Applications of a Bioenergetics Model to Yellow Perch (*Perca flavescens*) and Walleye (*Stizostedion vitreum vitreum*)[1,2]

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A simple energy budget equation is developed to yield a bioenergetics model designed to simulate fish growth. Parameters for the model are estimated from the literature for application to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). Simulations are presented that demonstrate model output as functions of body size, activity level, ration level, food quality, and environmental temperature. Sensitivity analyses identify the importance of food consumption, activity, and excretion as biological processes represented in the parameters. On the basis of temperature conditions in selected lakes and specified feeding levels, simulations are presented to quantify the importance of year-to-year variation of temperature in determining growth. In heterothermal systems, temperature selection by percids can have a significant effect on growth. For walleye on fixed rations, annual growth can vary from zero to twofold increments due entirely to differences in summer temperatures. Variations in food quality have lesser effects.

Key words: *Perca*, *Stizostedion*, bioenergetics model, growth, sensitivity, simulations

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Nous formulons une équation simple de budget énergétique conduisant à un modèle bioénergétique conçu pour simuler la croissance des poissons. Nous estimons les paramètres du modèle à partir de la littérature et les appliquons à la perchaude (*Perca flavescens*) et au doré jaune (*Stizostedion vitreum vitreum*). Nous décrivons des simulations démontrant les résultats du modèle comme fonctions de la grosseur du corps, du niveau d'activité, du niveau de ration, de la qualité de la nourriture et de la température ambiante. Des analyses de sensibilité démontrent l'importance de la consommation alimentaire, de l'activité et de l'excrétion comme processus biologiques représentés dans les paramètres. En nous fondant sur les conditions thermiques dans des lacs choisis et à des niveaux d'alimentation spécifiques, nous présentons des simulations permettant de quantifier l'importance des variations d'année en année de la température dans la détermination de la croissance. Dans des systèmes hétérothermes, le choix de la température par les percidés peut avoir un effet important sur la croissance. Chez des dorés jaunes maintenus à des rations fixes, la croissance annuelle peut varier de zéro à des augmentations du double résultant entièrement de différences dans les températures estivales. Les variations dans la qualité de la nourriture ont des effets moindres.

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A model of fish growth gives a better estimation of responses to environment than do population models because growth adjusts biomass more quickly than population density (Kerr 1971; Hall et al. 1970). For percid fishes such as the yellow perch, *Perca flavescens*, and walleye, *Stizostedion vitreum vitreum*, which are tolerant of a wide variety of habit conditions, a model of processes that regulate growth may be used as a sensitive tool in inferring ecological relationships.

A growth model has the capability of integrating a diversity of existing knowledge into a unified framework. This type of modeling has three

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phases. The first step is to mathematically state what is known about the growth-controlling processes that are to be incorporated. This requires a critical evaluation of the results of both laboratory and field studies. Second, the relations of these processes to independent variables must be evaluated. These relations comprise the model hypothesis. If the hypothesis is rigorous, validity of results will depend on validity of the analysis of subprocesses. Finally, the model itself is used as an analytical tool. A sensitivity analysis can indicate what parts of the current understanding of growth require further experimentation. Given a working simulation model, various ecological conditions may be evaluated with respect to their implications for fish growth.

The model described here represents modifications of the bioenergetics components of a population biomass model presented by Kitchell et al. (1974). Consumption and respiration are considered to be the processes that immediately control growth. Temperature and fish size are key variables determining the rates of these processes. Waste losses are modeled as functions of consumption and temperature.

A bioenergetics model hypothesis was chosen as a mechanistic approach to percid biology because it gives a rigorous framework relating the controlling processes to each other, to temperature, and to growth rates. We describe the functions used in the model, our assumptions in their use, and the kinds and sources of data employed as model parameters. We also provide examples of applications that may provide some insights into those factors important to the ecology of percid fishes.

Bioenergetics Approach

The specific growth rate of an individual, nonreproducing fish is calculated as weight increment per unit of weight per time and is defined by the equation

$$\frac{dB}{Bdt} = C - (R + F + U). \tag{1}$$

Specific growth rate is determined as the difference between specific rate of food consumption, C, and the sum of specific energy output rates, where

R = respiration or metabolism (including standard, active, and specific dynamic action components),
F = egestion,
U = excretion,
and
B = fish weight.

All units are expressed as equivalents in biomass and, for this model, are calculated on a per-day basis. The symbol ΔB is used to represent accomplished growth. Total rates can be calculated as the products of specific rates and fish weights. The following sections briefly describe each of the functions employed in solving Equation 1.

Consumption — The rate of feeding, C, is defined as a function of the maximum rate for an individual fish of a given size at a specified temperature, as follows:

$$C = C_{\max} P r_c \tag{2}$$

where $C_{\max} = a_1 B^{b_1}$, the maximum weight-specific ration at the optimum temperature, T_o, for consumption; a_1 and b_1 are regression constants,
P = a proportionality constant having values of 0 to 1.0, used to adjust the ration when fitting an observed growth curve,
and $r_c = (V^x)\ (e^{x(1-V)})$, a temperature-dependent proportional adjustment (i.e. 0 to 1.0) of consumption rate.

The function r_c is employed to fit a rate-response curve using three key parameters of biological importance (Kitchell et al. 1974). The slope estimate, Q, approximates a Q_{10} for the rate as it increases with increasing temperature over relatively low temperatures. The value of r_c reaches a maximum of 1.0 at the optimum temperature, T_o, and declines rapidly to zero at the maximum temperature, T_m. Terms for the temperature-dependence function are:

$$V = \frac{T_m - T}{T_m - T_o}$$

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

$$W = (\ln Q)(T_m - T_o)$$

$$Y = (\ln Q)(T_m - T_o + 2)$$

and T = ambient temperature.

The allometric function for feeding (and respiration, see below) is a major simplification of the earlier approach to bioenergetics modeling (Kitchell et al. 1974). The allometric consumption function reflects, in part, the change in stomach volume and digestion rates in relation to change in body weight (Brett 1971; Elliott 1976b). Maximum daily rations given by this function are expressed as proportions of fish body weights. This same function is assumed to apply when rations are less than maximum (i.e. $P < 1.0$).

