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Article

Effect of feeding history on metabolic rate of largemouth bass (*Micropterus nigricans*): implications for bioenergetics models

Steven H. Ranney[a], **Steven R. Chipps**[b], **and David H. Wahl**[c]

[a]Department of Natural Resource Management, South Dakota State University, Box 2140B NPS 138, Brookings, SD, 57007, USA; [b]U.S. Geological Survey, South Dakota Cooperative Fish and Wildlife Research Unit, Department of Natural Resource Management, South Dakota State University, Box 2140B NPS 138, Brookings, SD, 57007, USA; [c]Illinois Natural History Survey, Kaskaskia Biological Station, RR 1, Box 157, Sullivan, IL, 61951, USA

Corresponding author: **Steven R. Chipps** (email: steven.Chipps@sdstate.edu)

Abstract

Metabolic rate is a key parameter in fish energy budgets that strongly influences the output of bioenergetics models. In this study, we tested the hypothesis that metabolic rate varies with growth history of age-1 largemouth bass *Micropterus nigricans* Cuvier, 1828. Two groups of fish were fed alternating maintenance or ad libitum rations of fathead minnow *Pimephales promelas* Rafinesque, 1820, so that over a 9-week period, initial and ending size of fish was similar. After 9 weeks, oxygen consumption was measured using static, closed respirometry. Although final body weight was similar between the two groups (means, 104–108 g), specific oxygen consumption for fish fed maintenance rations (0.094 mg O_2 g^{-2} h^{-1}) was 38% less than that measured for fish fed ad libitum (0.152 mg O_2 g^{-2} h^{-1}). Bioenergetics estimates of food consumption were similar to observed values for fish fed ad libitum (~7% error), but for fish fed maintenance rations, the model overestimated food consumption by 65%. By accounting for changes in metabolic rate owing to reduced feeding, error in model estimates of food consumption was reduced. These findings shed new insight into factors associated with consumption-dependent error in bioenergetics models and highlight the importance of feeding history on metabolic rate of fish. Incorporating growth-dependent metabolism into bioenergetics models can improve model accuracy and allow fisheries biologists to make more informed decisions regarding fish growth and energetics.

Key words: metabolic rate, largemouth bass *Micropterus nigricans* Cuvier, 1828, restricted ration, bioenergetics

Introduction

Fish metabolism is a key component in fish energy budgets (Bevelhimer et al. 1985; Cech 1990). Although influenced primarily by fish weight and water temperature, other factors such as food availability, hypoxia, and stress are known to influence metabolic rate in fishes (Sloman et al. 2000; Richards 2010). Although not generally incorporated into fish bioenergetics models (BEMs), factors affecting metabolic rate in fishes can affect the accuracy of model output because of incomplete parameterization of the energy budget (Chipps and Wahl 2004). Dissolved oxygen and salinity concentration, for example, were shown to influence metabolism of Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus* Mitchill, 1815 and when incorporated in a BEM, improved model output (Niklitschek and Secor 2009).

The accuracy of BEMs is known to vary with feeding rate of fishes (Madenjian and O'Connor 1999; Chipps et al. 2000; Bajer et al. 2004*b*). In many instances, food consumption is overestimated when fish exhibit low feeding and growth rates (Madenjian and O'Connor 1999; Chipps and Wahl 2004; Bajer et al. 2004*b*). One hypothesis proposed to explain consumption-dependent error centers on the importance of waste losses in bioenergetics models (Bajer et al. 2004*a*). Although waste losses are often modeled as a constant proportion of consumed energy, they can vary with ration level, leading to error in model estimates (Elliott 1976; Wahl and Stein 1991; Bajer et al. 2004*a*). However, the magnitude of this error is generally low given the reduced sensitivity of waste loss parameters in BEMs (Bartell et al. 1986; Selch and Chipps 2007). Conversely, metabolism is a sensitive parameter in BEMs accounting for about 40%–45% of a fish's energy budget (Brett and Groves 1979; Chipps et al. 2022). Thus, error in metabolic rate measurements could have an appreciable influence on model reliability (Chipps et al. 2000).

Caloric restriction is known to reduce metabolic rate in a variety of animals, including fishes (Mehner and Wieser 1994; Heilbronn and Ravussin 2003; Fu et al. 2005). Following periods of starvation, metabolism in fishes generally

declines (Beamish 1964; Yengkokpam et al. 2008; Hvas et al. 2020) and although believed to be an adaptive response for conserving energy stores (Wieser et al. 1992), can have long-term costs related to oxidative stress (Salin et al. 2018). In mammals, caloric restriction is known to reduce resting metabolic rate (Yambayamba et al. 1996; Mueller and Diamond 2001). And similar responses have been observed in humans, where individuals on restricted diets have lower basal metabolic rates (Luke and Schoeller 1992). Changes in metabolic rate associated with periods of high (or low) food consumption can arise from physiological changes in the balance of demand (anabolic) and supply (catabolic) processes. Snakes, for example, can respond to the demand-side of starvation by reducing resting metabolic rate by up to 72% while simultaneously sparing important protein stores (supply-side) and using lipids for energy (McCue 2007). If similar patterns occur in fishes, feeding-related variation in metabolism could influence the accuracy of BEM predictions. In this study, we tested the hypothesis that resting–routine metabolism (RRM; Cech and Brauner 2011) varies with feeding history in largemouth bass *Micropterus nigricans* Cuvier, 1828 (see Kim et al. 2022 for revised species delimitation). We evaluated RRM of largemouth bass grown under two feeding regimes, an ad libitum or a maintenance ration of live fathead minnow *Pimephales promelas* Rafinesque, 1820. We then modeled food consumption using a bioenergetics model and compared model output with values measured in the laboratory.

