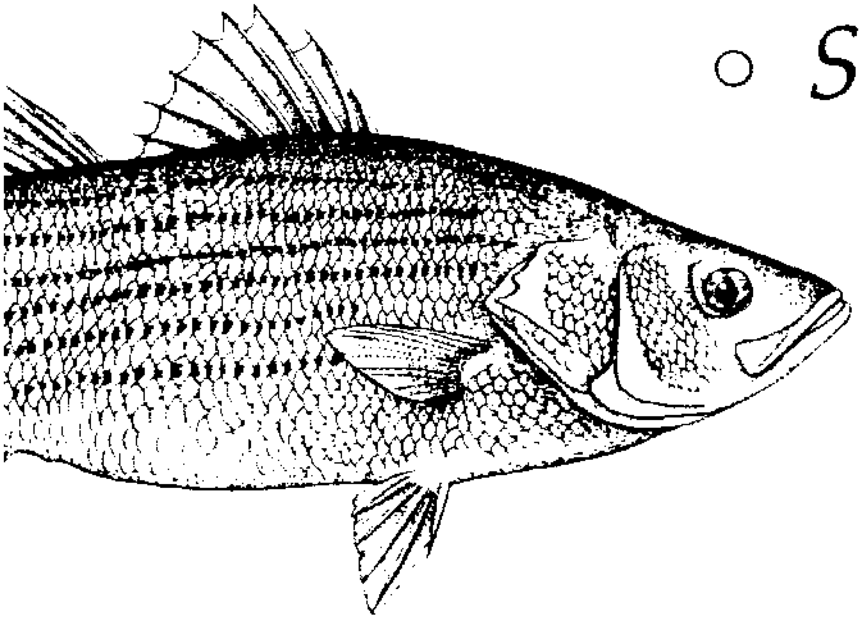
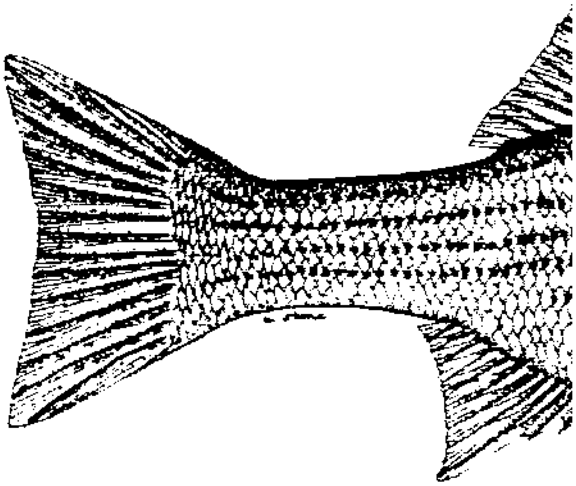
Parameter Valuation of a Bioenergetics Model for Striped Bass





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INTRODUCTION

The striped bass *Morone saxatilis* is a widely distributed sport and commercial fish species. Although native to the Atlantic Coast from Canada to Florida, the anadromous striped bass has been successfully established along the Pacific Coast and in freshwater reservoirs throughout much of the United States (Bain and Bain 1982; Axon and Whitehurst 1985). Striped bass are highly piscivorous, have high growth potential (to 30+ kg) and are relatively long-lived (to 15+ years). This combination of characteristics may cause striped bass to exert a heavy impact on forage-fish populations (Stevens 1969; Morris and Follis 1978; Summerfelt 1986). Quantitative assessment of the adequacy of prey supply to meet the forage demand of striped bass is required to determine stocking rates when establishing or maintaining freshwater populations or to estimate the production potential of self-sustaining populations (Moore 1988; Brandt et al. 1992).

Forage demand is the product of consumption by individual fish multiplied by the number of individuals in the population. Estimation of production potential requires as input the growth rate demonstrated or projected for average individuals in the population. Bioenergetics models are mass-balance energy equations that can be solved to estimate either consumption or growth of individuals and are well suited for addressing questions of forage demand and production potential. In a bioenergetics model, the energy in consumed food (C) is partitioned into its various fates:

$$C = G + R + W \qquad (1)$$

where G is somatic plus gonadal growth, R is total metabolic costs, and W is the energy contained in waste products. Metabolic and waste costs can be divided into subcomponents (Warren 1971). Metabolism consists of energy costs for basic maintenance (standard metabolism), activity, and digestion. Waste products are the total of nonassimilated energy egested as feces and assimilated energy later excreted as urea and ammonia.

