Comparison of Bioenergetics Parameters from Two Spring-Fed Riverine Largemouth Bass Populations

Jakob C. Tetzlaff*, William E. Pine III and Thomas K. Frazer

School of Forest Resources and Conservation, University of Florida, Box 110600, Gainesville, FL 32653, USA

Abstract: This study applies a new bioenergetics modeling framework put forth by Walters and Essington (this volume) which estimates bioenergetics parameters and consumption rates of fishes using commonly collected size-at-age and capture-recapture data from field studies. Bioenergetics model parameters and consumption rates are estimated for two populations of largemouth bass *Micropterus salmoides* with observed differences in growth patterns. We also compare consumption estimates from the bioenergetics model formulated by Walters and Essington with a more commonly employed bioenergetics model. We show that bioenergetics model parameters can be estimated with limited data on size-at-age and incremental growth when informative prior distributions on metabolic parameters are used. The general bioenergetics model revealed differences in bioenergetics parameters between the two largemouth bass populations that are well supported by auxiliary data on largemouth bass diets and observed prey abundance patterns. Lifetime growth and consumption estimates between the general bioenergetics model and Wisconsin bioenergetics model differed slightly. However, seasonal patterns in growth and consumption rates differed drastically between the two models. Estimating bioenergetics parameters using field data collected on specific populations of interests has the potential to allow for more realistic representation of seasonal growth and consumption patterns.

Key Words: Consumption, growth, metabolism, *Micropterus salmoides*.

INTRODUCTION

Bioenergetics models have become a widely used tool in fisheries management and research to estimate the consumption rates of fish [1-3]. Bioenergetics models are based upon simple balanced energy budgets where energy intake via food consumption is partitioned into one of three fates: metabolism, wastes, and growth [4, 5]. While a variety of models to describe these energy budgets and predict consumption have been proposed, the Wisconsin bioenergetics model [4] is widely used because of its relatively simple input parameters and the models ability to estimate consumption for a large number of fish species [1]. Variations of the Wisconsin bioenergetics model have been used extensively to quantify the consumption rates of predators. Knowledge of predator demand on prey fish populations has been used to better understand food web dynamics [6], assess ecosystem effects of nonnative predators [7], and inform stocking programs for sport fisheries [8]. In many applications, however, estimates of consumption are characterized by very high uncertainty and the models have not always performed well when compared to laboratory estimates of consumption [9-12].

The fact that many studies designed to evaluate bioenergetics have found disagreement between model predictions and independent estimates of consumption rates is not surprising. Many of the equations used within the bioenergetics modeling framework are simplifications of complex mechanistic relationships [2, 13]. In addition, due to the difficulty in estimating bioenergetics parameters for every fish species and every size-class of fish, parameter inputs used in these models are often borrowed between species, extrapolated across size classes, and assumed to be constant across populations. However, bioenergetics rates have been shown to vary between closely related species [14], across populations [15, 16], between size-classes [2, 16, 17], and among individuals [18]. Environmental factors such as temperature [2], dissolved oxygen [19], and salinity [20] also affect bioenergetics rates. While efforts should be taken to improve the predictive accuracy of bioenergetics models and identify common sources of model error [10], it is not possible for all sources of parameter uncertainty to be incorporated into a single species-specific bioenergetics model. The accuracy of species-specific bioenergetics models therefore depends on the ability of models to accurately depict growth and consumption across a wide range of sizes, abiotic variables, aquatic community structure and geographic locations.

Because of uncertainty in the applicability of generic models to individual studies, the ability to efficiently estimate bioenergetics model parameters directly from field data would improve the estimation procedures and ultimately model inference when bioenergetics models are used to address ecological or management questions. An alternative approach to bioenergetics modeling proposed by Walters and Essington [21] directly estimates bioenergetics parameters from commonly collected field measurements including size-at-age and growth increment data. While some bioenergetics parameters, such as those related to the allometric scaling of

---

*Address correspondence to this author at the School of Forest Resources and Conservation, University of Florida, Box 110600, Gainesville, FL 32653, USA; Tel: 352-392-1793; Fax: 352-393-3672;
E-mail: jctetz@ufl.edu

metabolism, have been shown to be relatively constant across fish populations [22-24], other bioenergetics parameters, such as those related to growth potential and energy allocation, have been shown to vary between populations and across geographic scales [15, 16, 25]. The modeling framework proposed by Walters and Essington [21] uses various generalizations of the von Bertalanffy growth model to estimate consumption and metabolism parameters from data collected on specific populations of interests, thus bypassing the need for using laboratory derived parameters or borrowing parameters from other species or populations.

The purpose of this paper was to fit the bioenergetics model formulated by Walters and Essington [21] (herein referred to as the general bioenergetics model) to observed growth data on two populations of largemouth bass *Micropterus salmoides* collected in adjacent spring-fed rivers along the Gulf coast of Florida. Specifically, we attempted to determine whether the general bioenergetics model could identify differences in bioenergetics parameters that are likely associated with observed differences in growth, prey availability patterns and prey sizes between the two populations of largemouth bass [26, 27]. The general bioenergetics model was fit under two scenarios according to different levels of *a priori* knowledge of bioenergetics parameter distributions. We used a hierarchical approach to fitting the general bioenergetics model to assess how parameter estimates and model uncertainty changed with increasing data. In addition, we compare estimates and patterns of consumption rates from the general bioenergetics model to those calculated from the Wisconsin bioenergetics model to examine how differing assumptions and input parameters between the two bioenergetics models influence consumption predictions. This study represents an example of how even limited information collected from traditional mark-recapture studies can be used in combination with size-at-age data to estimate bioenergetics parameters of consumption and metabolism for specific populations of interest.

METHODS

Data Collection

Largemouth bass were sampled in the Chassahowitzka and Homosassa rivers, spring-fed rivers along the west coast of peninsular Florida, as part of a long-term monitoring program [27]. Both systems are similar in their physical (temperature, size, discharge, depth, substrate) and chemical (nutrients, salinity) characteristics. Freshwater springs in the headwater reaches of both rivers serve as the origin of flow and water temperatures are fairly uniform throughout the year.

Major differences in shoreline development, riparian habitat, and vegetative characteristics exist between the two rivers. The Chassahowitzka River is, at present, undeveloped. In comparison, the Homosassa River has extensive shoreline development. Both rivers historically supported dense assemblages of rooted macrophytes including *Vallisneria americana*, *Sagittaria kurziana*, *Potamogeton pectinatus*, and *Najas guadalupensis* [28]. Trends in submersed aquatic vegetation in the Homosassa River show drastic declines over the past 11 years with current composition of submersed aquatic vegetation limited primarily to filamentous algae [28]. Submersed aquatic vegetation occurs throughout the majority of the freshwater portion of the Chassahowitzka River and is characterized by a patchy heterogeneous distribution. Differences in vegetative characteristics between rivers initiated population and community assessments of fishes beginning in 2007 [27].

Largemouth bass populations were sampled from January 2007 through January 2009. All fish were collected using boat electrofishing (Smith-Root Inc.; Mark IX GPP unit pulsed-DC; 20-30 A). Sampling was conducted one day each month on each river to obtain growth and diet information. Intensive three day mark-recapture studies were carried out in July 2007, January 2008, July 2008 and January 2009 to obtain abundance estimates of largemouth bass and prey species [27]. Most largemouth bass collected between January 2007 and January 2009 were weighed (g), measured (total length [TL]; mm), marked with individually numbered T-bar anchor tags (Hallprint Pty Ltd), and released. In October 2007 and February 2008 a majority of the largemouth bass collected were sacrificed for aging (N = 97 and 98 in the Chassahowitzka and Homosassa rivers, respectively). Diet samples were taken from at least 30 fish with total length greater than 200-mm during monthly samples between June 2007 and February 2008. Diet contents were collected with a gastric lavage technique. Prey items were sorted to lowest possible taxonomic order and dried at 60° for 48 hours. Diet composition was calculated as the percent dry weight of each prey group collected during each sampling event.

Bioenergetics Modeling

We fit the general bioenergetics model to growth increment data from capture-recapture studies and length-at-age data from otoliths (complete details of the model and likelihood functions used for fitting are described in Walters and Essington [21]). Essentially, the general bioenergetics model of Walters and Essington [21] is derived from the growth model of Paloheimo and Dickie [29] and incorporates temperature dependence of consumption and metabolism, as follows:

$$\frac{dW}{dt} = HW^{d}Q_c^{\frac{(T-10)}{10}} - mW^{n}Q_m^{\frac{(T-10)}{10}}. \qquad (1)$$

In this equation, HW^d describes the anabolic processes associated with food acquisition; where H represents the rate at which an animal acquires mass, W is the somatic mass, and d describes the allometric scaling of anabolic processes with mass. The second term, mW^n, represents the catabolic processes; where m is the rate at which an animal loses mass and n describes the allometric scaling of catabolism with mass. Q_c and Q_m represent consumption and metabolism coefficients of a Q_{10} relationship and allow anabolism and catabolism to increase or decrease with temperature (T).

