

Bioenergetics Modeling in the 21st Century: Reviewing New Insights and Revisiting Old Constraints

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Abstract.—The development and application of fish bioenergetics models have flourished in recent years, due in part to the complexity of the issues being faced by fisheries biologists. As with any model, the accuracy of bioenergetics models can be hampered by uncertainty in model parameters. A review of the literature showed that field and laboratory tests of bioenergetics models often result in poor agreement between model predictions and independent data. Nonetheless, bioenergetics modeling continues to be used to make important management decisions. Recent tests of model predictions have shown that parameter uncertainty is influenced by factors such as feeding rate, physiological adaptations, and prey composition and abundance. In an attempt to reduce the uncertainty in modeling applications, we propose a framework that highlights the importance of (1) model evaluation, (2) hypothesis-based parameter testing, and (3) improved communication between model developers and model users. Adherence to this framework will help reduce uncertainty in modeling applications and simultaneously contribute to a broader knowledge of fish physiology and feeding ecology.

Bioenergetics models provide a sound theoretical approach for estimating energy allocation in animals by partitioning consumed energy into three basic components: (1) metabolism, (2) wastes, and (3) growth (Winberg 1956). Because the models are based on mass-balance equations, they are often used to estimate growth or consumption given information on other variables. Bioenergetics models are particularly attractive for estimating food consumption by free-ranging fishes because of the time and effort required for more traditional approaches (Kitchell et al. 1977). Today these models are widely used as a tool in fisheries management and research; the availability of user-friendly software has led to the popularity of bioenergetics models (Figure 1; Hansen et al. 1997). Nonetheless, the proliferation of bioenergetics modeling has not been without controversy (Ney 1993). Expansion and application of bioenergetics models have generally proceeded without parallel efforts to evaluate model reliability. This disparity was first highlighted in a symposium organized by Bevelhimer and Wahl at the 1989 Annual Meeting of the American Fisheries Society. Several papers presented there and later published in the primary literature (Beauchamp et al. 1989; Boisclair and Leggett 1989; Wahl and Stein

1991) raised concerns about the accuracy and application of these models. As part of a 1992 symposium (Hansen et al. 1993), Ney (1993) conducted a review of models developed at that time and found poor agreement between field-derived measures of consumption or growth and bioenergetics estimates in four of six published studies. Ney (1993) proposed several directions for improvement and suggested that, in the meantime, the models should be used for making relative comparisons rather than quantitative predictions. In a summary paper, Hansen et al. (1993) called for additional field and laboratory tests of bioenergetics models.

The recent symposium organized by Hartman et al. (this issue) highlighted the diversity of models being developed and the increased number of ways in which these models are being used (e.g., Petersen and Kitchell 2001; Trudel et al. 2001; Harvey et al. 2002). Given the popularity of bioenergetics modeling, we felt it would be useful to revisit the concerns posed by Ney (1993) and assess progress made since that time. To accomplish this, we summarized studies from 1980 to 2004 that conducted laboratory or field tests of bioenergetics models. In 1992, only six studies had evaluated bioenergetics models (Ney 1993). Our analysis provided a much larger sample size ($n = 32$) upon which to judge model performance. We also explored how bioenergetics models are used in present-day applications by considering whether models were used as

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qualitative tools for hypothesis testing or quantitative tools for prediction. When used for the latter, we grouped studies based on whether the model in question had been evaluated. We discuss insights gained from model evaluations and conclude by proposing guidelines for the development and use of bioenergetics models that highlight the importance of model testing and the interface between research and management as a means for reducing model uncertainty.

Model Development

Like other mathematical models, bioenergetics models are simplifications of reality. How well they describe the real world depends on appropriate parameterization of the model and the accuracy of input data used to drive them (Bartell et al. 1986). Consider, for example, the variables used to estimate fish respiration. Respiration rate is usually measured across a range of fish sizes and water temperatures and then expressed as a function of these two variables. In most cases, such formulations provide reasonable estimates of respiration rate. But what if other factors, such as dissolved oxygen concentration, also affect respiration rate? Applying the model under variable oxygen concentrations, we might find that respiration rate is poorly defined because our parameter estimate is based on incomplete data. We could argue that this is a poorly parameterized model for ecological application or an inappropriate application of an otherwise descriptive model. In our view, the burden of rectifying this dichotomy lies with both model developers and users. Calibration of bioenergetics models, in itself, should not be the endpoint in model development. Rather, we argue that bioenergetics models need to be confronted with data as an important step in the model development process. Only by evaluating the performance of model output do we gain insights into model limitations; this knowledge can lead to improvements in model reliability by directing efforts at recalibrating model parameters and generating new hypotheses about parameter formulations (Hilborn and Mangel 1997).

Model Evaluation

Because bioenergetics models are based on a sound theoretical footing (e.g., thermodynamics), they provide a useful template for evaluating energy flow. Indeed, there is no evidence that conceptual models for mass-balance energy budgets are wrong (Ney 1993). When model output poorly represents observed data, one of several things may be true: (1) the model is incorrectly parameterized, (2) the input data used to drive the model are inaccurate, (3) the independent data

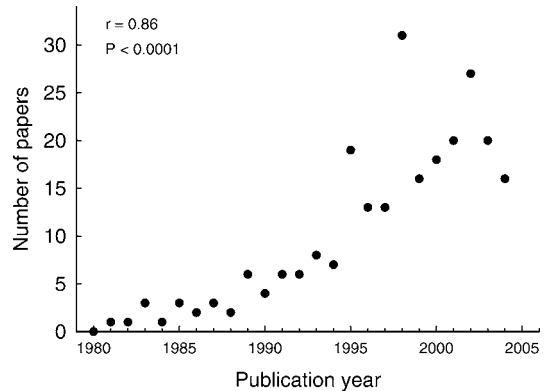


FIGURE 1.—Trends in the use of bioenergetics models from 1980 to 2004 as revealed by a literature search in BIOSIS with the keywords “bioenergetics” and “model.” The Pearson correlation coefficient and significance level are given.

being compared with the model results are wrong, or (4) some combination of the above.

Laboratory data, field observations, or both provide measures for model evaluation. Field evaluations account for natural feeding patterns and environmental effects, but represent a challenging means for model validation because accurate consumption estimates are difficult to obtain in free-ranging fishes (Diana 1983). Aside from being time and labor intensive, traditional methods for estimating food consumption rely on models and assumptions that could also be subject to error, thereby making it difficult to objectively evaluate bioenergetic model predictions. Admittedly, when discrepancies between field data and model predictions arise, it can be difficult to distinguish which of the previous outcomes (or explanations) was true. In the laboratory, sampling error can be significantly reduced, thus minimizing the influence of outcomes 2–4 above. For this reason, laboratory tests provide an important precursor to model corroboration because they help identify uncertainty in model output (Ney 1993; Madenjian et al. 2006). To characterize the performance of bioenergetics models, we reviewed published studies from 1980 to 2004 using electronic searches in BIOSIS with keywords “bioenergetic” and “model.” We chose this 24-year time period because it probably captured most, if not all, studies that evaluated bioenergetics models. During this period, a total of 32 studies compared model predictions with values observed in either the field or laboratory (Figure 1).