Respiration — The respiration rate is dependent upon body weight and ambient temperature; functions similar to those for consumption are used. In addition, both activity and feeding level affect respiration. Specific respiration, or metabolism, R, is given by

$$R = R_{\max} A r_R + SC \qquad (3)$$

where $R_{\max} = a_2 B^{b_2}$, the maximum weight-specific standard respiration rate at the optimum temperature for respiration; a_2 and b_2 are regression constants,

A = an activity parameter to specify respiration rates above standard (i.e. $A = 2.0$ indicates a Winberg II model, Fig. 4b),

$r_R = (V^x)\ (e^{x(1-V)})$, a temperature-dependent proportional adjustment of respiration similar to r_c of equation 2 but with different parameter values Q, T_o, and T_m,

and S = the specific dynamic action coefficient

Values of the allometric function, $R_{\max}$, are expressed as proportions of fish body weights. This reflects the well-known decrease in weight-specific metabolic rate as size increases (Winberg 1956). Specific dynamic action is defined as the metabolic cost of digestion, absorption, and deposition of consumed energy, and is assumed to be a constant proportion of the food consumption rate, C.

Egestion and excretion — Waste losses are defined as egestion, F, and excretion, U. Kitchell et al. (1974) assumed both values to be simple proportions of the feeding rate. A recently published, extensive study by Elliott (1976a) demonstrates that, for the brown trout, both vary as functions of feeding level and temperature. We assume the same to be true for percid fishes and express egestion and excretion rates as

$$F, U = C\alpha T^{\beta} e^{\gamma P} \qquad (4)$$

where α, β, and γ are regression constants, and C, T, and P are as defined above. Although the same formulation is used for both rates, the processes respond differently to the variables in Equation 4 as expressed in values for the coefficients α, β, and γ.

Implementing the Model

Two basic data sets are required to implement the model for simulation. Bioenergetics data describe components of the budget equation (Equation 1) as functions of the variables temperature, body size, food quality, and feeding rate (Table 1). Site-specific data are used to provide estimates of ambient temperatures, growth, and food availability. Much of the data employed in parameter estimation for perch was derived from experimental work on *Perca fluviatilis* (Solomon and Brafield 1972) and assumed to be applicable to *Perca flavescens* (Thorpe 1977). Similar data for walleye can be derived from Kelso (1972). Where data were available for one species but not the other, parameter values were assumed to be the same for the two.

The primary components of the model are functions of specified maximum consumption and respiration rates ($C_{\max}$, $R_{\max}$; Equations 2 and 3). We are not aware of direct measures of maximum food consumption rate reported for perch or walleye. Theoretically, the highest rates occur in the smallest free-swimming larvae and these are difficult to study in the laboratory. We estimated the coefficients for $C_{\max}$ using the method of Brett (1971) and extrapolation of data given by Solomon and Brafield (1972), Kelso (1972), and Swenson and Smith (1973). The resultant value of a_1 in Equation 2 was 0.25, so that a 1 g fish would consume a maximum daily ration of 25% of its weight at the optimum temperature. This value is comparable to maximum rations of 24% measured for the bluegill sunfish (McComish 1970) and 30% for sockeye salmon (Brett 1971). Value of the weight exponent, $b_1 = -0.27$, was similarly derived and approximates that reported for largemouth bass, where $b_1 = -0.3$ (Niimi and Beamish 1974).

The standard metabolic rate constant, b_2, was set equal to -0.2, a value typical of many fishes (Winberg 1956). Using basal respiration data for perch of a given weight (Solomon and Brafield 1972) and $b_2 = -0.2$, we extrapolated back to obtain a_2, the value for a 1 g fish. The specific dynamic action, S, component of total respiration was taken as a constant 15% of the food consumed; this is the reported value for both largemouth bass (Beamish 1974) and bluegill sunfish (Schalles and Wissing 1976).

Temperature optima and maxima for consumption and respiration were taken from sources

TABLE 1. Symbols and parameter values used to implement model equations applied to yellow perch (*Perca flavescens*).

Reference equation	Symbol	Parameter description	Parameter value
2	(C) a_1	Intercept for maximum consumption	0.25
	b_1	Slope for maximum consumption	−0.27
	T_o	Optimum temperature for consumption	
		young-of-year	29°C
		juveniles and adults	23°C
	T_m	Maximum temperature for consumption	
		young-of-year	32°C
		juveniles and adults	28°C
	Q	Slope for temperature dependence of consumption ($\simeq Q_{10}$)	2.3
3	(R) a_2	Intercept for maximum standard respiration	0.035
	b_2	Slope for maximum standard respiration	—0.20
	T_o	Optimum temperature for standard respiration	
		young-of-year	32°C
		juveniles and adults	28°C
	T_m	Maximum temperature for standard respiration	
		young-of-year	35°C
		juveniles and adults	33°C
	Q	Slope for temperature dependence of standard respiration ($\simeq Q_{10}$)	2.1
	S	Specific dynamic action coefficient	0.15
4	(F) α_1	Intercept for proportion of consumed food egested	0.158
	β_1	Coefficient for egestion vs. temperature	−0.222
	γ_1	Coefficient for egestion vs. feeding level	0.631
	(U) α_2	Intercept for proportion of consumed food excreted	0.0292
	β_2	Coefficient for excretion vs. temperature	0.58
	γ_2	Coefficient for excretion vs. feeding level	−0.299

summarized by Hokanson (1977). Optimum temperatures for consumption and growth of yellow perch are about 23°C (Schneider 1973), and this is equal to the average final laboratory temperature preferendum for this species (Neill and Magnuson 1974). Close correspondence between temperature preference and the optima for activity and growth is known for other fishes (Brett 1956). The ultimate upper incipient lethal temperature was used as maximum temperature for respiration and it sets the upper bounds on the system. The difference between T_o for consumption and T_m for respiration is 10°C; the midpoint between these, 28°C for adult perch, was arbitrarily chosen as both T_m for consumption and T_o for respiration. This is essentially equal to the maximum observed temperature preference for yellow perch (i.e. 29°C, lab; 27°C, field; Hokanson 1977). Values for Q were taken from Kitchell et al. (1974).

Elliott's (1976a) equations for egestion and excretion rates in brown trout as functions of temperature and ration were assumed to be applicable to percids. The partial regression coefficients β and γ were taken directly from Elliott and the intercepts α_1 and α_2 were adjusted to fit the curves through Solomon and Brafield's (1972) F and U estimates for *P. fluviatilis* eating *Gammarus* sp. at 14°C. The proportion of ingested food that is egested at $C_{\max}$ and 14°C is conveniently about equal to the value of α_1. Thus we set α_1 to the approximate known egestion values for each food type at 14°C (see Table 2 and related text).