The general bioenergetics model was fit to length-at-age and tag-recapture data to estimate parameters under two scenarios corresponding to different levels of *a priori* knowledge of parameter distributions (Table **1**). For the first scenario, as suggested by Walters and Essington [21], we fit the general bioenergetics model with informative uniform priors on both n ($0.75 \leq n \leq 1.0$) and Q_m ($1.8 \leq Q_m \leq 2.4$). Prior limits on n and Q_m were based on findings from Essington *et al.* [22]

Table 1. Uniform Prior Distributions Used for Both Fitting Scenarios of the General Bioenergetics Model. Point Estimates of Parameters Used in the Wisconsin Bioenergetics Model are Listed for Comparison

Parameter	Description	Scenario 1	Scenario 2	WI model	Units
H	Net food consumption rate per W^{-d}	1.0 – 15.0	1.0 – 15.0	-	$g\ g^{-1}\ yr^{-1}$
m	Standard metabolic rate per W^{-n}	0.5 – 8.0	0.5 – 8.0	-	$g\ g^{-1}\ yr^{-1}$
n	Metabolism power parameter	0.75 –1.0	0.50 – 1.0	-	–
d	Food consumption power parameter	0.5 – 1.0	0.3 – 1.0	-	–
Q_m	Proportional increase in metabolism per 10ºC temperature increase	1.8 – 2.4	1.0 – 4.0	2.25	–
Q_c	Proportional increase in feeding rate per 10ºC temperature increase	1.0 – 5.0	1.0 – 5.0	2.65	–

and Clarke and Johnston [23]. For this scenario, we fit the general bioenergetics model in a hierarchical fashion, using data from the first year of the study (Trial 1) and then using data from both years (Trial 2), in order to assess model fit with increasing data. In both trials, samples sizes for growth increment and length-at-age data were relatively low compared to other case studies used to fit the general bioenergetics model [30-32]. For the second scenario, we attempted to estimate all bioenergetics parameters: H, d, m, n, Q_c and Q_m. Posterior density functions for both scenarios were estimated using a Metropolis-Hastings Markov-chain Monte Carlo (MCMC) routine [33]. Four MCMC chains were run with different initial values of parameter estimates for 500,000 iterations, with a burn-in of 2,000 iterations and further thinned to leave 8,000 samples from each chain. To test for convergence, trace diagrams were visually inspected and the Gelman-Rubin convergence diagnostics were used [33].

Consumption estimated from the first scenario of the general bioenergetics model was compared with that from the Wisconsin bioenergetics model (Fish Bioenergetics 3.0) [4]. The Wisconsin bioenergetics model requires inputs of temperature, mean weight-at-age, and diet composition. Parameters related to mass and temperature dependence in consumption and respiration follow the largemouth bass model described by Rice *et al.* [34] (Table **2**). Mean weight-at-age was obtained from aged fish and fit to a von Bertalanffy growth model (Table **3**). Prey composition was calculated as percent dry weight of prey consumed by month. Energy densities (J/g wet mass) of prey were taken from Hanson *et al.* [4] and assumed to be constant over time. Energy density of largemouth bass was set at 4186 J/g wet mass and also assumed to be constant over time [34]. Consumption rates (g/g/day) were estimated for each age cohort independently by estimating a constant P-value (proportion of maximal consumption applied to each day of simulation). Individual cohorts were combined to represent lifetime consumption and growth estimates.

Both the general and Wisconsin bioenergetics models require information on timing of maturity and proportion of mass devoted to reproduction. Mass- and age-at-maturity were estimated as the mass or age at which 50% of individuals are mature and fit to data collected on mature adults in February 2008. The proportion of mass devoted to reproduction was estimated as 10%. Spawning date for the populations was set as March 1, hatch date was set as March 15 and length at hatch was set as 10 mm.

USGS automated temperature loggers were stationed on both rivers and recorded temperature at 15 minute intervals over the course of the study. A water temperature model,

$$T_t = \max\left[T_{winter}, T_{mean} + \left(T_{max} - T_{mean}\right)\sin\left(t - t_{\Delta}\right)\cdot 2\pi\right] \quad (2)$$

was fit to the time-series of measured temperatures from the Chassahowitzka and Homosassa rivers (Fig. **1**). Temperature used in both models was assumed to follow the same annual cycle throughout the lifetime of all fish in each river.

RESULTS

Model Fitting

In total, 108 and 93 largemouth bass were recaptured in the Homosassa and Chassahowitzka rivers, respectively. Growth increment data from fish recaptured at least 30 days following capture were collected from 73 largemouth bass from the Homosassa River and 44 largemouth bass from the Chassahowitzka River. Growth increment data were collected throughout the year and covered all seasons. A range of fish sizes were tagged throughout all seasons in each river. No relationship between size of fish tagged and temperature was observed. As expected, growth by largemouth bass was positively related to temperature in both river systems. However, this response was much more apparent in the Chassahowitzka River (Fig. **2**). Plots of length at tagging versus observed growth rate suggest higher asymptotic lengths for largemouth bass in the Chassahowitzka River (Fig. **3**).

Bioenergetics parameters were estimated with the general bioenergetics model for the Homosassa and Chassahowitzka river largemouth bass populations for two scenarios corresponding to different levels of *a priori* knowledge of parameter distributions (Table **1**). For the first scenario, the general bioenergetics model was fit to data collected from January 2007 to January 2008 (Scenario 1, Trial 1) as well for data collected from January 2007 to January 2009 (Scenario 1, Trial 2). The general bioenergetics model for Trial 1 was fit with 46 and 22 growth increment samples and 46 and 62 length-at-age samples from the Homosassa and Chassa-

Table 2. Parameters Used in Wisconsin Bioenergetics Model from Rice *et al*. [33]. Structures of the Indicated Equations can be Found in Hansen *et al.* [4]

Parameter	Description	Value	Units
Consumption Equation 2			
CA	Intercept of the allometric mass function	0.33	g g^{-1} d^{-1}
CB	Slope of the allometric mass function	-0.325	
CQ	Temperature for CK_1	2.65	°C
CTO	Temperature for 0.98 of Cmax on increasing curve	27.5	°C
CTM	Temperature for 0.98 of Cmax on decreasing curve	37	°C
Respiration Equation 1			
RA	Intercept for the allometric mass function	0.00279	g O_2 g^{-1} d^{-1}
RB	Slope of the allometric mass function	-0.355	
RQ	approximates Q_{10}	0.0811	$°C^{-1}$
RTO	Constant swimming speed at reference metabolism	0.0196	s cm^{-1}
RTM	Maximum (lethal) water temperature	0	
RTL	Cutoff temperature at which activity relationship changes	0	°C
RK_1	Swimming speed intercept above RTL	1	cm s^{-1}
RK_4	Mass-dependence for swimming speeds	0	
ACT	Intercept for the swimming speed-water temperature function below RTL	1	cm s^{-1}
BACT	Temperature-dependence coefficient for swimming seed-water temperature function below RTL	0	$°C^{-1}$
SDA	Proportion of assimilated energy lost to specific dynamic action	0.163	
Egestion/Excretion Equation 1			
FA	Intercept of proportion of consumed energy egested versus water temperature and ration	0.104	
UA	Intercept of proportion of consumed energy excreted versus water temperature and ration	0.068	
Predator Energy Density Equation 1			
E_{pred}	Energy density of predator	4186	J g^{-1}

howitzka rivers, respectively. The general bioenergetics model for Trial 2 was fit with 73 and 44 growth increment samples and 98 and 97 length-at-age samples from the Homosassa and Chassahowitzka rivers, respectively. For the second scenario (Table **1**), the general bioenergetics model was fit to all data collected on largemouth bass.