Field Tests

We found 17 studies in which field tests of bioenergetics models were conducted (Table 1). All but one of these studies estimated food consumption in

TABLE 1.—Summary of studies published since 1980 comparing field estimates with bioenergetics model predictions. All estimates are for food consumption except that for southern flounder, which is for growth. Positive values for percent differences indicate that model estimates were higher than field estimates.

Species	Percent difference	Months	Years	N	Age-classes	Analytical techniques	Reference
Sauger <i>Sander canadensis</i>	+2 to +770	12	2	1,114	2	0	Minton and McLean (1982)
Northern pike <i>Esox lucius</i>	+24 to +56	8	3	1,290	2	0	Diana (1983)
Largemouth bass <i>Micropterus salmoides</i>	+8	6	1	413	1	3	Rice and Cochran (1984)
Sockeye salmon <i>Oncorhynchus nerka</i>	+10 to +15	4	2	391	1	3	Beauchamp et al. (1989)
Yellow perch <i>Perca flavescens</i>	-51 to +3	5	1	4,200	3	1	Boisclair and Leggett (1989)
Walleye <i>Sander vitreus</i>	+40	1.5	1	360	1	1	Fox (1991)
<i>Esox</i> spp.	+39 to +52	6	3	2,933	1	3	Wahl and Stein (1991)
Baltic herring <i>Clupea harengus membras</i>	-30 to +89	4	1	1,885	1	1	Arrhenius (1998)
Walleye pollock <i>Theragra chalcogramma</i>	+5 to +17	1	1	300	1	0	Ciannelli et al. (1998)
Perch	0 to +162	1	1	240	1	0	Worischka and Mehner (1998)
Zander <i>Sander lucioperca</i>	+18 to +193	1	1	240	1	0	Worischka and Mehner (1998)
Northern pikeminnow <i>Ptychocheilus oregonensis</i>	-19 to -84	5	4	-	-	2	Petersen and Ward (1999)
Yellow perch	-25 to -50	6	2	5,315	4	2	Schaeffer et al. (1999)
Striped bass <i>Morone saxatilis</i>	+0.3 to +71	1	1	741	1	0	Hartman (2000)
Lake trout <i>Salvelinus namaycush</i>	+0.2	2-3	1	1,108	6	1	Madenjian et al. (2000)
Lake trout	+30 to +80	1	1	57	7	2	Trudel and Rasmussen (2001)
Southern flounder <i>Paralichthys lethostigma</i>	+50	1	1	28	1	1	Burke and Rice (2002)
Chinook salmon <i>Oncorhynchus tshawytscha</i>	+22	5	1	142	5	1	Madenjian et al. (2004)

the field and compared those estimates with the predictions of a bioenergetics model. Model predictions were obtained by inputting field estimates of fish growth. A single study used the model to predict growth and compared that with field estimates (Burke and Rice 2002). Field studies included a wide range of fish species across a number of trophic guilds (Table 1). Studies also included both juvenile and adult fishes. For comparative purposes, we calculated the percent difference between the model and field estimates reported in each study as $(\text{modeled value} - \text{observed value}) / \text{observed value} \times 100$ (Ney 1993).

Field tests of bioenergetics models generally revealed poor fits between model predictions and field estimates. The percent difference between field and model estimates ranged widely, from -84% to +770%. A few studies showed reasonable agreement (<15%) between field estimates and bioenergetics predictions; these included models for lake trout (+0.2%; Madenjian et al. 2000), largemouth bass (+8%; Rice and Cochran 1984), and sockeye salmon (+10%; Beauchamp et al. 1989). The remainder of the studies (82%) found substantially higher discrepancies, implying poor fits between field and model estimates. Moreover, in a majority of these studies (82%), model estimates of food consumption were higher than those calculated from field-derived diet data. The three exceptions were one study of northern pikeminnow (Petersen and Ward 1999) and two of yellow perch (Boisclair and Leggett 1989; Schaeffer et al. 1999).

To explore the factors associated with potential model error, we examined all of the studies published in the peer-reviewed literature that compared bioener-

getics predictions with field data. These studies probably vary both in the quality of data collected and in the rigor of statistical evaluation that could influence the level of agreement with bioenergetics model predictions. As a result, we summarized a number of metrics that could influence the precision of field estimates and agreement with model values, including the number of months and years of field data collected, sample size, the age-classes examined, and the number of analytical techniques used. We compared each metric across studies against the maximum percent difference (absolute value) reported for each study (Table 1) as well as the range in percent error. As might be expected, studies varied widely in both of these measures (Table 1). The majority of studies examined a single age-class with a few examining three or more. Expanding evaluations of model performance to examine multiple age-classes, particularly older ages, would be useful. A surprising number of studies (29%) did not use any statistical or analytical techniques to assess fits between model predictions and values determined in the field. We compared percent difference reported for these studies (Table 1) with those that used one or more analytical techniques and found higher maximum (*t*-test; $P = 0.05$) and greater range ($P = 0.05$) in percent difference for studies using no analytical techniques. Many studies calculated food consumption using multiple years of field data, but about half of these examined only a single year. Months examined within a year also varied substantially, ranging from 1 to 12 months. Examining a high number of months and years would be important for capturing temporal variation in food consumption

and could affect agreement with model predictions. We found increased disagreement between field estimates and model predictions when more months were included for both maximum (Pearson correlation: $P = 0.02$, $r = 0.56$) and range ($P = 0.02$, $r = 0.54$) in percent difference (Table 1). However, we found no relationship between either number of years ($P > 0.77$, $r = 0.02$ – 0.07) or total number of months (N of months \times N of years: $P > 0.07$, $r = 0.39$ – 0.44) sampled and the maximum or range in percent difference reported. These results suggest that disagreement between bioenergetics estimates and field data are largest when attempting to account for seasonal variation in food consumption.