Materials and methods

Fish source

Variation in fish body size presents a challenge when comparing RRM because of differences in absolute (i.e., $g\,O_2\,day^{-1}$) and allometric requirements (i.e., $g\,O_2\,g^{-1}\,day^{-1}$). To avoid this problem, we designed feeding trials so that mean body weight of fish that experienced different feeding histories was similar when RRM was measured. We obtained age-1 largemouth bass ($N = 24$, weight = 24.5 g, standard error (SE) = 1.8) from Blue Dog State Fish Hatchery in Waubay, South Dakota on 24 February 2007. All fish had been reared at the hatchery on an ad libitum ration of fathead minnow and were acclimated to laboratory conditions for 3 days. To maximize growth differences between fish fed maintenance ($n = 12$) or ad libitum ($n = 12$) rations beginning on 27 February (day 1), we assigned smaller fish to a maintenance ration and larger fish to an ad libitum ration. However, due to low variation in body size (i.e., ~90% were "smaller" fish), mean initial weight of fish fed maintenance rations ($\bar{x} = 23$ g, SE = 0.13, 95% confidence interval (CI), 22–23 g) was similar to that of ad libitum fed fish ($\bar{x} = 26$ g, SE = 2.2; 95% CI, 22–30 g) on day 1 of the experiment (Johnson 1999).

We randomly assigned each fish to individual, aerated aquaria (114 L) that were maintained on a recirculating, biofiltration system. Water temperature in the aquaria was gradually increased ($1\,^{\circ}C\,day^{-1}$) from 17 to 25 °C and submersible temperature loggers were used to measure mean hourly water temperature (Stowaway TidbiT, Onset Corp. Buzzards Bay, Massachusetts). Photoperiod was kept constant at 12 h light:12 h dark and fish were fed daily rations of live fathead minnow during morning hours (0900–1100). All animals used in this study were reared according to animal use and care guidelines established by South Dakota State University (Animal Welfare Assurance No. A3958-01).

We obtained high growth rates by feeding largemouth bass ad libitum rations of fathead minnow from 27 February (day 1) to mid-May 2007. Small fish were obtained during the same time period by feeding fish a restricted ration in an effort to maintain their body weight. When necessary, feeding was adjusted for fish on restricted rations to preclude any change in weight. By 19 March (day 20), differences in body size among fish fed ad libitum or restricted rations were becoming apparent, so we began measuring the weight of each fish (g) at 6–8 day intervals thereafter. Total length (mm) of each fish was measured at approximately monthly intervals and interpolated between dates to estimate energy density of largemouth bass (see Bioenergetics Modeling).

By 14 May 2007, two distinct size groups had emerged where mean body weight of small fish (33.8 g; $n = 12$, SE = 0.5) was only ~36% of that of large fish (94.1 g; $n = 12$, SE = 1.9). On 15 May (day 78), we switched the diet regimes and began our experimental feeding trials. Small fish, hereafter referred to as "ad libitum fish", were provided with ad libitum rations over the course of the experiment, whereas larger fish, hereafter referred to as "maintenance fish", were fed a restricted ration in an effort to maintain their body weight (i.e., no growth). We used a largemouth bass bioenergetics model (Rice et al. 1983; Rice and Cochran 1984) to approximate a maintenance ration for fish reared at 25 °C, and adjusted daily rations based on periodic measurements of fish weight (i.e., days 78, 102, 117, and 133). All fish were offered pre-weighed, live fathead minnows twice a day until mean body weight of ad libitum fish was statistically similar to the maintenance group (*t* test; SAS 2019). Maintenance fish consumed their ration almost immediately after introduction of prey, whereas ad libitum fish always had prey available to them. To estimate daily food consumption by each fish, uneaten minnows were removed from the tanks daily and weighed to the nearest 0.01 g. Daily food consumption was then estimated as the weight of minnows (in g wet weight) removed from the tank, subtracted from the weight of minnows offered to the fish each day. At the end of the feeding trial, we used fish weights on days 78, 102, 117, and 133 to compare growth rate between maintenance and ad libitum fish using a repeated measures Analysis of variance (ANOVA) (SAS 2019).

To determine whether activity between the two groups of fish was similar, we videotaped 16 randomly selected largemouth bass (8 per group) on days 134–135. A tripod-mounted video camera was set up over individual aquaria and recorded activity for 30 min during morning hours (0900–1200). To quantify activity, we randomly selected five continuous minutes from each videotaped period. We measured activity by overlaying an *x*–*y* grid on the video screen and counted the number of times (e.g., point tally) the fish crossed one of the axes. While we were setting up the camera above the aquaria, fish sought cover by hiding on the bottom of the tank near

the outflow standpipe before resuming normal behaviors of swimming slowly around the tank or resting near the bottom. After reviewing the videos, we observed that fish returned to their normal behaviors within 5 min; thus, we exclude observations from the first 5 min of each video. Points were summed for each fish, and we compared activity using a t test ($\alpha = 0.05$).

