

VARIABLE INTAKE, COMPENSATORY GROWTH, AND INCREASED GROWTH EFFICIENCY IN FISH: MODELS AND MECHANISMS

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Abstract. Resources fluctuate in space and time, and animals routinely experience temporally varying opportunities for resource intake, and variation in intake itself. We investigate consequences of such variation in intake on growth and growth efficiency (growth per unit intake) in juvenile hybrid striped bass. We observed, after statistically accounting for the effects of total consumption and initial body size, that individuals receiving a low ration followed by a higher ration (the fluctuating ration) grew faster than individuals receiving a temporally constant ration (the normal ration). To interpret this increase in growth efficiency, we consider a set of alternative models representing different physiological hypotheses of the growth process. Using a simple growth model, an analytical result shows that the fluctuating ration as typically applied in experiments (a low ration followed by a high ration), independent of any change in physiology, increases growth efficiency relative to individuals on the normal ration. Growth efficiency increases because cumulative maintenance costs are lower for individuals that stay small initially and then grow rapidly in comparison to individuals that grow steadily. Further, a statistical analysis of alternative models inferred that fish receiving a variable ration show higher assimilation and/or conversion efficiencies of food and lower mass-specific maintenance costs. Our analysis suggests that the lower cumulative maintenance costs incurred over a time interval with low consumption followed by high consumption act in association with higher assimilation-conversion efficiencies, and lower overall mass-specific maintenance costs to increase growth efficiency in hybrid striped bass.

Key words: *bioenergetics; compensatory growth; energy budget model; experiment; hybrid striped bass.*

INTRODUCTION

Individuals in natural populations face the challenge of obtaining and using resources that may fluctuate considerably in space and time, and understanding how individuals locate and exploit such resources is a basic issue in behavioral and evolutionary ecology. A related area, of interest in ecophysiology and life history evolution, explores the consequences of temporal variation in consumption that arises from such spatial and temporal variation in resource availability. In this paper, we address the effects of variable food intake on growth and growth efficiency in a juvenile fish.

In many experiments, food intake has been manipulated to fluctuate in time, and the subsequent growth responses of animals have been documented. A standard manipulation is to designate as the control group a set of individuals receiving ad libitum rations during the entire course of the experimental trial, and regard as the treatment group a second set of individuals receiving a restricted ration during the first segment of the trial followed by an ad libitum ration during the

second segment of the trial. In many of these experiments, the treatment group attains, by the end of the experimental trial, the same, or nearly the same, body size as the control group. The treatment group approaches or achieves the same body size, despite often large periods of restricted feeding, by growing at an increased rate relative to control individuals during the ad libitum feeding segment, and these periods of accelerated growth have been termed “compensatory growth” (Wilson and Osbourn 1960, Jobling and Johansen 1999, Hornick et al. 2000, Ali et al. 2003). Compensatory growth has been observed in numerous studies with birds and mammals (Wilson and Osbourn 1960, Hornick et al. 2000), as well as fish (Ali et al. 2003). Compensatory growth that leads to the same body size as controls can be termed “catch-up” growth, and “overcompensation” refers to compensatory growth that results in a larger body size than control individuals.

While the existence per se of the phenomenon of compensatory growth is important to animal production, the study of the evolutionary and physiological mechanisms underlying compensatory growth has also received attention (Wilson and Osbourn 1960, Sibby and Calow 1986, Jobling and Johansen 1999, Hornick et al. 2000, Ali et al. 2003). In particular, previous

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research has shown that fishes fed ad libitum after a period of restricted feeding exhibit an increase in consumption, and that this hyperphagic response contributes to compensatory growth. However, it is less clear whether individuals receiving a variable ration are more efficient physiologically (i.e., grow faster per unit body size per unit intake) relative to control individuals over the entire course of a feeding cycle. In fishes, for example, increases in growth efficiency during portions of the feeding cycle have been observed in two species (Russell and Wootton 1992, Zhu et al. 2001, 2003), while such results in other species have been absent, or ambiguous (Miglav and Jobling 1989a, b, Hayward et al. 1997, Gaylord and Gatlin 2001, Gaylord et al. 2001, Xie et al. 2001, Nikki et al. 2004). Empirical studies that identify the physiological mechanisms that may underlie any changes in growth efficiency are lacking.

Previous studies have modeled the process of compensatory growth, emphasizing mammals (Kyriazakis and Emmans 1992) and fish (Broekhuizen et al. 1994, Whitledge et al. 1998, Jones et al. 2002, Gurney et al. 2003). This previous theoretical work (Broekhuizen et al. 1994, Whitledge et al. 1998, Jones et al. 2002, Gurney et al. 2003) has focused on modeling consumption (e.g., the phenomenon of hyperphagia) and/or resource allocation as a function of energetic state. Missing from these earlier modeling studies is a statistical assessment, using experimental data, of alternative models representing alternative biological hypotheses of the physiological processes that drive growth metabolism in response to variable feeding schedules. Specifically, modeling approaches have not yet been applied in concert with experimental data to address how feeding regime affects growth efficiency via changes in physiology, an area of research that is of interest in both animal production and evolutionary ecology (Wilson and Osbourn 1960, Jobling and Johansen 1999, Hornick et al. 2000, Ali et al. 2003).

In the present study, we propose, *a priori*, a set of alternative models representing biological hypotheses concerning growth metabolism, and assess these models using experimental data (Akaike 1974, Schwarz 1978, Hilborn and Mangel 1997, Burnham and Anderson 2002). Thus, we extend previous work on growth energetics in two principal directions. First, by accounting for total *per capita* food consumption over the course of the experiment and initial body size as statistical covariates, we test whether individuals experiencing fluctuating food availability that varies from low to high grow more efficiently over the entire experimental period than individuals experiencing constant food availability. Second, by mathematical analysis and statistically fitting alternative growth models to our experimental data, we ask whether the growth responses exhibited by hybrid striped bass in our experiment can be attributed to the variable feeding schedule without changes in physiology, changes in

assimilation-conversion efficiency, alterations in maintenance costs, or some combination thereof. Our results offer new insights into the mechanisms associated with compensatory growth, and how organisms may respond physiologically to fluctuating resource availabilities.