Bioenergetics models have been developed for a number of fish species to address both autecological and synecological questions (Kitchell 1983), and a number of reviews have been published (Brett and Groves 1979; Elliot 1979; Cho et al. 1982; Brett 1983; Brafield 1985; Soofiani and Hawkins 1985; Ney 1990). The most frequent use of bioenergetics models in fisheries has been to estimate individual consumption and expand it to the population to determine forage demand. In this context, bioenergetics methodology has been used to quantify the impact of stocked salmonids on the forage base of Lake Michigan (Stewart et al. 1981), the potential demand of largemouth bass populations for gizzard shad in Ohio reservoirs (Carline et al. 1984), and the impact of walleye predation on the prey assemblage of a small Wisconsin lake (Lyons 1984) and Lake Erie (Hartman and Margraf 1992). The bioenergetics equation can be solved for growth rather than consumption to assess the effects of potentially limiting factors, notably temperature and prey availability (Kitchell et al. 1977; Rice et al. 1983; Brandt et al. 1992), or to predict comparative growth trajectories of species which are candidates for introduction (Bevelheimer et al. 1985).

Although a number of studies have been completed on the physiology of striped bass (reviewed by Westin and Rogers 1978; Setzler et al. 1980), no one has derived a complete energetics model for piscivorous sizes of this species. Eldridge et al. (1982) compiled an energy budget for striped bass embryos and larvae based on extensive laboratory research, and Tuncer et al. (1990) determined the energy budget of striped bass juveniles fed in a hatchery. In addition, Connolly and Tonelli (1985) developed a model to estimate the bioaccumulation of Kepone by striped bass in the James River estuary, Virginia. Although the latter model was adequate for their study, it would produce substantial error in other ecological applications, primarily because of inadequate respiration data and a potentially inaccurate value for assimilation efficiency.

We developed values for input parameters to a bioenergetics model for striped bass based on a compilation of data collected in several studies of striped bass metabolism and growth. Energetics information for several ecologically similar species was used to bridge various information gaps. We selected a basic version of the bioenergetics model developed by J. F. Kitchell and colleagues at the University of Wisconsin (Kitchell et al. 1977; Kitchell and Breck 1980; Stewart et al. 1983). Microcomputer software and a users manual have been developed for the Wisconsin bioenergetics model (Hewett and Johnson 1987; 1992) and are available from the University of Wisconsin Sea Grant Institute, Madison.

THE BIOENERGETICS MODEL

Overview

The equation we used to describe the energetics of striped bass is similar to that initially proposed by Ivlev (1939) and popularized by Winberg (1956). It has the general form:

$$C = G + R + SDA + F + U \qquad (2)$$

In this model, C and G are as in equation 1. Energy costs of standard metabolism and activity are combined in the R term, and the energetic costs of digestion are represented by the term SDA. The acronym SDA refers to specific dynamic action which is appropriately applied only to the energy released in deamination of proteins (Jobling 1985). In practice, "apparent SDA" also includes the energy used during mechanical digestion, assimilation and storage. Energy lost in waste products is represented by F for egested and U for excreted energy. All units for the equation are expressed in biomass equivalents, e.g., g/g/day.

The chief distinguishing feature of the Wisconsin bioenergetics model is that consumption is estimated directly as a proportion (P) of maximum possible ration for a given species at a particular weight and temperature. This innovation minimizes error potential when fitting the equation to known growth patterns. The P term is also sometimes interpreted as an estimate of feeding efficiency (Hewett and Johnson 1992). The Wisconsin model is usually run with a daily step length over the period of interest.

The basic version of the Wisconsin model for striped bass has 14 parameters which require input values (Table 1). Site-specific information is also needed for water temperature and energy content of predators and prey. Data on diet composition and predator growth rate may also be required, depending upon the application.

Consumption

In the Wisconsin model, the specific consumption rate for fish is a function of both weight and temperature and is a proportion of the physiological maximum consumption, C_{max}, such that:

$$C = C_{max} * P * r_c \tag{3}$$

where C_{max} = maximum consumption at the optimum temperature (T_{oc}). The term C_{max} is equivalent to $a_1 W^{b_1}$, where a_1 and b_1 are allometric constants and W is wet weight in grams. In equation 3, P is the proportionality constant of maximum ration that varies from 0 to 1, and r_c is a temperature dependent proportional scalar of consumption rate equivalent to $(V^X)(e^{X(1-V)})$ such that:

$$\frac{V = T_{mc} - T}{T_{mc} - T_{oc}} \tag{4}$$

$$X = \frac{W^2(1+(1+40/Y)^{0.5})^2}{400} \tag{5}$$

$$W = \ln Q_c\,(T_{mc}-T_{oc}) \tag{6}$$

and

$$Y = \ln Q_c(T_{mc}-T_{oc}+2) \tag{7}$$

The r_c function, developed by O'Neill et al. (1972), increases to a maximum value of 1.0 at the optimum temperature, T_{oc}, and declines to 0 at the maximum temperature for consumption, T_{mc}. As the value of r_c increases with increasing temperature up to T_{oc}, the slope of the function, Q_c, approximates a Q_{10} for the rate. The Q_{10} is a temperature coefficient used to describe a change in rate with an increase in temperature of 10°C. In total, the consumption component of this bioenergetics model requires input values for five parameters: a_1, b_1, T_{oc}, T_{mc}, and Q_c as well as for the actual temperature experienced by the fish, T.