Respirometry

On day 142 (18 July), after both groups of fish (ad libitum and maintenance) had attained similar body sizes, we measured RRM using static respirometry (Cech 1990). Respirometers consisted of transparent, rectangular 4.3 L plastic containers with a removable, four-hinged lid and a sealed gasket on one end (Sterilite®). Each respirometer was fitted with siphon tubes (inlet and outlet) to allow water to flow through the respirometer during fish acclimation, with both siphon tubes fitted with a clamp to seal off the respirometer during testing. Flow through the respirometer was achieved by opening the clamps from each siphon tube, placing the outlet tube into the aquarium's standpipe, and then increasing water flow slightly into the aquarium to account for water leaving the outlet siphon. Respirometers were also fitted with a small diameter water sampling tube to collect initial and final water samples to determine changes in oxygen concentration (Cech and Brauner 2011). The water sampling tube was fitted with a stopcock that formed a tight seal with a 60 mL syringe for collecting initial and final water samples. Siphon and water sampling tubes were sealed to the respirometers using clear silicone. Respirometers were approximately 31–40 times the volume of an individual fish (Cech 1990).

Because handling stress can have an important influence on oxygen consumption by fishes (Steffensen 1989), we introduced respirometers ($n = 24$) into each aquaria 2 weeks prior to testing so that fish would become acclimated to them. Placement of respirometers in the aquaria precluded any handling or transfer of fish from the aquaria, thereby reducing stress (Cech 1990). By leaving one end of the respirometer open, most fish quickly began to use them as cover and would often move in and out of the respirometer throughout the day.

Before measuring RRM, fish were starved for a minimum of 48 h to account for the effects of specific dynamic action (Beamish 1974). Based on work with largemouth bass fed at 25 °C (Beamish 1974; Tandler and Beamish 1980), this period provided ample time (i.e., >33 h) for oxygen consumption to return to baseline conditions following their last meal. Twenty-four hours prior to testing, fish were gently guided by hand into the respirometers if necessary. The respirometer was then closed and water flow was established through the respirometer during the remainder of the acclimation period (24 h).

To begin a trial, a 60 mL water sample was collected from the respirometer via the water sampling tube and evaluated for initial dissolved oxygen concentration (mg L^{-1}). Dissolved oxygen was determined using Winkler titrations with the azide modification (APHA 1998). After the initial sample was taken, water flow through the respirometers was ceased by clamping the inlet/outlet siphon tubes. Final oxygen concentration was then determined after 30–40 min by collecting a second water sample from the water sampling tube. To account for any residual water in the tube from the first sample, we discarded the first 10–15 mL of water from the syringe and collected the final 60 mL sample from the respirometer for titration. If final oxygen concentration in a respirometer fell below 5 mg L^{-1}, the trial was repeated for that fish (Klumb et al. 2003). All respirometry measurements were obtained in the afternoon, between 1400–1700 h.

We calculated RRM (mg O_2 h^{-1}) for each fish using the equation

$$\text{RRM} = \frac{[(I) - (F)] \times V}{T} - \text{BLANK} \quad (1)$$

where I is the initial O_2 concentration in water (mg L^{-1}), F is the final O_2 concentration in water (mg L^{-1}), V is the volume of the respirometer (L), T is the time elapsed (h), and BLANK is the mean oxygen consumption (mg O_2 h^{-1}) due to microbial activity (Cech 1990). To account for microbial metabolism in the respirometer, blank respirometry measurements were obtained from a fishless tank connected to the recirculating system. The tank and respirometer were identical to those housing fish, and blank (fishless) measurements ($n = 3$) were obtained on the same days as fish respirometry (days 142, 155, and 168). To account for the volume of largemouth bass in the respirometers, we assumed a displacement of 1 mL water per g of fish (Pope et al. 2001; Zweifel et al. 2010). Oxygen consumption was then divided by fish wet weight (g) and expressed as mg O_2 g^{-1} h^{-1} for each fish. We compared RRM between ad libitum and maintenance fish using a t test (SAS 2019). We also compared observed measurements of oxygen consumption to those predicted by the largemouth bass bioenergetics model using a paired t test (SAS 2019). Model estimates of standard metabolic rate (SMR) for largemouth bass were calculated for each fish using the equation

$$\text{R} = 0.348 \times \text{W}^{-0.355} \times \text{e}^{(0.0313\text{T})} \quad (2)$$

where R is the oxygen consumption (mg O_2 g^{-1} h^{-1}), W is the fish mass (g wet weight), and T is the water temperature in degrees Celsius (e.g., 25 °C; Rice et al. 1983).

Ad libitum feeding trial

To explore how RRM of largemouth bass on restricted rations changes if food availability increases, we switched all fish to an ad libitum feeding regime on day 143. We measured RRM again on days 155 and 168, after 13 and 26 days of ad libitum feeding by largemouth bass, respectively. Rearing and respirometry methods were identical to those previously described. After all feeding and respirometry trials were complete, we measured total length (mm) and wet weight (0.01 g) of all fish.

Table 1. Input values for Fish Bioenergetics 4.0 for age-1 largemouth bass (*Micropterus nigricans*) fed either ad libitum or maintenance rations of fathead minnows (*Pimephales promelas*).