The general bioenergetics model provided reasonable parameter estimates when informative priors were used on metabolism related parameters (Scenario 1, both trials; Figs. **4** and **5**). When priors were placed on the metabolism power parameter (*n*) and the Q_{10} parameter related to metabolism (Q_m) (Scenario 1), posterior distributions of all other parameters were well defined indicating that data were informative about the values of the parameters allowed to freely vary. Increased sample sizes for both length-at-age and growth increment data (Scenario 1 Trial 1 vs. Trial 2), led to tighter bounds on posterior distributions for both largemouth bass populations (Figs. **4** and **5**). Patterns in parameter estimates also remained consistent between the two trials for both largemouth bass populations (Figs. **4** and **5**). When the general bioenergetics model was used to estimate *H*, *m*, *n*, *d*, Q_m, and Q_c simultaneously, posterior distributions of all parameters had greater uncertainty and estimates of *n* and Q_m were unreasonably low (Scenario 2, Figs. **4** and **5**). Unconstrained

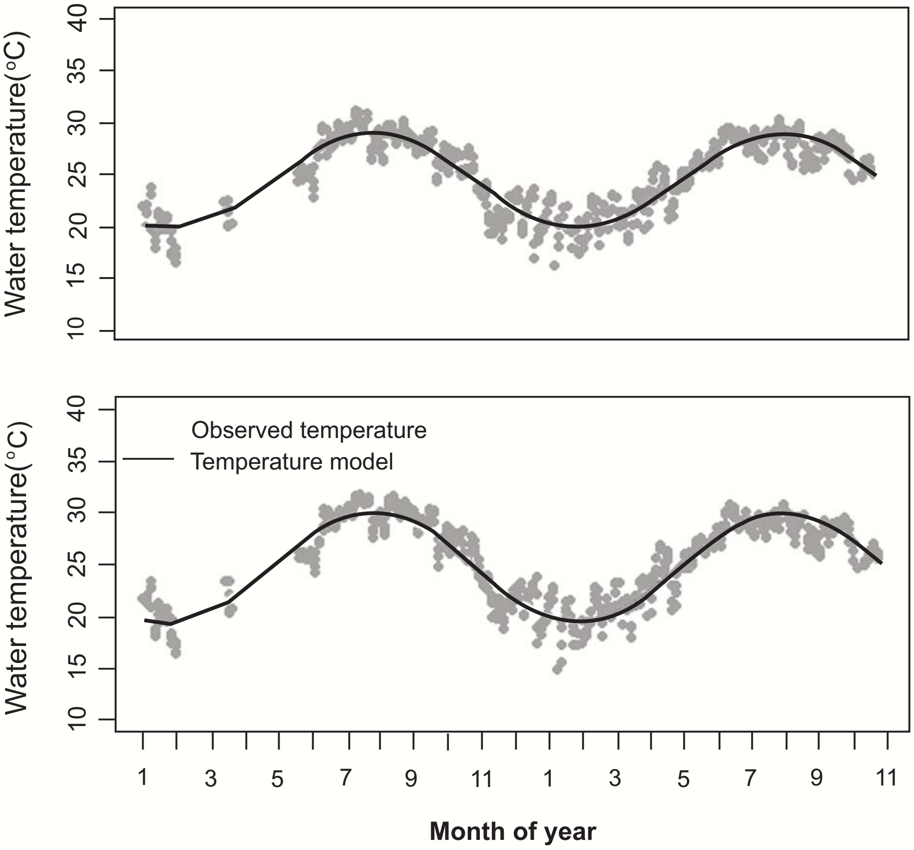

Fig. (1). Observed temperatures in the Chassahowitzka (top panel) and Homosassa (bottom panel) rivers. Solid line represents fitted temperature model used in both the general and Wisconsin bioenergetics models (Chassahowitzka River; T_{max} = 28.9, T_{mean} = 24.3, T_{winter} = 19.4, T_{Δ} = 0.69, Homosassa River; T_{max} = 29.9, T_{mean} = 24.6, T_{winter} = 19.0, T_{Δ} = 0.69).

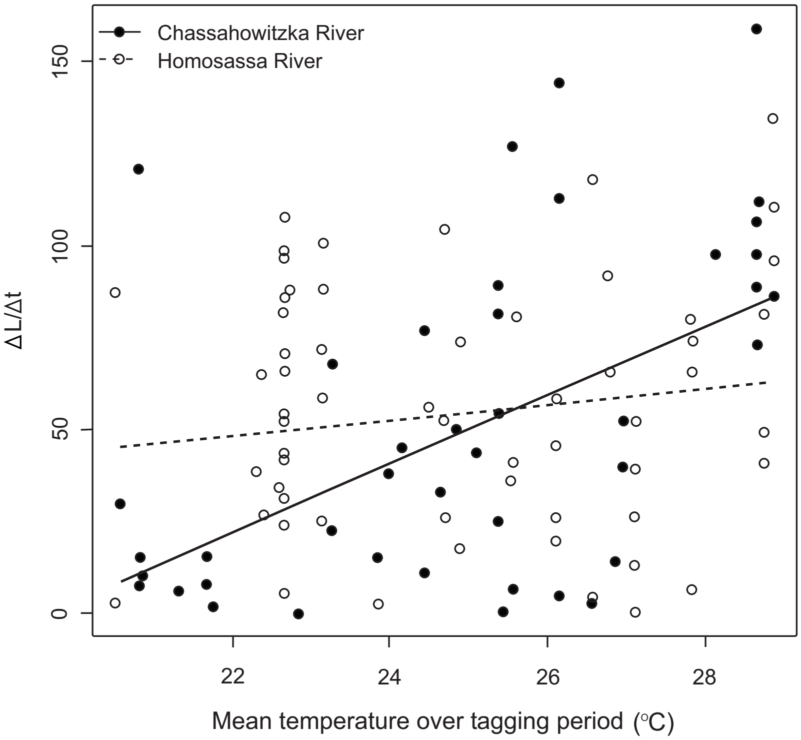

Fig. (2). Growth rate (ΔL/Δt) over a range of temperatures from tag return data on largemouth bass collected in the Chassahowitzka (closed circles; solid line) and Homosassa (open circles; dashed line) rivers.

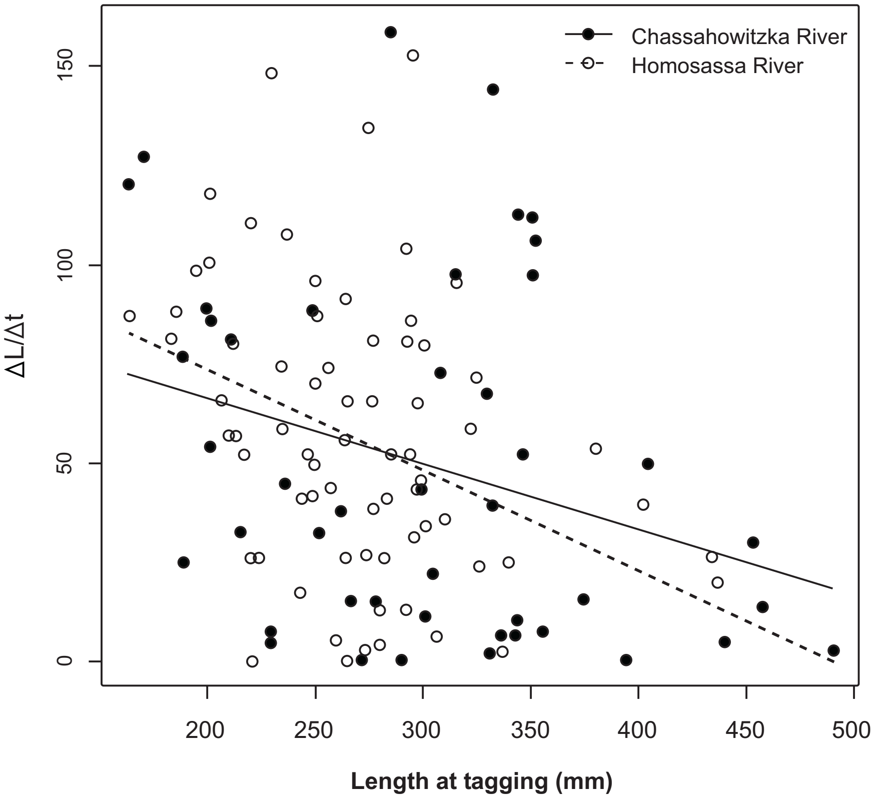

Fig. (3). Growth rate (ΔL/Δt) over a range of body sizes from tag return data on largemouth bass collected in the Chassahowitzka (closed circles; solid line) and Homosassa (open circles; dashed line) rivers.

parameter estimates were not possible due to confounding between consumption and metabolism parameters (*H* and *m*, *d* and *n*) (Scenario 2; Fig. **6**).

Posterior distributions of parameter estimates were robust to both starting values and priors when fit using all data except in the case when all parameters were allowed to vary (Figs. **4** and **5**). For the first scenario, posterior distributions of the metabolism parameter (*m*), metabolism power parameter (*n*) and the Q_{10} parameter related to metabolism (Q_m) were very similar between the two populations. Posterior distributions of the consumption parameter (*H*), the power parameter for consumption (*d*), and the Q_{10} parameter related to consumption (Q_c) showed consistent differences between the two largemouth bass populations (Fig. **7**). *H* was consistently lower and *d* and Q_c were consistently higher for the Chassahowitzka River largemouth bass population compared to the Homosassa River largemouth bass population.

The general bioenergetics model was fit to length increment and length-at-age data in order to estimate a complete growth trajectory for the two populations of largemouth bass (Fig. **8**). Comparing the estimated weight-at-age with observed weight-at-age shows the model estimated weight-at-age well despite the model being fit only to observed lengths. Estimated weight-at-age was higher in the Chassahowitzka River than the Homosassa River for all cases in which the model was fit. The general bioenergetics model predicted slightly higher consumption rates by largemouth bass in the Chassahowitzka River compared to the Homosassa River in all cases for which the model was fit.