Total sample size was also highly variable, but needed to be adjusted to account for the number of intervals examined to accurately reflect sampling effort. We divided sample size by the total number of months and number of age classes examined to determine the mean number of stomachs examined per month for each age-class. We found no relationship between this measure of sample size and differences between field observations and model predictions ($P > 0.74$, $r = -0.05$ to -0.08). In fact, some of the studies that had the largest sample sizes and used the most rigorous analytical techniques found the greatest disagreement between field estimates and model predictions. As an example, we highlight six studies, three with good agreement (largemouth bass, Rice and Cochran 1984; sockeye salmon, Beauchamp et al. 1989; Madenjian et al. 2000) and three with poor agreement (yellow perch, Boisclair and Leggett 1989; esocids, Wahl and Stein 1991; yellow perch, Schaeffer et al. 1999; Table 1), that all sampled over multiple months and years and employed a suite of analytical tools. Interestingly, the three studies that showed poor agreement between field and model estimates included 2–4 times as many stomachs per age-class per sampling interval (months and years). Based on these results, we believe that differences between predicted and observed values are not primarily related to issues with field estimates and that other factors inherent in making predictions with bioenergetics models must be considered.

Laboratory Tests

We found 15 studies in which laboratory tests of bioenergetics models were conducted, covering a wide range of species and life stages (Table 2). Three studies compared estimates of growth and seven assessed food consumption, with five comparing both growth and food consumption. About half the studies fed fish ad libitum rations, whereas the remainder varied feeding levels from maintenance to ad libitum. Percent

difference between observed and predicted values ranged from -110% to 122% for estimates of growth and from -63 to -328% for estimates of food consumption (Table 2); on the average, percent difference did not differ between growth or food consumption (t -test; $P > 0.40$ for maximum and range). As a result, in subsequent analyses we used estimates of error for both measurements to compare across studies, choosing only values for food consumption from any single study whenever they were both presented to allow more direct comparisons with field studies. Across all studies, disagreement between observed and predicted values from laboratory evaluations was comparable with that determined in the field. Unlike field studies, however, those in the laboratory revealed a more even distribution between studies that showed model under- and overestimates, and this was the case for both consumption and growth.

As with field studies, these laboratory studies probably varied both in the quality of data collected and in the rigor of statistical evaluation that could influence the level of agreement with bioenergetics model predictions. As a result, we summarized a number of metrics that could influence precision and agreement with model values, including number of days and intervals examined, number of experimental units used, the number of age-classes, ration levels and temperature ranges examined, and the number of analytical techniques used. The experimental units used for reporting percent error and sample sizes varied by study (e.g., individual fish, means within or across tanks). Whenever possible we either chose from the reported values or recalculated tabled values to avoid pseudoreplication and to maintain consistency in the data used to calculate both percent error and each of the metrics (Table 2). As with field studies, we compared each metric across studies against the maximum percent difference (absolute value) reported for each study (Table 2), as well as the range in percent error. Studies varied widely in most of the metrics examined (Table 2) except that most studies examined a single age-class with only a few examining two and none examining more than two. Limited number of studies with older age-classes is probably due to the difficulty of holding adult fish in captivity and suggests the need for additional laboratory tests with large fish. Unlike field studies, the majority of laboratory studies (86%) used at least one and often several statistical or analytical techniques to assess fits between model predictions and observed values. We compared percent difference reported for those studies that used none or one against those that used two or more analytical techniques. As might be expected given the greater overall analytical rigor possible in laboratory studies,

TABLE 2.—Summary of studies comparing laboratory estimates of food consumption (FC) or growth (GR) with bioenergetics model predictions. Positive values for percent differences indicate that model estimates were higher than laboratory estimates. For each study, we determined the number of days the experiment was conducted, the number of intervals over which fish were measured (INT), the number of experimental units (N) and analytical techniques (AT) used, the number of age-classes, the number of rations, and the temperatures examined.

Species	Estimate	Ration	Percent difference	Days	INT
Age-0 striped bass	FC	Ad libitum	-3 to +46	12	1
	GR	Ad libitum	-110 to +62	12	1
Age-1 striped bass, bluefish <i>Pomatomus saltatrix</i> , and weakfish <i>Cynoscion regalis</i>	FC	Varied	-11 to +16	12	1
	GR	Varied	-76 to +122	12	1
Largemouth bass	FC	Varied	-28 to +8	63	9
Powan <i>Coregonus lavaretus</i>	FC	Ad libitum	-37 to +33	4	1
Hybrid sunfish ^a	FC	No food 2-14 d	-18 to -25	105	1
	GR	No food 2-14 d	+24 to +37	105	1
Lake trout	FC	Varied	-33 to +59	364	12
Largemouth bass	GR	Varied	-70 to +44	182	3
Tiger muskellunge ^b	FC	25-100%	+4 to +328	140	10
Yellow perch	GR	Ad libitum	+23 to +27	135	9
	GR	No food 12 d	-21 to -23	135	9
Burbot <i>Lota lota</i>	FC	Ad libitum	-63 to +1	11	1
	GR	Ad libitum	0 to +11	11	1
Smallmouth bass <i>Micropterus dolomieu</i>	FC	Ad libitum	-17 to +13	21	1
	GR	Ad libitum	-17 to +13	21	1
White crappie <i>Pomoxis annularis</i>	FC	Varied	-43 to +224	70	1
	GR	Varied	+15 to +43	70	1
Western mosquitofish <i>Gambusia affinis</i>	FC	Varied	-33 to +181	11	1
Chinook salmon	FC	Ad libitum	-14 to +11	99	3
Largemouth bass	GR	Varied	-60 to +10	14	1

^a Green sunfish *Lepomis cyanellus* × bluegill *L. macrochirus*.

^b Northern pike × muskellunge *Esox masquinongy*.

we found no difference in the maximum (t -test; $P = 0.53$) and range of percent difference ($P = 0.80$) for studies using more statistical techniques.

The length of studies ranged from a low of 4 d (for larval fish) to close to a year, with longer studies generally sampling more intervals to estimate error rates against model predictions (Table 2). Unlike in the field studies, we found no relationship under more controlled laboratory conditions between the maximum or range in percent difference from model predictions and the total number of days (Pearson correlation: $P > 0.78$, $r < 0.08$), intervals ($P > 0.62$, $r < 0.14$), or days per interval ($P > 0.75$, $r < 0.10$) examined. We also found no relationship between the number of experimental units (Table 2) used to determine error rates and both measures of differences between laboratory estimates and model predictions ($P > 0.35$, $r < 0.24$). In general, laboratory studies appear to be using adequate numbers of experimental units to test bioenergetic models.