METHODS

Experimental study

We conducted a 120-d feeding and growth experiment with 16 juvenile hybrid striped bass (female white bass, *Morone chrysops*, crossed with male striped bass, *Morone saxatilis*; see Plate 1). The fish were housed individually in 130-L tanks within a freshwater culture system equipped with biological and ultraviolet filtration. Water temperature was maintained at $25.43^{\circ} \pm 0.55^{\circ}\text{C}$ (mean \pm SD), and the photoperiod was 12 h light : 12 h dark. Fish were acclimated to the individual-tank system with daily ad libitum feeding for two weeks using a floating, pelleted fish food (Zeigler Silver floating 5 mm pellets, #316540-36-44, Zeigler Bros. Inc., Gardners, Pennsylvania, USA). After acclimation, eight fish were randomly assigned to one of two groups. Total lengths (95.69 ± 5.76 mm) and wet masses (9.32 ± 1.54 g) were measured with individuals sedated in a buffered solution of quinaldine sulfate.

Individuals in one group received the normal ration and were fed ad libitum on a daily basis over the course of the experiment, excluding periods when body size measurements were taken. The ad libitum feeding proceeded by providing an individual fish one pellet at a time until feeding ceased for 2 min, and then recording the number of pellets consumed. Individuals in the second group received a fluctuating ration over the duration of the experiment. During the time intervals 1–27 d and 56–83 d, the “maintenance periods” (approximately the first and third months of the four-month experiment), individuals in the fluctuating-ration group received a maintenance diet consisting of one ad libitum feeding per week. During the time intervals 28–55 d and 84–120 d, the ad libitum periods (approximately the second and fourth months of the experiment), individuals in the fluctuating-ration group received a daily ad libitum feeding, identical to individuals in the normal ration group. Measurements of total length and wet mass were taken on days 0, 27, 55, 83, and 120, and fish from both groups were not fed during the 36 hours preceding measurements. At the end of the experiment, five fish drawn randomly from each treatment group were assayed, by a certified commercial laboratory, for body composition in terms of percent lipid, percent protein (Kjeldahl), and percent water, and a multivariate general linear model was used to test for the effect of treatment on body composition using total length on day 120 as a covariate.

Assessment of growth efficiency

We tested whether fish receiving the fluctuating ration grew faster over the course of the 120-d experiment



PLATE 1. Hybrid striped bass (female *Morone chrysops* crossed with male *Morone saxatilis*). Photo credit: M. E. Picha.

than fish of the same initial body size that consumed an equal amount of food under the normal ration. To make use of both of our body size measurements, we fit a statistical model to both wet mass and total length data simultaneously. Specifically, we assume that our measurement of wet mass on day 120, $S^\circ(120)$, is described by a normal distribution with mean

$$\mu_s = \beta_s S^\circ(0) + \beta_c C^\circ(120) \quad (1)$$

and variance σ_s^2 , where $S^\circ(0)$ is observed wet mass on day 0 (the superscript $^\circ$ denotes empirically observed quantities, which must be distinguished from model solutions discussed in the next section), $C^\circ(120)$ is observed total consumption after 120 days, β_s is a parameter that models the effect of initial wet mass on growth, and β_c is a parameter that models the effect of total consumption on growth. The parameter β_s can be interpreted as a mass-specific maintenance cost over a finite time interval (units: mass lost per initial body mass), and the parameter β_c can be interpreted as a growth efficiency over a given time interval (units: mass gained per mass consumed). Eq. 1 is the mean response in an ANCOVA model having dependent variable $S^\circ(120)$, covariates $S^\circ(0)$ and $C^\circ(120)$, and zero intercept. We assume that total length on day 120, $L^\circ(120)$, is related to wet mass via a power law of the form $L = aS^b$. Accordingly, $L^\circ(120)$ is assumed to have a lognormal distribution with parameters

$$\begin{aligned} \mu_L &= \ln(a) + b \ln[\mu_s] \\ &= \ln(a) + b \ln[\beta_s S^\circ(0) + \beta_c C^\circ(120)] \end{aligned} \quad (2)$$

and σ_L^2 , where a and b are parameters for the power

law relating length to mass, and \ln denotes the natural logarithm. Eq. 2 is the mean response in an ANCOVA-type model obtained for natural log-transformed length data having dependent variable $\ln[L^\circ(120)]$, intercept $\ln(a)$ and covariates $S^\circ(0)$ and $C^\circ(120)$ acting through the function $b \ln[\beta_s S^\circ(0) + \beta_c C^\circ(120)]$. Under this model, the mean of $\ln[L^\circ(120)]$ is

$$\begin{aligned} E\{\ln[L^\circ(120)]\} &= \ln(a) + b \ln\{E[S^\circ(120)]\} \\ &\approx \ln(a) + bE\{\ln[S^\circ(120)]\} \end{aligned} \quad (3)$$

where E denotes the operation of calculating a mean assuming very large sample size (i.e., E denotes expectation, Casella and Berger 1990). We note that the last term in Eq. 3 can be obtained using a Taylor series approximation for computing the expectation $E\{\ln[S^\circ(120)]\}$, and our numerical calculations for our particular data set suggest that this is a reasonable approximation. Hence, this model for length produces essentially the same mean value for $\ln[\text{length}]$ as the standard power law model that regresses $\ln[\text{length}]$ on $\ln[\text{mass}]$. Accordingly, we construct a bivariate distribution for mass and length on day 120 by taking the product of the normal density for $S^\circ(120)$, and the lognormal density for $L^\circ(120)$, essentially fitting two ANCOVAs with shared parameters (β_s and β_c) simultaneously. The likelihood for a pair of body size observations from a single fish, $[S^\circ(120), L^\circ(120)]$, is then

$$\frac{\exp\left\{-\frac{[S^\circ(120) - \mu_s]^2}{2\sigma_s^2}\right\}}{\sqrt{2\pi\sigma_s^2}} \cdot \frac{\exp\left\{-\frac{[\ln[L^\circ(120)] - \mu_L]^2}{2\sigma_L^2}\right\}}{L^\circ(120)\sqrt{2\pi\sigma_L^2}}$$

and the overall likelihood is the product of these terms taken over all 16 individuals (2 treatments \times 8 individuals = 16). This approach allows for both length and mass to be interpreted simultaneously in terms of the parameters of interest, β_S , β_C , a , and b , and the effects of the experimental treatments on these parameters.