Table 1. Symbols and parameter values of the bioenergetics model for striped bass.

Symbol	Parameter Description	Values
	Consumption, C_{max}	
a_1	Coefficient for weight relationship to maximum consumption	0.33
b_1	Exponent for weight relationship to maximum consumption	-0.30
T_{co}	Optimum temperatures for consumption	25, 22, 20*
T_{cm}	Maximum temperatures for consumption	30, 27, 25*
Q_c	Slope for temperature dependence of consumption	2.26
	Standard Metabolism, R_{max}	
a_2	Coefficient for weight relationship of standard metabolism	.02192
b_2	Exponent for weight relationship of standard metabolism	-0.234
T_{ro}	Optimum temperatures for standard metabolism	30, 27, 25*
T_{rm}	Maximum temperature for standard metabolism	35, 32, 30*
Q_r	Slope for temperature dependence of standard metabolism	2.5
	Activity Metabolism, A	
A	Active metabolism multiplier of standard metabolism	2.0
	Digestion Metabolism, SDA	
S	Coefficient for apparent specific dynamic action	0.172
	Egestion, F	
f	Coefficient for proportion of consumed food egested	0.104
	Excretion, U	
u	Coefficient for proportion of assimilated food excreted	0.068

* Temperatures for juvenile, subadult, and adult striped bass, respectively.

Intercept and Coefficient for Weight Dependence of Consumption

The relationship of maximum daily consumption to fish weight is usually described in *ad libitum* feeding trials. However, no study has adequately assessed the weight dependence of C_{max} for striped bass, and as a result, a_1, and b_1, could not be derived from available data. We assumed a value of 0.33 for a_1, the same value derived by Rice et al. (1983) from the studies of Niimi and Beamish (1974) on largemouth bass, *Micropterus salmoides*. The intercept of the function relating maximum consumption to weight at the optimum temperature, a_1, can be interpreted as the percent of maximum daily ration (i.e., 33%) consumed by a 1 g striped bass. This value is a reasonable approximation. Rogers and Westin (1978) observed newly feeding striped bass larvae to consume 25% of their body weight per day, on a dry weight basis, of live *Artemia* nauplii at 22°C. Assuming a similar relationship between dry and wet weights as determined for larger juveniles in their study, this value would equate to approximately 40% on a wet weight basis. That these larvae weighed less than 1 g indicates this value would be less than 40% for a 1 g fish. Our assumed value for a_1 is greater than the a_1 values of 0.25 and 0.26, assumed for walleye (Kitchell et al. 1977) and derived for lake trout, *Salvelinus namaycush* (Stewart et al. 1983), respectively. However, it is reasonably close to 0.3, the value measured for lamprey *Petromyzon marinus* (Kitchell and Breck 1980), sockeye salmon *Oncorhynchus nerka* (Brett 1971), and assumed for skipjack tuna *Katsuwonus pelamis* (Kitchell et al. 1978).

Maximum daily consumption declines with increasing size on a specific weight (g/g) basis: b_1 is negative. We set this weight dependence exponent for maximum consumption at -0.30 for striped bass based on a review of derived values for other species. These ranged from a low of -0.18 for esocids (Bevelheimer 1983) to a high of -0.327 for lake trout (Stewart et al. 1983) and included intermediate values for walleye (-0.27; Kitchell et al. 1977) and largemouth bass (-0.325; Rice et al 1983).

Slope for Temperature Dependence of Consumption

The value of Q_c, the slope of the r_c function, was derived from data measured by Cox and Coutant (1981) in laboratory experiments with juvenile striped bass. They measured consumption rates for 13 groups of eight to ten juvenile striped bass fed an unrestricted ration of fathead minnows at constant temperatures ranging from 16°C to 34°C. These data, presented as consumption per group on a gram per day basis, were regressed against temperatures up to 25°C, the optimum temperature for consumption by juvenile striped bass (see page 15). The slope of the line ($N=6$, $r^2 = 0.857$, $p=0.0081$) was equal to 0.0814, which equates to a Q_c of 2.26 ($e^{0.0814 \cdot 10}$). This Q_c is very close to 2.3, the value used for bluegill *Lepomis macrochirus* (Kitchell et al. 1974), walleye and yellow perch *Perca flavescens* (Kitchell et al. 1977), and sea lamprey (Kitchell and Breck 1980). The temperature dependence coefficient used by Rice et al. (1983) for largemouth bass equates to a Q_c of 2.65.

