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Evaluation of a *Mysis* bioenergetics model

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Direct approaches for estimating the feeding rate of the opossum shrimp Mysis relicta can be hampered by variable gut residence time (evacuation rate models) and non-linear functional responses (clearance rate models). Bioenergetics modeling provides an alternative method, but the reliability of this approach needs to be evaluated using independent measures of growth and food consumption. In this study, we measured growth and food consumption for M. relicta and compared experimental results with those predicted from a Mysis bioenergetics model. For Mysis reared at 10°C, model predictions were not significantly different from observed values. Moreover, decomposition of mean square error indicated that 70% of the variation between model predictions and observed values was attributable to random error. On average, model predictions were within 12% of observed values. A sensitivity analysis revealed that Mysis respiration and prey energy density were the most sensitive parameters affecting model output. By accounting for uncertainty (95% CLs) in Mysis respiration, we observed a significant improvement in the accuracy of model output (within 5% of observed values), illustrating the importance of sensitive input parameters for model performance. These findings help corroborate the Mysis bioenergetics model and demonstrate the usefulness of this approach for estimating Mysis feeding rate.

INTRODUCTION

Bioenergetics models provide an efficient, cost-effective means for estimating growth and food consumption by aquatic animals. Based on balanced energy budgets, bioenergetics models have been applied to address a variety of ecological questions, such as contaminant uptake in fishes (Stow and Carpenter, 1994), nutrient regeneration (Kraft, 1993; Chipps and Bennett, 2000) and food web interactions (He *et al.*, 1993; Schindler *et al.*, 1993; Johannsson *et al.*, 1994). Although application of bioenergetics modeling has increased, many models have not been adequately evaluated using independent field or laboratory data [but see (Rice and Cochran, 1984; Beauchamp *et al.*, 1989; Hartman and Brandt, 1993; Whitledge and Hayward, 1997)]. The evaluation of bioenergetics models is a crucial step for ensuring the accuracy of model predictions as well as enabling researchers to identify and correct potential sources of error (Ney, 1993).

For invertebrate predators such as the widely distributed opossum shrimp *Mysis relicta*, direct approaches for estimating the feeding rate can be hampered by variable gut residence time [evacuation rate models; (Murtaugh, 1984; Chipps, 1998)] and non-linear functional responses [clearance rate models; (Folt *et al.*, 1982; Rudstam, 1989)]. As a result, bioenergetics modeling provides an attractive approach for estimating the feeding rate of *Mysis*, but needs to be evaluated to determine the reliability of model output. In this paper, we compare estimates obtained from a *Mysis* bioenergetics model to observations of *Mysis* growth and food consumption from laboratory rearing experiments. We discuss the accuracy of food consumption estimates obtained from the model and identify potential sources of variation affecting model output.

METHOD

Feeding and growth

Mysis relicta were collected from Lake Pend Oreille, Idaho, USA, on 15 December 1996 and transported to the

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laboratory in coolers filled with 5°C lake water. In the laboratory, *Mysis* were transferred to a 5 l jar filled with dechlorinated 5°C well water, reared in the dark for ~4 weeks and fed thawed *Daphnia pulex* at 2- to 4-day intervals.

Growth studies were initiated on 16 January 1997. To obtain *Mysis* wet weight (wt), we pipetted mysids ($N = 10$) into 100 ml beakers filled with 5°C water. *Mysis* were decanted onto a 5 × 5 cm, 150-μm-mesh cloth, and excess water was blotted away from the underside of the cloth. Each *Mysis* (10.7–14.5 mm) was then carefully weighed to the nearest 0.0001 g (range = 0.007–0.020 g wet wt), placed into one of 10 jars filled with 650 ml of water, and maintained in a dark incubation trough at 5°C. Water temperature in the incubation trough was slowly increased over 5 days from 5 to 10°C, and *Mysis* were allowed to acclimate to 10°C for an additional day. Previous studies with *Mysis* revealed that an acclimation rate of 1°C day^{-1} resulted in significantly different feeding rates at 4 and 10°C (Chipps, 1998). When *Mysis* were not acclimated at 1°C day^{-1}, feeding rates were similar at 4 and 12°C (Rudstam *et al.*, 1999). The optimal temperature range for *Mysis* feeding and growth is 9–12°C (Chipps, 1998; Rudstam *et al.*, 1999).