We use the bivariate model just described to test two main hypotheses. First, we assess treatment effects on the growth responses to the covariates initial body size and total consumption by testing for treatment effects on the parameters β_S and β_C (i.e., we test for heterogeneity of slopes across treatments). Second, we ask if mass and length respond differently to the treatments by testing whether the power law parameters a and b depend on treatment. For example, fluctuating-ration fish may add length at the expense of mass, and hence appear thin relative to normal-ration fish, or vice versa. We assess these hypotheses statistically by fitting the bivariate model to our length and mass data using maximum likelihood. We employ a standard backward elimination scheme, as in PROC REG in SAS (SAS 2001), to identify the significant independent variables in our model, allowing the parameters β_S , β_C , a , and b to depend on treatment. We computed test statistics using likelihood ratios, and assess these test statistics using Chi-squared distributions (Casella and Berger 1990).

Assessment of alternative growth models

The bivariate model described above allows a summary analysis of growth over the 120-d duration of the experiment; it does not explore the additional information available from our measurements of body size and daily per capita consumption measurements. Accordingly, we analyzed and fit a set of simple growth models to our measurements of wet mass, taking into account our daily measurements of per capita consumption.

We model the physiological change of a single state variable, wet mass (e.g., Kitchell et al. 1977, Rice et al. 1983, Kyriazakis and Emmans 1997, Whitley et al. 1998, West et al. 2001, Skalski and Gilliam 2002, Ricklefs 2003). The change in total wet mass, $S(t)$, can be written as a static mass budget model (cf. dynamic energy budget models, Kooijman 2000):

$$\frac{dS}{dt} = kI(t) - \omega S(t) \quad (4)$$

where the k is the assimilation-conversion efficiency, $I(t)$ is consumption (assumed to be a known function of time, either from empirical data, or a model of the consumption process) and ω is a mass-specific maintenance rate. The parameter k is an instantaneous measure of growth efficiency (analogous to the finite rate β_C , units: mass gained per mass consumed) and ω is an instantaneous mass-specific metabolic rate of a fasting animal (analogous to the finite rate β_S , units: mass

lost per body mass per time). We refer to Eq. 4 as Model 0, our null mass budget model.

We developed several simple extensions of our null model, Eq. 4, with each extension representing a physiological hypothesis, and assessed via statistical model fitting the ability of each model to predict fish growth in our feeding experiment. A fundamental issue in studies of compensatory growth is whether physiological changes, beyond hyperphagia, underlie the compensatory response. Model 1, a four-parameter model, represents a form of this hypothesis by assuming that the normal and fluctuating-ration groups have different physiologies by extending Model 0 to have physiological parameters k and ω specific to each treatment group. The parameters are $(k, \omega) = (k_n, \omega_n)$ for fish receiving the normal ration and $(k, \omega) = (k_f, \omega_f)$ for fish receiving the fluctuating ration. A further elaboration on this idea, Model 2, posits that the physiology of the fish receiving the fluctuating ration not only differs from the normal ration group, but also depends on whether the current feeding schedule is the ad libitum period (one ad libitum feeding per day) or the maintenance period (one ad libitum feeding per week). Accordingly, Model 2 assumes that $(k, \omega) = (k_n, \omega_n)$ for fish receiving the normal ration, $(k, \omega) = (k_m, \omega_m)$ for fish in the maintenance period under the fluctuating ration regime (the subscript 1 symbolizes low feeding), and $(k, \omega) = (k_h, \omega_h)$ for fish in the ad libitum period under the fluctuating ration regime (the subscript h symbolizes high feeding).

Models 0, 1, and 2 are isometric in the sense that the parameter ω does not depend on body size, and therefore does not change as an individual grows. In this regard, Models 0, 1, and 2 represent a departure from many existing mass budget models that often represent this kind of physiological parameter as an allometric, or nonlinear, function of body size, usually by means of a power function (e.g., Kitchell et al. 1977, Rice et al. 1983, Kyriazakis and Emmans 1992, Broekhuizen et al. 1994, Jones et al. 2002). Accordingly, we consider allometric versions of Models 0, 1, and 2, where the parameter ω is allowed to vary as a power function of body size. Model 0A is an allometric version of Model 0 with $(k, \omega(S)) = (k, \omega_0 S^{\omega_1})$, yielding three parameters (k, ω_0, ω_1) . Model 1A is an allometric version of Model 1 with $(k_n, \omega_n(S)) = (k_n, \omega_{n0} S^{\omega_{n1}})$ and $(k_f, \omega_f(S)) = (k_f, \omega_{f0} S^{\omega_{f1}})$, yielding six parameters $(k_n, \omega_{n0}, \omega_{n1}, k_f, \omega_{f0}, \omega_{f1})$. Model 2A is an allometric version of Model 2 with $(k_n, \omega_n(S)) = (k_n, \omega_{n0} S^{\omega_{n1}})$, $(k_{f1}, \omega_{f1}(S)) = (k_{f1}, \omega_{f10} S^{\omega_{f11}})$, and $(k_{fh}, \omega_{fh}(S)) = (k_{fh}, \omega_{fh0} S^{\omega_{fh1}})$, yielding nine parameters $(k_n, \omega_{n0}, \omega_{n1}, k_{f1}, \omega_{f10}, \omega_{f11}, k_{fh}, \omega_{fh0}, \omega_{fh1})$. Consumption is often not measured in growth studies, and is frequently modeled as an allometric function of body size (e.g., Kitchell et al. 1977, Rice et al. 1983, Kyriazakis and Emmans 1992, Broekhuizen et al. 1994, Jones et al. 2002, Gurney et al. 2003). However, consumption, obviously, is a strong predictor of growth, but varies considerably among individuals

