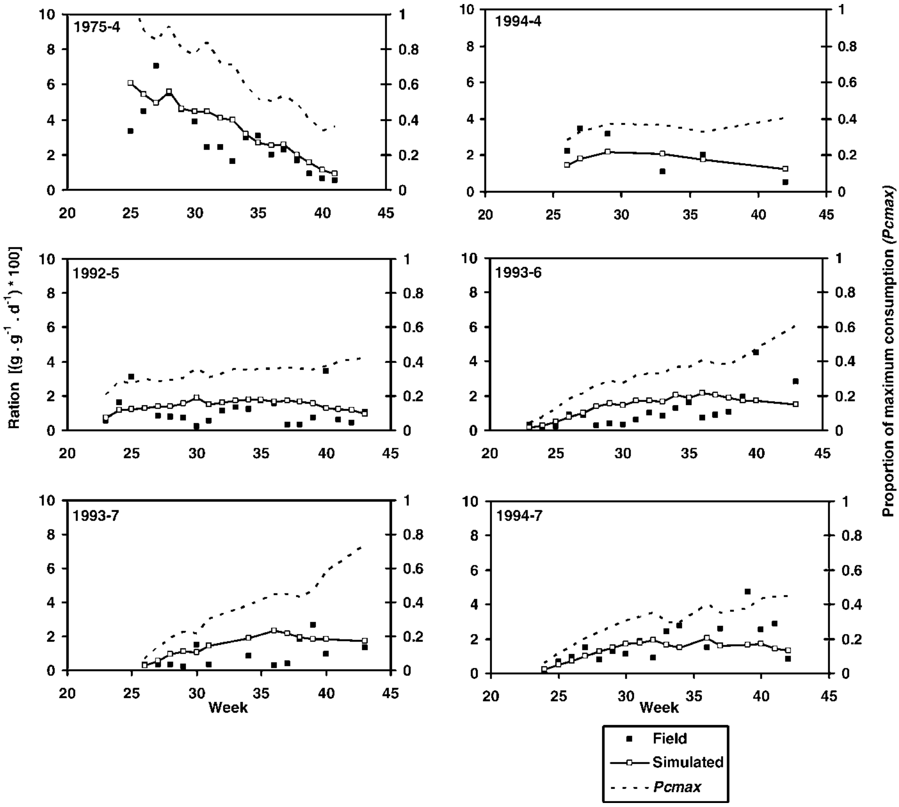

FIGURE 3.—Continued.

simulations and 12.0% (range, –20.1% to +30.9%) for strong year-classes (1971, 1987, and 1991). Of the 1990s simulations, the absolute values of SRCDs were lowest for 1994. The RCDs ranged among weeks from –92.8% to +363.6%, the averages for RCDs within year and age ranging from −14.1% to +106.5%. Unlike the SRCDs, the RCDs were positive for most simulations (simulations overpredicted field rations).

The ANOVA for the effect of the class variables on $p - f_3$, indicated no significant interactions between the variables and that year and week were significant ($P <$ 0.0001). From the multiple linear regressions, using backwards stepwise elimination effects on $p - f_3$, the final model explained about 32% of the variance and included five independent variables: walleye average weight, walleye weekly growth increment, lake temperature, prey energy density, and diet proportion of gizzard shad (Table 3). The AIC method indicated that the top-ranked model included the same independent variables as those from the backwards elimination procedure. The evidence ratios showed that the top-ranked model was 1.86 times better supported than the second ranked model (Table 4; six independent variables), which also included the independent variable representing number of walleyes in weekly diet samples, a variable not found significant in the backwards elimination procedure.

Plots of each significant independent variable on $p - f_3$ lacked obvious trends. Less than 10% of the data points in each relationship appeared to be influencing any significant trend obtained from the above regression analyses. There were significant correlations ($P \geq$ 0.05) between field ration size and all of the independent variables tested except temperature, and numerous significant correlations were present among the independent variables.