Unlike with study duration, we did find positive relationships between percent error and the number of ration and temperature treatments examined. Laboratory tests of bioenergetic models have included a wide range of temperatures, ranging from 4 to 35°C (Table 2). We found increased disagreement between laboratory estimates and model predictions when a broader range of temperatures were examined for both

maximum (Pearson correlation; $P = 0.01$, $r = 0.62$) and range ($P = 0.005$, $r = 0.66$) in percent difference (Table 2). Similarly, when more individual temperature treatments were examined we also found higher percent differences as determined by the maximum ($P = 0.05$, $r = 0.66$) and range ($P = 0.002$, $r = 0.70$) values. The number of ration levels examined and the total number of unique treatments (ration levels, temperatures and ages combined) were also positively related to maximum ($P < 0.04$, $r > 0.67$) and range ($P < 0.004$, $r > 0.68$) in percent error. These results clearly suggest that disagreement between bioenergetics models and laboratory data are largest when attempting to account for a range of temperatures and variable ration levels on model estimates. These effects appear to be more important than study duration and the number of experimental units examined in laboratory studies.

Insights Gained from Model Evaluations

Four patterns emerged from our review of field and laboratory tests of bioenergetics models: (1) uncertainty in model predictions varies considerably among and within species; (2) disagreement between observed and predicted values was similar for field and laboratory tests; (3) bioenergetics estimates of food consumption were generally higher than those determined from field-based sampling; and (4) the error in bioenergetics esti-

TABLE 2.—Extended.

Species	N	AT	Age-classes	Ration	Temperature (°C)	Reference
Age-0 striped bass	28	0	1	1	7, 20	Hartman and Brandt (1993)
	28	0	1	1	7, 20	Hartman and Brandt (1993)
Age-1 striped bass, bluefish <i>Pomatomus saltatrix</i> , and weakfish <i>Cynoscion regalis</i>	22	0	2	1	19–25	Hartman and Brandt (1995)
	22	0	2	1	19–25	Hartman and Brandt (1995)
Largemouth bass	8	3	1	2	22, 27	Whitledge and Hayward (1997)
Powan <i>Coregonus lavaretus</i>	22	1	1	1	10–15	Huuskonen et al. (1998)
Hybrid sunfish ^a	3	1	1	3	24	Whitledge et al. (1998)
	3	1	1	3	24	Whitledge et al. (1998)
Lake trout	12	2	2	3	3–10	Madenjian and O'Connor (1999)
Largemouth bass	79	2	1	2	2–15	Wright et al. (1999)
Tiger muskellunge ^b	40	1	1	4	7.5–25	Chipps et al. (2000b)
Yellow perch	20	1	2	1	21	Bajer et al. (2003)
	20	1	2	1	21	Bajer et al. (2003)
Burbot <i>Lota lota</i>	12	3	2	1	12–19	Paakkonen et al. (2003)
	12	3	2	1	12–19	Paakkonen et al. (2003)
Smallmouth bass <i>Micropterus dolomieu</i>	3	2	2	3	22, 27	Whitledge et al. (2003)
White crappie <i>Pomoxis annularis</i>	6	1	2	3	23–30	Bajer et al. (2004a)
	6	1	2	3	23–30	Bajer et al. (2004a)
Western mosquitofish <i>Gambusia affinis</i>	18	2	1	3	10–35	Chipps and Wahl (2004)
Chinook salmon	12	2	1	1	12	Madenjian et al. (2004)
Largemouth bass	18	3	1	2	12–32	Slaughter et al. (2004)

mates increases when trying to account for variable water temperatures and feeding rates. Based on this summary, it is clear that attempts to corroborate bioenergetics models will continue to be met with mixed success.

Ney (1993) highlighted several areas that he believed reduced the reliability of bioenergetics models when used for predictive purposes, and we agree with those assessments. He argued that borrowing parameter values from other species (see also Trudel et al. 2004) and extrapolating models beyond the limits of their design (e.g., extrapolating from small fish to large fish) should be avoided. Ney (1993) also called for work on the activity components of energy budgets and stressed the importance of accurate field data (e.g., water temperature and seasonal prey energy density) when using bioenergetics models. These ideas provide direction for improving the reliability of bioenergetics models by focusing attention on the quality of information needed to assemble and drive the models. Here, we focus on the importance of parameter uncertainty in bioenergetics models and highlight three issues that contribute to model error as evidenced by recent studies.

Consumption-Dependent Error

The link between ration size and the accuracy of bioenergetics models has been well documented (Madenjian and O'Connor 1999; Chipps et al. 2000b; Bajer et al. 2004b; Chipps and Wahl 2004; Madenjian

et al. 2006). This phenomenon, termed “consumption-dependent error,” appears to be widespread among bioenergetics models and occurs when model accuracy varies as a function of food consumption (Bajer et al. 2004b). Moreover, the same general pattern appears across a range of species; namely, that bioenergetics models overestimate food consumption for fishes feeding at low rations and underestimate food consumption for fishes feeding a high rations (Table 3). Several hypotheses have been proposed to explain the influence of ration size on the accuracy of model predictions. Logically, several authors have pointed to consumption-dependent parameters in bioenergetics models as the source of error in model estimates (Wahl and Stein 1991; Chipps et al. 2000b; Bajer et al. 2004b). The idea that consumption-dependent parameters such as egestion, excretion, and specific dynamic action should be modeled as a function of ration size rather than fixed proportions of consumed energy is not new (Elliot 1976; Wahl and Stein 1991; Chipps et al. 2000b). For many bioenergetics models, estimates of waste losses are based on limited data from few species and are assumed to represent a constant proportion of consumed energy. In many taxa conversion efficiency declines at high ration levels, implying that waste losses should not be modeled as fixed proportions of consumed energy (Wahl and Stein 1991; Chipps et al. 2000b). Indeed, reducing waste losses (as a percentage of consumed energy) for fish fed low rations reduces

TABLE 3.—Summary of laboratory studies examining the errors between model predictions and observed values for fish fed either high (ad libitum) or low (<50% maximum) ration levels. All estimates are for food consumption except that for yellow perch, which is for growth. Positive values indicate that model estimates were higher than observed values.

Species	Low ration	High ration	Reference
Lake trout	+40 to +59	-33 to -13	Madenjian and O'Connor (1999)
Tiger muskellunge	+59	+4	Chipps et al. (2000b)
Smallmouth bass	+13	-17	Whitledge et al. (2003)
Yellow perch	-23 to +20	+22 to +27	Bajer et al. (2003)
White crappie	+82 to +218	-19	Bajer et al. (2004a)
Western mosquitofish	+58 to +181	-33 to +25	Chipps and Wahl (2004)

the amount of energy needed to balance the model, in turn, reducing the tendency of models to overestimate food consumption. Of the 33 models available in Fish Bioenergetics 3.0 (Hanson et al. 1997), only eight models (24%) incorporate effects of ration size and water temperature on estimates of waste loss.

