Development and Evaluation of a Bioenergetics Model for the Inland Silverside in Freshwater Systems

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Abstract.—Consumption and respiration parameters were fit for inclusion in a bioenergetics model developed to predict the growth of the inland silverside *Menidia beryllina*. Although this model accurately predicted inland silverside growth through the initiation of spawning, it failed to predict the growth of reproductively active inland silversides. Model simulations provided initial evidence that a single model cannot predict the lifetime growth patterns of this species. Instead, a two-stage model is probably necessary to account for the physiological differences between the prespawning and active-spawning stages. In addition, the bioenergetics models of short-lived (life span, <2 years) fishes may need to include a better means for assessing the direct energy expenditure for reproduction.

The inland silverside *Menidia beryllina* is a euryhaline, zooplanktivorous, short-lived fish species that inhabits rivers and coastal estuaries along the east and Gulf coasts of the United States. The species has been stocked extensively within southern reservoirs as a forage fish for littoral predators. It is categorized as opportunistic in the Winemiller and Rose (1992) triangular life history model. Inland silversides have evolved to be rapid colonizers after disturbances because of their short generation time, great reproductive effort, small body size, and small-batch fecundity. Prespawning inland silversides require high energy input to provide for rapid growth. This rapid growth enables them to survive winter, escape predation, and reach reproductive size in time for the breeding season the following spring. As adults, inland silversides require energy to meet the demands of both somatic and reproductive growth. With increases in somatic size there is an increase in reproductive capacity that provides more room for egg production (Slatkin 1984). After the reproductive season, few reproducing adults survive, suggesting a metabolic burnout (Huber and Bengtson 1999) that gives rise to two growth periods. The first growth period (27% of total growth) occurs while the inland silverside is a juvenile before the onset of winter, and the second (73% of total growth) occurs while the inland silverside is an adult after the winter (Huber and Bengtson 1999).

Application of a bioenergetics model developed for estuarine inland silversides (Peck et al. 2003) is limited because the model does not incorporate the effects of temperature on metabolic activities and is applicable only when the water temperature is 25°C. Our interest was in developing a temperature- and size-dependent bioenergetics model for the inland silverside because of both its importance as prey for piscivores in southern reservoir communities and its interesting life history strategy. Thus, our study objective was to fit consumption and respiration parameters across a range of temperatures for use in a bioenergetics model for the inland silverside and to apply the model to a wild population. Through the use of simulations, we investigated the ability of the bioenergetics model to model the lifetime growth of inland silversides in freshwater systems.

Methods

Fish collection and laboratory acclimation.—Inland silversides were collected from Buffalo Springs Lake (33°31′N, 101°42′W), a reservoir in Lubbock County, Texas, on 12 October 2002 for model development and from White River Lake (33°28′N, 101°05′W), a reservoir in Dickens County, Texas, on 6 July 2004 for laboratory evaluation. Inland silversides were captured with a seine (1.8 × 9.1 m, 5-mm mesh) and transported to the laboratory in an aerated holding tank. The photoperiod in the laboratory was controlled by timed halogen lights set for a 14-h-light : 10-h-dark cycle. Fish were allowed to acclimate to laboratory conditions for a minimum of 2 weeks after capture. During acclimation, they were fed

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freeze-dried brine shrimp *Artemia* spp. and crushed Tetramin flake food (Tetra, Blacksburg, Virginia) daily. For model development, fish were placed into 94.6-L tanks that were immersed in 1,136-L water baths to minimize temperature fluctuations. The temperature within each water bath was changed at a rate of 1°C/d until it reached final temperatures of 10, 15, 20, 25, and 30°C. After the target temperature was reached, fish were allowed an additional 2 weeks of acclimation before experiments began. Inland silversides were then transferred to respiration and consumption chambers, as described below. For model evaluation, groups of six inland silversides were held in 10 ($N = 60$) 37.9-L aquaria with individual aeration for an additional week at $22 \pm 0.5°C$ after the 2-week laboratory acclimation.