Optimum and maximum temperature for consumption (T_{co} and T_{cm}) and respiration (T_{ro} and T_{rm}) vary with life stage in striped bass. Choice and rationale for selection of these values is deferred until the respiration component of the model has been considered.

Respiration

Metabolic cost of standard plus active metabolism vary with fish size and water temperature. We used a model functionally similar to that developed by Kitchell et al. (1977) to derive the specific respiration rate (R) for striped bass standard plus activity metabolism:

$$R = R_s * A * r_r \qquad (8)$$

Here R_s = the specific standard respiration rate equivalent to the allometric weight relationship, $a_2W^{b_2}$, where a_2 and b_2 are species-specific constants. The parameter A is a multiplier of standard metabolism to account for activity costs, and r_r is a temperature-dependent proportional adjustment of respiration rate ranging from 0 to 1. This value is derived with the same equations as for r_c (equations 4 through 7) except that optimum and maximum temperature for respiration (T_{ro} and T_{rm}) replace T_{co} and T_{cm} and Q_r, the slope of the temperature-dependence function, replaces Q_c. Therefore, the respiration component of this bioenergetics model requires input values for six parameters (a_2, b_2, A, T_{ro}, T_{rm}, and Q_r).

Coefficient and Exponent for Weight Dependence of Standard Metabolism

The parameter a_2 is the intercept of the line relating maximum specific standard metabolism to weight at the optimum temperature, T_{ro}, for respiration (i.e., specific standard metabolism of a 1 g fish at T_{ro}). For consistency with the microcomputer versions of the Wisconsin bioenergetics model (Hewett and Johnson 1987, 1992), we calculated a_2 on the basis of g O_2/g fish/day. These microcomputer models then convert oxygen consumption to energy consumption by oxycalorific coefficients (e.g., 13.56 joules/mg O_2; Rice et al. 1983). Energy is translated to weight in the model output depending on the energy density (joules/g) of the fish.

Rice and Breck (unpublished manuscript) used multiple linear regression techniques to synthesize fish respiration data for striped bass from the laboratory work of Kruger and Brocksen (1978). Kruger and Brocksen (1978) determined the oxygen consumption of striped bass at three water velocities (1, 5, and 10 cm/s) and at five water temperatures (8, 12, 16, 20, and 24°C); sizes of striped bass ranged from 22.5 to 68.4 g. The derived equation from their data was:

$$R = .0014\ W^{-0.234}\ e^{0.0917T}\ e^{0.0[illegible]SS} \qquad (9)$$

where W=weight (grams), T=temperature (°C), and SS=swimming speed (cm/s). For a 1 g striped bass at 30°C, the optimum temperature for respiration without activity (0 cm/s), a_2, is equal to 0.02192 gm O_2/day.

This a_2 value compares favorably with the work of Klyashtorin and Yarzhombek (1975), who studied the respiration of striped bass (0.3 to 22 g) at different temperatures and oxygen concentrations. Their data indicated that a 1 g fish would consume 0.0132 to 0.0168 g O_2/g day at 22°C (interpolated from Figures 4 and 5 in Klyashtorin and Yarzhombek 1975). Using the equation derived from Kruger and Brocksen (1978), a 1 g striped bass at 22°C would consume

0.0105 g O_2/g day. The close similarity between the results of these very different investigations indicates that our value for a_2, 0.02192, is a realistic approximation.

The weight dependence coefficient (b_2) of -0.234 was derived from Kruger and Brocksen (1978) and used in our modeling simulations of striped bass metabolism. Although only a small range of weights was experimentally tested (22.5 to 68.4 g), the value is very close to -0.2, the value postulated by Winberg (1956) to describe the weight dependence of metabolism for a representative fish species, and used by Kitchell et al. (1977) for walleye. The weight dependence coefficient also agrees well with other studies on striped bass metabolism. Converting the value of 0.72 (Eldridge et al. 1982) to a specific rate equates to a value of -0.28 for larval striped bass. Klyashtorin and Yarzhombek (1975) measured a b_2 value of -0.25 for juvenile striped bass. Our coefficient is substantially greater than -0.355, the weight dependence exponent derived for largemouth bass by Rice et al. (1983) from the data of Beamish (1970), but within the range of values used to model salmonid metabolism, -0.295 to -0.217 (Stewart 1980).