Model Applications

Environmental temperatures constitute a major determinant of growth under specified feeding regimes. Unfortunately, many extensive field studies of growth, population dynamics, and production have not included or reported temperature data. Our applications of the model are restricted to those sites where water temperature data have been reported. An adequate simulated profile of surface water may be derived from four known parameters: average date of ice disappearance, date and values for maximum midsummer temperature, and average day of first complete ice cover. With this information, the temperature curve for the ice-free period can be simulated using a skewed sine function. Actual daily temperatures or interval data with linear interpolation between observations can be used for the model. In these simulations we employ data from Lake Erie (Jobes 1952; Burns 1976) and Oneida Lake (Forney 1977). Using reported growth rates, we used the model to evaluate hypotheses regarding fish growth in these systems.

We used the parameters described in the preceding section and summarized in Table 1 to perform simulations that demonstrate model outputs (Fig. 1–5) as functions of the variables temperature, body size, activity, and ration level.

For a 10 g yellow perch feeding at maximum levels, all components of the energy budget equation are expressed as functions of temperature (Fig. 1). Maximum growth rate occurs at about 22°C, and growth declines rapidly between 22 and 28°C. The relationship of growth and temperature as shown here agrees closely with that observed by McCormick (1976) for juvenile yellow perch. Starvation is assumed to be represented by standard respiration rates at temperatures greater than 28°C; this provides a conservative estimate of weight loss during starvation since excretory and other losses are not simulated.

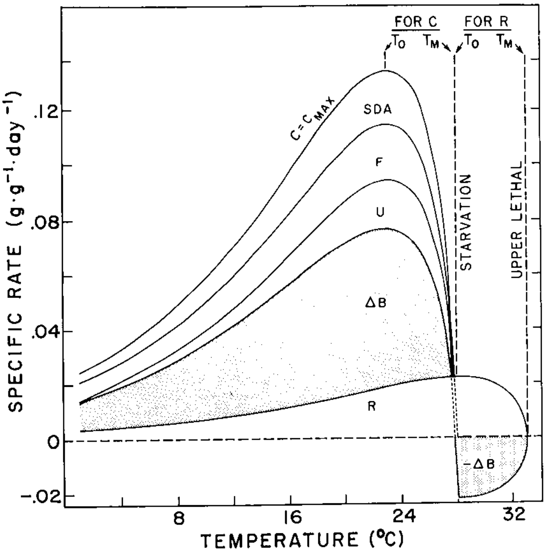

FIG. 1. Model output of the relations between temperature and all component rates of the energy budget for a 10 g yellow perch. Symbols are those given in Equation 1. Parameters are those summarized in Table 1.

Changes in weight-specific rates for energy budgets at maximum rations are displayed as a function of fish weight to demonstrate the allometric effect (Fig. 2). Optimum temperature for consumption was set at 23°C and for respiration at 28°C. All rates decline rapidly over the 1–50 g size range and more slowly for fish greater than 50 g. Small fish have a greater scope for growth than large fish because the C and R functions converge with increasing size (i.e. $|b_1| > |b_2|$).

Egestion and excretion of invertebrate (e.g. *Gammarus*) foods vary as a function of temperature and ration level. At maximum rations ($P = 1.0$), the proportion egested declines as temperature increases while that excreted increases with rising temperature (Fig. 3). The cumulative net loss as waste varies only slightly (26–32%) with more than 30% lost at very low and high temperatures. Maximum absorption efficiency would occur at high temperatures but would be offset by a relatively high excretory loss. Hence, the temperature range of 4 to 12°C appears most efficient for growth at minimum waste loss rates. Both loss rates are altered by consumption levels less than maximum to yield increased efficiency at reduced rations.

We combined all functions to simulate the effect of temperature on estimated maintenance rations for fish of 1 g to 1 kg (Fig. 4a). Maintenance rations are inversely related to body size as suggested by the simulations of allometric effects (Fig. 2). They are highest at about 27°C

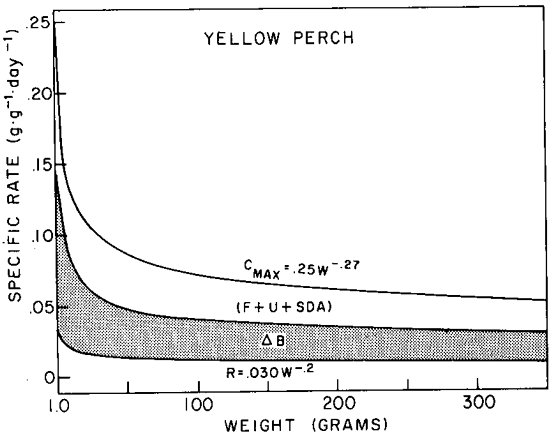

FIG. 2. Relations between body size and components of the energy budget for yellow perch at 23°C. Allometric functions for maximum consumption and respiration rates are from Equations 2 and 3.

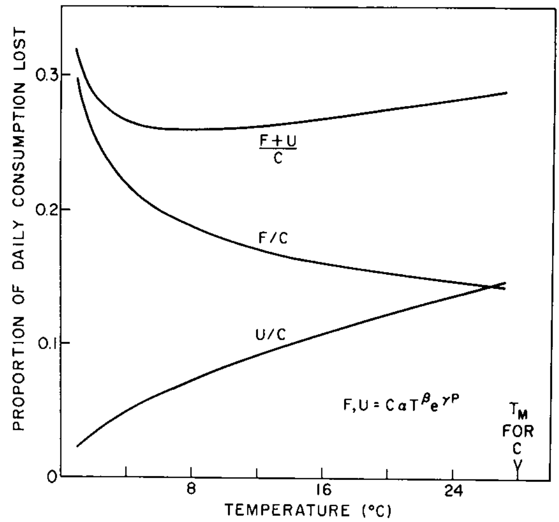

FIG. 3. Proportions of consumed food egested and excreted and their sums as functions of temperature. Calculated values are based on Equation 4.

for all sizes, being greater than 6% of body weight for a 1 g fish and about 1.5% for a 1 kg fish. Maintenance rations at low temperatures (<4°C) would be about 1% and 0.2% for 1 g and 1 kg fish, respectively. The inference of reduced maintenance rations at temperatures greater than 27°C reflects the decline in feeding rates observed at high temperatures and the resultant reduction in losses to egestion, excretion, and specific dynamic action (Fig. 1).

Ware (1975) discusses the continuing controversy regarding estimates of activity and metabolic levels ascribed to free-living fishes. Winberg (1956) proposed that the level of laboratory-determined standard metabolism (Winberg I) be doubled (Winberg II) in estimating respiratory energy utilized by fishes in nature. Many subsequent studies have applied this procedure as a rule of thumb (Mann 1969). Ware (1975) proposed that pelagic, juvenile fishes had activity levels equivalent to Winberg III.