Mechanisms affecting fish metabolism have also been proposed to explain the influence of ration size on the accuracy of model output (Brett and Groves 1979; Madenjian and O'Connor 1999). In a laboratory study of lake trout bioenergetics, model estimates of food consumption were lower than observed values for fish fed rations ad libitum (Madenjian and O'Connor 1999). Because activity was considered negligible, the authors postulated that increases in standard metabolism may occur for fish feeding at high rates and therefore affect model accuracy. Similarly, metabolic compensation (i.e., reduced metabolic rate) may occur for fish maintained on low rations, thus explaining why model predictions tend to overestimate food consumption at low feeding rates (Chipps and Wahl 2004).

Studies have shown that consumption-dependent error can also propagate in bioenergetics models independently of physiological changes. In a study of juvenile tiger muskellunge, the simulated error in metabolic rate had more influence on model accuracy for fish fed low rations than for fish fed ad libitum because it accounted for a higher proportion of the total energy budget (Chipps et al. 2000b). Moreover, recent studies have shown that fish fed fluctuating rations grow significantly faster than those fed similar amounts on a constant ration (Whitledge et al. 1998; Skalski et al. 2005). As a result, estimates of model error were higher for fish exhibiting a compensatory growth response (fluctuating ration) and were believed to be associated with physiological responses not accounted for in bioenergetics models (Whitledge et al. 1998). In a related study, however, Skalski et al. (2005) argued that the increase in growth occurred independently of any physiological changes because fish fed fluctuating rations initially remained smaller for a longer period of time, thus incurring lower cumulative maintenance costs over the growth interval.

Many of the hypotheses involving consumption-dependent error remain untested. Given the scope of this problem we believe that prioritizing research in this area will significantly improve the reliability of model estimates. As a start, we argue that bioenergetics models need to incorporate the effects of ration size on metabolic functions. Specifically, relationships among growth, metabolic rate (standard and activity) and waste losses inherent in bioenergetic models need to be determined as a function of ration size. Resolving these issues will be especially important when applying bioenergetics models to field conditions where consumption rate is known to be variable.

Physiological Adaptations

Regional differences in species physiology can have an important influence on the accuracy of parameter estimates. Although little attention has been paid to this topic, evidence suggests that physiological responses differ between populations. Munch and Conover (2002) found that regional differences among populations of Atlantic silverside *Menidia menidia* accounted for significant variation in weight-dependent consumption and the proportion of energy lost to excretion and egestion. All else being equal, northern populations of silversides consumed 37% more than southern populations at 24°C (Munch and Conover 2002). Differences in consumption and metabolism have also been observed as a function of latitude for muskellunge (Clapp and Wahl 1996) and walleye (Galarowicz and Wahl 2003). Although incorporating these effects into bioenergetics models is straightforward, information on regional physiological differences is often lacking for many species.

Subtle physiological adaptations can also have an important influence on accuracy of bioenergetics model predictions. In juvenile muskellunge, metabolic rate was significantly lower in winter months compared with that in spring and summer at the same water temperature (Chipps et al. 2000a). Hence, single-season estimates of fish metabolism may affect the reliability of model output if the model is applied outside of the range for which parameters are defined.

Similarly, in most bioenergetics models, physiological responses to environmental conditions are driven by water temperature. Yet factors such as dissolved oxygen concentration, salinity, and turbidity are known to affect physiological responses, but they are not usually included in parameter formulations (Cech et al. 1985; Niklitschek 2001; Sweka and Hartman 2001). In western mosquitofish, respiration rate varied significantly with dissolved oxygen concentration (Cech et al. 1985) and had important implications for model application (Chipps and Wahl 2004). These examples illustrate some of the constraints on existing models, but more importantly should prompt model developers to include hypothesis testing as a component of parameter estimation and model users to question whether the model is appropriately specified for the application being considered (see A Framework for Model Development and Application below).

Effect of Prey Composition and Abundance

Activity rate multipliers are often used in bioenergetics models to account for fish activity but have long been criticized as a variable (unknown) component of fish energy budgets (Boisclair and Leggett 1989; Boisclair and Sirois 1993; Madon and Culver 1993). Recent studies using glycolytic enzymes (lactate dehydrogenase) have linked activity levels in fish with variability in prey composition and abundance (Sherwood et al. 2002; Selch and Chipps 2007; Rennie et al. 2005). In a study of fast and slow growing yellow perch populations, Rennie et al. (2005) showed that fish from a fast growing population consumed less food than perch from a slow growing population. They attributed slow growth to increased activity levels resulting from differences in prey composition and abundance. Similarly, prey size and morphology are known to affect capture success (Wahl and Stein 1988; Einfalt and Wahl 1997) and can influence activity level in fish predators (Sherwood et al. 2002). In a laboratory study using largemouth bass predators and bluegill prey, activity levels of largemouth bass scaled positively with prey size (Selch and Chipps 2007). Subsequent bioenergetics modeling revealed substantial error in model predictions for bass foraging on large bluegills, presumably due to increased activity costs of capturing large prey that were not accounted for in the model.

In their present form, bioenergetics models do not account for the influence of prey composition or abundance on feeding-related activities. However, in most modeling platforms activity can be modeled as a function of prey density if relationships between activity and prey abundance are known. In a study with juvenile walleyes, Madon and Culver (1993)

showed that fish activity scaled positively with zooplankton biomass. They demonstrated that fits between observed and predicted food consumption were improved by modeling activity as a function of prey biomass. These examples highlight the influence of prey composition and abundance on foraging-related activity and demonstrate that model performance can be improved by accounting for these effects in parameter formulations.

Bioenergetics models have also been linked with foraging models to test hypotheses about factors affecting fish growth. These linked (or mechanistic) models account for prey composition and abundance via functional feeding responses and can provide important insights into factors constraining fish growth. In a study with brown trout *Salmo trutta*, Hayes et al. (2000) combined a bioenergetics model with a detailed foraging model to identify factors affecting lifetime growth rate of drift-feeding brown trout. A similar approach was used with a bioenergetics model for sockeye salmon to evaluate the influence of water temperature, prey density, and vulnerability to predation on the growth rate of kokanee (lacustrine sockeye salmon; Stockwell and Johnson 1997, 1999). Although the modeling formulations and data requirements for foraging models can be complex, when combined with bioenergetics modeling, they provide a powerful approach for evaluating the influence of prey abundance and composition on growth rate of fishes.