For field analysis, 25 inland silversides were collected from Buster Long Lake, Texas (33°32′N, 101°55′W), with a bag seine (1.8×9.1 m, 5-mm mesh) during 1700–2200 hours weekly from 15 May to 14 October 2003. Fish were immediately euthanized and kept on ice until they could be processed. In the laboratory, inland silverside mass (g), standard length (SL; cm), and gender (mature male, mature female, or immature) were recorded.

Model development.—Daily incremental growth was modeled as

$$\frac{dW}{t} = \frac{J_a(1 - u)C - J_o(\text{ACT} \cdot R + S \cdot C)}{J_f};$$

where

dW/t = change in fish wet mass (g/d)
J_a = energy density of prey (J/g wet mass)
u = fraction of energy lost to egestion and excretion
C = daily consumption (g wet prey/d)
J_o = oxycaloric conversion (J/mg O$_2$)
ACT = activity multiplier
R = daily respiration (mg O$_2$/d)
S = specific dynamic action (mg O$_2$/g wet prey)
J_f = energy density of fish (J/g wet mass)

Respiration and consumption were modeled as functions of temperature (°C) and wet-fish mass (g). Parameters for respiration and consumption were assumed to have a normal distribution and were fitted to the observed data using maximum likelihood.

Respiration parameters.—Respiration parameters were estimated from 90 inland silversides (standard length [SL], 3.86–7.26 cm) at 10, 15, 20, 25, and 30°C. Before individual respiration rates were determined, the inland silversides were starved to allow complete gastric evacuation. To ensure that no food was metabolized in the gut during the respiration trials, fish in tanks cooler than 20°C were starved for 2–3 d and fish in tanks warmer than 20°C were starved for 1 d. Respiration of the inland silversides was estimated by placing individual fish into 500-mL respirometers constructed from clear Lexan pipe. Each apparatus was fitted with an inflow and outflow hose (inside diameter, 7 mm) for water exchange and a smaller outflow hose (inside diameter, 3 mm) with a stopcock, from which water samples were drawn. Each fish was allowed to acclimate to the respiration chamber for 1 h. During acclimation, water was exchanged in the apparatus to prevent depletion of dissolved oxygen (DO) and to minimize stress to the fish. Water exchange was accomplished by siphoning water through the inflow and outflow hoses on the enclosed respirometer. After the acclimation period, water exchange was stopped and the initial DO concentration was measured with a Yellow Springs Instruments Model 95 dissolved oxygen meter from a 100-mL water sample that was drawn from the respiration chamber. The chamber was left undisturbed for 1 h, and the final DO level was measured from another 100-mL water sample. A fishless control chamber was used for each temperature to determine the biological oxygen demand (BOD). Total oxygen consumption for each inland silverside was determined by calculating the difference between initial and final DO measurements after correcting for the BOD. After the respiration trial was completed, each inland silverside was euthanized and mass and length were measured.

The respiration parameters were fit to the equation

$$R = A_r \cdot W^{B_r} \cdot e^{(\theta_r \cdot T)};$$

where

A_r = intercept for respiration
W = fish wet mass (g)
B_r = mass-dependent coefficient for respiration
θ_r = temperature-dependent coefficient for respiration
T = water temperature (°C)

Consumption parameters.—Consumption was estimated from 48 inland silversides (SL, 3.60–6.61 cm) at 10, 15, 20, 25, and 30°C. Individual inland silversides were placed into 12-L rectangular consumption chambers submersed in a water bath to maintain constant temperature (10, 15, 20, 25, and 30°C). Each aerated consumption chamber was provided with 3 L of water. Fish were allowed to acclimate to the chambers for 24 h.

Live daphnia *Daphnia magna* (purchased from the Carolina Biological Supply Co. and cultured in the laboratory) were used as prey during the consumption trial. At the beginning of the consumption trial, adult *Daphnia* were harvested from the culture tanks with a

TABLE 1.—Components of the bioenergetics model for inland silversides.