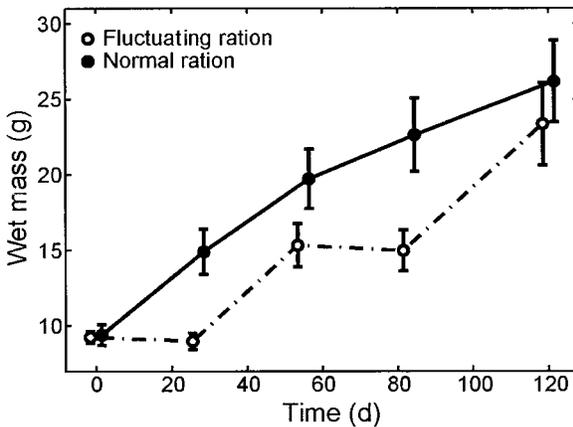


FIG. 1. Wet mass (mean \pm SE) of juvenile hybrid striped bass receiving normal and fluctuating rations during a 120-d feeding and growth experiment.

(e.g., Miglavs and Jobling 1989a, Russell and Wootton 1992, Whitley et al. 1998, Nikki et al. 2004). Because our focus is on growth efficiency based on empirically measured consumption, and we have daily measures of consumption, we treat consumption as a covariate (i.e., a known input into the model) rather than attempt to predict it as a dependent variable, as has been done in studies that lack detailed consumption data (e.g., Kitchell et al. 1977, Rice et al. 1983, Broekhuizen et al. 1994, Jones et al. 2002, Gurney et al. 2003).

Given this set of models and their underlying hypotheses, we fit model predictions of growth to our experimental data. We have five observations of wet mass for each individual fish, $S^o(0)$, $S^o(27)$, $S^o(55)$, $S^o(83)$, and $S^o(120)$, providing four time intervals during which growth can be modeled and predicted, yielding 64 observations (including repeated measures of individuals) of changes in body size (eight replicate fish \times two treatments \times four time intervals). We predicted the final body size for each interval using the observed initial body size for that interval as the initial condition in the differential equations. A model solution of this form can be represented as $S(t_{i+1}, S^o(t_i))$, where t_{i+1} is the time at the end point of the i th interval, t_i is the time at the beginning point of the i th interval, and $S^o(t_i)$ is the observed body size at the beginning point of the i th interval. The isometric models (Models 0, 1, and 2) are linear and can be solved analytically. However, the allometric models are nonlinear and must be solved numerically. We approximated solutions to the differential equations for all models using Euler's method with a fixed time step of one day (Kincaid and Cheney 1996). We fit the models by maximum likelihood, representing $S^o(t_{i+1})$ as having a normal distribution with mean $S(t_{i+1}, S^o(t_i))$ and constant variance. Hence, the likelihood for the wet mass data from one fish over the four time intervals is the following:

$$\prod_{i=1}^4 \frac{\exp\left\{-\frac{[S^o(t_{i+1}) - S(t_{i+1}, S^o(t_i))]^2}{2\sigma^2}\right\}}{\sqrt{2\pi\sigma^2}}$$

where σ^2 is the variance and the overall likelihood is the product of the individual likelihoods taken over all 16 individuals. This statistical approach models the times series of wet mass observations for each individual using a process error model where observations at time t_{i+1} are conditional on observations at time t_i (see Hilborn and Mangel 1997).

We used the model selection criterion of Schwarz (1978), the Bayesian Information Criterion (BIC), to make our statistical inferences by computing BIC differences (Burnham and Anderson 2002). Smaller values of the BIC for a particular model i relative to the BIC value for an alternative model j lead to the inference that model i provides a better description of the data than model j . The BIC takes both goodness-of-fit (via the likelihood) and model parsimony (via number of parameters) into account, decreasing as the likelihood increases, and increasing as the number of model parameters increases.

RESULTS

Assessment of growth efficiency

The hybrid striped bass demonstrated what could be considered, in the context of compensatory growth studies in fish, the canonical growth response. Individuals receiving the normal ration grew at a rate that decreased over time, whereas individuals receiving the fluctuating ration illustrated a step-like response that was associated with their variable feeding schedule (Fig. 1). The average body sizes, measured as mean wet mass, did not differ between the treatment groups at the beginning ($t = 0.19$, $df = 15$, $P = 0.85$) and end ($t = 0.73$, $df = 15$, $P = 0.47$) of the experiment according to a t test. No difference was detected in the final body composition of the fish between the two treatments (Wilks' $\Lambda = 0.80$, $P = 0.89$). Evaluated at the mean of the covariate (total length = 137 mm), body composition (mean \pm SE) for fish receiving the normal ration was $16.43 \pm 0.55\%$ protein, $4.28 \pm 0.70\%$ fat, and $74.02 \pm 0.44\%$ water, while fish in the fluctuating ration treatment were $17.20 \pm 0.54\%$ protein, $3.54 \pm 0.69\%$ fat, and $74.20 \pm 0.43\%$ water.