Each *Mysis* was initially fed a fixed ration of five *D. pulex* day^{-1} [$\bar{x}$ dry wt = 0.028 mg, SE = 0.0012; (Chipps, 1997)], but on day 6 of the experiment we increased the daily ration to 10 *D. pulex* day^{-1} because all *Daphnia* were being consumed by individual mysids. We increased the ration size to ensure that *Mysis* would experience measurable growth over the feeding trial. *Daphnia pulex* were collected from a local reservoir using a 1-mm-mesh D-net and then frozen in filtered lake water. This gear sampled larger *D. pulex* ($\bar{x}$ length =1.80 mm), helping to reduce variability in body size [95% CI = 1.67–1.89 mm; (Chipps, 1997)]. The mean dry wt of *Daphnia* was estimated using the equation:

$$W = 0.028L - 0.022$$

where W is dry wt in milligrams and L is *Daphnia* length in millimeters (Richman, 1958).

Jars containing *Mysis* were examined daily, and uneaten *D. pulex* and accumulated fecal pellets were removed by siphoning. Feeding experiments continued until all *Mysis* had produced at least two molts (~50 days). Two mysids died during the experiment and were not included in the analysis. At the end of the feeding trials, *Mysis* were starved for 18–24 h and then weighed (wet) to the nearest 0.0001 g.

Comparisons with model output

We used the Wisconsin bioenergetics model to estimate *Mysis* food consumption (Rudstam, 1989; Hanson *et al.*, 1997). Actual food consumption (g dry wt) was estimated by multiplying the total number of *D. pulex* consumed by their mean dry wt (0.028 mg). To account for variability in *D. pulex* size, we also calculated cumulative consumption based on the lower (0.025 mg) and upper (0.030 mg) 95% confidence limit (CL) for mean body mass of *D. pulex*.

Bioenergetic estimates of food consumption were computed using initial and ending wet wt of *Mysis* as input. Owing to the delicate nature of *Mysis* and their susceptibility to handling mortality, they were only weighed at the beginning and end of the feeding trial. Other parameters required in the bioenergetics model included predator and prey energy densities, water temperature and proportion of prey items in the diet. Water temperature (10°C) and proportion of prey items (100% *Daphnia*) were held constant during the feeding trials.

Energy density of *Mysis* was modeled from values reported by Lasenby (Lasenby, 1971). For juvenile *M. relicta* in Char Lake, Lasenby (Lasenby, 1971) reported an energy value of 20.92 kJ g^{-1} dry wt (3.14 kJ g^{-1} wet wt). We used information reported by Richman to obtain energy density of *D. pulex* (Richman, 1958). On a dry wt basis, the mean energy density of 1.80 mm *D. pulex* is 21.23 kJ g^{-1} dry wt (Richman, 1958). For modeling purposes, wet wt energy densities are generally used as input because fish and invertebrates consume and become satiated by prey in their wet state (Luecke and Brandt, 1993). We computed a wet wt energy density of 2.123 kJ g^{-1} wet wt for *D. pulex* by assuming a dry:wet wt ratio of 10% for *Daphnia* prey (Dumont *et al.*, 1975). This value was then adjusted to 1.868 kJ g^{-1} wet wt to account for an estimated 12% energy loss associated with freezing and thawing of *D. pulex* prey (Luecke and Brandt, 1993). Because wet wt energy density, and hence consumption estimates, were sensitive to the dry:wet wt ratio of prey (Luecke and Brandt, 1993; Stockwell *et al.*, 1999), we multiplied bioenergetic food consumption estimates by 0.10 to convert consumption back to dry wt. In studies with fish, the dry:wet wt ratio of *Daphnia* removed from stomach contents is generally higher than that calculated from field samples (Luecke and Brandt, 1993; Stockwell *et al.*, 1999). This phenomenon can lead to significant errors in prey energy density, and hence bioenergetic estimates, when water loss due to ingestion is unknown. For this reason, we compared consumption estimates on a dry wt basis since these values were not affected by assumptions regarding water content of prey. The dry:wet wt ratio of 0.10 was used only to compute a reasonable wet wt energy density as the required input for the model.