Equation	Symbol	Description	Value
$R = A_r \cdot W^{B_r} \cdot e^{(\theta_r \cdot T)}$	R	Daily respiration (mg O_2/d)	
($\sigma^2 = 0.1575$, $R^2 = 0.78$)	A_r	Intercept for R	8.592
	W	Fish wet mass (g)	
	B_r	Mass-dependent coefficient	0.5472
	θ_r	Temperature-dependent coefficient	0.0363
	T	Temperature (°C)	
$C = A_C \cdot W^{B_C} \cdot e^{(\theta_c \cdot T)}$	C	Daily consumption (g wet prey/d)	
($\sigma^2 = 0.0456$, $R^2 = 0.72$)	A_c	Intercept for C	0.0071
	B_c	Mass-dependent coefficient	0.1786
	θ_c	Temperature-dependent coefficient	0.0833
$\dfrac{dW}{t} = \dfrac{[J_a(1-u)C] - J_o(\text{ACT} \cdot R + S \cdot C)}{J_f}$	$\dfrac{dW}{t}$	Daily growth (g/d)	
	J_a	Energy density of prey (J/g wet mass)	2,513
	u	Egestion and excretion	0.027
	ACT	Activity multiplier	1.9220
	J_o	Oxycaloric conversion (J/mg O_2)	0.0136
	S	Specific dynamic action (mg O_2/g wet prey)	0.17
	J_f	Energy density of fish (J/g wet mass)	4,776

50-µm mesh net and concentrated into 1 L of water. A 50-mL sample was collected from the concentrated *Daphnia* and preserved in a 4% sucrose-buffered formalin solution (Haney and Hall 1973) to estimate the biomass of the entire *Daphnia* sample. The first 30 *Daphnia* were measured from each sample placed into the consumption chamber, and the mean length of each sample was calculated to estimate the average mass of *Daphnia* in the chamber. Live *Daphnia* were then rinsed into 0.5 L of water and fed to inland silversides three times (~33% of the total at each feeding) during the day. After 24 h, fish were removed from the consumption chambers and euthanized, and mass and length were measured. The remaining *Daphnia* were recovered from the consumption chambers by filtering water through a 50-µm mesh and then preserved. The preserved *Daphnia* were counted and measured with an ocular micrometer at 10× magnification. The first 30 *Daphnia* were measured from each consumption chamber, and the mean length of each sample was calculated to estimate the average mass of *Daphnia* in the chamber. *Daphnia* mass was estimated using the linear regression equation (McCauley 1984)

$$\log_e W = 1.8268 + 2.7854 \overline{\log_e L},$$

where $\log_e W$ is the natural logarithm of *Daphnia* mass (µg) and $\overline{\log_e L}$ is the geometric mean of the natural logarithm of length of individuals in the sample (mm).

Biomass was estimated from the equation

$$\text{Biomass} = e^{\log_e W} \cdot N,$$

where N is the number of *Daphnia* in the sample.

Biomass consumed was estimated as the change in *Daphnia* biomass from the initial estimate to the final estimate. The consumption parameters were fit to the equation

$$C = A_c \cdot W^{B_c} \cdot e^{(\theta_c \cdot T)},$$

where A_c is the intercept for consumption, B_c is the mass-dependent coefficient for consumption, and θ_c is the temperature-dependent coefficient for consumption.

To assess the fit of respiration and consumption parameter values, we used a linear hypothesis test (i.e., intercept = 0, slope = 1; Fox 1997) of predicted versus observed values.

Other parameters.—We obtained values for three parameters from other published bioenergetics models. The activity multiplier (ACT) value, 1.92, was obtained from the bioenergetics model for the Atlantic silverside *Menidia menidia* (Munch and Conover 2002), a closely related species, as was done in the original inland silverside bioenergetics model (Peck et al. 2003). A constant value of 0.17 was used as the value for the specific dynamic action (SDA) (Kitchell et al. 1977). The egestion and excretion (u) value of 0.27 was obtained from the bioenergetics model for western mosquitofish *Gambusia affinis* (Chipps and Wahl 2004; Table 1). We did not borrow the egestion and excretion parameter from the Atlantic silverside model because this value (i.e., $u = 0.02$) was especially small and fell outside the usual range for this parameter in published literature. *Daphnia* were assigned an energy density of 2,513 J/g wet mass (Cummins and Wuycheck 1971). The energy density of the inland silversides was estimated from the equation developed by Hartman and Brandt (1995) as

$$J = 45.29D^{1.507},$$

where J equals the energy density (J/g wet mass) and D is the percent dry mass of the inland silversides. The mean dry mass (mean = 22%) was estimated from 100 inland silversides that were dried for 6 d at a constant temperature of 60°C. The equation yielded an energy density for the inland silversides to be 4,776 J/g wet mass. The standard value for oxycaloric conversion is 0.0136 J/mg O_2 (Elliot and Davidson 1975).