Model Comparisons

Predicted growth patterns of largemouth bass differed between the two bioenergetics models. Compared with the predicted size-at-age from the general bioenergetics model, the Wisconsin bioenergetics model estimate was generally similar for ages 1-4 but higher for older ages in both rivers (Fig. **9**). The Wisconsin bioenergetics model predicted that largemouth bass lost weight in late summer in both rivers and had high weight gain prior to spawning in the spring. The general bioenergetics model predicted that weight gain for largemouth bass was greatest throughout the summer. Observed weight-increment data from tagged fish suggests that largemouth bass do not lose weight over summer months in either river with growth generally greatest at higher temperatures (Fig. **2**).

Median consumption estimated using the general bioenergetics model was lower than that estimated using the Wisconsin bioenergetics model for both populations (Fig. **10**). Estimates of consumption for largemouth bass ages 1 to 7 from the general bioenergetics model (Scenario 1, Trial 2) ranged from 64% to 72% that of the Wisconsin consumption estimate for the Chassahowitzka River and 62% to 74% for the Homosassa River. In addition to magnitude, patterns of consumption also varied between models. The general bioenergetics model predicted greater seasonality in consumption than the Wisconsin model for both largemouth bass populations. The Wisconsin bioenergetics model also predicted a decrease in consumption rates during summer months for both populations, whereas the general bioenerget-

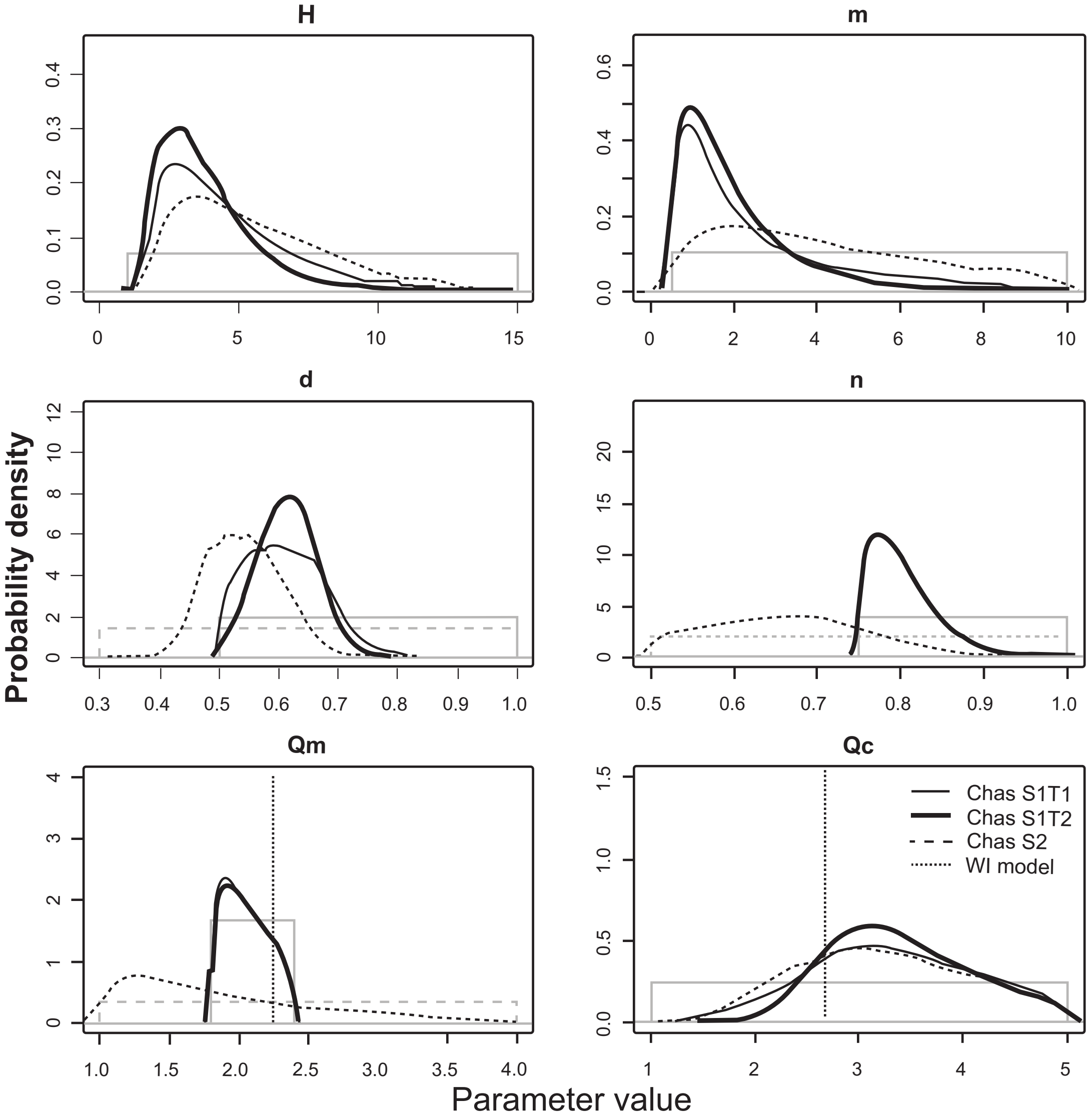

Fig. (4). Posterior probability densities of bioenergetics parameters for the Chassahowitzka River largemouth bass population for two scenarios in which the general bioenergetics model was fit. The first scenario (S1: Trial 1 (T1); solid thin line, Trial 2 (T2); solid thick line) was fit with informative priors on metabolic parameters (n and Q_m). The second scenario (S2; dashed line) was fit without informative priors. Prior probability density functions are grey lines and posterior probability densities are black lines. Wisconsin bioenergetics model estimates are shown as vertical dotted lines.

ics model predicted peak consumption rates during summer months for both populations.

DISCUSSION

The bioenergetics model formulated by Walters and Essington [21] provided reliable fits to observed length increment and length-at-age data for both largemouth bass populations of interest. For this dataset, informative priors on metabolic parameters were required to obtain realistic parameter estimates. While posterior density distributions of parameter estimates were wide, patterns in parameter estimates were consistent across all fitting scenarios. Despite small sample sizes, posterior distributions of parameter estimates were robust to both starting values and parameter priors. The general bioenergetics model fit the observed growth patterns and consumption estimates agreed well with published literature on largemouth bass [34-37]. The general bioenergetics model also accurately depicted observed seasonal differences in growth patterns between the two populations.

Informative priors on metabolic parameters were required in order to obtain reasonable estimates of consumption parameters due to confounding between metabolism and consumption in the data. Informative priors were used to restrict the range of possible solutions to those that were biologically plausible. When the metabolic parameters n and Q_m were constrained to reasonable values based on laboratory studies (n: 0.75-1.0, Q_m: 1.8-2.4), posterior distributions for H, m, d and Q_c appear to be well defined indicating that data were informative about the values of these parameters. When the model was allowed to run unconstrained, credible intervals on all parameters increased. Due to small sample sizes of tag-recapture data, there was likely not enough information in the data to inform all parameter estimates. Increasing