Model Applications

Relative versus Absolute Uses

The development and application of bioenergetics models has increased appreciably since the early 1980s. Our review of the literature revealed that the number of published studies increased from a few per year in the early 1980s to about 20 per year in the 2000s (Figure 1). Clearly, bioenergetics modeling has become widely used as a tool in fisheries research and management. Yet when confronted with data, few models seem to reliably track feeding or growth under variable conditions. Indeed, many bioenergetics models remain untested, prompting us to question how they are being used in present day applications. To explore this question, we reviewed the literature during the decade since the last bioenergetics symposium and located articles that used bioenergetics models. We performed an electronic search of journals in fisheries science and ecology using the BIOSIS database. We included the search terms "bioenergetic" and "model", for papers published between 1994 through 2004. Out of 17 journals searched, we chose 6 journals that contained the majority of relevant articles: *Canadian Journal of*

Application of Bioenergetics Models

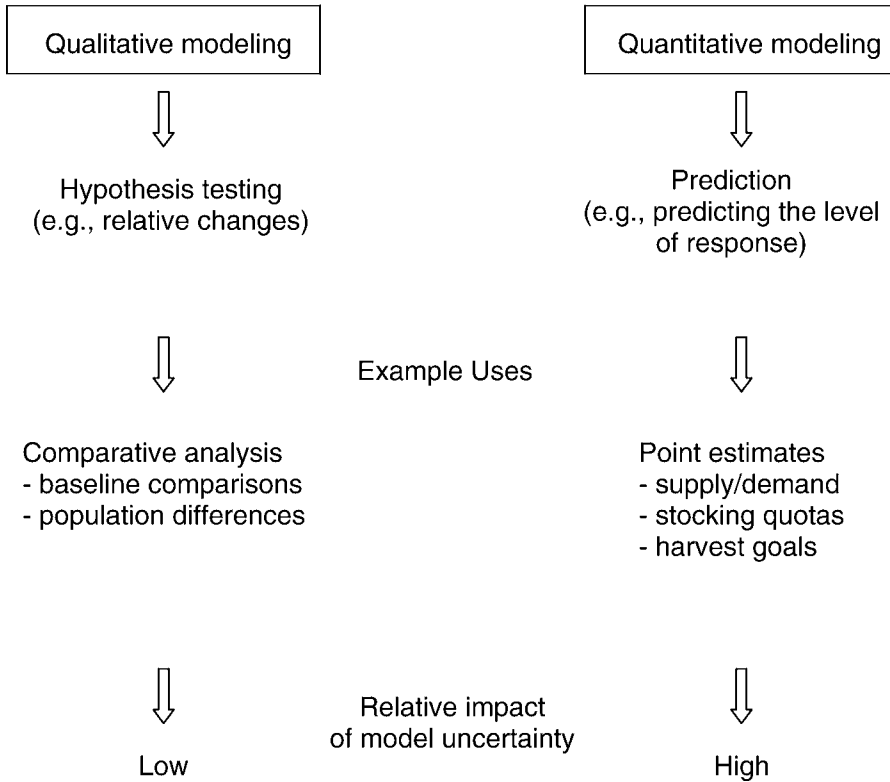


FIGURE 2.—Overview of qualitative versus quantitative applications of bioenergetics models in fisheries research and assessment.

Fisheries and Aquatic Sciences (CJFAS), *Ecological Applications* (EA), *Ecological Modeling* (EM), *Journal of Fish Biology* (JFB), *North American Journal of Fisheries Management* (NAJFM), and *Transactions of the American Fisheries Society* (TAFS). Since BIOSIS only searched title, abstract, and keyword fields for each reference article, we also conducted a visual issue-by-issue search in three of the journals containing most of the relevant articles during the 10-year period (CJFAS, NAJFM, and TAFS). This yielded additional papers not cited in the electronic search. We categorized each study on the basis of whether it used bioenergetics modeling to generate quantitative predictions (e.g., for setting harvest goals, stocking requirements, or balancing predator-prey demand) or served as a tool for hypothesis testing (Figure 2).

The use of bioenergetics modeling varied strongly by the journal in which the study was published (Figure 3). Studies published in management-related journals

(i.e., NAJFM and EA) had a much higher percentage of papers using models to generate quantitative predictions. In these cases, models were used to address questions such as predation mortality due to consumption or to determine stocking rates based on estimates of prey demand. In contrast, studies that used bioenergetics models to explore hypotheses about such topics as the effects of climate change on food consumption or comparisons of feeding rates across populations represented a larger proportion of the studies published in CJFAS, EM, and JFB.

Previous authors have suggested that the accuracy of model output could limit the application of models and that they should not be used to answer important management questions that require absolute measures without further testing and evaluation (Wahl and Stein 1991; Ney 1993). To assess whether this advice was being followed, we reviewed each of the 44 studies published during 1994–2004 that generated quantita-

tive predictions to see if they used a model that had been evaluated. For the purpose of these comparisons, we used a liberal definition of reliability—any single-species model for which the agreement between model output and independent data from any laboratory or field study was less than 15% was considered reliable. Using this criterion, we considered the models for largemouth bass, sockeye salmon, walleye pollock, and lake trout to be reliable. All of the other models evaluated had a range of uncertainty greater than 25%, in most cases substantially larger (Tables 1, 2). The majority of the studies that used bioenergetics models to generate predictive estimates did not use models we considered reliable (89%, 39 out of 44). Of the five studies that did, four were with sockeye salmon and the fifth was with largemouth bass. These summaries suggest that bioenergetics models continue to be used for predictive purposes in guiding management decisions despite lack of any evidence that they provide reasonable estimates of growth or food consumption. Moreover, with the exception of salmonine studies in the Great Lakes (Stewart and Ibarra 1991; Rand and Stewart 1998), there have been few follow-up attempts to evaluate the success of management decisions that were based on bioenergetics predictions.

The details of model formulation and constraints on model use are not always transparent to users. Ironically, the computing technology and software programs that have made bioenergetics models so accessible and easy to use can also contribute to misuse. Of those studies making quantitative predictions, the majority (82%, 36 out of 44) used commercially available software (i.e., Fish Bioenergetics 3.0). Encouragingly, a substantial number of these authors (43% of the studies) modified the parameters in the model in some fashion before applying the model to their particular question. However, most of the modifications were simply updates to temperature-dependent functions using more recently published data. The increased accessibility to bioenergetics models has made it easy to perform complex calculations and we encourage their use as a tool for qualitative comparisons. However, when using bioenergetics models to generate predictive estimates, we propose a precautionary approach that embraces, rather than averts, potential uncertainty in model output. These concerns are beyond those related to extrapolation of model results to the population level (i.e., estimates of population size), which is also difficult.