Model evaluation.—The predicted inland silverside mass was compared with actual growth in a laboratory validation trial. At the start of the trial, the total mass per tank (six fish per tank) was measured by placing each group into a tared container holding water and Stress Coat Conditioner (Aquarium Pharmaceuticals Inc.) to minimize the stress of handling. After mass was measured to the nearest 0.1 g, the fish were returned to their respective tanks. This weighing process was repeated every 7 d for a total of seven times. Fish were fed freeze-dried *Artemia* ad libitum twice daily. Wet mass (g) predicted by the freshwater bioenergetics model was regressed against the mean observed inland silverside wet mass. The fit of the bioenergetics model to observed growth was evaluated by a linear hypothesis test (i.e., intercept = 0, slope = 1; Fox 1997) of the natural log of predicted values versus the natural log of observed values.

Model application.—Starting in July, we projected growth of the inland silversides using our bioenergetics model under a range of P_{Cmax} (proportion of maximum consumption) values to investigate the differences in mass between males and females at the beginning of the growing season (May). In deriving predictions with bioenergetics models, it is important to incorporate the variation owing to the uncertainty in the data sets from which the models were made (Munch and Conover 2002). We numerically integrated the stochastic model

$$\frac{dW}{t} = \left\{ Ja(1-u)C\exp\left(E_c - \frac{\sigma_c}{2}\right) \right.$$
$$\left. - J_o[\text{ACT} \cdot (R + E_R) + S \cdot C] \right\}/J_f,$$

where E_C and E_R are normally distributed random variables sampled independently at each time step and σ_C is the error for consumption, as described in Munch and Conover (2002). The simulated mass of the inland silversides was the mean from 1,000 iterations at each time step (i.e., daily). The initial wet mass of the inland silversides was 0.3897 g, and the temperatures used were the approximate mean temperatures for each month in Buster Long Lake. Diet composition and stomach capacity information for the inland silversides was obtained from Chizinski et al. (2007). Growth
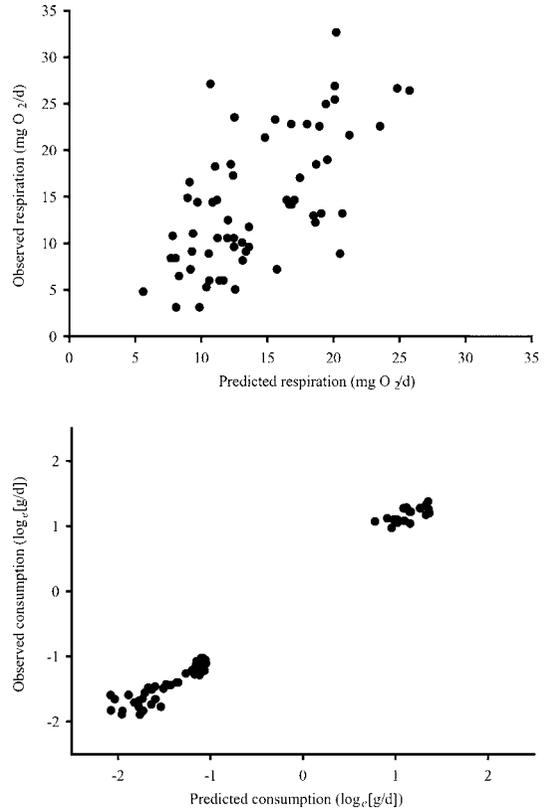

FIGURE 1.—Predicted versus observed respiration (upper panel) and consumption of *Daphnia* (wet mass; lower panel) for nonreproducing inland silversides in a laboratory setting.

estimations were simulated at a range of values for P_{Cmax} from 0.2 to 1.0.