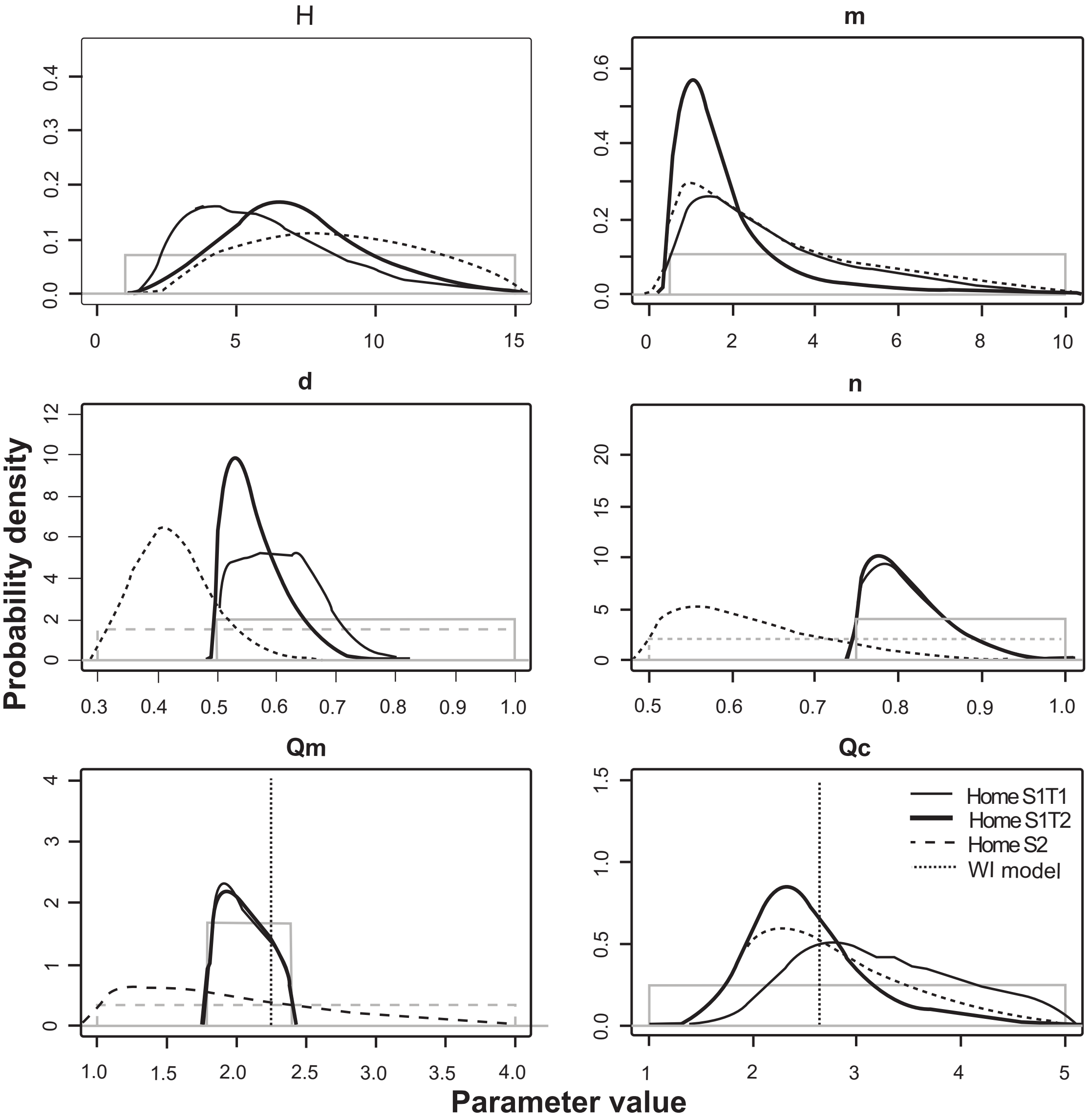

Fig. (5). Posterior probability densities of bioenergetics parameters for the Homosassa River largemouth bass population for two scenarios in which the general bioenergetics model was fit. The first scenario (S1: Trial 1 (T1); solid thin line, Trial 2 (T2); solid thick line) was fit with informative priors on metabolic parameters (n and Q_m). The second scenario (S2; dashed line) was fit without informative priors. Prior probability density functions are grey lines and posterior probability densities are black lines. Wisconsin bioenergetics model estimates are shown as vertical dotted lines.

sample sizes for both growth increment and size-at-age data led to better defined posterior distributions and reduced uncertainty in parameter estimates. An important result is that patterns in posterior distributions did not change between the first and second trials of scenario 1. This is likely due to growth increment data being collected over a wide contrast in temperatures for both populations [21]. While increased sample sizes would have likely decreased credible limits of parameter estimates, patterns in parameter estimates between populations remained consistent for all fitting scenarios.

Consistent differences in consumption related parameters between populations were evident for all general bioenergetics model scenarios. These differences included a higher net food consumption rate (*H*), slower increase in food consumption with body size (*d*), and lower response in food consumption to temperature (Q_c) for largemouth bass in the Homosassa River. Since both rivers are subject to very similar temperature regimes, differences in seasonal and lifetime growth patterns are likely the result of differences in prey availability patterns and available prey sizes between the two rivers. Differences in consumption parameter estimates imply that largemouth bass in the Homosassa River have higher consumption rates (*H*) in comparison to largemouth bass in the Chassahowitzka River, but exhibit a slower increase in consumption rate with body size (*d*). Moreover, largemouth bass in the Homosassa River experience less seasonal variation in prey abundance (Q_c) compared to largemouth bass in the Chassahowitzka River. Differences in consumption related parameters between the two populations are supported by field observations of differences in prey consumption and prey abundance patterns for largemouth bass between rivers [26, 27].

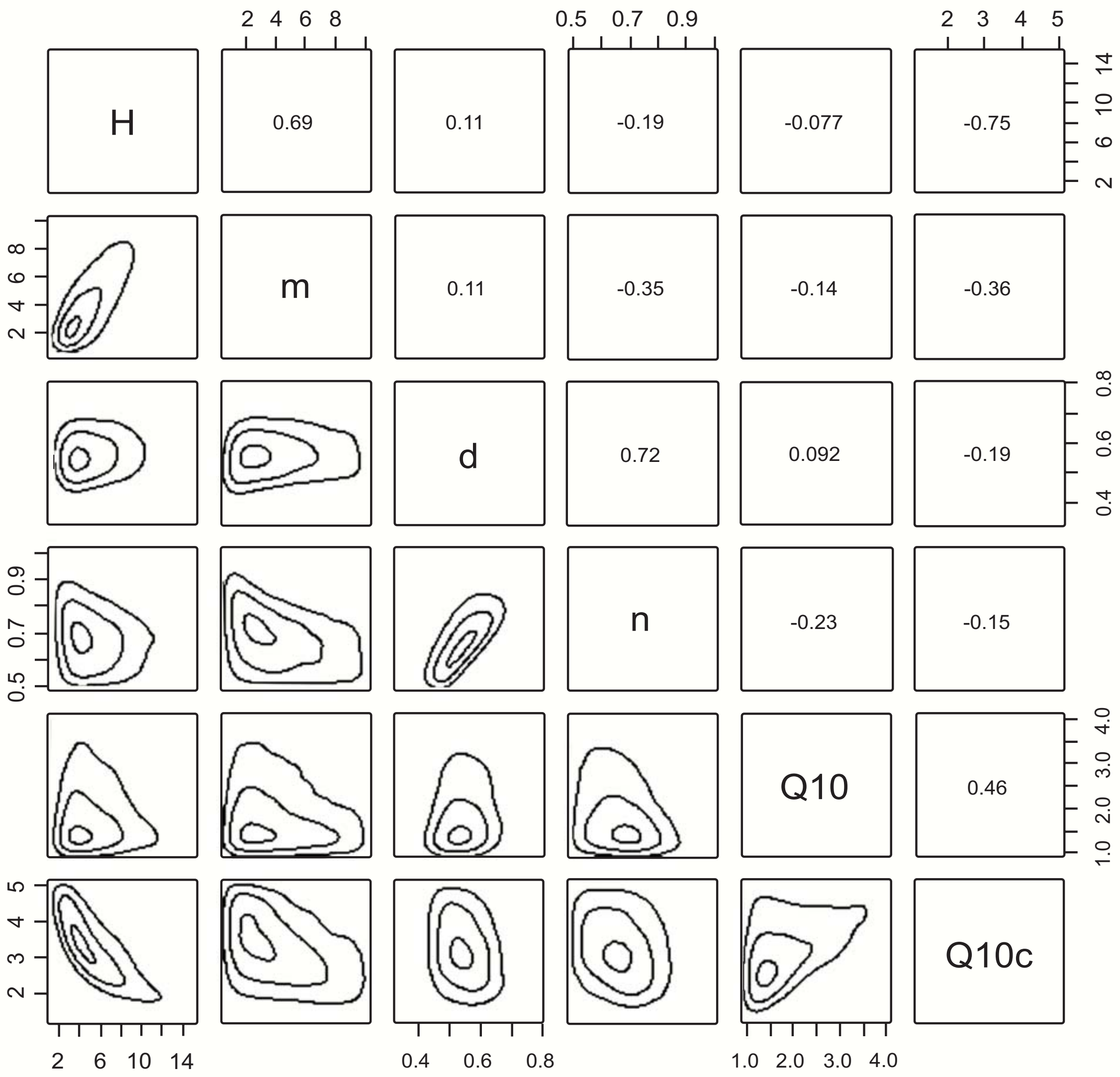

Fig. (6). Correlation matrix of parameter combinations from the general bioenergetics model when fit without informative priors on metabolic parameters using data from the Chassahowitzka River largemouth bass population. Contours represent the 0.9, 0.5 and 0.2 correlation regions. Notice the confounding in parameter values between H/m and d/n.

Largemouth bass diets collected in the Homosassa River were more likely to contain prey and had greater numbers of prey items compared to largemouth bass of similar sizes in the Chassahowitzka River suggesting that largemouth bass in the Homosassa River exhibit greater feeding activity [26]. However, largemouth bass in the Homosassa River consumed smaller sizes of prey items compared to largemouth bass in the Chassahowitzka River [26]. Differences in prey sizes relative to predator sizes between the two populations were most evident for larger individuals. In addition, total prey abundance for largemouth bass in the Homosassa River was less seasonal than in the Chassahowitzka River due to large imports of saltwater prey species during winter months in the Homosassa River [27]. Prey abundance of freshwater species was highly seasonal in both systems with significantly decreased abundance in winter months compared to summer months [27].