To assess the bioenergetics of variable activity, we simulated growth rates at each of three activity levels as a function of temperature (Fig. 4b) for a 10 g yellow perch consuming maximum rations. At high activity levels (III), maximum specific growth rate (~2% day^{-1}) occurs at about 20°C. At low activity levels, those we assume to be equivalent to standard respiration rates (I), maximum growth is nearly 6% at 23°C. The optimum temperature for maximum specific growth rate declines slightly as activity levels increase. With the exception of results given in Fig. 4b, all simulations presented herein assume a Winberg I model ($A = 1.0$).

We specified fixed ration levels in simulations of growth by a 10 g yellow perch at various temperatures. Rations were set equal to $C_{\max}$ at temperatures where specified rations exceeded $C_{\max}$. The results are expressed as specific growth rates for rations of 1% of body weight to maximum (13%) (Fig. 5a). Growth rate declines

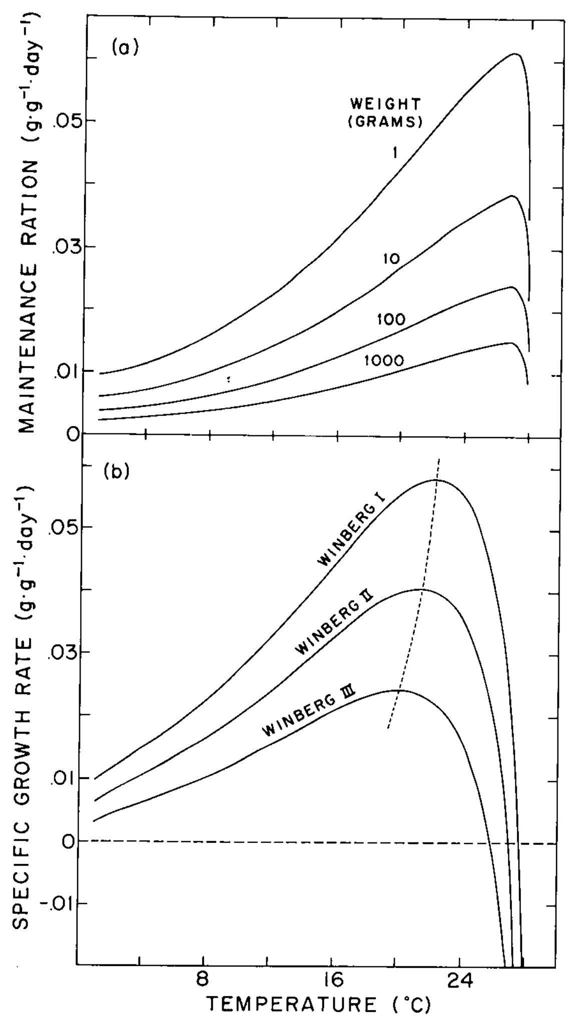

FIG. 4. (a) Relations between temperature and estimated maintenance rations for perch of four weights when maintenance $= R/1.0 - (F/C) - (U/C) - S$). Adult temperature parameters were used for the 1 g fish to facilitate comparison. (b) Specific growth rates at maximum rations for a 10 g perch as functions of temperature and multiples of the standard respiration rate used to estimate levels of activity in nature.

with increasing temperature at all ration levels. The zero growth line in Fig. 5a represents maintenance rations as a function of temperature ranging from 1% at 8°C to nearly 4% at 27°C.

We calculated and plotted gross and net conversion efficiency isopleths for the specified ration levels. Gross conversion efficiency (Fig. 5b) exceeds 45% at the highest rations obtained over the 4–20°C temperature range. Net conversion efficiencies (Fig. 5c) exceed 64% at low ration levels and temperatures less than about 10°C. Net efficiencies are lowest (<58%) at high ration levels and high temperatures.

Elliot (1976b) found that highest gross conversion efficiency for brown trout also occurred at maximum rations and intermediate temperatures. Our simulation results and Elliot's laboratory observations both contrast with the observation that fingerling sockeye salmon have maximum gross conversion efficiency at ration levels less than maximum (Brett et al. 1969). The data of Brett et al. indicate a reduction in assimilation efficiency as ration approaches the maximum for a given temperature. Brown trout also have lower assimilation at high rations (Elliot 1976a) but still have highest gross conversion efficiency at maximum rations and intermediate temperatures.

The difference between Elliot's (1976b) results and those of Brett et al. (1969) may be due, in part, to differences in their experimental designs. Elliot fed natural foods to individual fish whereas Brett et al. fed a pellet diet to a large group of fish and periodically subsampled the group to determine growth. Since Brett et al. did not recover and quantify uneaten food in all experiments, it is possible that they progressively overestimated the actual quantities consumed by a tank population when rations approached the maximum for a given temperature. It is also possible that the assimilation efficiency of sockeye salmon eating pellet diets is somewhat different from that of brown trout eating natural foods.

Sensitivity Analysis

Methods and assumptions — A single parameter analysis of sensitivity was done to evaluate the relative importance of input parameters for yearly growth output. We simulated growth of age I+