Results

Model Parameters

Respiration.—The best-fit allometric and temperature-dependent respiration function was $R = 8.592 \cdot W^{0.5472} \cdot e^{(0.0363 \cdot T)}$ (Table 1). This model provided a reasonable fit ($R^2 = 0.78$, $n = 41$) with the data, and all parameter coefficients were significant ($P < 0.0001$). The linear hypothesis test showed no significant bias ($F = 0.0659$; df = 73, 75; $P = 0.9363$) in the predicted versus observed consumption parameter values (Figure 1).

Consumption.—The best-fit allometric and temperature-dependent consumption function was $C_{max} = 0.0071 \cdot W^{0.1786} \cdot e^{(0.0833 \cdot T)}$ (Table 1). This model provided a reasonable fit ($R^2 = 0.72$, n = 34) with the data, and all parameter coefficients were significant ($P < 0.05$). The linear hypothesis test showed no significant bias ($F = 0.204$; df = 41, 43; $P = 0.8163$)
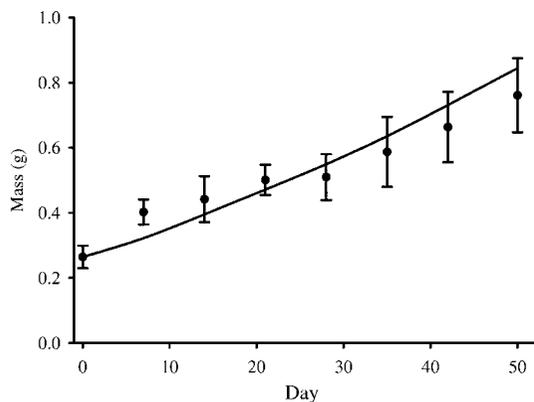
Figure 2.—Predicted (solid line) and observed (circles) wet mass ± SE of inland silversides held at 24.26 ± 0.36°C for 50 d and fed freeze-dried *Artemia* spp. ad libitum. Each point represents the mean mass of 60 inland silversides.

in predicted versus observed consumption parameter values (Figure 1).

Model Validation

Inland silversides grew an average of 0.0099 g/d in the validation trial. Daily water temperatures were 24 ± 0.36°C for the duration of the 50-d laboratory validation trial. The linear hypothesis test showed no significant bias ($F = 3.4767$; df = 6, 8; $P = 0.0998$) in predicted and observed weight over time (Figure 2). However a pattern was observed in the residuals of the model validation: the model underpredicted early in the trial and overpredicted later in the trial.

Field Estimates

Adult inland silversides.—Weekly water temperatures increased from May (21°C) to July 2003 (28°C) in Buster Long Lake. The mean sizes of adult females (SL, 7.14 cm; SE = 0.18; $n = 10$) and adult males (SL, 6.90 cm; SE = 0.06; $n = 39$) were similar in May (*t*-test: df = 47; $t = -1.54$; $P = 0.13$). However, the mean mass values for adult females (4.16 g; SE = 0.28; $n = 10$) and adult males (3.15 g; SE = 0.08; $n = 39$) were not similar in May (*t*-test: df = 47; $t = -4.88$; $P < 0.001$). In July, the mean sizes of adult females (SL, 8.25 cm; SE = 0.59; $n = 9$) and adult males (SL, 6.64 cm; SE = 0.19; $n = 30$) were not similar (*t*-test: df = 37; $t = -4.48$; $P < 0.001$). The mean mass values for adult females (5.93 g; SE = 0.36; $n = 9$) and adult males (3.18 g; SE = 0.21; $n = 30$) continued to be dissimilar (*t*-test: df = 37; $t = -6.30$; $P < 0.001$) in July.

Dietary data for adult inland silversides were obtained from Chizinski et al. (2007). The adult females' dietary composition was dominated by Copepoda in every month sampled except July. In

July, the predominate prey in the adult female inland silversides was Cladocera (75% by mass). In contrast, the dietary composition of the adult male inland silversides was predominately Cladocera during May, June, and July and Copepoda during August and September. The median stomach fullness of the female inland silversides ranged between 31% and 58% of stomach capacity between May and July; male inland silverside fullness was less, ranging between 6% and 25%.