Observed differences in prey abundance patterns and sizes of available prey between the two rivers were reflected in observed seasonal and lifetime growth patterns of largemouth bass and predicted by the general bioenergetics model. The general bioenergetics model was able to use information from length increment data collected over multiple seasons to estimate these trends in growth and consumption patterns. The general bioenergetics model also successfully identified observed differences in both size allometry in consumption and seasonal patterns in prey abundance using growth increment and temperature data without information on prey populations or largemouth bass diet data which are required by other bioenergetics approaches.

Consumption as estimated from the general bioenergetics model was lower than that estimated from the Wisconsin bioenergetics model for largemouth bass in both rivers. Differences between predicted consumption rates from the two models were not unexpected due to slight differences in assumptions regarding size allometry of energy expenditure and consumption as well as temperature dependence of respiration and consumption between the two models. Posterior

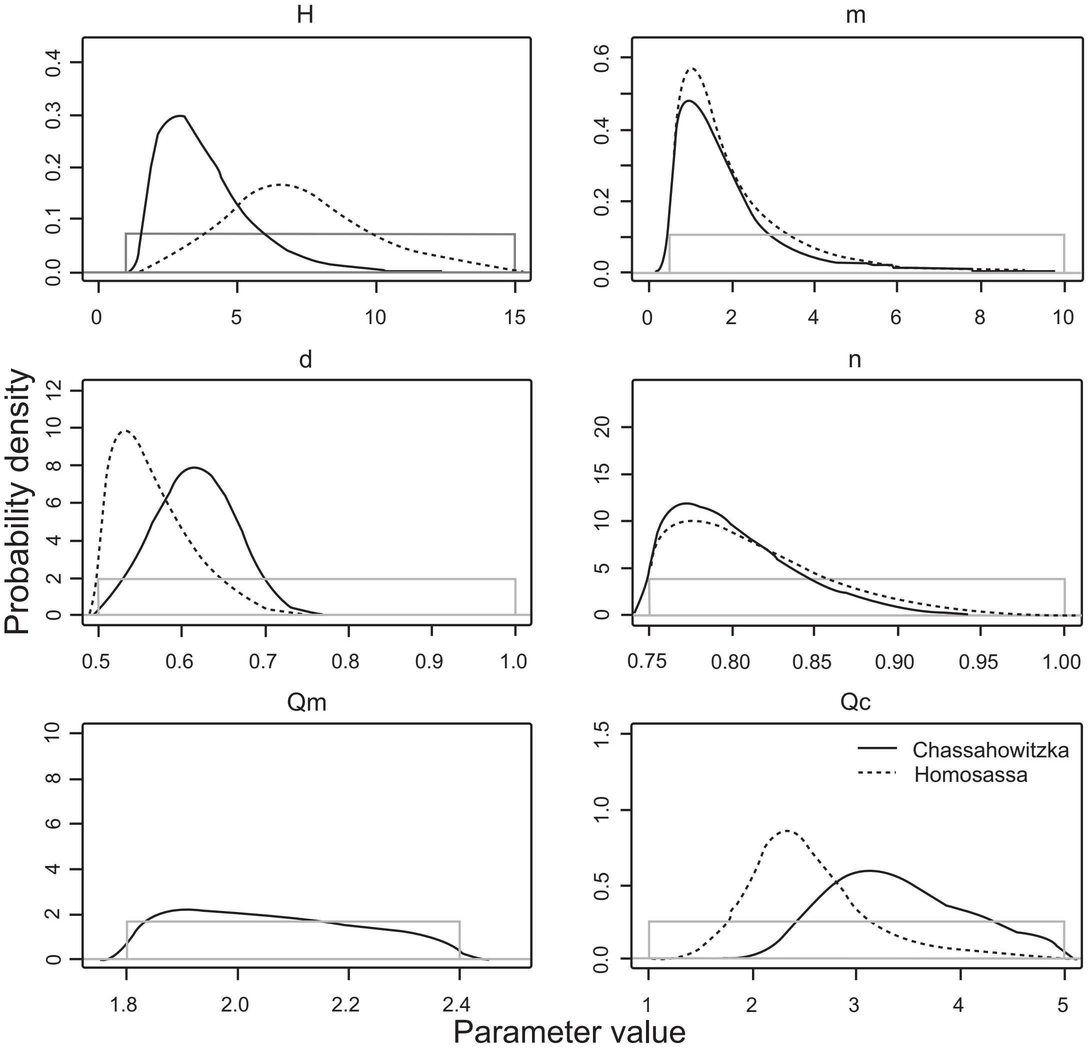

Fig. (7). Comparison of posterior probability densities of bioenergetics parameter estimates between the Chassahowitzka River and Homosassa River largemouth bass populations when the general bioenergetics model is fit with informative priors on metabolic parameters (*n* and Q_m).

distributions of bioenergetics parameters from the general bioenergetics model differed from those used in the Wisconsin bioenergetics model. However, even when the general bioenergetics model is fixed with parameter estimates used in the Wisconsin model (Q_m=2.25, and Q_c=2.65), estimates of consumption between the two models did not converge. One possible reason for the lack of convergence may be due to differences in model structure. The Wisconsin bioenergetics model, for example, uses a simple exponential relationship to describe the temperature dependence of metabolism [34]. Hanson *et al.* [4] suggest that respiration should be modeled using a temperature dependent function rather than the simple exponential function. In the case reported herein, the Wisconsin bioenergetics model may have overestimated respiration rates at higher temperatures. If so, higher consumption rates would be required to balance the energy budget.

The general bioenergetics model predicted maximum consumption and growth during summer months, whereas the Wisconsin model predicted the opposite pattern with decreased consumption and weight loss during this same time period. These differences likely occur because observed field temperatures consistently exceeded the laboratory estimated temperature for maximum consumption for largemouth bass used in the Wisconsin bioenergetics model [4, 34]. If the temperature time series as measured in the field is indicative of what was actually experienced by most largemouth bass, then the laboratory estimated relationship for temperature-dependent consumption in the Wisconsin bioenergetics model is not appropriate for the largemouth bass populations in this study. When the CTO parameter in the Wisconsin bioenergetics model is increased from 27.5 to 30.0, predicted patterns of consumption between the two bioenergetics models were very similar. Growth increment data and diet information supported the patterns predicted by the general bioenergetics model, with maximum growth and consumption occurring during summer months.

As is often the case, all physiological parameters for the Wisconsin bioenergetics model were obtained from the literature [1, 3]. The validity of borrowing physiological parameters, even for the same species, however, has repeatedly been questioned [1, 12, 14]. In our investigation, we applied

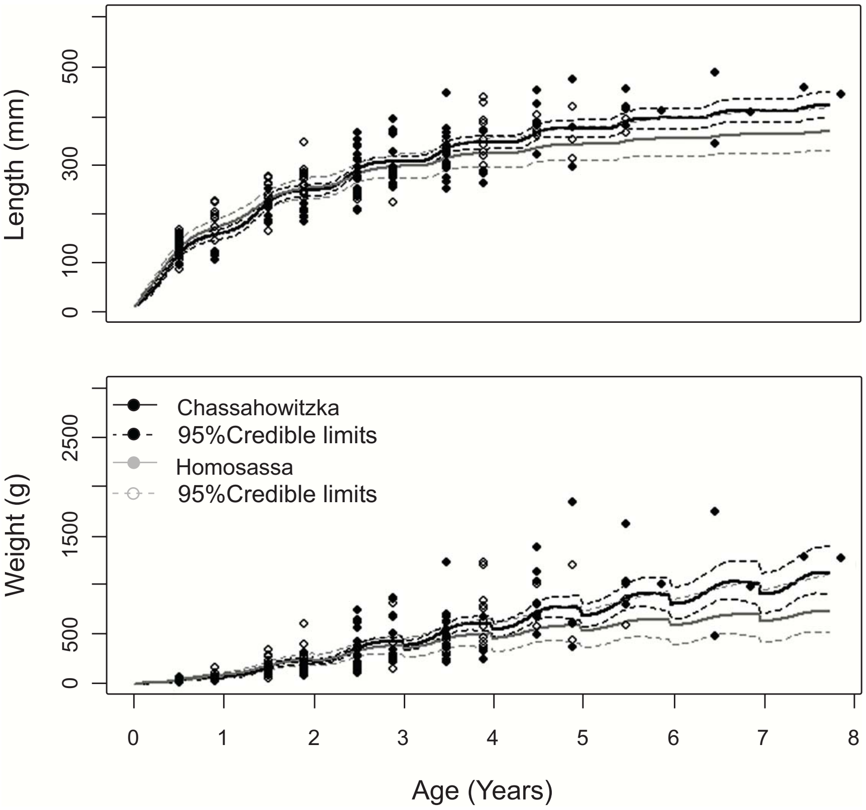

Fig. (8). Observed length-at-age (points; top panel) and weight-at-age (points; bottom panel) of largemouth bass captured in the Chassahowitzka (closed points) and Homosassa rivers (open points) and estimated length- and weight-at-age from the general bioenergetics model (Chassahowitzka River; black line, Homosassa River; grey line). Dashed lines represent Bayesian posterior 95% credible limits.