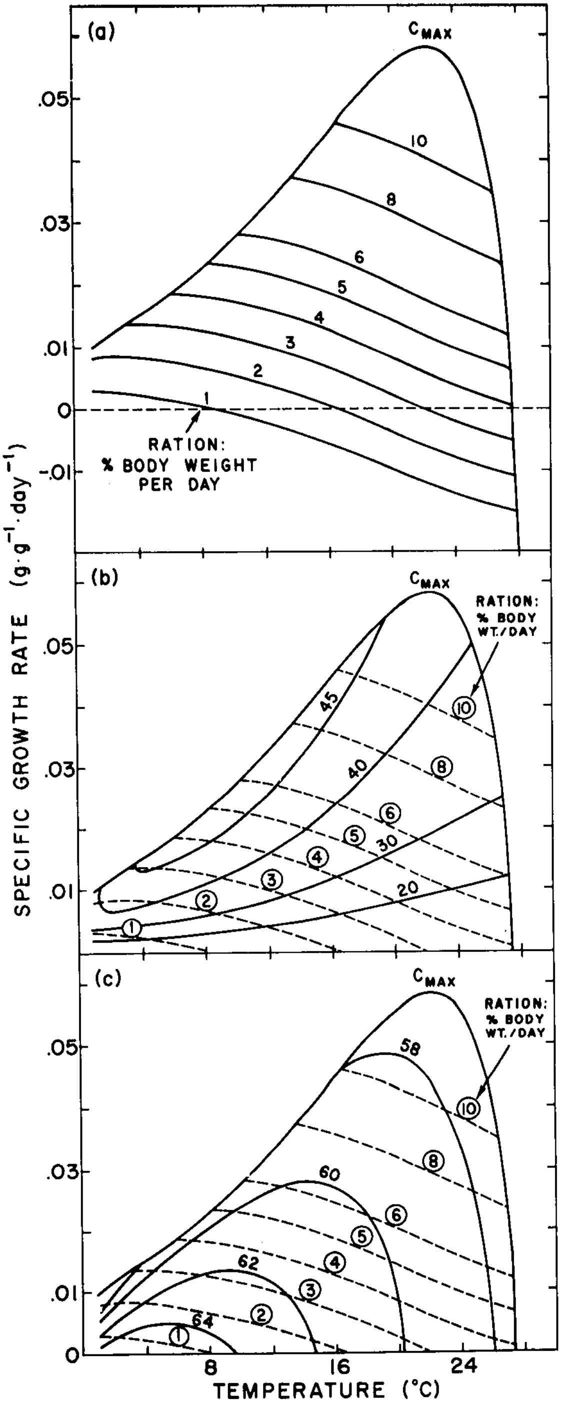

FIG. 5. (a) Specific growth rates for a 10 g perch as functions of temperature and specified ration levels ranging from 1% of body weight to maximum. (b) Relations between gross conversion efficiency (isopleths, %) and temperature for a 10 g perch when gross efficiency (%) = $(\Delta B/C) \times 100$. Isopleths (solid lines) are plotted from simulations at those specified ration levels represented by broken lines. (c) Relations between net growth efficiency (isopleths, %) and temperature as described for Fig. 5b when net efficiency (%) = $[\Delta B/(C - \text{Maintenance})] \times 100$.

yellow perch in western Lake Erie using the parameter values for adult fish in Tables 1 and 3 as nominal values. The simulation used a temperature curve (Fig. 8b) derived from observed temperatures in western Lake Erie. We assumed that perch orient to their preferred temperature, and that water of this temperature was available throughout the summer although surface temperatures higher than preferred were observed. Under these conditions simulated growth of a yearling perch with a starting weight of 9 g was 51 g in 1 yr for a final weight of 60 g.

Each parameter was separately varied ±10% and the simulation rerun. Temperature inputs, such as optimum temperature for consumption (T_o) and preferred temperature (T_p), were varied ±1 deg. C.

The model sensitivity of yearly growth for each parameter is

$$s(p) = \frac{p \cdot \Delta(\Delta B)}{\Delta B \cdot \Delta p},$$

where $s(p)$ = yearly growth sensitivity for p,
p = nominal value of parameter p (Table 1),
Δp = input deviation of parameter p,
ΔB = nominal yearly growth ($B_1 - B_o$),
$\Delta(\Delta B)$ = change in simulated yearly growth due to Δp,
B_o = weight at beginning of year,
and B_1 = weight at end of year.

Since $p = 10 \cdot \Delta p$ (except for temperature parameters), sensitivities for parameters were calculated by

$$s(p) = \frac{10 \cdot \Delta(\Delta B)}{\Delta B}$$

A sensitivity of $s(p) = \pm 1.0$ means that a change of parameter p by 10% causes a resultant 10% change in simulated yearly growth. Sensitivities of $|s(p)| > 1.0$ indicate higher sensitivities of simulated growth to p; values of $|s(p)| < 1.0$ indicate lower sensitivities. For example, $s(p) = -0.5$ means that, for a 10% change (or error of estimate) of input parameter p, simulated yearly growth decreased by 5%.

Results and conclusions — Results of the sensitivity analysis (Fig. 6) can be interpreted with respect to both the internal operation of the modeling equations and the intrinsic function of each parameter. Analysis of internal operation is of most utility in evaluating the degree of success with which the model simulates the intended bioenergetic relationships. As such, this type of analysis is most useful to the modeler and is discussed only briefly. A second use of the sensitivity analysis is to assess the importance of the relations between the biological meaning of each parameter and the output, yearly fish growth.

The sensitivities calculated are self-normalizing and give a good measure of the relative importance of each parameter to simulated annual fish growth (Fig. 6). These results are strictly applicable only to the specific simulation analyzed. For conditions of other lakes, year-classes, and growth assumptions, the results may be considerably different. For instance, the model sensitivities for changes of 1 deg. C in maximum temperatures of respiration and consumption are low for the Lake Erie simulations, but might be very high for systems with higher summer temperatures.

We emphasize that this analysis is done for yearly growth sensitivity. If yearly growth is known and the model is used to estimate consumption, sensitivities of consumption output to errors of parameter estimates would be much lower. Preliminary results indicate that estimation of consumption in this manner provides accurate output despite relatively large uncertainties in the values of nonconsumption related parameters. We consider that the model will be a powerful tool for evaluating predator–prey systems.

For the simulations performed, parameters with highest overall sensitivity are P and a_1. Although they operate identically in the model, each has a different meaning. The parameter a_1 defines the amount of food a perch can eat; P is the proportion of a_1 that a perch actually eats. High sensitivities of P and a_1 do not adversely affect the operation of the model as it was used for simulations presented below, since P is the parameter

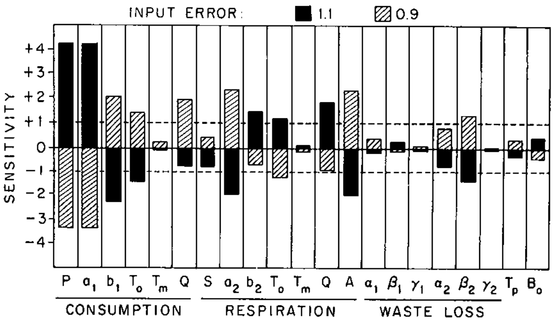

FIG. 6. Normalized sensitivities to 10% changes (1.1 × or 0.9 × nominal value) of each parameter used to simulate yearly growth for age I+ yellow perch in the western basin of Lake Erie. In addition to the parameters given in Table 1, others are defined in the equation series and text.

used to fit observed growth. The sensitive respiration parameters a_2 and A have the same operational relation to each other as do a_1 and P. The assymetry of both Q sensitivities stems from the extreme nonlinearity of the temperature dependence of both respiration and consumption.

Sensitivity of the model to errors in the estimate of different parameters varies considerably. The degree to which these sensitivities represent uncertainty in estimation of yearly fish growth is related to how well the phenomenon represented by the parameter is known. For example, growth is highly sensitive to errors in A, the level of in situ metabolism, which is poorly known. Refinement of the lethal temperature parameter (T_m for respiration), which is well known and has a low sensitivity, would not contribute substantially to our present understanding of the growth process.