Discussion

Where BEM rations were corroborated with field or laboratory estimates of daily ration, good agreement was generally attributed to deviations (SRCDs) less than 20% relative to observed values (Ney 1993; Madenjian and O'Connor 1999; Whitledge et al. 2006). In this study, seven of eight simulations produced using the Kitchell et al. (1977) BEM that had average field rations greater than 1.6 $g \cdot g^{-1} d^{-1}$ had SRCDs

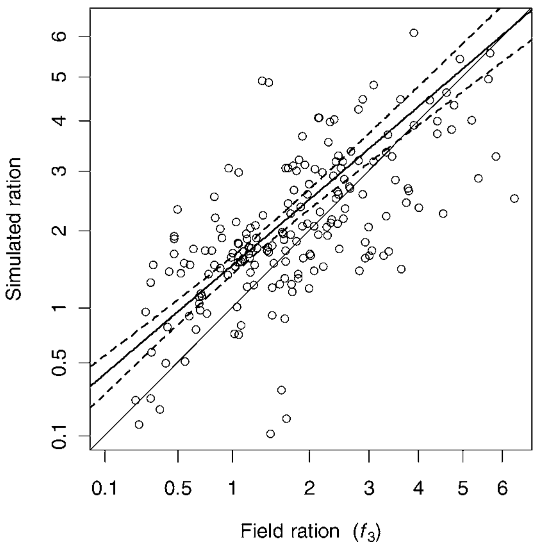

FIGURE 4.—Weekly simulated versus field rations for walleyes. The 45° line represents unity; the other solid line is the major axis regression line, and the dashed lines indicate the 95% confidence interval.

between −1.3% and +22.2%. When field ration size was less than 1.6 $g \cdot g \cdot^{-1} d^{-1}$, the SRCDs increased to more than 28%. Field ration size was highly variable among weeks and even with smoothed data, differences between weeks ranged as high as 627%. Deviations between predicted and observed field rations ($p - f_3$) were different among years and weeks, but age and weight had no effect on their size or sign. Weight, growth, temperature, prey energy density, and amount of gizzard shad consumed accounted for 32% of the variance between predicted and field rations. Field ration size was significantly correlated to all of the independent variables tested except temperature. Low ration size and high interannual variability in prey availability during the 1990s (Fitzgerald et al. 2006) likely obscured any expected effect of temperature on ration size. The 1992 simulations for age-1 and age-2 walleyes and all of the 1994 simulations produced the lowest SRCDs among the years modeled. Compared with the other years, age-specific walleye growth was low for the 1992 age-1 and age-2 simulations and field rations were relatively high for the 1994 simulations.

At moderate field rations (f_3 = 3.67–6.34%) the predicted and field rations ($p - f_3$) were not significantly different, but at lower rations (<3.67%) the predicted values overestimated field rations (Figure 4). While walleyes in this study consumed low to moderate rations, Hurley's (1986) field rations for juvenile and adult walleyes from the Bay of Quinte, Lake Ontario, were among the highest reported in the literature and provided an opportunity to determine whether the walleye BEM underestimated high daily ration values. Hurley's (1986) study was the only other published comparison of field and BEM rations for adult walleye and he found that the simulated rations consistently underestimated (>75%) field values. Fox (1991) and Johnston (1999) compared field rations with BEM rations for age-0 walleyes using a range of respiration and consumption parameters from the literature. In Fox's (1991) comparisons for walleyes from 0.06 to 0.56 g, field rations ranged from 2% to 49% per day and the Kitchell et al. (1977) model, on average, overestimated field values by more than 70%. In Johnston's (1999) comparisons of 0.0025–0.050 g walleyes, field rations ranged from 40% to 250% per day, and BEM predicted values were, on average, 33% below in situ pond estimates. Our results and other published walleye comparisons exhibited patterns consistent with previous laboratory BEM analyses for lake trout, white crappie, yellow perch, Eurasian perch, western mosquitofish *Gambusia affinis*, and hybrid sunfish (green sunfish *Lepomis cyanellus* × bluegill *L. macrochirus*) (Madenjian and O'Connor 1999; Bajer et al. 2003, 2004a, 2004b; Chipps and Wahl 2004; Whitledge et al. 2006) that found systematic overestimation of consumption at low rations, underestimation of consumption at high rations, and good agreement at moderate rations.