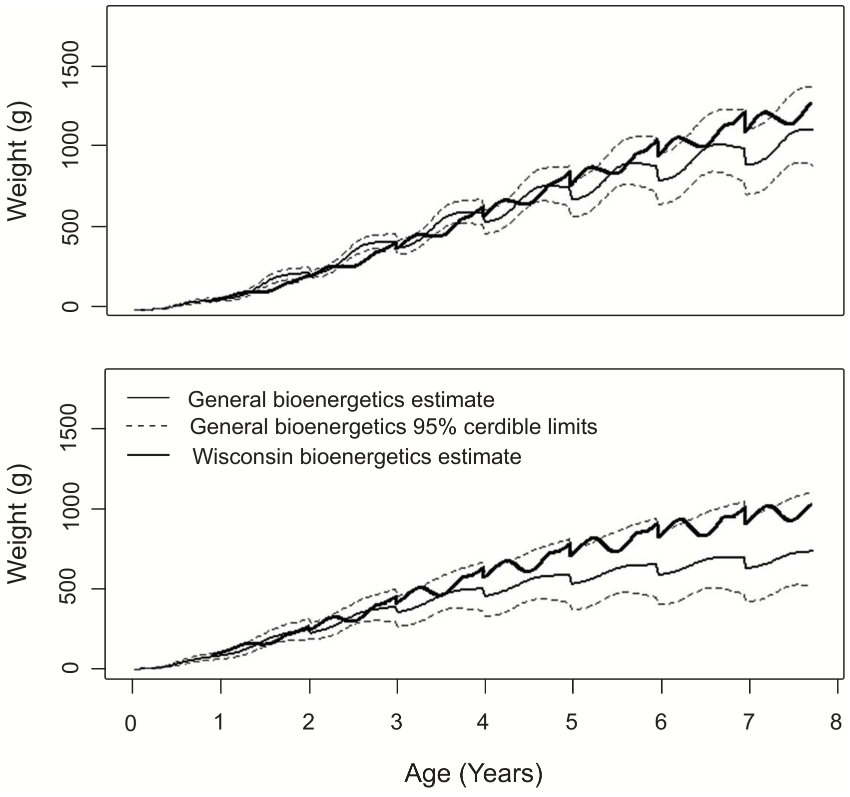

Fig. (9). Predicted weight at age for the Chassahowitzka River (top panel) and Homosassa River (bottom panel) largemouth bass populations from the general bioenergetics model (thin line) and Wisconsin bioenergetics models (solid line). Dashed lines represent Bayesian posterior 95% credible limits for the general bioenergetics model.

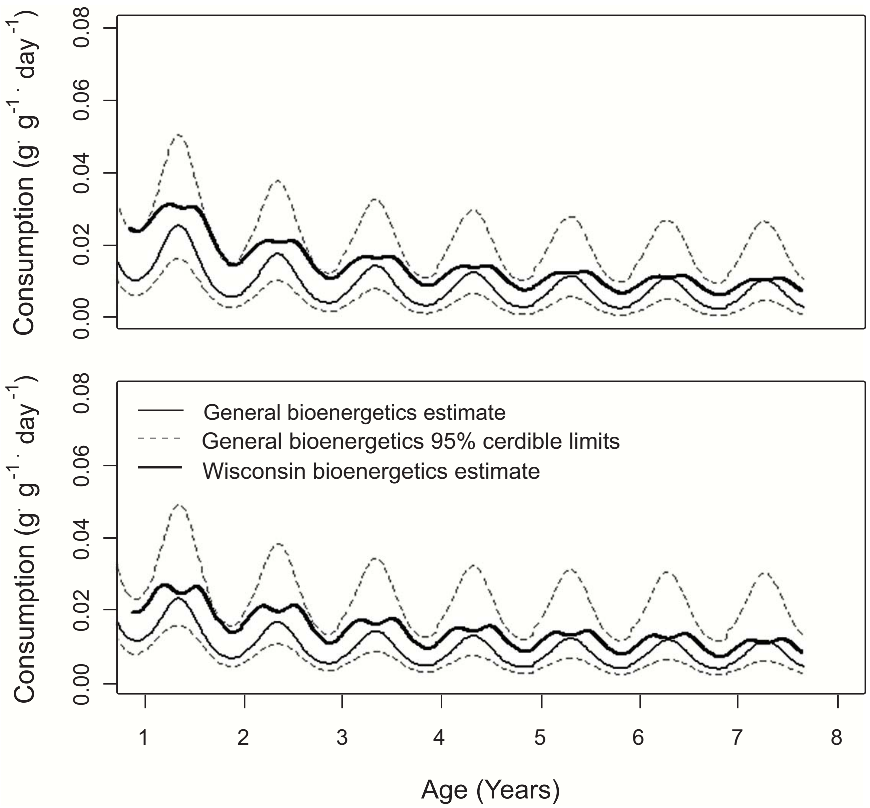

Fig. (10). Daily consumption estimates for the Chassahowitzka River (top panel) and Homosassa (bottom panel) River largemouth bass populations from the general bioenergetics model (thin line) and Wisconsin bioenergetics models (solid line). Dashed lines represent Bayesian posterior 95% credible limits for the general bioenergetics model.

Table 3. Weight-Length Parameters (*a* and *b*), von Bertalanffy Parameters (L_∞, *k*, and t_o) and Mass at Maturity for Largemouth Bass from the Chassahowitzka and Homosassa Rivers

Parameter	Description	Chassahowitzka	Homosassa	Units
a	Intercept coefficient of length-weight relationship	1.28 e^{-5}	1.28 e^{-5}	g mm^{-b}
b	Power coefficient of length-weight relationship	3.0	3.0	-
L_∞	Average asymptotic body length	525	455	mm
k	Growth coefficient	0.26	0.33	yr^{-1}
t_o	Theoretical age at length = 0	-0.52	-0.72	yr
Wma	Mass at maturity	230	230	g

the Wisconsin bioenergetics model, which was developed using input parameters for northern largemouth bass (*Micropterus salmoides salmoides*), to model Florida largemouth bass (*M. s. floridanus*) bioenergetics. Differences in growth rates between different strains of largemouth bass (Florida, northern, and their F_1 hybrid) have been shown to be independent of environmental factors, with northern largemouth bass having greater growth rates than Florida largemouth bass [16, 38-40]. In addition, northern and Florida largemouth bass populations display different patterns in the rate at which they convert food to growth [16]. These growth differences may have a significant effect on the consumptive demand predicted by the Wisconsin bioenergetics model.

Regional differences in physiology can also have an important influence on the accuracy of consumption estimates [15]. Geographic variation in the genetic capacity for growth has been demonstrated for numerous fishes [41-43]. Garvey and Marschall [25], for example, showed that growth patterns of largemouth bass differed across latitudes due to differences in energy allocation decisions. Accounting for local adaptation in growth physiology may markedly improve the performance of bioenergetics models [15]. We recognize, however, that it is impractical to measure all model parameters for each species and locale [1, 12, 15]. The general bioenergetics model circumvents issues related to parameter borrowing and regional differences in physiology by estimating physiological parameters directly from growth increment and size-at-age data collected on the population of interest, thus offering an alternative to developing individual models. However, this approach needs to be corroborated with laboratory evaluations across a range of species and conditions [12].

The purpose of this paper was to assess whether the general bioenergetics model put forth by Walters and Essington [21] could provide reasonable bioenergetics parameters and consumption estimates for two populations of largemouth bass. The general bioenergetics model predicted differences in consumption parameters and consumption patterns between the two populations that are supported by field consumption data and prey availability patterns. Differences in patterns and magnitude of consumption estimates between the general bioenergetics model and Wisconsin bioenergetics model are likely due to a combination of factors and such differences merit further evaluation. It is likely, however, that differences between the two models will be population-specific rather than species-specific. As with other types of models, it has been suggested that bioenergetics models are most useful as a tool for hypothesis testing and should be used for making qualitative comparisons rather than quantitative predictions [1, 12]. The ability of the general bioenergetics model to estimate bioenergetics parameters directly from field length increment and length-at-age data offers potential advantages to current bioenergetics models. First, the general bioenergetics model does not rely on laboratory derived estimates or require borrowing of estimates from other populations. Second, the incorporation of growth increment data should allow for more precisely defined seasonality in consumption and growth. Third, the Bayesian parameter estimation allows uncertainty in parameter estimates to be incorporated into management recommendations [30]. Finally, the use of data commonly collected in many population assessments should allow for seamless integration into a framework for testing hypotheses that require estimates of fish consumption rates.