New research is most needed on those relationships which are most critical to fish growth (high sensitivity) and which are least well known. We attempt to identify areas of greatest need for research using these considerations. The availability of estimates for a given parameter is a complex function of the adequacy and frequency of measurement. Parameter sensitivities and our subjective judgments of the availability of estimates are classified as high, moderate, or low. The need for further research was judged by the following algorithm:

	Availability of Estimate		
Sensitivity	*High*	*Moderate*	*Low*
High	Moderate	High	High
Moderate	Low	Moderate	High
Low	Low	Low	Moderate

The results of this exercise are presented in Table 2. We conclude that the highest priority for percid research should be to determine the allometric specific rate functions (aB^{-b}) for maximum consumption and routine metabolism. These rates are highest in young-of-the-year fishes and the first year-class contributes a high proportion of the total production in many systems (e.g. Chadwick 1976). Estimates of the metabolic cost of daily activity ($\sim A$) in the field are difficult to make but might be worth pursuing as such measures might contribute importantly to our knowledge of ecological bioenergetics. The moderate sensitivity of excretion parameters was an unexpected result. Waste losses have been adequately evaluated for only one fish species, the brown trout (Elliot 1976a). Comparable studies on percids and other fishes may be useful.

TABLE 2. Summary of sensitivity analysis of model parameters and implications of need for further research. Qualitative evaluations are given as high (H), moderate (M), or low (L). Parameter symbols are those given in Table 1 and the text.

Parameter	Sensitivity	Availability of estimate	Need for further research
Consumption			
a_1	H	L[a,b]	H
b_1	H	M[a]	H
P	H	L[b,c]	H
T_o	M	H	L
T_m	L	L[a]	M
Q	M	M	M
Respiration			
A	H	L[b,c]	H
a_2	H	M[a]	H
b_2	M	M[a]	M
T_o	M	H	L
T_m	L	H	L
Q	M	H	L
S	M	M[a,b]	M
Waste Losses			
α_1	L	L[a]	M
β_1	L	L[a]	M
γ_1	L	L[a]	M
α_2	M	L[a]	H
β_2	M	L[a]	H
γ_2	L	L[a]	M
T_p	L	H	L
B_o	L	H	L

[a] Known for other species; derived by extrapolation of available yellow perch data.

[b] Measured in laboratory; poorly known and variable under natural conditions.

[c] Specified for simulations.

Simulated Growth of Lake Erie Yellow Perch

Applications of the model to available data are presented in this section and in the following two sections. Assumptions made are given as hypotheses and the simulation results should be viewed as such. Although many applications are possible, those presented are best viewed as examples chosen to demonstrate various components of the model.

Methods and assumptions — We conducted two simulations of yellow perch growth in Lake Erie (Fig. 7). In the first simulation, growth data presented by Jobes (1952) were fitted with the model using parameter values given in Tables 1 and 3 together with a water-temperature curve (Fig. 8b) for the western basin of the lake. Weight of fish at annulus formation was based on Jobes' data pooled for both sexes. For the second

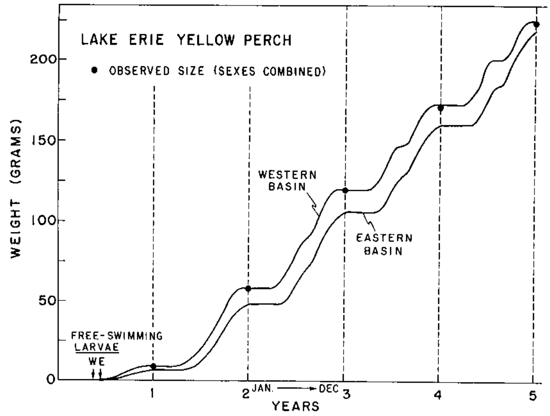

FIG. 7. Simulated growth of yellow perch under the thermal conditions of western and eastern Lake Erie. Observed growth data are from Jobes (1952); parameter values, from Tables 1 and 2; annual temperature data (Fig. 8b), from Burns (1976).

simulation, we used a water-temperature curve (Fig. 8b) for the extreme eastern end of Lake Erie; all other parameters were the same as in the first simulation. The eastern end of Lake Erie has an annual thermal cycle approximately one month behind that of the western basin (Burns 1976). Maximum summer temperatures of 23 °C in the eastern basin were lower than those (24 °C) recorded for the western basin during 1970. We assumed homothermous conditions in both areas of the lake.

Temperature optima and maxima for consumption and respiration rates of young-of-the-year fish were used for first-year growth. All other age-classes were assumed to be physiologically adult (Table 1). Young-of-the-year fish were assumed to prey exclusively on invertebrates. For the second year of growth the diet was assumed to be 50% invertebrates and 50% fishes. All older fish were assumed to be exclusively piscivorous. Values of α_1 for egestion were varied from 0.158 for invertebrates (Solomon and Brafield 1972) to 0.05 for fish prey (Kelso 1972) to estimate changes in food quality.

To begin the growth simulations, we assumed that spawning was initiated by spring water temperatures of 11 °C (Hokanson 1977), that hatching required 10 days, and that larvae were free swimming (weighing 0.04 g) 5 days after hatching. Simulations of growth were, therefore, begun 15 days after 11 °C was first determined in the annual thermal cycle. During winter months, consumption was assumed to be equivalent to maintenance rations; therefore, no growth occurs at temperatures $\leqslant 2.0$ C (Fig. 7). Values for P (Equation 2, Table 3) were adjusted for each year-class to yield the simulation results given in Fig. 7. Values for P approximate the ratio of the maximum potential and estimated (or realized) daily rates of food consumption.