Prespawning inland silversides.—Weekly water temperatures decreased from July (28°C) to October 2003 (22°C) in Buster Long Lake. Prespawning inland silversides caught in seines during July (Chizinski et al., in press) had a mean length of 3.29 cm (SL, SE = 0.07, $n = 86$) and a mean mass of 0.39 g (wet mass, SE = 0.02, $n = 86$). In October, prespawning inland silversides had a mean length of 5.62 cm (SL, SE = 0.12, $n = 75$) and a mean mass of 1.73 g (wet mass, SE = 0.10, $n = 75$).

Dietary data for prespawning inland silversides were obtained from Chizinski et al. (2007). The dietary composition of prespawning inland silversides was dominated by Copepoda every month sampled from July to October. The diet primarily consisted of small Copepoda species (e.g., *Chyodorus* spp.) that gradually increased with the size of the fish. Median stomach fullness ranged between 31 and 66% of stomach capacity for prespawning inland silversides between July and October.

Model Comparisons

Based on the field data, the generated mass was similar to that of the observed inland silverside mass. Bioenergetics estimates of growth were 0.8415 g (95% confidence interval = 0.8344–0.8484 g) in August, 1.3352 g (1.3248–1.3456 g) in September, and 1.6392 g (1.6212–1.6446 g) in October. Observed inland silversides were 0.7357 g (0.6187–0.8528 g) in August, 1.2031 g (1.004–1.4021 g) in September, and 1.728 g (1.5272–1.9287 g) in October.

According to our simulations, female inland silversides must feed at a mean $P_{C\max}$ of 0.90 or more to achieve the mean mass of 4.16 g, whereas male inland silversides require a mean $P_{C\max}$ of 0.60 to achieve the mean mass of 3.15 g (Figure 3).

Discussion

The ability of our inland silverside bioenergetics model to predict growth was corroborated by our 50-d laboratory validation trial and field observations of prespawning inland silversides from July to October. In both instances, the models adequately predicted growth by estimating inland silverside mass within 1 standard

error. Although the model provided meaningful predictions, we did see a slight divergence between observed and predicted values. Early in the laboratory validation trial, the model tended to predict mass at the lower end of the range of the observed values, whereas later in the trial the model tended to predict mass at the upper end of the range. The opposite trend was evident in the field observations of inland silversides in Buster Long Lake. The model tended to overpredict mean mass in August and September and underpredict mean mass in October. The model behavior may be a compilation of errors introduced through the borrowing of several parameters from other species (i.e., mosquitofish and Atlantic silverside). Further effort will be needed to obtain species-specific estimates of parameters for improved fit of modeled growth. Additionally, monthly means of temperature, stomach capacity, and prey composition were used in the simulation, which reduced day-to-day variation. Using daily estimates also may have improved the fit-to-model observed values.

Chizinski et al. (2007) described temporal intraspecific resource partitioning by immature and adult male and female inland silversides. Male, female, and immature inland silversides partitioned the available plankton prey through changes in prey selection and through a dramatic decrease in male stomach fullness during the period when male and female energy demands were large, thus reducing potential competition between the two sexes. Resource partitioning corresponded to the two growth periods of the inland silverside. Our inland silverside bioenergetics model accurately predicted the growth of prespawning inland silversides during this first period of rapid growth. The simulations also predicted the proportion of maximum consumption necessary to achieve the observed adult masses during the second growth period. The simulated values needed to reach the observed masses of adult male and female inland silversides (Figure 3) are well above published values of P_{Cmax}, which typically range from 25% to 52% (Kitchell et al. 1977; Beauchamp et al. 1989; Chipps and Wahl 2004). Additionally, these values are well above the percent stomach fullness observed for this species in the wild (Chizinski et al. 2007) and present a very unlikely scenario.