Slope for Temperature Dependence of Standard Metabolism

The temperature dependence coefficient for striped bass metabolism, 0.0917, derived from Kruger and Brocksen (1978) data, equates to a Q_{10} of 2.5. This value approximates Q_{10} for the r_2 function and is slightly higher than 2.0, the Q_{10} equal to the temperature dependence derived by Klyashtorin and Yarzhombek (1975), as calculated for striped bass by Lewis et al. (1981). Comparable Q_{10} values used by other researchers include 2.1 for bluegill (Kitchell et al. 1974), walleye and yellow perch (Kitchell et al. 1977), and lamprey (Kitchell and Breck 1980) and 1.8 to 2.0 for salmonids (Stewart 1980). The temperature dependence coefficient derived for largemouth equates to a Q_{10} of 1.4 (Rice et al. 1983).

Activity Multiplier of Standard Metabolism

Winberg's (1956) review of piscine metabolic research led him to conclude that a multiple of standard metabolism could be used to calculate the additional metabolic costs resulting from activity. He assumed a value of 2.0 (Winberg II multiplier) for the activity parameter. In the absence of sufficient information on the activity metabolism of striped bass, we assumed that the same value was applicable to striped bass respiratory costs.

Although there is no physiological basis for the assumption that activity metabolism is a constant proportion of standard metabolism, numerous studies have assumed this relationship. Choice of multiplier has usually been based on the investigators' perceptions of the lifestyle patterns of their target species. Penczak et al. (1984) used a value of twice standard metabolism to estimate the total metabolism of fish species in two Polish rivers. Similarly, Kitchell et al. (1978) cited research indicating that a value twice standard metabolism might be a reasonable estimate of activity metabolism for tuna. An activity multiplier of less than two has been used for less mobile fishes. Stewart (1980) used a swim speed model to estimate that activity multipliers for lake trout ranged from 1.4, at low temperature and small size, to 1.9, at high temperature and large size. Kitchell et al. (1977) assumed an A equal to 1.0 (i.e., negligible activity costs) for walleye and yellow perch based on field data that indicated little locomotor activity. Sauger *Stizostedion canadense* in Tennessee (Minton and McLean 1982) and northern pike *Esox lucius* in Alberta (Diana 1983) were also assumed to have activity multipliers of 1.0.

Direct estimates of activity costs have been made by determining the other components of the energy budget from laboratory and field studies and then solving the equation for activity. Results indicate that activity costs can be highly variable over time and among populations. Adams et al. (1982) found that activity metabolism varied with time of year as well as sex in largemouth bass, ranging from 0.18 to 1.44 times standard metabolism ($A = 1.18$ to 2.44). Similarly, Boisclair and Leggett (1989) reported that activity costs among twelve populations of yellow perch ranged from zero ($A = 1.0$) to almost three times standard metabolism.

An alternative approach to estimating activity costs is to incorporate swimming speed in the respiration component of the bioenergetics equation (see equation 9). This approach assumes that swimming encompasses all activity, which is probably a reasonable assumption for pelagic fishes such as striped bass. We rejected this alternative on two grounds: 1) lack of accurate field data on striped bass swimming effort; and 2) the likelihood that swimming ability of striped bass increases sharply with age. Neumann et al. (1981) hypothesized, based on laboratory results indicating juvenile striped bass were weak swimmers although adults exhibited extensive coastal migrations, that swimming ability of striped bass with increasing age could best be described by a sigmoidal curve. Additional complexities include the confounding factors of aerobic vs anaerobic metabolism (Webb 1978; Priede 1985), and the fact that striped bass are facultative ram ventilators (Freadman 1979). Research consisting of swim speed measurements for striped bass at various sizes, temperatures and speeds, as well as optimal (or standard) swimming speeds and field measurements of activity, are necessary to adequately characterize the activity metabolism of striped bass.

Our value of A (2.0) is probably a reasonable estimate for striped bass. Kruger and Brocksen (1978) determined that a value of five times the standard metabolic rate would equal the metabolic cost of a juvenile striped bass at the maximum swimming speed of 60 cm/s (as measured by Painter and Wixcom 1967). At more reasonable swimming speeds, 10 to 20 cm/s, oxygen consumption would range from 1.6 to 2.8 times the standard metabolic rate, assuming oxygen consumption at activity varies directly with the specified weight and temperature dependence coefficients of standard respiration.

Optimum and Maximum Temperatures

Values of T_{oc}, T_{mc}, T_{or}, and T_{mr}, the optimum and maximum temperatures for consumption and respiration, respectively, define the temperature-dependent proportional adjustments, r_c and r_r. Temperature values for striped bass were derived from research conducted by personnel of the Oak Ridge National Research Laboratory. Optima and maxima were determined in a manner similar to that used for walleye and yellow perch (Kitchell et al. 1977).