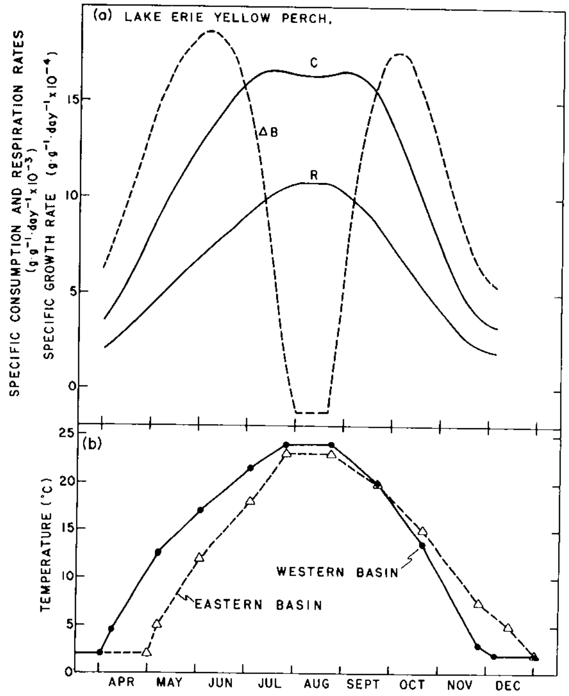

FIG. 8. (a) Simulated specific rates of food consumption, respiration, and growth for age IV+ yellow perch in western Lake Erie. (b) Cycles of surface water temperature for western (83°, W L.) and eastern (79°, W L.) Lake Erie during 1970. Data are from Burns (1976) with linear interpolations between observations.

TABLE 3. Weight data and parameter values used to simulate growth of yellow perch in Lake Erie.

Age-class	Weight (g) at annulus formation	α_1 for egestion	P for consumption
I	9	0.158	.522
II	58	0.100	.378
III	119	0.050	.309
IV	172	0.050	.284
V	224	0.050	.279

Results and conclusions — Simulation results for the thermal regime of western Lake Erie yield a virtually linear growth response for juvenile perch during those times of the year when growth occurs. For older, larger perch, growth is rapid during spring, slows or ceases during midsummer and resumes during fall months. Simulated growth of young-of-the-year perch suggests food consumption rates approximately one-half the estimated maxima ($P = 0.522$). Values for P decrease with age, implying an increasingly severe food limitation.

We determined specific rates of respiration, food consumption, and growth during the fifth year of growth (Fig. 8a). Although maintenance rations are lower for larger fish (Fig. 4), the allometric relations of food consumption and respiration rates make growth of larger fish markedly reduced by high midsummer temperatures. A distinctly bi-modal growth response emerges as size increases. Kitchell et al. (1974) discussed a similar bi-modal growth pattern observed in adults of many fish species. Also, see Forney (1977) on Oneida Lake walleye.

Respiration rates given in Fig. 8a generally reflect correspondence with existing water temperature. Consumption also parallels thermal conditions except during midsummer months, when the rates are nearly constant. As a result, the net energy available for growth is substantially reduced and a negative energy budget arises for maximum temperature conditions during August. A strongly bi-modal growth pattern results with growth during spring being greater than that during fall due to the allometric relations proposed for consumption and respiration.

Simulated growth of perch under the thermal regime of eastern Lake Erie (Fig. 7) emphasizes the thermal effect. Perch in the eastern basin are smaller at a given age than those in the western basin due to: (1) delayed hatching (assumed for the simulation) resulting in a reduced growing season during the first year and a smaller initial size for each subsequent year, and (2) reduced growth rates for young-of-the-year and juveniles (age I+) due to the lower thermal regime. For older fish, the differences are reduced; growth in the eastern basin shows less midsummer reduction, reflecting the lower maximum temperature.

Simulated Growth of Oneida Lake Walleye

Methods and assumptions — To evaluate applications of the model to walleye and to short-term growth data, we simulated growth of age III+ fish in Oneida Lake (Forney 1977) during that period of the year when growth occurred (May–September). Parameters given in Table 1 were assumed applicable to walleye except that thermal optima and maxima were reduced 1 deg. C for respiration and consumption; e.g. $T_o = 22°C$, $T_m = 27°C$ for C; and $T_o = 27°C$, $T_m = 32°C$ for R (Koenst and Smith 1976; Hokanson 1977). Assuming a 240-day ice-free period, a maximum midsummer temperature of 24°C, and an initial weight of 280 g, a value for $P = 0.4425$ yielded a final weight of 517 g, which is equivalent to that observed.

Using 27°C (Forney 1977) as the midsummer maximum, we also simulated walleye growth employing the same parameters as those for the 24°C simulation. Lastly, we assumed that walleye would behaviorally thermoregulate during midsummer, maintaining themselves in 22°C water when surface water temperatures exceeded 22°C during a cycle with a maximum of 27°C.

Results and conclusions — Although the 24°C simulation (Fig. 9) was fitted to the initial and final weights, the simulated growth underestimates the observed. The 22°C simulation, in which behavioral thermoregulation was assumed, more closely corresponds to the growth data for midsummer through late summer. High temperatures of the 27°C simulation result in weight loss during midsummer. Although growth occurs in spring and fall, net change in weight is negative under the ration levels specified.

It is important to note that all three simulations assume that only temperatures and body size determine ration levels. That condition is specified in a constant value of P. Intraseasonal changes

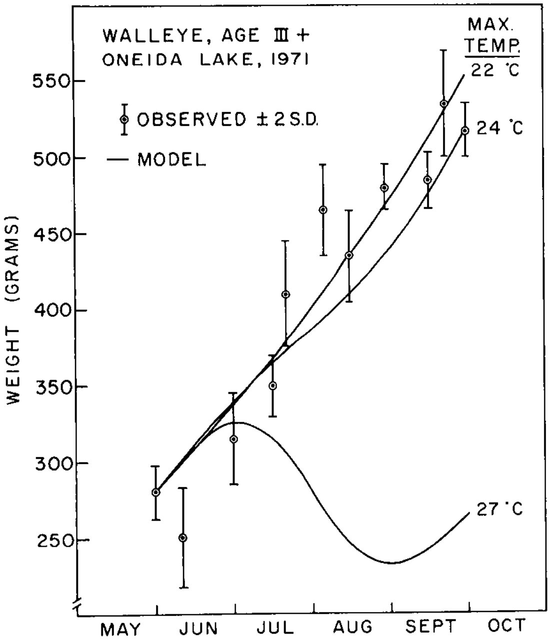

FIG. 9. Simulated and observed growth of age III+ walleye in Oneida Lake during 1971. Observed data are from Forney (1977). See text for explanation of assumptions regarding maximum summer temperatures. Water temperature during the ice-free period was simulated with a skewed sine function.

in food availability are not simulated. The observed data undoubtedly represent greater variation in actual feeding rates than that assumed by the simulations. However, the assumption of equivalent rations points to the very significant effect on growth rates of year-to-year and seasonal variation in temperature. Within the observed range, differences of only a few degrees in maximum summer temperatures can have marked effect on annual growth. Access to temperatures optimal for growth and behavioral thermoregulation in heterothermal environments may yield growth rates substantially different from those expected from the assumption of random distribution throughout the epilimnion.