A Framework for Model Development and Application

We offer several recommendations as a framework for the development and application of bioenergetics

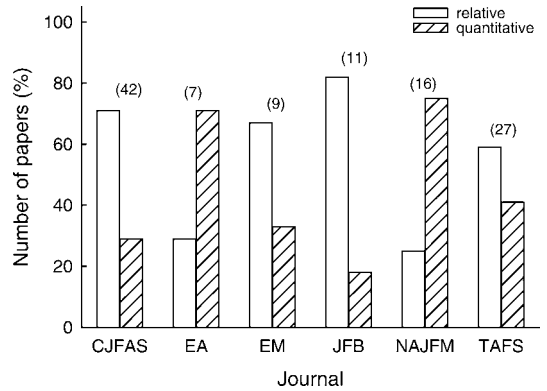


FIGURE 3.—Percentages of papers by journal during 1994–2004 that used bioenergetics models to make relative comparisons or quantitative estimates based on the results from bioenergetics modeling. The total number of papers examined from each journal is given in parentheses. See text for journal abbreviations.

models. To reduce the uncertainty in modeling applications, we highlight the importance of (1) model evaluation under a broad range of conditions, (2) hypothesis-based parameter testing, and (3) enhanced communication between model developers and users as a process for improving the dissemination of information. We focus our attention on modeling applications used for predictive purposes. Given the current state of uncertainty with many models, we believe that bioenergetics modeling is most powerful as a tool for qualitative assessment. Nonetheless, bioenergetics models are frequently used to generate quantitative predictions for guiding management decisions, and it is here that we propose guidelines for reducing uncertainty in modeling applications.

We begin by illustrating the five basic steps of the modeling process (Figure 4). For consistency, we use the definitions presented in Haefner (2005) for the following terms: (1) conceptual model, (2) mathematical model, (3) model verification, (4) model calibration, and (5) model evaluation. Model formulation begins with a conceptual model of the parameters of interest; in the classical view of energy budgets, this is given as $C = M + A + SDA + U + F + G$, where consumed energy (C) is balanced by the energy lost to metabolism (M), activity (A), specific dynamic action (SDA), excretion (U), or egestion (F) and that transformed into growth (G). The conceptual model is then expressed mathematically and translated into computer code to construct a quantitative model, a process that is termed verification. Calibration, in turn, is the process of parameter estimation; in most cases, controlled observations (experiments) are used to

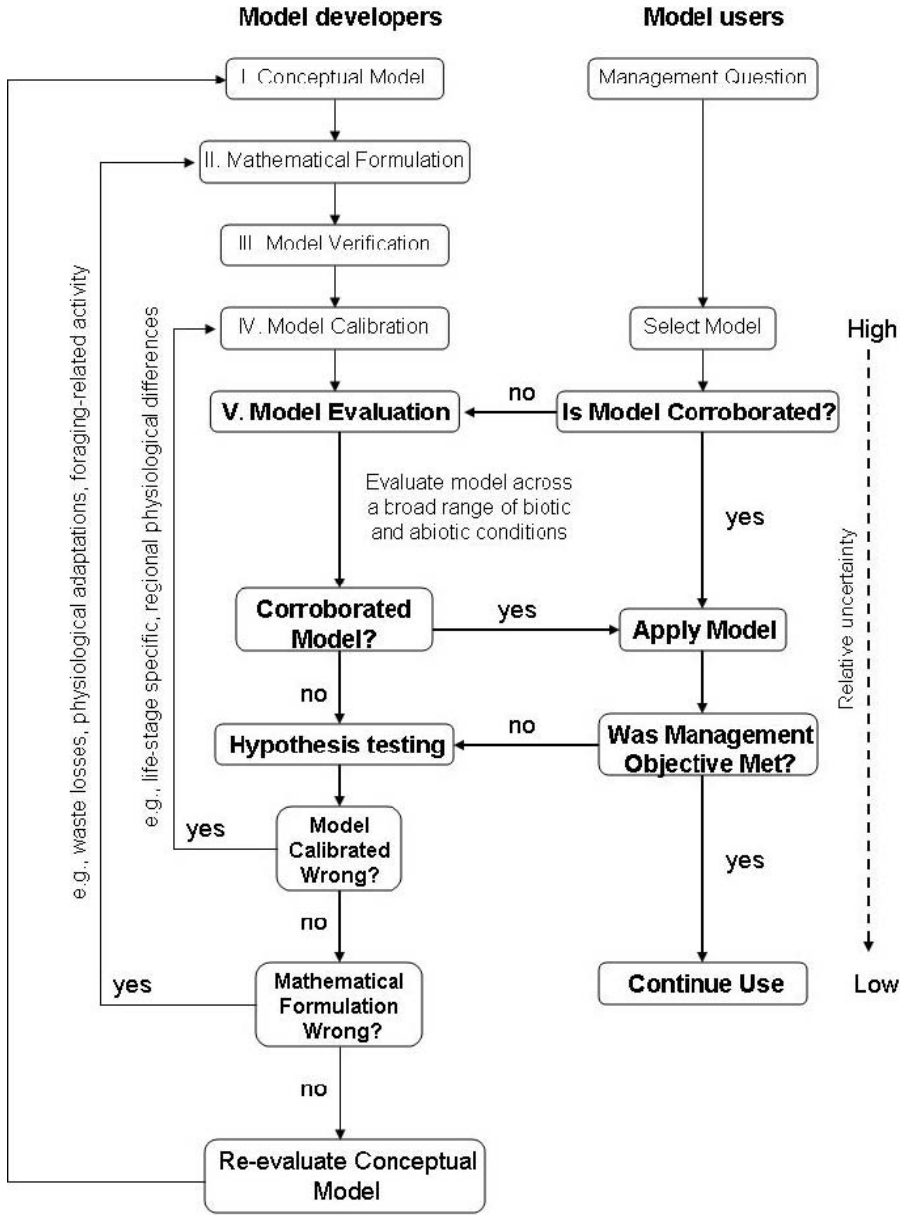


FIGURE 4.—Conceptual framework for reducing uncertainty in bioenergetics modeling applications (adapted from Haefner 2005). The flow diagram on the left depicts the general modeling process from conceptualization to evaluation. The steps associated with evaluation and parameter testing are in bold type to highlight their importance in model development. The flow diagram on the right depicts the steps that should be taken before model use or that provide feedback to model developers. The interactions between model development and use (horizontal arrows) are crucial to establishing the level of uncertainty associated with predictions (dashed arrow). To this end, it is important that model users document the success or failure of management decisions based on bioenergetics predictions.

quantify relationships and develop predictive equations for estimating model parameters (e.g., regression constants; Haefner 2005). Finally, the model is evaluated using independent data in an attempt to

validate model output. However, because models are never truly validated (Hilborn and Mangel 1997; Berkson et al. 2002), we use the term “corroborated” to refer to models that, when compared with indepen-

dent data, provide reasonable agreement to observed values. Generally speaking, the development of most bioenergetics models has been considered complete once the models have been calibrated. Indeed, there are few instances where models have been adequately evaluated as part of the development process.