We used three statistical approaches to compare model predictions to observed values (Rice and Cochran, 1984; Wahl and Stein, 1991; Whitledge and Hayward, 1997). First, we compared estimates of food consumption to model values using a non-parametric, paired sign test (Statistical Analysis Systems, 1999). Second, sources of error in model predictions were evaluated by decomposition of mean square error (MSE). Using least squares regression of actual values on model estimates, MSE represents the variance around the 1:1 line (Wahl and Stein, 1991). This variance is partitioned into three components: (1) error associated with differences in the means (m); (2) error associated with the slope differing from unity (s); and (3) error associated with random variation (r). Finally, we used the reliability index k to determine how close (within a factor of k) model predictions were to actual values (Leggett and Williams, 1981; Rice and Cochran, 1984; Wahl and Stein, 1991). Statistically, the reliability index is accurate to a factor of k if 68% of observed values fall between $1/k$ and k (Leggett and Williams, 1981).

RESULTS AND DISCUSSION

Observed versus predicted consumption

Daily consumption of *D. pulex* prey ranged from 0.119 to 0.206 mg dry wt *Mysis*$^{-1}$ day^{-1} ($\bar{x}$ = 0.146 mg dry wt *Mysis*$^{-1}$ day^{-1}). These values were similar to rates reported for 5–12 mm *M. relicta* fed a mixed zooplankton assemblage [0.09–0.36 mg dry wt *Mysis*$^{-1}$ day^{-1}; (Cooper and Goldman, 1980)]. On a cumulative basis, food consumption ranged from 5.600 to 10.332 mg dry wt *Mysis*$^{-1}$ with an average value of 7.161 mg *Mysis*$^{-1}$ (Table I). Cumulative consumption estimates based on the lower and upper CLs for the mean mass of *D. pulex* averaged 6.480 and 7.705 mg *Mysis*$^{-1}$ (Table I).

We converted *Mysis* wet wt (WW) to dry wt (DW) using the equation (Chipps, 1997):

$$DW = \left(\frac{WW}{1.14}\right)^{1.37}$$

and then computed gross conversion efficiency as growth (mg dry wt) divided by total consumption (mg dry wt). On a dry wt basis, conversion efficiency ranged from 7 to 29% ($\bar{x}$ = 15%). These values were within the range reported for *M. relicta* [16–29% (Hakala, 1979)] and *Mysis mixta* [10–15% (Rudstam, 1989; Gorokhova, 1998)]. However, differences in *Mysis* size, time of year and type of prey consumed can affect gross conversion efficiency, making it difficult to compare values across studies.

Model estimates of cumulative food consumption ranged from 6.109 to 13.235 mg dry wt *Mysis*$^{-1}$ (Table I). On average, model estimates were within 12% of observed values (range = −7.5–28.1%; Table I) and provided a reasonable fit to observed data (k = 1.15; Table II). Predicted cumulative consumption was similar to observed values (Fisher's sign test, $M = -2$, $P = 0.28$) with most of the variation between observed and predicted values attributed to random error (Table II).

Sensitivity of bioenergetic parameters

Several sources of error can affect the accuracy of model output. The energetic cost of processing food (specific dynamic action, SDA) remains unknown for *Mysis*, but is likely to be between 17 and 20% of assimilated energy (Rudstam, 1989). Additionally, information regarding the energetic costs of excretion (U) and molting in *Mysis* has not been experimentally determined (Rudstam, 1989). Based on a sensitivity analysis, we found that errors in

Table I: Observed and predicted food consumption for eight M. relicta fed D. pulex at 10°C

Mysis growth		No. of dayss	No. of *Daphnia* eaten	Observed cumulative consumption (mg dry wt)	Modeled cumulative consumption (mg dry wt)	Percent difference
Initial mass (g wet wt)	Final mass (g wet wt)					
0.014	0.019	50	295	8.260 (7.485–8.916)	9.777	18.3
0.020	0.027	50	369	10.332 (9.357–11.118)	13.235	28.1
0.007	0.016	49	243	6.804 (6.164–7.375)	8.626	26.7
0.008	0.012	47	200	5.600 (5.064–6.054)	6.309	12.6
0.012	0.014	50	240	6.720 (6.054–7.155)	7.366	9.6
0.008	0.011	50	236	6.608 (5.944–7.045)	6.109	–7.5
0.008	0.013	47	220	6.160 (5.614–6.605)	6.818	10.6
0.009	0.013	47	243	6.804 (6.164–7.375)	6.735	–1.0
0.011	0.016	49	255	7.161 (6.480–7.705)	8.121	12.2

Modeled consumption was estimated from the *Mysis* bioenergetics model. Values in parentheses represent lower and upper consumption estimates based on variability in mean *Daphnia* size. Percent difference was computed as (model observed)/observed × 100. Means are given in the last row.