Model day	Water temperature (°C)	Prey energy density (J g^{-1} wet weight)	Mean largemouth bass weight* (g wet weight)		Mean largemouth bass energy density (J g^{-1} wet weight)	
			Ad libitum ($n = 12$)	Maintenance ($n = 12$)	Ad libitum ($n = 12$)	Maintenance ($n = 12$)
78	26.7	3341 (31)	33.8 (0.4)[a]	94.1 (1.8)[b]	5366 (26)	5665 (42)
102	25.3	3341 (31)	61.0 (0.9)[a]	99.7 (1.5)[b]	5643 (29)	5854 (36)
117	24.3	4052 (133)	79.0 (1.5)[a]	103.6 (1.4)[b]	5817 (33)	5973 (34)
133	24.6	3816 (82)	103.9 (3.0)[a]	106.6 (1.4)[a]	6002 (40)	6099 (33)
142	25.2	3816 (82)	107.9 (2.9)[a]	103.9 (1.8)[a]	6106 (44)	6170 (33)

Note: Values in parentheses represent 1 standard error. Model day 78 corresponds to 15 May 2007. *For each model day, differences in fish weight between ad libitum and maintenance-fed largemouth bass are denoted by a superscript; values with the same letter are not significantly different (Tukey's honestly significant difference test, adjusted for false discovery rate; $p > 0.05$).

Bioenergetics modeling

We modeled food consumption for individual fish using a largemouth bass bioenergetics model (Rice et al. 1983; Deslauriers et al. 2017) and compared these estimates to observed values measured in the laboratory. Information on fish size (growth) was used as input in the model to estimate food consumption over four modeling periods (days 78–102, 102–117, 117–133, and 133–142). Other input parameters included mean daily water temperature, energy density of prey (fathead minnow), and energy density of largemouth bass (Table 1).

We quantified the energy density of fathead minnows (J g^{-1} wet weight) using bomb calorimetry (Parr Instrument Company, Moline, Illinois). Five replicate samples of fathead minnow (3–5 fish/sample) were used to quantify average energy density on each of three dates (days 78, 117, and 133) and used as input in the bioenergetics model. To obtain initial and ending energy density values of individual largemouth bass without sacrificing them, we estimated energy density for each fish on day 78 and 168 using the equation

$$\text{(3)} \quad \text{J g}^{-1}\text{ wet weight} = (\text{TL} \times 0.0194 + 2{,}367)$$

where TL is the total length (mm) of largemouth bass (Garvey et al. 1998).

Evaluating model accuracy

We used decomposition of mean square error (MSE) as a diagnostic check of the degree and sources of error in model predictions (Wahl and Stein 1991; Chipps and Wahl 2004). Using least-squares regression of observed versus predicted consumption, MSE represents the variance around the 1:1 line. The error is partitioned into three components: (1) error associated with differences in means (m); (2) error associated with the slope differing from unity (s); and (3) error associated with random variation (r) (Rice and Cochran 1984; Chipps and Bennett 2002). For models that have no systematic bias, the means and slope components of the model will equal zero and the random variation component will equal one (Mincer and Zarnowitz 1969). We calculated MSE using the formula

$$\text{(4)} \quad \begin{aligned} \text{MSE} &= \left(\frac{1}{n}\right)\sum_{i=1}^{n}(P_i - A_i)^2 \\ &= \left(\bar{P} - \bar{A}\right)^2 + \left(S_P - rS_A\right)^2 + \left(1 - r^2\right)S_A^2 \\ 1 &= \frac{\left(\bar{P} - \bar{A}\right)^2}{\text{MSE}} + \frac{\left(S_P - rS_A\right)^2}{\text{MSE}} + \frac{\left(1 - r^2\right)S_A^2}{\text{MSE}} \\ 1 &= m + s + r \end{aligned}$$

where n is the number of paired observations; P_i and A_i are predicted and actual values; $\bar{P}$ and $\bar{A}$ are the means of P_i and A_i; S_P, and S_A are the standard deviations of P_i and A_i; and r is the correlation coefficient (Mincer and Zarnowitz 1969). To evaluate systematic errors (m and s), we regressed observed values on predicted values and used Bonferroni joint CIs to test the joint hypothesis that regression parameters had an intercept of 0 and a slope of 1 ($\alpha = 0.05$; Neter et al. 1985). If the joint hypothesis is rejected, differences between means and slopes are tested separately (Rice and Cochran 1984; Selch and Chipps 2007).

Results

Feeding and growth

Daily food consumption by individual largemouth bass fed ad libitum averaged 5.2 g day^{-1} ($n = 12$, SE = 0.2) and ranged from 3.2 to 9.9 g day^{-1} during the 64-day feeding trial. Fish fed maintenance rations consumed an average of 1.7 g day^{-1} ($n = 12$, SE = 0.02) with daily consumption ranging from 1.4 to 2.1 g day^{-1}. Mean total food consumption for ad libitum fish, summed from days 78 to 142, was 303 g compared to 97 g for maintenance fish (Table 2). Fish fed maintenance rations consumed about 32% of that measured for ad libitum fish.