Treating initial wet mass and total consumption (i.e., total absolute consumption over the 120-d experiment) as covariates in a bivariate statistical model, the backward model selection procedure selected a model which predicts that fish receiving the fluctuating ration grow faster, on a given total intake, than fish receiving the normal ration. In particular, the parameter β_5 is significantly different from zero ($\chi^2 = 30.28$, $P < 0.001$) but does not differ across treatments ($\chi^2 = 0.17$, $P = 0.682$), while the parameter β_C is different from zero ($\chi^2 = 87.66$, $P < 0.001$) and differs across treatments

($\chi^2 = 10.47$, $P = 0.001$). Accordingly, fish receiving the fluctuating ration showed a stronger response to total consumption than fish receiving the normal ration, and these individuals have, on average, a higher growth efficiency in the sense of more mass gained at any given initial body size and level of total consumption (Fig. 2A, the slopes are growth efficiencies). Thus, the order per se in which food is consumed, holding total quantity fixed, affects growth, with fish fed at low levels followed by high levels growing more than individuals fed at a constant intermediate level.

We found no evidence that the power law relationship relating length to mass depends on treatment by acting on the parameters a ($\chi^2 = 1.62$, $P = 0.203$) and b ($\chi^2 = 0.05$, $P = 0.819$) individually, or jointly ($\chi^2 = 1.75$, $P = 0.417$). Instead, the fish in the two treatment groups gained total length and mass in similar proportions by the end of the 120-d experiment (Fig. 2B).

Analysis and statistical fitting of alternative growth models

The results from the application of the bivariate model indicate that, with “all else equal” (i.e., initial body size, total food consumption), fish receiving the fluctuating ration grow faster, and are thus in some sense more efficient physiologically than fish receiving the normal ration. Without any additional data analysis, we can gain some insight as to how fish might achieve higher growth on a variable ration without any associated change in physiology. We proceed by first considering a hypothetical experiment in which two fish, labeled Fish 1 and Fish 2, both of initial size S_0 grow according to Model 0 (the isometric model in which physiological parameters do not differ across treatments) and consume C grams of food during a period of duration T . Fish 1 consumes a constant quantity each day, so that $I(t) = C/T$, while Fish 2 has variable consumption, not feeding during the first half of the period, followed by high feeding during the second half of the period so that $I(t) = 0$ for $0 \leq t \leq T/2$ and $I(t) = 2C/T$ for $t/2 < t \leq T$. Since k and ω are constants, Model 0 predicts body sizes at time T given by the solutions

$$S(T) = S_0 e^{-\omega T} + \frac{kC}{\omega T} (1 - e^{-\omega T})$$

for Fish 1, and

$$S(T) = S_0 e^{-\omega T} + \frac{2kC}{\omega T} (1 - e^{-\omega T/2})$$

for Fish 2. Growth over a period of duration T is $S(T) - S_0$, and the difference in growth between Fish 2 and Fish 1 (Fish 2 growth minus Fish 1 growth) is:

$$\begin{aligned} & \frac{kC}{\omega T} [2(1 - e^{-\omega T/2}) - (1 - e^{-\omega T})] \\ &= \frac{kC}{\omega T} (e^{-\omega T} - 2e^{-\omega T/2} + 1) \\ &= \frac{kC}{\omega T} (e^{-\omega T/2} - 1)^2 > 0 \end{aligned} \quad (5)$$

(i.e., a positive number), thus showing that the growth of Fish 2 is always greater than the growth of Fish 1 for any $0 < T$. This result shows that a fluctuating consumption regime per se, in the form of a low feeding period followed by a high feeding period, independent of any change in physiology, results in an increase in growth efficiency over a finite time period. The increase in growth occurs because individuals on the variable ration are smaller for most of the period (because they add mass only during the second half of the period), and hence incur lower cumulative maintenance costs over the period (since maintenance costs increase with body size). This analysis provides one mechanism that may underlie increases in growth efficiency such as those observed in our experiments (Fig. 2A). This mechanism seems not to have been considered in previous work.

The difference in growth indicated in Eq. 5 is a unimodal function of the ω and T , reaching its maximum when $\omega T \approx 2.51$ (notice that ω and T always occur via the product ωT). Hence, assuming that the experimental duration T is not very large, the growth difference predicted by Eq. 5 will be an increasing function of ω for most biologically realistic values of ω . For example, in a 60-d experiment, the growth difference increases until the maintenance rate reaches about 4% per day ($\omega T = 0.04 \times 60 \approx 2.5$). The implication is that, all else equal, the effect of a variable ration per se, in the form of a low feeding period followed by a high feeding period, should be larger for species and life stages (e.g., juveniles) with higher mass-specific maintenance costs.

The mechanism just described does not invoke any change in physiology to achieve a change in growth efficiency. We now explore models that include changes in physiological rates. Considering all six alternative models, the best model according to the BIC criterion is Model 2, followed by Model 1 (Table 1). These results support the inference that the fluctuating ration is having an effect on the physiological parameters k (the assimilation-conversion efficiency) and ω (the mass-specific maintenance cost). Model 2 predicts isometric maintenance costs and alterations in physiology associated with the two feeding periods (maintenance and ad libitum) in the fluctuating ration. Specifically, fish receiving the fluctuating ration grew more efficiently in response to increasing consumption during ad libitum periods than during maintenance periods, and grew more efficiently than fish receiving the normal ration (as indicated by the different slopes in Fig. 3A, which are interpretable as growth efficiencies). Further, fish