Table II: Statistical comparisons between actual food consumption and that predicted by a Mysis bioenergetics model

Statistical test	Actual versus		
	Model	Adjusted model (lower 95% CL)	Adjusted model (upper 95% CL)
Reliability index (*k*)	1.15	1.13	1.32
Mean square error	6.05	4.73	11.51
Mean (*z*)	0.84 (14.0)	0.07 (1.6)	5.27 (46.0)
Slope (*s*)	0.94 (15.6)	0.39 (8.4)	1.98 (17.0)
Random error (*r*)	4.26 (70.3)	4.26 (90.0)	4.26 (37.0)
Paired sign test			
(α = 0.016)			
P	0.28	0.72	0.0078

Three different statistical approaches were used to compare actual and model values: (i) the reliability index (*k*); (ii) decomposition of MSE; and (iii) a non-parametric, paired sign test. Adjusted model values represent comparisons between model output and actual values using the lower and upper 95% CL for *Mysis* respiration rate. Values in parentheses represent the proportion of total MSE attributed to the mean, slope or random error.

estimating these parameters are not as sensitive as those associated with estimating prey energy density and *Mysis* respiration (Table III). To obtain 10–15% changes in predicted food consumption, errors in SDA and *U* would have to be as large as 50–70%. Assuming that errors are not that large, prey energy density and the intercept value in the *Mysis* respiration equation were the most sensitive input parameters in our modeling scenario.

Respiration rates for *M. relicta* have been quantified at oxygen concentrations ranging from 3 to 11 mg l^{-1} (Sandeman and Lasenby, 1980). Using these data, we estimated 95% CIs around the mean intercept value (0.00182) used in the equation:

$$R = 0.00182W^{-0.161}e^{0.0752T}$$

where R is respiration (g O_2 g^{-1} day^{-1}), W is *Mysis* wet wt (g) and T is temperature [°C; (Rudstam, 1989)]. The CL around the intercept value ranged from 0.0015 to 0.0022. Using the lower estimate of 0.0015, we obtained predicted food consumption estimates that were, on average, 4.8% less than observed values, thus reducing the discrepancy between observed and predicted food consumption and improving the accuracy of model output (Figure 1; Table II). Similarly, variation in observed consumption had an appreciable influence on agreement between observed and predicted values, although this variation was not as significant as that associated with *Mysis* respiration rate (Figure 2). These observations demonstrate that uncertainty (95% CL) in sensitive parameters can have an important influence on agreement between observed and predicted values. By accounting for this variation, agreement between observed and predicted consumption was improved, helping to corroborate the *Mysis* bioenergetics model (Table II).

Table III: Sensitivity analysis for the Mysis bioenergetics model

Parameter	Value[a]	Value (+10%)	Value (–10%)	% change in bioenergetic output	
				(+10%)	(–10%)
Consumption					
Intercept *a*	0.0360	0.0390	0.0320	<1	<1
Slope *b*	–0.3720	–0.3350	–0.4090	<1	<1
Respiration					
Intercept *a*	0.0018	0.0020	0.0016	8	–9
Slope *b*	–0.1610	–0.1450	–0.1770	5	6
Temperature *t*	0.0750	0.0827	0.0676	7	6
SDA	0.1800	0.1980	0.1620	3	3
Egestion	0.1500	0.1650	0.1350	2	2
Excretion	0.1800	0.1980	0.1620	3	3
PRY[b]	1.87	2.06	1.68	–9	11
PRED[c]	3.14	3.45	2.82	2	–2

Individual parameters were varied ±10% and the percent change in predicted food consumption was determined from baseline conditions where initial and final mass were the average of eight mysids reported in Table I. SDA represents specific dynamic action, PRY represents prey energy density (kJ g^{-1} wet wt) and PRED represents *Mysis* energy density.
[a]From Rudstam (Rudstam, 1989).
[b]Prey energy density from Richman (Richman, 1958).
[c]*Mysis* energy density from Lasenby (Lasenby, 1971).