Although the model accurately predicted growth of the prespawning inland silversides, it failed to predict the growth of actively spawning adults. Model simulations provided initial evidence that the disparity in growth predictions cannot be driven solely by differences in feeding and diet and suggest that a single model cannot predict the lifetime growth patterns in the inland silverside. An appropriate solution would be the fitting of two models (prespawning and actively
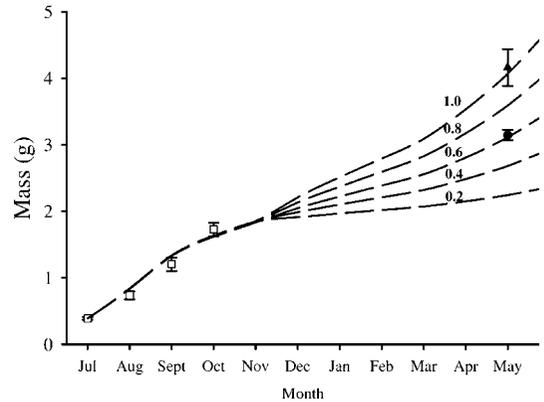

FIGURE 3.—Stochastic simulations with the inland silverside bioenergetics model in Buster Long Lake, Texas, using monthly mean water temperatures and dietary composition. The dietary composition and stomach fullness for inland silversides for July through November were obtained from Chizinski et al. (in press). The growth estimates for inland silversides for November to May were simulated at P_{Cmax} (proportion of maximum consumption) values ranging from 0.2 to 1.0. The specification of the model is described in the text. The squares represent the mean $\pm$ SE prespawning inland silverside wet mass (g); the circle represents the mean $\pm$ SE male inland silverside mass; and the triangle represents the mean $\pm$ SE female inland silverside mass.

spawning) incorporating the physiological differences between the two phases. In theoretical investigations of the von Bertalanffy (VB) growth model, several authors have suggested that a single model is not appropriate for modeling lifetime growth (Day and Taylor 1997; Czarnoleski and Kozlowski 1998; Lester et al. 2004). Day and Taylor (1997) argued that a two-equation growth model is necessary to fully account for the allocation of surplus energy into somatic growth in immature fish and for the allocation of a portion of the surplus energy to reproduction in adults. In contrast to our findings, Lester et al. (2004) found that the VB growth equation accurately predicted the somatic growth of adult fish but failed to predict the growth of immature individuals. Lester et al. (2004) also suggested that the VB equation predicts growth in teleosts because most length-at-age data are dominated by postmaturation individuals. We believe that something similar may be occurring within the bioenergetics modeling literature. Most models have been developed on longer-lived species and, therefore, model predictions of long-term growth are fairly accurate because the length of time in simulations is dominated by the postmaturation phase. In fish species such as the inland silverside, the period of active spawning is much shorter than the period of prespawning. Thus, because

so much energy is devoted to reproduction postmaturity, a separate bioenergetics model is probably needed to account for the physiological changes that occur postmaturation.

Bioenergetics models have been developed for numerous species and have aided biologists in modeling energy allocation in fishes. In many instances, these models accurately predict growth, consumption, and metabolism given known food supplies and water temperature. These linear models predict that the total energy available for individual investment in somatic growth and reproduction equals the total amount of food consumed minus the energetic losses from metabolism and waste. Many bioenergetics models allocate most energy into somatic growth, whereas few bioenergetics models (e.g., Chipps and Wahl 2004; Bevelhimer 2002) have incorporated a modeling component to predict the investment of energy into reproduction. The bioenergetics models that include reproductive investment forecast energetics investment using the gonadosomatic index (GSI) as a proxy. However, as used in bioenergetics models, GSI fails to incorporate many of the temporal aspects of reproduction (i.e., the buildup of reproductive investment before spawning) that are associated with single and multiple spawners. This proxy also fails to include many of the behaviors (e.g., nest building and reproductive displays) associated with reproduction that could also affect growth predictions from the models (Hinch and Collins 1991). The most prevalent problem in assessing energetic allocation patterns in reproduction using a bioenergetics framework is the absence of direct measurements of reproductive expenditure. Without a direct measure, parameterization and inclusion into the modeling framework are difficult. Furthermore, many bioenergetics models have been developed on longer-lived (lifespan, >2 years) species with moderate reproductive investment and, thus, biases from reproduction may be negligible. In organisms with a concentrated life history, we would expect to see larger biases in bioenergetics simulations of lifetime growth. The results presented in this study identify a need for a two-phase bioenergetics model for predictions of lifetime growth in short-lived species. Although a postspawning model may be needed to predict lifetime growth, our model accurately predicts growth of prespawning inland silversides.