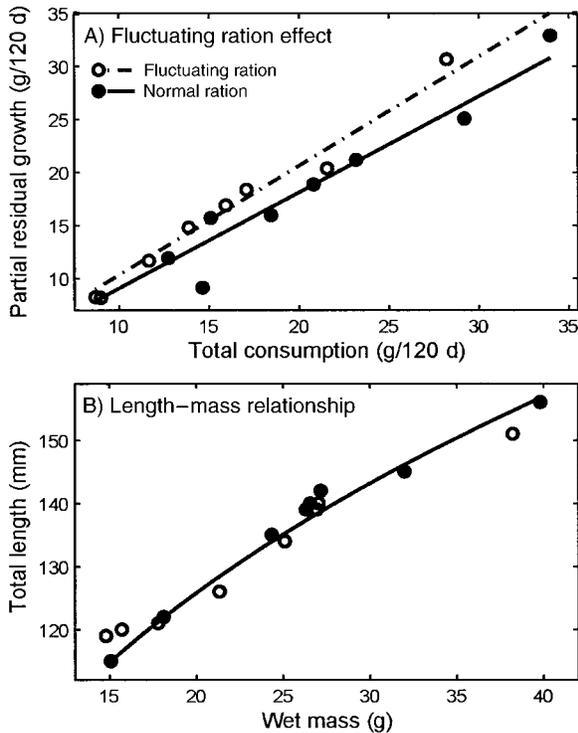


FIG. 2. (A) Partial residual growth of juvenile hybrid striped bass receiving normal (solid circles, solid line) and fluctuating (open circles, dot-dash line) rations as a function of total consumption over the 120-d experiment. The symbols denote partial residual growth for each fish, computed as observed growth minus the predicted linear effect of initial body size. The lines denote predicted partial residual growth. Both regression lines have zero intercept, but they have significantly different values for the slope parameter β_c , indicating that fish receiving the fluctuating ration grew more efficiently than fish receiving the normal ration. (B) The total lengths and wet masses of hybrid striped bass at the end of the 120-d experiment in the form of a length-mass curve. Open circles represent the fluctuating ration; solid circles represent the normal ration. The line denotes the maximum likelihood power law parameterized with estimates of a and b .

receiving the fluctuating ration lost less mass as a function of body size (mass loss that can be attributed to maintenance costs) during ad libitum periods than during maintenance periods, and they also lost less mass than fish receiving the normal ration (as indicated by the different slopes in Fig. 3B, which are interpretable as mass-specific maintenance costs over a finite time interval). The best-fit parameter estimates for Model 2 predict precisely these results (Table 2). In particular, mass-specific maintenance (the ω 's) declines during the ad libitum periods on the fluctuating ration, and increases during maintenance periods, relative to fish on the normal ration, thereby producing the body size effect in Fig. 3B. Assimilation-conversion efficiency (the k 's) increases during the ad libitum periods under the fluctuating ration relative to the normal ration, thereby, in concert with the changes in ω , producing the con-

sumption effect in Fig. 3A. The parameter k in Model 2 is estimated to be small during maintenance periods, but because consumption is low during these periods the small k has a weak effect on overall growth. Models involving allometric maintenance costs generally performed poorly, and, overall, there is little evidence for a nonlinear relationship between growth and body size (Fig. 3B), as would be predicted by an allometric model of maintenance costs. Accordingly, our inference is that maintenance costs are well-described by an isometric model over the range of body sizes that we studied (9–40 g).

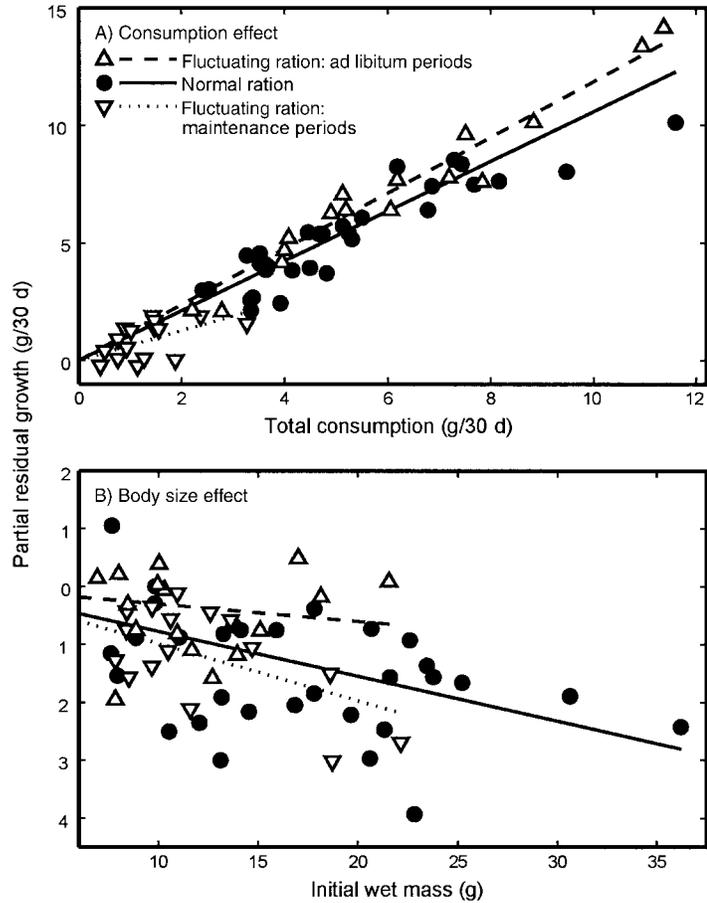
The model selection results and the data in Fig. 3 indicate that growth physiology is altered by feeding regime. However, as just illustrated with Eq. 5, the feeding regime per se also affects growth efficiency over the time scale of the entire experiment even in the absence of any associated change in physiology. We can roughly partition the cause of this increase in growth between these two causative processes as follows. Averaging over all individuals, the mean total consumption over the 120-d experiment was about 18.3 g. At this level of total consumption, the linear model in Fig. 2A predicts a growth increase of about 2.3 g. The effect of the fluctuating ration per se can be calculated using Model 0, which predicts no alteration in physiology, to predict the growth of individuals feeding on the fluctuating and normal rations. Employing average consumption schedules for the two treatments, Model 0 predicts a difference in growth of about 1.3 g, or about one-half of the 2.3-g effect, for individuals with total consumption equal to 18.3 g. The joint effects of the fluctuating ration per se and alterations in physiology can be calculated using Model 2. For individuals with total consumption equal to 18.3 g, Model 2 pre-

TABLE 1. Values of the standardized Bayesian Information Criterion (Δ BIC) for the six alternative mass-budget models describing growth in the feeding experiment with hybrid striped bass.