The framework we present depicts a classical view of the modeling process (Figure 4). With regard to bioenergetics models, however, we emphasize two important components: (1) the model evaluation phase and (2) interactions between model developers and model users. In the evaluation phase it is important that models are tested across a broad range of conditions (e.g., water temperature, feeding rate, prey density), paying careful attention to the accuracy of the input data used to drive it. Indeed, variation in input parameters (i.e., 95% confidence limits) should be included whenever possible by bracketing model predictions to account for the uncertainty in external variables (Hartman and Hayward 2007). When model predictions provide poor fits (e.g., >25%) to observed data, model developers should question whether (1) the model is appropriately calibrated or (2) alternative parameter formulations are needed, with the ultimate goal of corroborating model output. For the latter, we advocate that model developers pay particular attention to issues involving consumption-dependent error, physiological adaptations, and foraging-related activity (e.g., prey type and abundance). Once a model has been evaluated it is important that model users recognize potential limitations to its performance. How well did the model perform? Under what conditions was the model evaluated? Did the authors make any adjustments to model parameters or suggest limitations to model application? In many of the studies we reviewed, the authors offer advice for dealing with model uncertainty that either helps improve the reliability of model output (Bajer et al. 2004a; Madenjian et al. 2006; Whitley et al. 2006) or identifies specific constraints to model use (Chipps et al. 2000b; Chipps and Wahl 2004). As with all models it is important to recognize the constraints associated with model use; models corroborated using laboratory data under a narrow set of conditions may be less reliable in field situations than those corroborated under a broad range of conditions in both the field and laboratory. While the latter would be considered an acid test of a bioenergetics model, in most cases corroborated models should be used only within the range of conditions under which they were evaluated. Hence, we emphasize that model users consider the conditions and constraints affecting model reliability. An effort to adhere to our proposed framework will be required by both model developers and model users.

Model developers need to incorporate model evaluation as an important step in the development process and translate these results into a context useful for management application (Mace and Sissenwine 2002). It follows that model users must recognize the limitations of model predictions and question how uncertainty in bioenergetics estimates influences management decisions. Effective communication between these two groups is critical for the development and application of modeling technologies—something we believe has been underappreciated with regard to the proliferation of bioenergetics modeling.

Case Study of an Esocid Model

To demonstrate the application of our framework, we offer a case history of an esocid bioenergetics model. Our example focuses on a post hoc evaluation of a bioenergetics model developed for esocid fishes (Bevelhimer et al. 1985) where field and laboratory tests of model output and subsequent work with age-0 muskellunge have improved our understanding of esocid energetics. To calibrate the esocid model developed by Bevelhimer et al. (1985), Wahl and Stein (1991) adjusted parameter estimates for activity metabolism and waste loss to account for juvenile fish physiology and piscivory. They then evaluated the model by comparing field estimates of growth and food consumption with those generated by the model. They found that field-derived estimates of food consumption were consistently lower (39–52%) than those generated from the bioenergetics model during two field seasons. A number of mechanisms were proposed to explain these discrepancies, including variable waste loss, seasonal variation in metabolic rate, the influence of different prey taxa on foraging activity, and a combination of these factors (Wahl and Stein 1991). Several years later, we evaluated the same model in the laboratory across a broad range of water temperatures and ration levels, where direct observations of juvenile tiger muskellunge feeding and growth ($n = 40$ fish) could be compared with model output. Like Wahl and Stein (1991) we found that observed food consumption was 30–75% lower than that generated by the model (Chipps et al. 2000b). Moreover, our laboratory work revealed that accuracy of model predictions varied with season and ration level, leading us to hypothesize that mathematical formulations, particularly for metabolism and waste loss, needed to be revisited as proposed by Wahl and Stein (1991). In winter months (<10°C), for example, the model overestimated food consumption by 113–328% compared with only 4–58% during summer months (>20°C; Chipps et al. 2000b). Because parameters for fish metabolism had been calibrated across the range of water temperatures we

examined (Bevelhimer et al. 1985), we were interested why the model performed so poorly at low water temperatures. Does seasonal variation in metabolism, which has been documented for other fishes (Evans 1984), account for the seasonal variability in model accuracy? To test this hypothesis we conducted laboratory experiments using age-0 muskellunge and found that respiration rate varied with season independently of water temperature (Chipps et al. 2000a). Indeed, for a 100-g muskellunge reared at 10°C, respiration rate was 65% lower during winter than in summer months (Chipps et al. 2000a). Incorporating these seasonal metabolic changes in the esocid bioenergetics model reduced the error rate (percent difference) by about 50% and improved the reliability of model output (S. Chipps, unpublished). Although feeding history (e.g., ration level) was not examined, we suspect that it also influences metabolism, waste losses, or both; if so, incorporating these effects into parameter formulations would further improve the reliability of model output.

The results from such detailed evaluations taught us several lessons: (1) the value of combined field and laboratory testing as a means to evaluate model reliability, (2) the variation of model accuracy with biotic and abiotic factors, and (3) the importance of treating model parameters as hypotheses (that is, do parameter formulations capture all the important physiological drivers?). This iterative process of conjecture and testing illustrates the importance of model evaluation in the development and application of bioenergetics models. Taken together, these efforts also help reduce uncertainty in modeling applications by highlighting constraints to model reliability that model users can incorporate in the decision-making process.

Conclusions

Our review indicated that tests of bioenergetics models continue to be met with mixed success. Indeed, more often than not we found poor fits between model predictions and field or laboratory data. To improve model performance, we encourage model developers to include evaluation and hypothesis-based parameter testing as important components of the development process. As we have learned, these efforts reveal how well models perform across variable conditions and shed light on factors affecting bioenergetic predictions that have implications beyond assessing model accuracy. Aside from work with salmonids (Elliot 1976; Brett and Groves 1979), little attention has been paid to the dynamics of energy budget components (waste losses, metabolism, feeding, and growth). Yet, factors such as ration size, metabolic adaptations, and foraging-related activity have an important influence

on accuracy of model predictions. Quantifying these effects helps reduce the uncertainty in bioenergetics models in addition to enhancing our knowledge of fish physiology and feeding ecology.

Finally, as with other models, it is important to recognize that there is uncertainty in bioenergetics estimates. Although bioenergetics modeling provides a powerful tool for fisheries assessment, it does not free model users from recognizing the influence of model uncertainty on management decisions (Ney 1993). In this context we encourage model users to consider the importance of model evaluation and the relative uncertainty associated with model estimates as outlined in our framework. In our view, the application of bioenergetics models will be better served by relying more on the evaluation process and less on the traditional "black box" approach to model use.

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