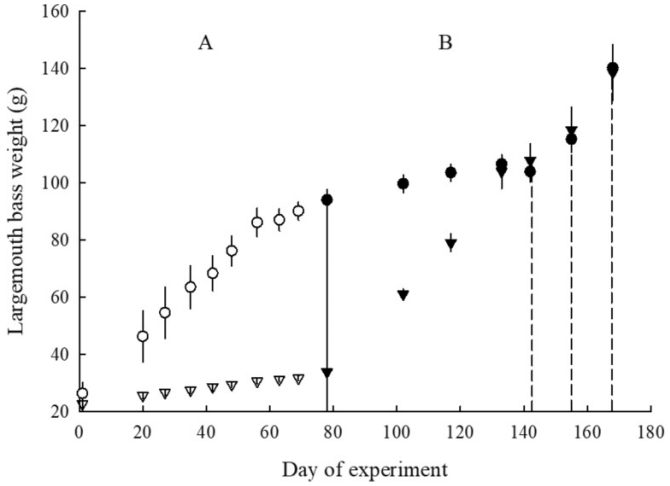
Mean growth rate during the 64-day trial was significantly different between ad libitum and maintenance-fed fish (repeated measures ANOVA, $F_{[1,22]} = 400.6$; $p < 0.0001$). Ad libitum fish grew an average of 0.97 g day^{-1}, whereas maintenance fish grew only 0.14 g day^{-1}. However, by the end of the feeding trial (day 142), mean size of ad libitum fish was similar to that of maintenance fish (t test, $t_{[0.05,22]} = 1.11$; $p = 0.28$; Fig. 1).

Table 2. Mean observed and modeled food consumption for largemouth bass (*Micropterus nigricans*) fed either ad libitum or maintenance rations of fathead minnows (*Pimephales promelas*).

Simulation interval	Food consumption (g of fathead minnows largemouth bass^{-1})					
	Ad libitum ration ($n = 12$)			Maintenance ration ($n = 12$)		
(Model day)	Observed (g)	Model (g)	% difference	Observed (g)	Model (g)	% difference
78–102	92 (0.2)	90 (2)	−2	43 (0.1)	61 (2)	70
102–117	77 (3)	67 (3)	−13	28 (0.1)	43 (1)	64
117–133	98 (6)	93 (6)	−5	25 (0.3)	44 (1)	68
133–142	36 (1)	31 (1)	−14	2 (0.1)	14 (2)	450
Totals	303	281	−7	98	162	67
142–155	53(5)	58 (4)	9	56 (3)	56 (3)	0
155–168	64 (6)	83 (4)	29	82 (4)	91 (4)	10

Note: Observed values represent laboratory measures of food consumption, whereas model values were predicted using a largemouth bass bioenergetics model (Rice and Cochran 1984; Deslauriers et al. 2017). Percent difference was calculated as (model − observed)/observed*100. Values in parentheses represent 1 standard error. Model day 78 corresponds to 15 May 2007.

Fig. 1. (A) Mean weight of age-1 largemouth bass (*Micropterus nigricans*) fed a surplus (open circles, $n = 12$) or restricted ration (open triangles, $n = 12$) of fathead minnows (*Pimephales promelas*) from day 1 to 78 (day 1 corresponds to 27 February 2007). (B) On day 78 (solid vertical line), when two distinct sizes of largemouth bass were achieved, daily rations were reversed so that smaller fish were fed a surplus ration (ad libitum ration, solid triangle) and larger fish were fed a restricted ration (maintenance ration, solid circle). On day 142 (dashed vertical line), when both groups of largemouth bass were similar in size, resting–routine metabolic rate (RRM) was measured. After day 142, both groups of fish were fed ad libitum rations and RRM was measured again on day 155 and day 168 (dashed lines). Error bars on solid and triangle symbols represent 95% confidence intervals.



Respirometry

Oxygen consumption due to microbial metabolism in the respirometers (i.e., blanks) averaged 0.19 mg O_2 h^{-1} (SE = 0.02) and represented a relatively low percentage of background oxygen consumption (0.8%–3.5%) compared to that consumed by fish. Although fish were of similar size by day 142, mean oxygen consumption differed significantly between largemouth bass fed ad libitum or maintenance rations ($t_{[0.05,22]} = 4.3$; $p = 0.0003$). Oxygen consumption ranged from 0.09 to 0.20 mg O_2 g^{-1} h^{-1} for ad libitum fish and from 0.04 to 0.12 mg O_2 g^{-1} h^{-1} for maintenance fish at 25 °C. On the average, oxygen consumption by maintenance fish was about 38% lower than that measured for fish fed ad libitum rations (Fig. 2).

Mean observed oxygen consumption for fish fed ad libitum rations (0.15 mg O_2 g^{-1} h^{-1}; SE = 0.01) was similar to SMR given by eq. 2 (0.14 mg O_2 g^{-1} h^{-1}; SE = 0.001; paired t test, $t_{[0.05,11]} = 0.61$; $p = 0.55$). However, mean oxygen consumption for fish fed maintenance rations (0.09 mg O_2 g^{-1} day^{-1}; SE = 0.008) was significantly lower than SMR predicted by the model (0.14 mg O_2 g^{-1} d^{-1}; SE = 0.001; paired t test, $t_{[0.05,11]} = 6.5$; $p < 0.0001$).