The pattern in consumption and growth deviations observed in this and other studies indicates that growth

TABLE 4.—Akaike weights for the best models including the variables in Table 3. All other models had evidence ratios larger than 10. The term Δ_i stands for the difference between a model's Akaike information criterion value (AIC) and that of the top-ranked model, which had an AIC value of −51.6. Evidence ratios = quotients of the Akaike weights for the top-ranked model divided by that for each other model.

Model rank	Variables	R^2	Δ_i	Akaike weight	Evidence ratio
1	Wt, *G*, Temp, PreyEn, %GS	0.316	0	0.40	
2	#WAE, Wt, *G*, Temp, PreyEn, %GS	0.319	1.24	0.21	1.86
3	Wt, *G*, Temp, PreyEn, %INV, %GS	0.317	1.84	0.16	2.51
4	*G*, Temp, PreyEn, %GS	0.296	2.88	0.09	4.22
5	#WAE, Wt, *G*, Temp, PreyEn, %INV, %GS	0.32	3.09	0.08	4.69
6	#WAE, *G*, Temp, PreyEn, %GS	0.299	4.16	0.05	8.00

efficiency is higher at low ration and lower at high ration than predicted by the BEM. Chipps et al. (2000) observed that gross conversion efficiency (GCE) exhibited a dome-shaped response to ration level for age-0 tiger muskellunge (muskellunge *Esox masquinongy* × northern pike *E. lucius*), with a peak at 75% of maximum consumption. The GCE estimated from their model output, however, increased continuously with ration size, a trend that would lead to underprediction of consumption at high rations. Growth efficiency can change with predator or prey activity, ration size, feeding periodicity, the nutrient content of prey, and following periods of starvation (Paloheimo and Dickie 1966; Kelso 1972; Kerr 1982; Whitledge et al. 1998; Metcalfe et al. 2002; Blake et al. 2006). Most BEMs lack adjustments for ration-dependent assimilation efficiency or for nutrient concentration of prey (e.g., fatty acid type, vitamins, and minerals). Bioenergetic models also lack adjustments for metabolic depression which may occur at very low ration levels (Beamish 1964; Glass 1968; Mehner and Wieser 1994; O'Connor et al. 2000; Chipps and Wahl 2004) and lead to overestimation of maintenance or submaintenance rations. Activity influenced by feeding is another potential source of error in BEMs; however, Whitledge and Hayward (1997) and Madenjian and O'Connor (1999)observed that activity was not an important factor in the ration-dependent errors observed in their BEMs for largemouth bass and lake trout, respectively.

A possible source of error in our field estimates of daily ration that may account for some of the overestimation error in simulated rations at low feeding levels was the way the invertebrate proportion of the walleye diets was handled for the 1992–1994 simulations. In our field estimates of daily ration the invertebrate portion was not adjusted for evacuation rate, which probably biased ration estimates downward when invertebrates made up a substantial proportion of diets. Percentage composition of invertebrates in the diets was negatively related to daily ration and consumption of invertebrates was greatest in June (simulation weeks 21–25). In most of the instances in which invertebrates made up more than 20% of the diet, daily ration was less than 1% of walleye body weight. Diet corrections due to evacuation were needed only during weeks 23–25 with multipliers during that time ranging from 1.1 to 1.4. If the invertebrate proportion of the ration was adjusted for evacuation during this period, only 20 out of 189 ration estimates would have been adjusted and only five of those would have caused a greater than 25% shift in the difference between the predicted and field estimates of daily ration, which would have further been diminished by the three-interval averaging technique for daily ration (f_3) we employed in our error analyses.

Bajer et al. (2003, 2004a, 2004b) suggested that the cause of the observed deviations was within the consumption dependent parameters F, U, and SDA, whereas Madenjian and O'Connor (1999) discounted the effects of these parameters on those deviations. Measured and simulated values used for F, U, and SDA range from about 10–30%, 4–15%, and 6–19%, respectively, of gross energy ingested (Elliott 1976; Beamish and Trippel 1990; Rudstam et al. 1994; Hanson et al. 1997). However, the consumption deviations observed in our model and Bajer et al.'s (2003, 2004a, 2004b) work often exceeded the maximum values for all three parameters combined, decreasing the likelihood that F, U, and SDA alone are responsible. The offsetting temperature and ration-size dependence of F and U (Elliott 1976; Kitchell et al. 1977) and an inverse relation between ration size and SDA (Beamish and Trippel 1990) further diminish the likelihood that these parameters alone could produce the observed errors.