ACKNOWLEDGEMENTS

We thank the Florida Fish and Wildlife Conservation Commission for providing funding for the original field study through a State Wildlife Grant (07002) to the University of Florida. This manuscript was greatly improved by comments and suggestions from an anonymous reviewer.

REFERENCES

[1] Ney JJ. Bioenergetics modeling today: growing pains on the cutting edge. Trans Am Fish Soc 1993; 122: 736-48.

[2] Hansen LJ, Boisclair D, Brandt SB, *et al.* Applications of bioenergetics models to fish ecology and management: where do we go from here? Trans Am Fish Soc 1993; 122: 1019-30.

[3] Hartman KJ, Hayward, RS. In: Guy CS, Brown ML, Eds. Analysis and interpretation of freshwater fisheries data. Bioenergetics: Am Fish Soc 2007; pp. 515-60.

[4] Hanson PC, Johnson TB, Schindler DE, Kitchell JF. Fish Bioenergetics 3.0. Madison, WI: University of Wisconsin, Sea Grant Institute; 1997. Report No.: No. WISCU-T-97-001.

[5] Kitchell JF, Stewart DJ, Weininger D. Application of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum*). J Fish Res Board Can 1977; 34: 1922-35.

[6] Harfmart KJ, Brandt SB. Predatory demand and impact of striped bass, bluefish, and weakfish in the Chesapeake Bay: applications of bioenergetics models. Can J Fish Aquat Sci 1995; 52: 1667-87.

[7] Johnson BM, Martinez PJ, Hawkins JA, Bestgen KR. Ranking predatory threats by nonnative fishes in the Yampa River, Colorado, via bioenergetics modeling. N Am J Fish Manag 2008; 28: 1941-53.

[8] Jones ML, Koonce JF, O'Gorman R. Sustainability of hatchery-dependent salmonine fisheries in Lake Ontario: the conflict between predator demand and prey supply. Trans Am Fish Soc 1993; 122: 1002-8.

[9] Bajer PG, Whitledge GW, Hayward RS, Zweifel RD. Laboratory evaluation of two bioenergetics models applied to yellow perch: identification of a major source of systematic error. J Fish Biol 2003; 62: 436-54.

[10] Bajer PG, Whitledge GW, Hayward RS. Widespread consumption-dependent systematic error in fish bioenergetics models and its implications. Can J Fish Aquat Sci 2004; 61: 2158-67.

[11] Madenjian CP, O'Connor DV, Pothoven SA, *et al.* Evaluation of a Lake Whitefish bioenergetics model. Trans Am Fish Soc 2006; 135: 61-75.

[12] Chipps SR, Wahl DH. Bioenergetics modeling in the 21st century: Reviewing new insights and revisiting old constraints. Trans Am Fish Soc 2008; 137: 298-313.

[13] Hartman KJ, Kitchell JF. Bioenergetics modeling: progress since the 1992 symposium. Trans Am Fish Soc 2008; 137: 216-23.

[14] Trudel M, Geist DR, Welch DW. Modeling the oxygen consumption rates in Pacific salmon and steelhead: an assessment of current models and practices. Trans Am Fish Soc 2004; 133: 326-48.

[15] Munch SB, Conover DO. Accounting for local physiological adaptation in bioenergetic models: testing hypotheses for growth rate evolution by virtual transplant experiments. Can J Fish Aquat Sci 2002; 59: 393-403.

[16] Slaughter JE IV, Wright RA, DeVries DR. The effects of age-0 body size on the predictive ability of a largemouth bass bioenergetics model. Trans Am Fish Soc 2004; 133: 279-91.

[17] Whitledge GW, Hayward RS, Zxeifel RD, Rabeni CF. Development and laboratory evaluation of a bioenergetics model for subadult and adult smallmouth bass. Trans Am Fish Soc 2003; 132: 316-25.

[18] Tyler JA, Bolduc MB. Individual variation in bioenergetic rates of young-of-year rainbow trout. Trans Am Fish Soc 2008; 137: 314-23.

[19] Cech JJ, Massingill MJ, Vondracek B, Linden AL. Respiratory metabolism of mosquitofish, *Gambusia affinis*: effects of temperature, dissolved oxygen, and sex difference. Environ Biol Fish 1985; 13: 297-307.

[20] Wuenschel MJ, Jugovich AR, Hare JA. Metabolic responses of juvenile gray snapper (*Lutjanus griseus*) to temperature and salinity: physiological costs of different environments. J Exp Mar Biol Eco 2005; 231: 145-54.

[21] Walters CJ, Essington TE. Recovery of bioenergetics parameters from information on growth. Open Fish Sci J 2009; (this issue).

[22] Essington TE, Kitchell JF, Walters CJ. The von Bertalanffy growth function, bioenergetics, and the consumption rates of fish. Can J Fish Aquat Sci 2001; 58: 2129-38.

[23] Clark A, Johnston NM. Scaling of metabolic rate with body mass and temperature in teleost fish. J Anim Eco 1999; 68: 893-905.

[24] Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. Toward a metabolic theory of ecology. Ecology 2004; 85: 1771-89.

[25] Garvey JE, Marschall EA. Understanding latitudinal trends in fish body size through models of optimal seasonal energy allocation. Can J Fish Aquat Sci 2003; 60: 938-48.

[26] Tetzlaff JC. Energetic consequences of habitat loss: trade-offs in energy acquisition and energy expenditure by *Micropterus salmoides*. Masters Thesis University of Florida, Gainesville, Florida, USA, 2008.

[27] Frazer TK, Pine WE III, Lauretta MV, *et al.* Increased nutrient loading of spring-fed coastal rivers: effects on habitat and faunal communities. Annual Report: Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida 2008; pp. 1-74.

[28] Frazer TK, Notestein SK, Pine WE III. Changes in the physical, chemical, and vegetative characteristics of the Homosassa, Chassahowitzka and Weeki Wachee Rivers. Final Report: Southwest Florida Water Management District, Tampa, Florida 2006; pp. 1-163.

[29] Paloheimo JE, Dickie LM. Food and growth of fishes I. A growth curve derived from experimental data. J Fish Res Board Can 1965; 22: 521-42.

[30] van Poorten BT, Walters CJ. Estimation of bioenergetics parameters using capture-recapture data with comparison to estimates from a laboratory-based model. Open Fish Sci J 2009; (this issue).

[31] Flowers JF, Pine WE III, Tetzlaff JC. Bioenergetics approach to describing Gulf sturgeon growth in two Florida rivers. Open Fish Sci J 2009; (this issue).

[32] Coggins LJ, Pine WE III. Development of a Temperature-dependent growth model for the endangered humpback chub using capture-recapture data. Open Fish Sci J 2009; (this issue).

[33] Gelman A, Carlin JB, Stern HS, Rubin DB. Bayesian Data Analysis. New York: Chapman and Hall 1995.

[34] Rice JA, Breck JE, Bartell SM, Kitchell JF. Evaluating the constraints of temperature, activity and consumption on growth of largemouth bass. Environ Biol Fishes 1983; 9: 263-75.

[35] Rice JA, Cochran PA. Independent evaluation of a bioenergetics model for largemouth bass. Ecology 1984; 65: 732-9.

[36] Whitledge GW, Hayward RS. Laboratory evaluation of a bioenergetics model for largemouth bass at two temperatures and feeding levels. Trans Am Fish Soc 1997; 126: 1030-5.

[37] Neal JW, Noble RL. A bioenergetis-based approach to explain largemouth bass size in tropical reservoirs. Trans Am Fish Soc 2006; 135: 1535-45.

[38] Isely JJ, Noble RL, Koppelman JB, Phillip DP. Spawning period and first-year growth of northern, Florida, and intergrade stocks of largemouth bass. Trans Am Fish Soc 1987; 116: 757-62.

[39] Williamson JH, Carmichael GJ. An aquacultural evaluation of Florida, northern, and hybrid largemouth bass, *Micropterus salmoides*. Aquaculture 1990; 85: 247-58.

[40] Phillip DP, Whitt GS. Survival and growth of northern, Florida, and reciprocal F_1 hybrid largemouth bass in central Illinois. Trans Am Fish Soc 1991; 120: 58-64.

[41] Conover DO, Present T. Countergradient variation in growth rate: compensation for length of the growing-season among Atlantic silversides from different latitudes. Oecologia 1990; 83: 316-24.

[42] Conover DO, Brown JJ, Etisham A. Countergradient variation in growth of young striped bass (*Morone saxatilis*) from different latitudes. Can J Fish Aquat 1997; 54: 2401-9.

[43] Jonassen TM, Imsland AK, Fitzgerald R. Geographic variation in growth and food conversion efficiency of juvenile Atlantic halibut related to latitude. J Fish Biol 2000; 56: 279-94.

Received: January 01, 2009 Revised: July 01, 2009 Accepted: July 17, 2009