Acknowledgments

References

Beauchamp, D. A., D. J. Stewart, and G. L. Thomas. 1989. Corroboration of a bioenergetics model for sockeye salmon. Transactions of the American Fisheries Society 118:597–607.

Bevelhimer, M. S. 2002. A bioenergetics model for white sturgeon *Acipenser transmontanus*: assessing differences in growth and reproduction among Snake River reaches. Journal of Applied Ichthyology 18:550–556.

Chipps, S. R., and D. H. Wahl. 2004. Development and evaluation of a western mosquitofish bioenergetics model. Transactions of the American Fisheries Society 133:1150–1162.

Chizinski, C. J., C. G. Huber, M. Longoria, and K. L. Pope. 2007. Intraspecific resource partitioning by an opportunistic strategist, inland silverside *Menidia beryllina*. Journal of Applied Ichthyology 23:147–151.

Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalents for investigations into ecological energetics. Internationale Vereinigung für Theoretische und Angewandte Limnologíe Verhandlungen 18:1–158.

Czarnoleski, M., and J. Kozlowski. 1998. Do Bertalanffy's growth curves result from optimal resource allocation? Ecology Letters 1:5–7.

Day, T., and P. D. Taylor. 1997. Von Bertalanffy's growth equation should not be used to model age and size at maturity. American Naturalist 149:381–393.

Elliot, J. M., and W. Davidson. 1975. Energy equivalents of oxygen consumption in animal energetics. Oecologia (Berlin) 19:195–201.

Fox, J. 1997. Applied regression, linear models, and related methods. Sage Publications, Thousand Oaks, California.

Haney, J. F., and D. J. Hall. 1973. Sugar-coated *Daphnia*: a preservation technique for Cladocera. Limnology and Oceanography 18:331–333.

Hartman, K. J., and S. B. Brandt. 1995. Estimating prey energy density of fish. Transactions of the American Fisheries Society 124:347–355.

Hinch, S. G., and N. C. Collins. 1991. Importance of diurnal and nocturnal nest defense in the energy budget of male smallmouth bass: insights from direct video observations. Transactions of the American Fisheries Society 120:657–663.

Huber, M., and D. A. Bengtson. 1999. Interspecific differences in growth and reproductive tissues during the breeding season in *Menidia menidia* and *M. beryllina*. Journal of Fish Biology 55:274–287.

Kitchell, J. F., D. J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). Canadian Journal of Fisheries and Aquatic Sciences 34:1922–1935.

Lester, N. P., B. J. Shuter, and P. A. Abrams. 2004. Interpreting the von Bertalanffy model of somatic growth

in fishes: the cost of reproduction. Proceedings of the Royal Society of London B 271:1625–1631.

McCauley, E. 1984. The estimation of the abundance and biomass of zooplankton in samples. Pages 228–265 *in* J. A. Downing and F. H. Rigler, editors. A manual on methods for the assessment of secondary productivity in freshwaters, 2nd edition. Blackwell Scientific Publications, Boston.

Munch, S. B., and D. O. Conover. 2002. Accounting for local physiological adaptation in bioenergetics models: testing hypotheses for growth rate evolution by virtual transplant experiments. Canadian Journal of Fisheries and Aquatic Sciences 59:393–403.

Peck, M. A., R. S. Katersky, L. M. Menard, and D. A. Bengtson. 2003. The effect of body size on food consumption, absorption efficiency, respiration, and ammonia excretion by the inland silverside, *Menidia beryllina* (Cope) (Osteichthyes: Atherinidae). Journal of Applied Ichthyology 19:195–201.

Slatkin, M. 1984. Ecological causes of sexual dimorphism. Evolution 38:622–630.

Winemiller, K. O., and K. A. Rose. 1992. Patterns of life history diversification in North American fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences 49:2196–2218.