As in Madenjian and O'Connor (1999), for moderate rations our predicted consumption averaged over entire simulations agreed reasonably well (−1 to +22% deviation) with the in situ estimates. Unlike laboratory analyses in which feeding could be closely monitored and measured (Bajer et al. 2004b), our analyses relied on field estimates that were quite variable between sample dates. Like those analyses, however, our application exhibited systematic and often large deviations between simulated and observed consumption that were related to observed ration size. Our results extend the observations of Bajer et al. (2003, 2004a, 2004b) and Madenjian and O'Connor (1999) from laboratory to field BEM analyses. Results from comparing studies that exhibited the systematic deviations indicate that one or more parameters affecting growth efficiency are either missing or wrong. Further analyses of the consumption-dependent parameters in BEMs (F, U, and SDA), respiratory response to ration, and the effects of growth-limiting nutrients on growth pattern and assimilation efficiency may probably improve energy balance analyses. In the short term, although not a satisfying answer to the cause of the prediction errors, corrections of the type formulated by Bajer et al. (2004a) and Whitledge et al. (2006) can increase the accuracy of simulations. In the absence of studies identifying the cause of the deviations, the growing number of studies showing evidence of ration-dependent error in BEMs (Madenjian and O'Connor 1999; Chipps et al. 2000; Bajer et al. 2003, 2004a, 2004b; Whitledge et al. 2003, 2006; Chipps and Wahl 2004; Madenjian et al. 2006) indicates that caution should be exercised in applying uncorrected BEMs to both slow- and fast-growing fish populations.

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Appendix follows

Appendix: Walleye Growth Curve Computation

TABLE A.1.—Walleye weights (g) used in the computation of the polynomial growth curves. The coefficient of variation (CV) is equal to the SD divided by the average weight times 100.