Cox and Coutant (1981) found that 25°C was the optimum temperature for consumption and growth of juvenile striped bass. This value is in agreement with the work of Cech et al. (1984). Although there has been no adequate measure of upper incipient lethal temperature, juvenile striped bass died at temperatures above 35°C (Davies 1973). We considered 35°C as the upper incipient lethal temperature and the maximum temperature for respiration, T_{mr}. A temperature of 30°C, midpoint between 25°C and 35°C, was chosen to represent the maximum temperature for consumption (T_{mc}) and the optimum temperature for respiration (T_{or}).

These terms should correspond to the highest preferred temperature of striped bass. The 30°C value is midpoint between 29°C and 31°C, the highest preferred temperatures of juvenile striped bass acclimated at 24° (Texas Instruments 1976).

There is a marked ontogenetic shift in thermal preferenda with age of striped bass. Temperature selection of subadult (ages 2-4) striped bass ranged from 20-24°C (Coutant and Carroll 1980) but dropped to 18-22°C for adults (ages 5-10) in freshwater impoundments (Schoich and Coutant 1980). Because thermal preferenda and optima are equivalent for most species (Beitinger and Fitzpatrick 1979), we used the midpoint of these ranges, 22°C and 20°C as T_{oc} for consumption by subadult and adult striped bass, respectively. The values of T_{mc}, T_{or}, and T_{mr} for subadult and adult striped bass were scaled accordingly. The respective values (°C) for juvenile, subadult, and adult striped bass were 25, 22, and 20 for T_{oc}, 30, 27, 25 for T_{mc} and T_{or}, and 35, 32, and 30 for T_{mr}.

Digestion Metabolism, SDA

The metabolic costs of digestion, absorption, and assimilation of food plus specific dynamic action (SDA) are considered additional respiratory costs and defined as apparent SDA (Beamish 1974). Many investigators have modeled apparent SDA as a proportion of total consumption or ingested energy. However, error may result when the diet changes from invertebrates to fish or becomes heterogeneous because assimilation efficiency can change with food type (Stewart et al. 1983). Therefore, we modeled SDA as a proportion (S) of the assimilated energy for striped bass such that

$$SDA = S(\text{Consumption-Egestion}) \qquad (10)$$

We assumed that S was independent of both temperature and ration size (Stewart et al. 1983). Beamish (1974) determined that SDA was 17.2% of metabolizable energy for fish on a piscivorous diet, and we used this value for striped bass. Most bioenergetics models for piscivorous fishes have also used 0.172 as the coefficient for apparent SDA, although some have ranged as low as 0.14 (Hewett and Johnson 1992).

Excretion and Egestion

We modeled egestion (F) for striped bass with a function identical to that used for largemouth bass by Rice et al. (1983), as derived from the work of Beamish (1972):

$$F = f\,C \qquad (11)$$

where f=proportion of consumed energy (C) egested. We set the value of f equal to 0.108. Tuncer et al. (1990) reported that juvenile striped bass (2-18 g) fed pelletted food had egestion rates averaging 10.8% (f=0.108) in laboratory trials at 24°C; results were very similar at two different ration levels. This coefficient of egestion is virtually identical to the value (f = .104) reported by Beamish (1972) for largemouth bass.

Like egestion, excretion varies as a function of size, temperature, and ration. Excretory products are chiefly ammonia and urea. We modeled excretion (U) as a proportion of utilizable energy:

$$U = u\,(C\text{-}E) \qquad (12)$$

where u=proportion of utilizable energy (consumption - egestion) that is excreted. Juvenile striped bass fed pelletted food in laboratory trials demonstrated an average u value of 0.066 (derived from Tuncer et al. 1990), and we used this value of the excretion coefficient in our model. Rice (1981) used an excretion coefficient of 0.068 for largemouth bass, substantiating our selection. The combined effect of total waste loss, egestion plus excretion, varies little with temperature because F and U respond in opposite ways to temperature change (Kitchell et al. 1977). Therefore, assuming constant proportions of consumed or assimilated energy is reasonable.

MODEL IMPLEMENTATION AND REFINEMENT

For illustrative purposes, the bioenergetics model for striped bass was implemented for a 100 g fish at maximum ration (Figure 1). As expected, maximum specific rates for all functions, except respiration, occur at 25°C, the optimal temperature for consumption. Specific respiration rates continue to rise to 30°C, then rapidly decline. Specific rates of all functions decrease with increasing weight of striped bass (Figure 2).

This striped bass bioenergetics model has been used to make inferences about potential stocking strategies for striped bass based on the available supply of forage fishes in a Virginia reservoir (Moore 1988). In addition, the model has been used to simulate striped bass growth in Chesapeake Bay (Brandt et al. 1992).