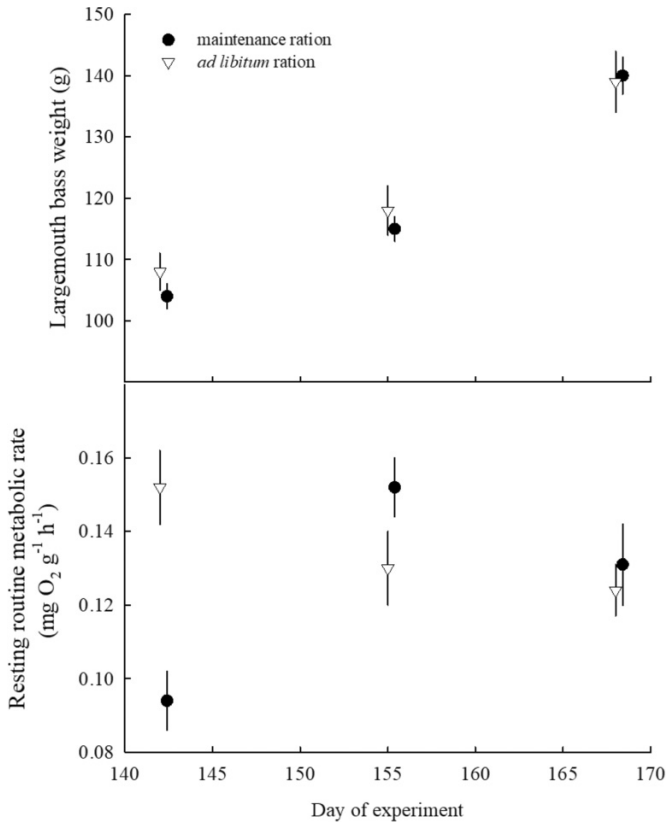
Ad libitum feeding trial

On day 142, we began feeding both groups of fish an ad libitum ration, and measured fish weight and oxygen consumption after 13 (day 155) and 26 days (day 168) for both maintenance (hereafter, *adjusted*) and ad libitum fish. Mean weight of *adjusted* (140.2 g) and ad libitum fish (138.6 g) was similar after 13 ($t_{[0.05,22]} = 0.73$; $p = 0.47$) and 26 days ($t_{[0.05,22]} = -0.277$; $p = 0.78$), and we found no differences in RRM after both groups of fish were maintained on an ad libitum feeding regime for 13 ($t_{[0.05,22]} = -1.6634$; $p = 0.11$) or 26 days ($t_{[0.05,22]} = -0.5714$; $p = 0.57$; Fig. 2). Interestingly, specific oxygen consumption increased for fish on adjusted rations from day 142 to 155, despite their larger body size on day 155, implying that growth from surplus feeding increased metabolic demand. In contrast, specific oxygen consumption decreased for fish fed ad libitum (and ultimately fish fed adjusted ration) by the end of the experiment, which would be expected as body size increases.

Bioenergetics modeling

Mean energy density of fathead minnows varied during the feeding trials. To account for this, we used energy density values of 3341, 4052, or 3816 J g^{-1} wet weight as input on days 78, 117, and 133 for prey energy density. For largemouth bass,

Fig. 2. Upper panel: mean weight of age-1 largemouth bass (*Micropterus nigricans*) fed ad libitum ($n = 12$) or maintenance ($n = 12$) rations of fathead minnows (*Pimephales promelas*) for 64 days. After day 142, all largemouth bass were fed ad libitum rations of fathead minnows until the end of the experiment on day 168. Lower panel: mean resting–routine metabolic rate of largemouth bass was measured on days 142, 155, and 168 when mean weight of fish from both treatments was similar. Day 1 corresponds to 27 February 2007. Error bars on symbols represent 1 standard error.

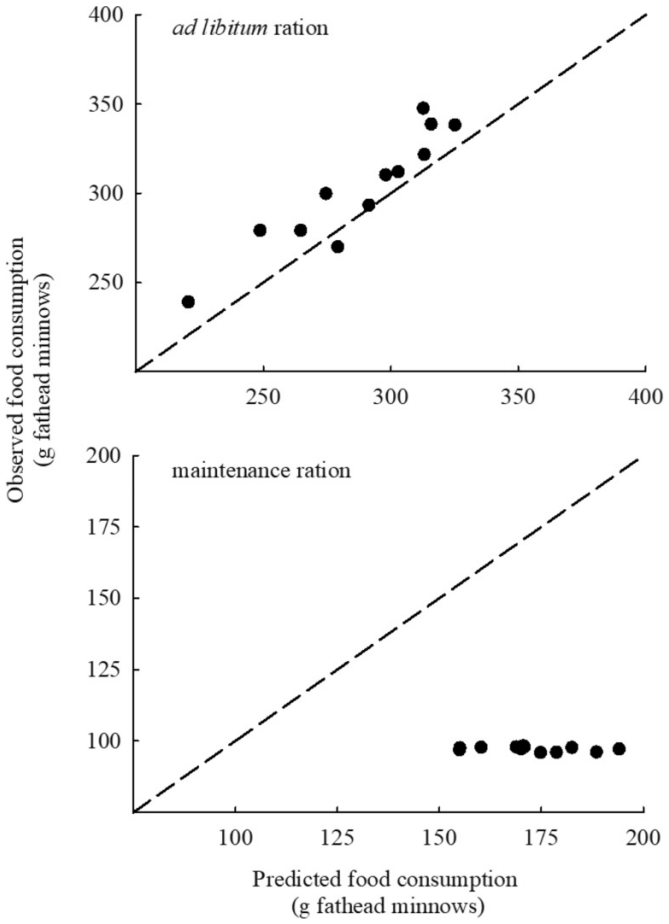


we estimated mean initial energy densities of 5366 J g^{-1} wet weight for ad libitum fish and 5665 J g^{-1} for maintenance fish. Final energy densities were 6106 J g^{-1} wet weight for ad libitum fish and 6170 J g^{-1} wet weight for maintenance fish (Table 1).