Effects of food quality — To assess the relative importance of prey quality we varied the value of the egestion constant, α_1, to represent an all-fish diet ($\alpha_1 = .05$), an all-invertegrate diet ($\alpha_1 = .15$) and a mixed diet ($\alpha_1 = .10$). Each was simulated under the three thermal regimes and parameter values used for Oneida Lake. We assumed the energy cost of predation to be the same for all prey types.

Variations in food quality under a given thermal regime result in relatively small differences in total growth (Table 4). Given the same prey, thermal conditions can account for substantially greater differences in growth. The optimal condition of piscivory and thermoregulation results in fish twice the final size of those grown under conditions of an all-invertebrate diet with high midsummer temperatures.

Comparative Growth Responses

Although our model does not explicitly allow for competitive interactions, a simple comparative growth response under equivalent environmental conditions can provide some insights regarding competition between percids and sympatric fishes optimally adapted to other thermal regimes.

TABLE 4. Simulated final weights (g on day 269, October 1) of age III+ walleye in Oneida Lake, New York, as functions of varied thermal conditions and prey type. Initial fish weight was 280 g on May 30 (day 150). See text for details of assumed conditions of each simulation.

Maximum Temperatures	Proportion egested (α_1)		
	.05	.10	.15
24°C	517	479	443
27°C	265	250	235
22°C	551	509	470

Methods and assumptions — For simulation of these relations we used a hypothetical cold-water or salmon-like fish having 15°C as T_o for consumption and 19°C as T_o for respiration. Temperature maxima for the salmonid were 19°C for C and 23°C for R. For a hypothetical warmwater or centrarchid-like fish, we used thermal parameters given by Kitchell et al. (1974) for bluegills: $T_o = 27$, $T_m = 31$ for C; $T_o = 30$, $T_m = 34$ for R. All other parameters and those for a percid fish were taken from Table 1. Growth was simulated using the annual thermal regime (Fig. 8b) of western Lake Erie; an initial weight of 100 g was assumed and April 1 was designated as the beginning of the growing season. Two feeding levels were simulated with $P = 0.38$ or 0.25 for all three fish types (Fig. 10).

Results and conclusions — For the lower ration level, the warmwater or centrarchid-like fish appeared to be at maintenance rations throughout the April through December simulation period. The salmonid-like fish grew slightly in spring but lost weight during the warm summer months. The percid fish grew during spring and fall to a final weight of 119 g. At the higher rations levels, all three fish grew. However, the salmonid lost weight during periods of high temperature. Both the centrarchid and percid fish grew throughout the simulation period.

Three important conclusions arise from the simulation results. 1) In years when rations are relatively low, the seemingly slight growth advantage of the percid fish becomes cumulative. Assuming a parallel of growth, other components of fitness, and, ultimately, competitive superiority,

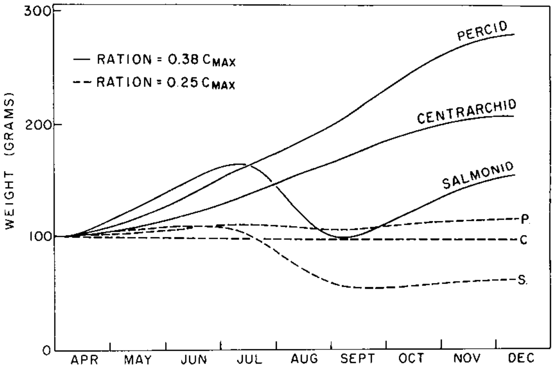

FIG. 10. Simulated growth at two ration levels for hypothetical warmwater, coldwater, and percid fishes in the western basin of Lake Erie.

slight differences in growth during any single year may ultimately result in dominance by one form over its competitors. 2) To accomplish annual growth equivalent to that of a percid in Lake Erie, the coldwater and warmwater fishes must consume substantially higher rations. 3) The most successful fishes in a homothermous system such as the western basin of Lake Erie are probably those with maximum growth rates at or about the maximum observed temperature.

These generalizations are most applicable to homothermous systems. As concluded from the Oneida Lake simulation, growth responses in a thermally stratified lake might be noticeably different. In heterothermous lake systems, the maximum growing season for a species may be at the southern limits of its range. These lakes provide near optimum water temperatures at some depth for the longest part of the year even though surface waters may become warm enough to retard growth. The largest individuals of any given species should be found near the periphery of the range dictated by high temperatures. This seems to be true for yellow perch and walleye (Scott and Crossman 1973).

General Discussion

As proposed, the model is best applied in attempts to evaluate growth responses of an average or typical member of the population under the average of environmental conditions. Implementation of reproduction and mortality functions allows simulations of the entire population. A known growth curve, a record of thermal experience during the observed period, plus estimates of feeding rates and prey types are the site-specific data sets neded for adequate applications of the model. Known components may be used to simulate an unknown. For instance, growth and temperature data are sufficient to estimate consumption and, hence, effect of a predator on its prey. Growth data are most readily available, complete thermal records and food habits studies less so, and measures of feeding rates scarce. The variation in growth which we hypothesize may be due to variation in temperature alone (Fig. 9) suggests that regular temperature measurement should become an integral part of future population and growth studies. Food habits studies have greatest value when employed in determining rates of feeding (Table 4, Fig. 5a).

The model is sufficiently general for application to a wide variety of fishes. To fully implement the energy budget model as conceived, critical data sets required for a given species include respiration and maximum consumption rates as functions of body size and temperature, plus egestion and excretion as functions of temperature and ration levels. These functions provide the boundaries to the scope for growth. Each species may have its characteristic bioenergetic boundaries, and once these are determined a greater understanding of the distributional and behavioral ecology of the species may be attained. Except for the excellent studies on salmonids (Brett et al. 1969; Elliot 1976b), bioenergetics data at temperatures near the upper and lower tolerance levels of most fishes are generally lacking. Also, a need exists for research on the bioenergetics of young-of-the-year fish.

The process of parameter determination would clearly be facilitated by an abundance of experimental data. Unfortunately, such data for percids are not available for many of the parameters in the equation series. Where data are lacking, we can only extrapolate from existing information and use the resultant formulation as an untested hypothesis. All parameters employed in our model may be directly measured; the extrapolations and assumptions are open to rigorous experimental evaluation.

Acknowledgments

J. Koonce, Case Western Reserve University, defined and implemented an earlier version of the model. D. Balsiger, University of Wisconsin, wrote the computer program and a user's guide for its application. This research was funded by the National Oceanic and Atmospheric Administration, Office of Sea Grant, Department of Commerce, through an institutional grant to the University of Wisconsin.

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