However, the values we present for the parameters of this striped bass bioenergetics model can probably benefit from further refinement. The problems that afflict valuation for most species-specific bioenergetics models presently in use also pertain to our model: species borrowing, reliance on juvenile fish, and uncertainty about activity metabolism (Ney 1990). Values for several parameters were obtained either by direct substitution from an unrelated species (e.g., the coefficient of weight dependence for maximum consumption) or by selection of an intermediate value from the range reported for various species (the exponent of weight-dependence for maximum consumption). However, the similarity in reported values for some physiological parameters among fish species with comparable lifestyles suggests that species borrowing may sometimes be reasonable.

The bioenergetic parameter values that we were able to obtain or derive from studies of striped bass resulted from laboratory observations of juvenile fish. How well these values apply to large adult striped bass is unknown. Virtually all bioenergetics models for fishes which grow to large size suffer from the same uncertainty, because the logistics of laboratory studies using large specimens are difficult. However, the need for accurate valuation of bioenergetic parameters for large fish is critical, especially for the allometric weight-dependent functions of

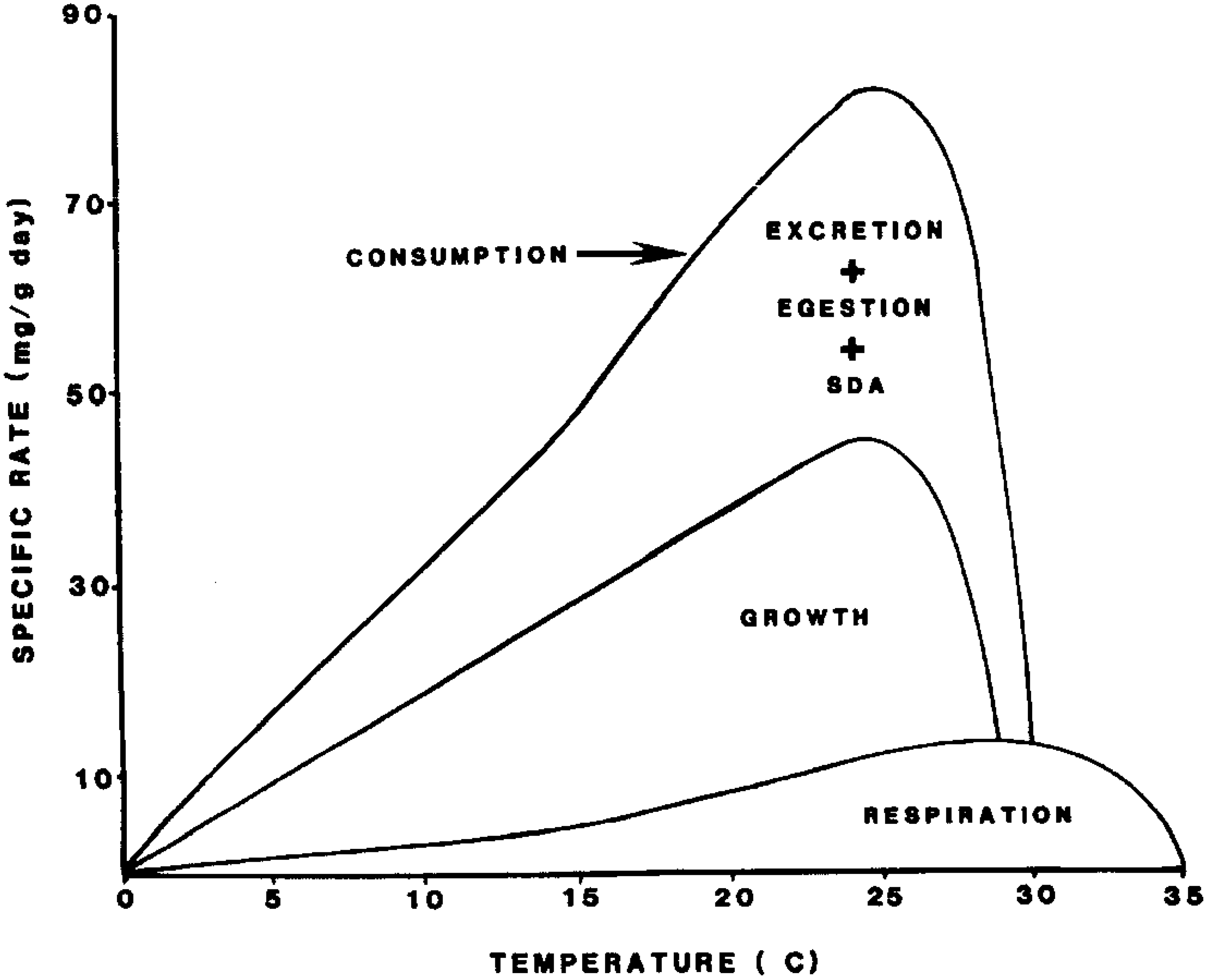

Figure 1. Model output for the energy budget of a 100 g striped bass as a function of water temperature.