Model version	No. parameters	Δ BIC	Evidence ratio	Model rank
Isometric models				
0	2	10.97	241	4
1	4	3.56	6	2
2	6	0	1	1
Allometric models				
0A	3	13.39	808	6
1A	6	10.13	158	3
2A	9	11.19	269	5

Notes: The Δ BIC values have been computed by subtracting the BIC value for Model 2, the best-fitting model with the smallest value of the BIC, from the BIC values for each of the six models. The model version column indicates the model fit to the experimental data, the parameters column denotes the number of physiological parameters employed in each model, the evidence ratio for each model relative to Model 2 is calculated following Burnham and Anderson (2002), and the model rank column denotes the rank of the fit of the model by the BIC.

FIG. 3. Comparison of fish growth during maintenance and ad libitum periods on the fluctuating vs. normal ration over four ~1-mo intervals during which growth was measured. Partial residual growth is plotted against total consumption and initial body size; lines denote the best-fit predictions from Model 2. (A) The consumption effect (growth minus the predicted linear effect of body size) shows that the fluctuating ration affects physiology. As in Fig. 2A, for a given level of total consumption, fish on the fluctuating ration during ad libitum periods grew more efficiently in response to intake than fish on the normal ration, but there was no evidence of such increased growth efficiency during maintenance periods. (B) The body size effect (growth minus the predicted linear effect of total consumption) also shows that the fluctuating ration affects physiology. For fish on the fluctuating ration during ad libitum periods, the penalty for larger body size, in terms of mass lost, was ameliorated relative to fish on the normal ration; during maintenance periods, those fish showed no such amelioration. Actual fits of the model to the data are more accurate than those portrayed here because statistical fitting accounts for among-individual variation in daily consumption (two individuals may consume the same total amount of food but have different daily consumption patterns) that cannot be depicted in this two-dimensional graph.



dicts a difference in growth of about 2.8 g, which corresponds approximately to the observed effect of 2.3 g. Hence, the fluctuating ration per se, in the absence of any associated change in physiology, can account for about half of the observed increase in growth, and the joint effects of the fluctuating ration per se and alterations in physiology can account for the entire observed increase in growth.

DISCUSSION

Our study integrates a feeding and growth experiment using hybrid striped bass with model fitting and analysis to explore the mechanisms underlying their growth on a variable feeding schedule that induces compensatory growth. Analysis with a bivariate model indicates that, after statistically accounting for the lin-

TABLE 2. Maximum-likelihood parameter estimates for the isometric growth models, Models 0, 1, and 2, and the allometric growth models, Models 0A, 1A, and 2A.

Model	Normal ration	Fluctuating ration	
		Maintenance periods	Ad libitum periods
Isometric models: (\hat{k} , $\hat{\omega}$)			
0	(1.32, 0.0040)	(1.32, 0.0040)	(1.32, 0.0040)
1	(1.10, 0.0027)	(1.52, 0.0053)	(1.52, 0.0053)
2	(1.10, 0.0027)	(0.67, 0.0035)	(1.20, 0.0010)
Allometric models: (\hat{k} , $\hat{\omega}_0$, $\hat{\omega}_1$)			
0A	(1.33, 0.0086, 0.24)	(1.33, 0.0086, 0.24)	(1.33, 0.0086, 0.24)
1A	(1.11, 0.0036, 0.09)	(1.49, 0.0125, 0.32)	(1.49, 0.0125, 0.32)
2A	(1.11, 0.0036, 0.09)	(0.66, 0.0034, 0.00)	(1.24, 0.0266, 0.98)

Notes: The isometric parameters are k , the assimilation-conversion efficiency; and ω , the mass-specific maintenance rate. The allometric parameters are k , the assimilation-conversion efficiency; ω_0 , the allometric constant for maintenance rate; and ω_1 , the allometric exponent for maintenance rate. In the allometric model, the maintenance cost per unit time for an individual with mass S is $\omega_0 S^{1-\omega_1}$.

ear effects of total consumption and initial body size, individuals receiving a ration that alternates between weekly and daily ad libitum feedings (the fluctuating ration) grow faster than individuals receiving daily ad libitum feedings (the normal ration). Thus, for a given initial body size and total consumption, fish receiving the fluctuating ration grow faster than fish receiving the normal ration, and, in this sense, grow more efficiently. Our model fitting and analysis indicate that the positive effect of the fluctuating ration on growth is attributable to both the effect of the consumption schedule per se on cumulative maintenance costs, and an associated change in physiology characterized by an increase in assimilation-conversion efficiency and decrease in mass-specific maintenance costs during the ad libitum periods.

Measurements of individual consumption rates are needed to estimate growth efficiencies, and, relative to the number of compensatory growth studies published on fish, few studies report such measurements (Ali et al. 2003). Among studies that report growth efficiencies, the results are mixed, with some reporting periods of increased growth efficiencies for fish receiving a variable ration (Russell and Wootton 1992, Zhu et al. 2001, 2003), and others reporting little difference among feeding treatments (Miglav and Jobling 1989a, b, Hayward et al. 1997, Gaylord and Gatlin 2001, Gaylord et al. 2001, Xie et al. 2001, Nikki et al. 2004). Growth efficiencies are typically calculated for a set of specific time intervals corresponding to changes in feeding regime, as in Fig. 3A. However, we are not aware of any study that has reported, for a given initial body size and total consumption, an increase in growth over the entire duration of a study that can be attributed to a variable feeding regime, as in Fig. 2A. Moreover, while there is some evidence in the literature for increased growth efficiencies during some portions of a feeding cycle in fish receiving variable rations, tests among putative mechanisms underlying any increases in growth efficiency have been lacking.