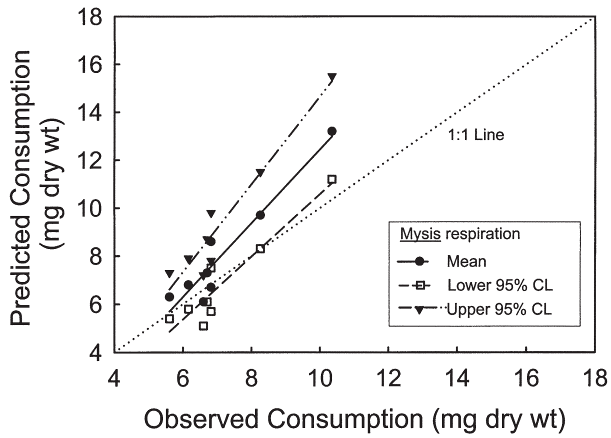

Fig. 1. Comparison of predicted versus observed food consumption estimates for eight *Mysis* reared at 10°C. The three lines show variation in bioenergetic model predictions as a function of variation in *Mysis* respiration rate. Predicted values were obtained by modeling *Mysis* consumption using the mean, lower and upper 95% CL for *Mysis* respiration rate. The dotted line represents the 1:1 line.

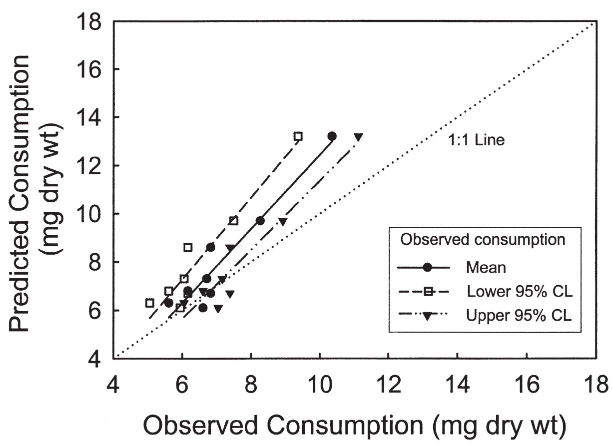

Fig. 2. Comparison of predicted versus observed food consumption estimates for eight *Mysis* reared at 10°C. The three lines show variation in observed food consumption as a function of variation in mean *Daphnia* size. Observed consumption was computed using the mean, lower and upper 95% CL for *Daphnia* size. The dotted line represents the 1:1 line.

The sensitivity of temperature-dependent functions for food consumption and respiration was not examined in this study. Tests of other bioenergetic models have revealed that the accuracy of bioenergetic predictions can vary across seasons (Chipps *et al.*, 2000) and feeding rates (Whitledge *et al.*, 1998). Temperature effects may be less important for vertically migrating *Mysis*, because they migrate to colder water (usually 4°C) during the day. As a result, the mean daily water temperature experienced by most *Mysis* populations is generally limited, ranging from ~3°C in winter to 9°C in summer (Rudstam, 1989; Chipps and Bennett, 2000). Moreover, errors in bioenergetic estimates at temperatures <10°C would probably have less influence on annual estimates of cumulative food consumption because growth and food consumption are reduced at lower temperatures (Rudstam, 1989; Chipps *et al.*, 2000).

Corroboration of the *Mysis* bioenergetics model

Modeling output revealed that the accuracy of the *Mysis* model was within the range reported for other bioenergetics models. In laboratory tests of largemouth bass (*Micropterus salmoides*) (Whitledge and Hayward, 1997) and striped bass (*Morone saxitilis*) models (Hartman and Brandt, 1993), differences between observed and predicted values ranged from –28 to 8% and 6 to 33%, respectively. Similarly, a sockeye (*Oncorhynchus nerka*) bioenergetics model provided reliable estimates of food consumption that were within 10–15% of field-derived consumption estimates (Beauchamp *et al.*, 1989). Recent application of the *Mysis* model revealed that the model performed well at predicting *M. mixta* growth when accurate measurements of food consumption were used as input (Gorokhova, 1998).

At optimal temperatures for feeding and growth, the *Mysis* model produced reasonable estimates of food consumption. The greatest challenge to application of the model, however, may lie in the accurate quantification of *Mysis* diets. In populations where *Mysis* exhibit a high degree of omnivory (Grossnickle, 1982), gut fluorescence techniques may be particularly useful for quantifying the proportion of phytoplankton in *Mysis* diets (Rudstam *et al.*, 1989; Rudstam and Hansson, 1990). Given accurate information on diet composition and energy content of prey, the *Mysis* bioenergetics model provides reliable estimates of food consumption, strengthening the validity of the bioenergetics approach for estimating *Mysis* feeding rate.

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