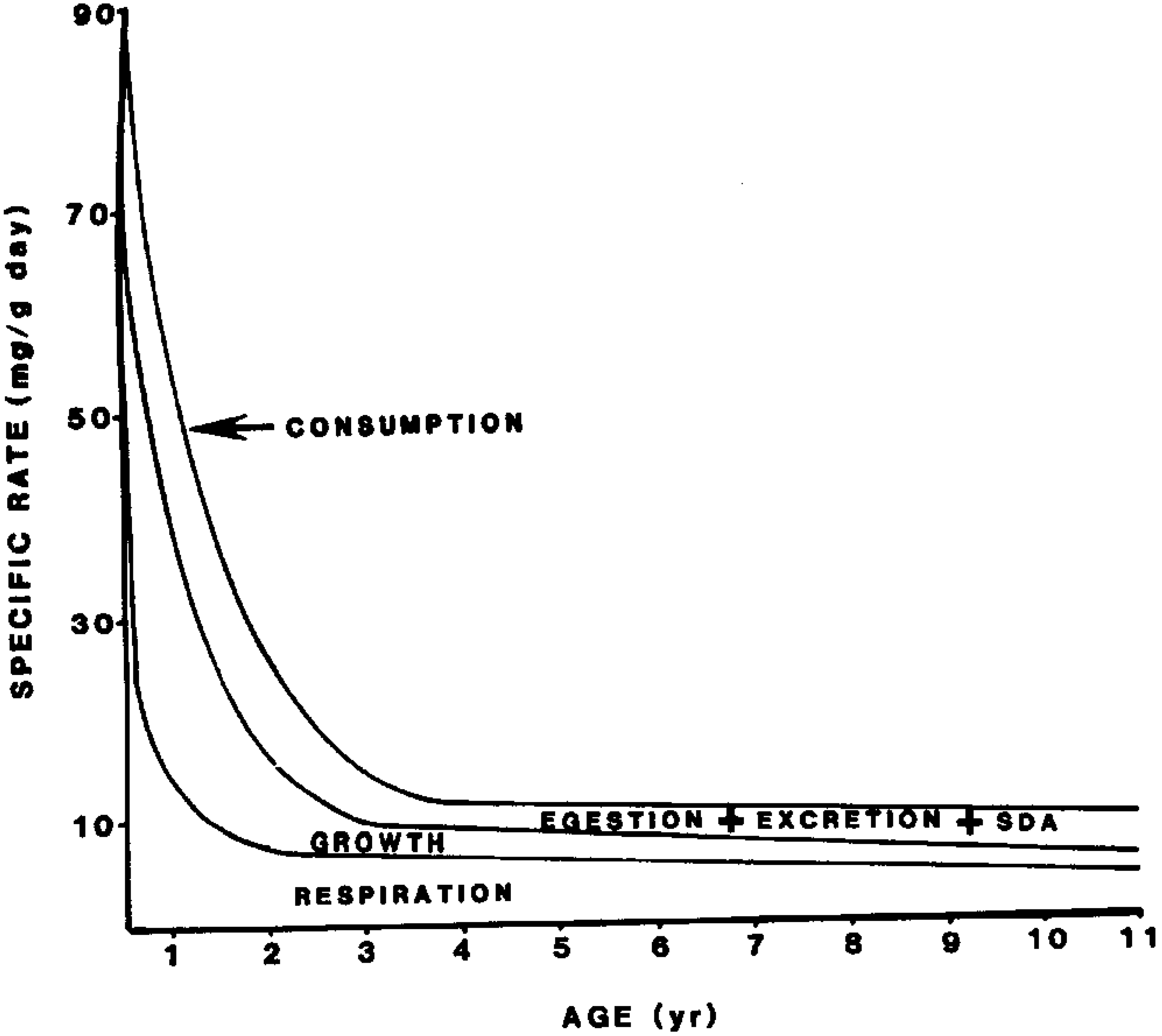

Figure 2. Model output for striped bass at the optimum temperature for consumption (T_{∞}) as a function of body size.

maximum consumption and standard metabolism; errors in these parameters can have a strong influence on model predictions (Bartell et al. 1986).

The energetic costs of activity also are poorly quantified in most bioenergetics models. Whether activity costs are negligible, exceed, or are equal to costs of standard metabolism will have an obvious impact on model output for consumption or growth. Determination of true activity costs of noncaptive fish can be accomplished only by intense field study (Boisclair and Leggett 1989; Lucas et al. 1991).

Despite these uncertainties, we believe that the striped bass model in its present form has many applications. However, we strongly encourage field corroboration of this bioenergetics model. How accurately does it predict consumption or growth for striped bass in freshwater, estuarine and marine systems? The answers will determine both the need for and the nature of future refinements in the valuation of the model.

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