Bioenergetics estimates of food consumption for fish fed ad libitum rations ranged from 31 to 93 g and were similar to observed food consumption that ranged from 36 to 98 g (Table 2). Total food consumption predicted by the model over the 65 day period (days 78–142) averaged 281 g (±95% CI = 264–298 g), similar to observed values that averaged 303 g (95% CI = 283–323 g). On the average, the model performed well, as bioenergetics estimates of total food consumption were within 7% of observed values (Table 2). Regression of observed on predicted values revealed that the 95% joint CI included an intercept of 0 ($\beta_0 = 18.9 \pm 24.9$) and a slope of 1 ($\beta_1 = 1.05 \pm 0.082$) for fish fed ad libitum rations (Fig. 3).

For maintenance fish, the model predicted food consumption values ranging from 14 to 61 g, compared to observed values that ranged from 2 to 43 g. Total food consumption

Fig. 3. Relationship between observed food consumption and predicted food consumption for age-1 largemouth bass (*Micropterus nigricans*) fed ad libitum ($n = 12$; top panel) or maintenance rations ($n = 12$; bottom panel) of fathead minnow (*Pimephales promelas*) for 64 days (experiment days 78–142). Predicted food consumption was estimated using the largemouth bass bioenergetics model (Rice et al. 1983) in Fish Bioenergetics 4.0 (Deslauriers et al. 2017). Dashed line represents the 1:1 line.



predicted by the model averaged 162 g (±95% CI = 18) and was notably greater than mean, observed total food consumption of 98 g (±95% CI = 1) resulting in appreciable error (77%) in model output (Table 2). Decomposition of MSE showed that most of the variability between observed and predicted values was due to systematic error associated with the means ($z = 97\%$), whereas random error ($r = 0.01\%$) and error due to differences in the slope ($s = 2.4\%$) were relatively low. Regression of observed on predicted values revealed that the 95% joint CI did not include an intercept of 0 ($\beta_0 = 101.4 \pm 55.9$) and a slope of 1 ($\beta_1 = -0.02 \pm 0.58$; Fig. 3).

Output from the bioenergetics model did not appear to be linked to differences in fish activity patterns among largemouth bass. Activity level of largemouth bass was similar between ad libitum and maintenance-fed fish ($t_{[0.05,\ 14]} = 0.62$; $p = 0.25$). Ad libitum fish crossed the x–y grid an average of 28 times ($n = 8$, SE = 3.8) compared to fish fed maintenance

rations that crossed the *x*–*y* axis an average of 25.4 times ($n = 8$, SE = 1.9).

Discussion

Metabolic equations in fish energy budgets are scaled to account for body weight, water temperature, and swimming speeds but often neglect other important physiological adaptations (Chipps and Wahl 2008). In this study, we found that oxygen consumption by largemouth bass was strongly linked to feeding history and was lower among fish fed restricted rations. Bioenergetics modeling supported this finding; the model appreciably overestimated food consumption, implying that metabolic rate was overestimated for fish fed maintenance rations. These observations support the notion that consumption-dependent error in bioenergetics models (Chipps et al. 2000; Bajer et al. 2004*a*; Chipps and Wahl 2008) is linked to variation in fish metabolism.

The largemouth bass bioenergetics model used here has been tested in both field (Rice and Cochran 1984) and laboratory settings (Whitledge and Hayward 1997; Selch and Chipps 2007). Previous studies have shown that the model provided reliable estimates of food consumption when feeding rates exceeded 2% body weight day^{-1} (Whitledge and Hayward 1997; Selch and Chipps 2007; this study). However, at very low feeding rates when fish exhibit little to no growth (i.e., maintenance fish = 1.2% body weight day^{-1}), the model performed poorly (see also Wright et al. 1999). These discrepancies can be explained, in part, by the methodology used to parameterize oxygen consumption by largemouth bass. In the original work to quantify largemouth bass metabolism, Beamish (1970) held fish in the laboratory and fed them to satiation (ad libitum) for at least 1 month. Fish were then starved for 48 h prior to measuring oxygen consumption. Because the model was parameterized using well-fed fish, it performs well for fish exhibiting reasonable feeding and growth rates. However, the model failed to capture energy allocation for fish exhibiting little to no growth. In our view, this highlights the importance of developing and testing bioenergetics parameters across a range of feeding and growth rates (Bajer et al. 2003; Chipps and Wahl 2008).

Metabolic rate in fishes can account for up to 50% of the total energy budget (Brett and Groves 1979). As a result, it could be under strong selective pressure when feeding rate varies in the natural environment. A variety of studies have shown that metabolic rate of fishes declines after periods of starvation (e.g., Mehner and Wieser 1994; Rios et al. 2002; Hvas et al. 2020). A related study with juvenile blue catfish *Ictalurus furcatus* (Valenciennes, 1840) found that ration size had no effect on SMR of blue catfish after 4 months; however, body size of blue catfish varied by the end of the feeding trial and fish fed the most restricted ration were smaller when SMR was measured (Nepal et al. 2021). Because smaller fish have greater mass-specific metabolic rates than larger fish, different-sized fish could preclude the ability to detect metabolic differences due to feeding history.