Age	Week	*n*	1992	CV	Age	Week	*n*	1993	CV	Age	Week	*n*	1994	CV
1	23	9	100.22	38.33	2	24	29	127.90	27.40	1	26	8	52.88	28.90
1	24	4	113.00	12.72	2	25	25	133.36	28.02	1	32	4	77.25	38.13
1	26	4	101.00	26.16	2	26	17	161.06	38.59	1	33	6	76.67	34.58
1	27	4	120.25	39.97	2	27	38	137.21	28.49	1	35	4	59.75	14.23
1	28	8	85.88	38.82	2	28	34	139.62	31.25	1	36	6	103.00	22.51
1	29	26	61.50	51.08	2	29	12	152.58	35.49	1	37	5	149.40	53.09
1	30	11	88.00	37.74	2	30	31	128.13	21.32	1	38	7	134.43	32.39
1	31	9	81.44	48.79	2	31	14	133.14	23.88	1	39	8	128.50	34.52
1	32	7	71.29	44.81	2	32	14	150.50	30.12	1	41	7	163.43	47.61
1	33	6	97.83	46.37	2	33	16	153.38	20.47	1	42	11	120.36	34.57
1	34	16	93.75	56.49	2	34	18	159.17	22.50	3	19	41	285.44	19.01
1	35	7	97.57	27.35	2	35	9	165.78	36.92	3	23	10	287.90	9.58
1	36	8	118.25	28.80	2	36	4	232.75	16.52	3	24	9	217.78	14.93
1	37	22	111.73	28.19	2	37	10	203.10	11.87	3	25	4	236.75	14.72
1	38	20	110.90	32.12	2	38	11	209.55	19.30	3	26	14	242.36	15.20
1	39	13	128.85	22.44	2	39	23	263.30	17.92	3	27	32	269.28	18.21
1	40	22	139.91	32.16	2	40	35	260.09	19.10	3	28	16	287.44	23.89
1	41	24	173.54	33.63	2	43	43	336.16	18.93	3	29	15	276.60	20.12
1	42	19	155.79	31.37	3	24	4	302.50	33.24	3	30	9	279.56	13.72
1	43	4	292.50	19.34	3	25	6	328.33	13.56	3	31	14	293.00	16.69
2	23	15	195.93	30.79	3	26	4	351.75	16.45	3	32	11	280.82	27.06
2	24	10	218.10	21.55	3	27	10	350.60	17.24	3	33	23	288.43	19.23
2	28	7	308.71	17.59	3	28	4	337.25	19.29	3	34	11	326.55	11.82
2	29	11	240.91	24.56	3	30	5	291.80	17.75	3	35	20	339.80	13.29
2	32	7	234.57	23.48	3	37	4	361.75	10.41	3	36	15	319.87	18.66
2	36	6	276.00	11.83	3	38	5	338.20	15.60	3	37	20	360.00	16.76
2	40	4	284.75	28.32	3	39	6	423.33	22.21	3	38	7	366.57	23.94
2	41	6	378.17	17.66	3	43	18	428.22	17.23	3	39	23	353.30	13.54
2	42	6	292.67	29.05	6	23	14	570.13	19.20	3	40	12	351.17	14.03
2	43	16	352.31	12.61	6	24	8	629.63	22.69	3	41	21	399.00	20.41
3	23	12	351.75	22.85	6	25	21	598.19	21.11	3	42	38	378.03	22.14
3	24	10	361.90	26.70	6	26	22	615.73	16.27	4	19	8	433.25	16.75
3	27	4	357.25	13.17	6	27	17	627.00	19.58	4	26	4	507.00	17.82
3	28	6	411.33	23.31	6	28	8	526.50	15.50	4	27	5	388.40	8.92
3	29	5	346.00	25.28	6	29	28	533.18	14.51	4	29	5	394.60	15.74
3	30	4	361.50	40.22	6	30	14	594.28	15.93	4	33	4	472.00	13.43
3	34	4	311.00	12.27	6	31	9	511.33	14.01	4	36	5	471.60	10.20
3	41	5	562.60	10.36	6	32	4	636.25	21.25	4	42	5	489.20	32.75
3	43	6	483.83	11.48	6	33	4	670.25	14.39	7	19	14	647.93	10.73
5	23	40	590.65	16.88	6	34	6	476.50	15.02	7	24	4	728.75	22.87
5	24	30	599.67	17.78	6	35	5	666.20	19.18	7	25	9	629.67	19.89
5	25	16	574.13	20.20	6	36	10	599.10	22.35	7	26	9	660.78	11.14
5	26	29	579.07	15.30	6	37	10	590.40	20.93	7	27	9	573.33	18.61
5	27	21	515.05	14.85	6	38	14	534.29	14.69	7	28	9	619.33	18.71
5	28	30	597.53	19.92	6	39	5	672.40	12.26	7	29	7	516.00	14.34
5	29	34	564.82	19.88	6	40	20	654.35	18.21	7	30	6	487.00	11.72
5	30	11	558.18	17.48	6	43	46	648.74	19.12	7	31	4	573.75	10.32
5	31	32	616.53	17.15	7	24	4	508.50	26.06	7	32	5	480.40	13.20
5	32	32	606.78	18.95	7	25	15	877.80	28.67	7	33	8	485.25	12.58
5	33	16	638.19	15.96	7	26	6	843.17	26.72	7	34	5	648.20	25.76
5	34	7	564.00	5.33	7	27	5	712.60	19.22	7	36	7	541.86	12.23
5	35	15	597.20	15.39	7	28	5	703.40	16.70	7	37	7	629.86	13.83
5	36	15	646.73	18.11	7	29	5	732.00	20.01	7	39	7	628.86	25.08
5	37	4	667.50	13.89	7	30	8	797.88	29.65	7	40	6	695.67	15.03
5	38	11	648.00	28.31	7	31	6	805.50	33.67	7	41	4	645.50	23.29
5	39	13	569.54	14.26	7	34	4	722.75	24.75	7	42	13	587.62	20.53
5	40	7	700.57	16.55	7	36	4	637.50	10.75					
5	41	7	571.14	12.31	7	37	5	758.60	10.54					
5	42	7	643.57	15.19	7	38	8	781.75	16.15					
5	43	25	700.40	21.69	7	39	4	752.00	13.74					
					7	40	7	1,047.86	56.09					
					7	43	16	802.69	34.94					