Our mathematical analysis shows that a variable ration per se, without any associated change in physiology, can lead to higher overall growth efficiency through a savings in maintenance costs when a low feeding period is followed by a high feeding period. Fish receiving a variable ration that begins with low food intake and ends with high food intake are smaller during a larger portion of a given time interval than fish receiving the same total amount of food as a constant daily ration. Consequently, fish on the variable ration incur lower cumulative maintenance costs during a given time interval (because maintenance costs are proportional to body size), and, because they eat the same total quantity of food, grow larger. The results of Muller and Nisbet (2000) show that the changes in growth efficiency discussed here can have important population-level implications, and our analytical results and data analysis corroborate and complement

their numerical simulations. Finally, an important prediction that follows from our mathematical analysis is that, all else equal, the effect of a variable ration per se should be larger for species and life stages with higher maintenance costs, an idea that seems not to have been recognized and warrants empirical assessment.

In terms of physiology, our results also imply that the fluctuating ration induces a change in physiology that increases overall growth efficiency. Specifically, assimilation-conversion efficiency (the parameter k) increases during the ad libitum periods of the fluctuating ration, and mass-specific maintenance costs (the parameter ω) decrease during these same periods. Although previous studies have speculated that increases in growth efficiency are driven by reduced maintenance costs (Russell and Wootton 1992, Zhu et al. 2001, 2003), our results attribute increases to both an increase in assimilation-conversion efficiency and a decrease in maintenance costs for fish on a fluctuating ration. Previous studies indicate that respiration rate declines during periods of complete food deprivation (e.g., Wieser et al. 1992, O'Connor et al. 2000, Ali et al. 2003), perhaps indicating lower maintenance costs, the absence of respiration associated with processing food (i.e., specific dynamic action, or cost of growth; Wieser 1994), and/or reduced activity. One study (Wieser et al. 1992) suggests that respiration rates rapidly return to normal levels after re-feeding is initiated. Our observation of higher maintenance costs during maintenance periods of the fluctuating ration differs from these food deprivation studies, but is consistent with the idea of an initial increase in respiration associated with the stress of suddenly lacking a consistent source of food (Wieser et al. 1992, Ali et al. 2003), e.g., increased searching for food. We are not aware of any studies that directly measure (e.g., using labeled feed) assimilation-conversion efficiencies on fish receiving variable rations. Wieser (1994) discusses some evidence in endotherms that metabolic efficiencies increase for animals on a restricted feeding schedule, but noted that such evidence is lacking in ectotherms. Detailed information on the growth and respiration responses of animals to different feeding schedules (Ali et al. 2003), including responses to manipulations of both feed quantity and nutritional composition, is presently lacking and is needed to assess these ideas.

While there are many studies of mass and energy budget models, few have been directed towards the phenomenon of compensatory growth. These models (Broekhuizen et al. 1994, Jones et al. 2002, Gurney et al. 2003) focus on changes in body composition by partitioning the body into two components, reserve weight and structural weight. An interesting comparison between these earlier models and our present results involves the specification of consumption (the term $I(t)$ in Eq. 4). Our theoretical result given in Eq. 5, along with our model fitting and the data in Fig. 2A,

shows that the effect of the fluctuating ration, without any change in physiology, is sufficient to produce higher growth relative to individuals on the normal ration (termed overcompensation) when individuals receiving the fluctuating ration consume the same total quantity of food as individuals receiving the normal ration. On average, individuals receiving the fluctuating ration consumed less than individuals receiving the normal ration, so we did not observe overcompensation at the population-level average, as depicted in Fig. 1. However, several individuals receiving the fluctuating ration consumed more food than individuals receiving the normal ration (Fig. 2A). Because there is substantial phenotypic variance in consumption in our data set and many others (e.g., Miglavs and Jobling 1989a, Russell and Wootton 1992, Whitley et al. 1998, Nikki et al. 2004), we can not rule out the possibility that population genetic forces, including natural and/or artificial selection, genetic drift, and mutation, could act to produce a population that exhibits growth overcompensation due to hyperphagia acting alone. In contrast, the hyperphagic response assumed by Gurney et al. (2003) leads to overcompensation only in the presence of associated changes in resource allocation. However, by our statistical model fitting, we detect changes in physiology that work in association with hyperphagia to further increase growth efficiency for fish on the fluctuating ration. Whether the changes in physiology that we infer are associated with the resource allocation mechanisms portrayed in previous models (Broekhuizen et al. 1994, Jones et al. 2002, Gurney et al. 2003) is unknown and worthy of investigation.

More generally, it remains to be seen whether the mathematical rules underlying hyperphagia and resource allocation employed in models (Broekhuizen et al. 1994, Jones et al. 2002, Gurney et al. 2003) are better descriptions of empirical data than some other alternative hypotheses. An interesting prospect for future work is to test the mathematical forms for hyperphagic response and resource allocation posited in these studies against alternatives derived from life history theory (e.g., Sibly and Calow 1986, Shertzer and Ellner 2002). Indeed, Shertzer and Ellner (2002) show that individuals with allocation strategies that depend on structural and reserve components jointly have higher fitness than individuals with allocation strategies that depend on structural or reserve components either individually, or via their ratio. In comparison, the allocation mechanisms assumed in existing compensatory growth models assume that the allocation strategy depends solely on structural components (Gurney et al. 2003), or on the ratio of structural and reserve components (Broekhuizen et al. 1994, Jones et al. 2002). Further, while many studies often show that temporal variation in environmental conditions has negative impacts on populations (e.g., Muller and Nisbet 2000, Shertzer and Ellner 2002), our results give an example in which fish can grow more efficiently with a variable

food supply. The relevance of these results to growth physiology, life history evolution, ecology and animal production is intriguing, and should be a focus of future work.

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