Unlike studies of starvation, the link between restricted food ration and reduced metabolic rate in fishes has not been well documented. The physiological mechanisms that drive these changes are not well understood. Studies of other vertebrates suggest that many metabolic processes are regulated on various time scales by food intake (Secor and Diamond 1998). In mammals, for example, lower resting metabolic rate during food restriction is believed to result from a reduction in the metabolic rate of active tissues (i.e., reduced cellular metabolism; Shetty 1990; Selman et al. 2001; Lambert and Merry 2003). Changes in metabolism are likely regulated by hormones that are sensitive to changes in food intake such as catecholamines, peptides, glucagon, and insulin (Shetty 1990). When prolonged food restriction results in loss of body weight, further reductions in metabolism become more closely tied to the loss of metabolically active tissue until energy balance is restored (Shetty 1990). Thus, a reduction in energetically expensive cellular biochemical processes could be adaptive during periods of reduced energy intake (Secor and Diamond 1998) and could explain why metabolic rate varies as a function of food intake in largemouth bass. This adaptive response also provides a plausible explanation for why metabolic rates were similar among both groups of bass following ad libitum feeding (i.e., 12 and 25 days post-ad libitum feeding). Increased food intake is associated with rapid, energetically expensive responses in gastrointestinal hormones, nutrient transporters, and hydrolases in the gut that contribute to increased cellular metabolism, tissue growth, and thus higher metabolic rate (Secor and Diamond 1997; Secor and Diamond 1998).

Although oxygen consumption by largemouth bass appeared to respond quickly (<2 weeks) to increased food intake, we were unable to determine how quickly it declined when fish experience restricted rations. Ration size for maintenance fish was kept constant (~1.7 g day^{-1}), yet mean body weight of fish increased by about 8 g. Body weight increase could be attributed to difficulties in providing a true "maintenance" ration for each fish (i.e., ration size was greater than actual maintenance requirements). However, for fish fed restricted rations, improved metabolic efficiency owing to a lower metabolic rate could increase their scope for growth, and thus growth would be expected to increase under a constant ration level. Improved metabolic efficiency may explain observed growth patterns in maintenance fish because as they grew, the ratio of energy intake-to-energy demand would decrease if metabolic rate remained unchanged. Changes in metabolic rate could be beneficial when foraging rate is reduced, allowing fish to grow or perhaps survive through periods in which it may not have been able to otherwise (Wright et al. 1999; Hervant and Renault 2002).

Some studies suggest that poorly parameterized values for egestion, excretion, and specific dynamic action (SDA) are the source of consumption-dependent errors in bioenergetics models (Bajer et al. 2003; Bajer et al. 2004*a*). This is a logical hypothesis because (1) bioenergetics models for many species have borrowed these parameter values from other taxa (e.g., brown trout *Salmo trutta* Linnaeus, 1758; Ney 1993; Bajer et al. 2004*a*) and (or) (2) these parameters are often modeled as a constant proportion of food consumption (Kitchell et al. 1977) or as a combined function of fish mass, water temperature, and ration size (Elliot 1976). Nonetheless, sensitivity analyses show that waste–loss parameters

have less influence on bioenergetics model predictions than metabolism (Rice et al. 1983; Bartell et al. 1986). Indeed, to fit model predictions to observed data for maintenance fish, we would have to set values for egestion, excretion, and specific dynamic action all to zero—an unlikely explanation given that estimates for these parameters have been well documented for largemouth bass (Beamish 1972, 1974) and that setting these values to zero implies no waste loss or heat increment.

Model predictions have been shown to be sensitive to errors in metabolic rate (Rice et al. 1983; Bartell et al. 1986). For fish fed maintenance rations, adjusting the intercept value in eq. 2 by the observed, 38% reduction in metabolism (i.e, reducing the intercept value from 0.348 to 0.215), resulted in reduced mean error between observed and total predicted food consumption from 77% to 24%. These findings imply that energy savings via a reduction in metabolic rate accounted for a large proportion (>75%) of the error in model predictions for largemouth bass. Because consumption-dependent error in bioenergetics models can be linked to metabolic variation, incorporating consumption-dependent metabolism in BEMs would help reduce phenomena associated with consumption-dependent error and improve model accuracy (Chipps and Wahl 2008).

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Data availability

The datasets analyzed for the study are available from the senior author upon reasonable request (steven.ranney@gmail.com).

Author information

Author ORCIDs

Steven R. Chipps https://orcid.org/0000-0001-6511-7582

Author contributions

Conceptualization: SHR, SRC, DHW
Data curation: SHR, SRC
Formal analysis: SHR, SRC, DHW
Funding acquisition: SRC
Investigation: SHR, SRC, DHW
Methodology: SHR, SRC, DHW
Project administration: SRC
Resources: SRC
Software: SHR, SRC
Supervision: SRC
Validation: SHR, SRC
Writing – original draft: SHR, SRC, DHW
Writing – review & editing: SHR, SRC

Competing interests

The authors declare there are no competing interests.

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