A SIMPLE METHOD FOR ESTIMATING THE FOOD CONSUMPTION OF FISH POPULATIONS FROM GROWTH DATA AND FOOD CONVERSION EXPERIMENTS[1]

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ABSTRACT

Experimental data on the gross food conversion efficiency of fishes (K_1 = growth increment/food ingested) are usually reduced to a model of the form $K_1 = aW^b$; it is shown that the model $K_1 = 1 - (W/W_\infty)^\beta$ has a number of advantages over the traditional model.

The new model can be used to compute the food consumption per unit biomass of an age-structured fish population, by relying on the first derivative of the von Bertalanffy growth formula (VBGF) to express growth increments, and the identity of W_∞ in the VBGF and in the model expressing K_1 as a function of weight.

Computed examples, using published growth and mortality parameters, and the results of food conversion experiments were used to obtain consumption estimates in a carnivorous grouper (*Epinephelus guttatus*) and an herbivorous angelfish (*Holacanthus bermudensis*). Results were shown to be most sensitive to the parameter β. Various applications of this simple model are discussed, particularly as a method to estimate key inputs in J. J. Polovina's ECOPATH model.

A multiple-regression extension of the basic model is presented which accounts for the impact of factors other than body weight on values of K_1 and β. This method is illustrated with an analysis of data on dab (*Limanda limanda*).

Estimating the quantity of food eaten during a certain period by a fish population from field data is usually a difficult task and various sophisticated methods developed for this purpose have data requirements which can make their routine application impossible (Beverton and Holt 1957; Ursin 1967; Daan 1973, 1983; Andersen 1982; Armstrong et al. 1983; Rice et al. 1983; Stewart et al. 1983; Pennington 1984; Majkowski and Hearns 1984). Polovina (1984) recently presented a technique for construction of ecosystem models which is structured around a well-documented computer program called ECOPATH (Polovina and Ow[3]). In situations where classical fishery data are sparse this technique has the potential of becoming a standard method for consolidating and examining the data available on aquatic ecosystems. ECOPATH estimates equilibrium biomass (B), annual production

(P), and annual consumption (Q) for each group in the model. ECOPATH requires a number of data inputs for each group treated in the model and usually the most difficult to obtain is the average food consumption per unit biomass (Q/B) of each group. The present study derives a method to estimate Q/B through a combination of experimental and field data that are easily obtained. In the process, a model is derived which will allow for more information to be extracted from feeding experiments than has hitherto been the case.

MODEL FOR REDUCING EXPERIMENTAL DATA ON THE CONVERSION EFFICIENCY OF FISHES

Usually laboratory or pond feeding experiments lead to estimates of K_1, the gross conversion efficiency, which are obtained, for short intervals, from

$$K_1 = \text{growth increment/food ingested} \quad (1)$$

(Ivlev 1939, 1966).

Usually, K_1 declines with body size (other factors affecting K_1 are discussed below) and it has become

a standard procedure to plot empirical values of K_1 obtained against the corresponding body weights, i.e., the mean weights (W) corresponding to each growth increment, or

$$\log_{10} K_1 = \log_{10} a + b \log_{10} W \qquad (2)$$

which leads to the model

$$K_1 = aW^b. \qquad (3)$$

(See Sprugel 1983 for a method to correct the bias due to log transformation in this and the other models below.) A discussion of this model may be found in Jones (1976) (see Figure 1a for an example).

This model has three liabilities, the first of which is the most serious:

1) The parameters "a" and "b" have no biological meaning, i.e., cannot be predicted from one's knowledge of the biology of a given fish. Converse-
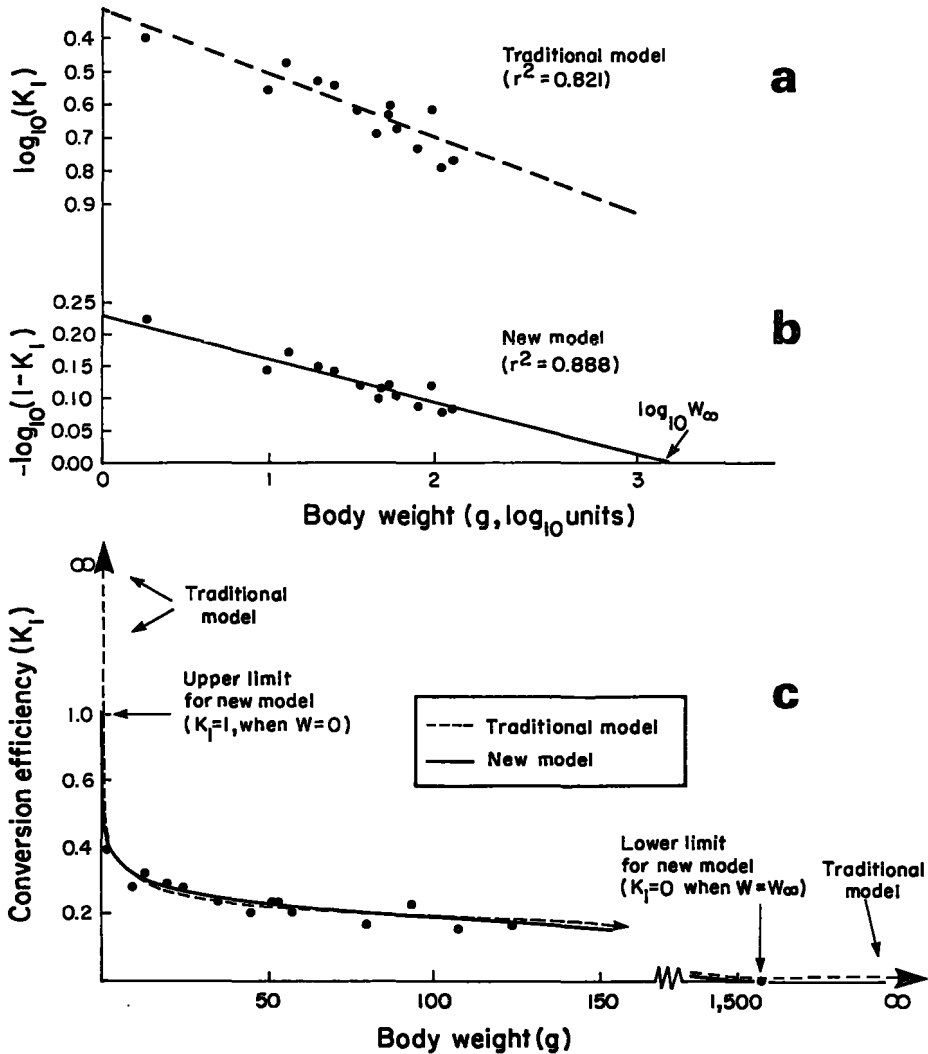

FIGURE 1.—Relationship of gross food conversion efficiency (K_1) and body weight (W) in *Channa striata*. a) Plot of $\log_{10}K_1$ on $\log_{10}W$, as needed to estimate parameters "a" and "b" of traditional model for prediction of K_1 from body weight. b) Plot of $-\log_{10}(1-K_1)$ on $\log_{10}W$, as needed to estimate parameters W_∞ and β of new model. c) Comparison of the two models. Note that both fit the data well over the range for which data points are available, but that the traditional model provides nonsensical results beyond this range (see text). Based on the data in Pandian (1967).

ly, these parameters do not provide information which can be interpreted via another model.

2) The model implies values of $K_1 > 1$ when $a^{-1/b} > W > 0$, which is nonsensical.

3) The model implies that, except when $W = 0$, K_1 is always > 0, even in very large fish, although it is known that fish cannot grow beyond certain species-specific and environment-specific sizes, whatever their food intake.

The new model proposed here has the form

$$K_1 = 1 - (W/W_\infty)^\beta \qquad (4)$$

with β as a constant and W_∞ as the weight at which $K_1 = 0$. The model implies that $K_1 = 1$ when $W = 0$, whatever the values of β and W_∞ (see Discussion for comments on using values other than 1 as upper bound for K_1 in Equation (4)). The new model can, as the traditional model, be fitted by means of a double logarithmic plot:

$$C = \beta \log_{10} W_\infty - \beta \log_{10} W \qquad (5)$$

where $C = -\log_{10} (1 - K_1)$, the sign being changed here to allow the values of C to have the same positive sign as the original values of K_1. Interestingly, it also appears that negative values of K_1 (based on fish which lost weight), which must be ignored in the traditional model, can also be used in this model (as long as they do not drag the mean of all available K_1 values below zero, see Table 1), although their interpretation seems difficult.

The new model requires no more data, nor markedly more computations than the old one. It produces "possible" values of K_1 over the whole range of weights which a given fish can take. The values of W_∞, which represent the upper bound of this range can be estimated from

$$W_\infty = \text{antilog}_{10} (C \text{ intercept}/|\text{slope}|). \qquad (6)$$

Thus, while β has no obvious biological meaning, the values of W_∞ obtained by this model do have a biological interpretation, which is, moreover, analogous to the definition of W_∞ in the von Bertalanffy growth function (VBGF) of the form

TABLE 1.—Data on the food conversion efficiency of *Channa striata* (= *Ophiocephalus striatus*) (after Pandian 1967), *Epinephelus striatus* (after Menzel 1960), and *Holacanthus bermudensis* (after Menzel 1958).

Body weight (g)[1]	Food conv. (K_1)[2]	Transformed data		$C = -\log_{10}(1-K_1)$	Species and remarks
		$\log_{10} W$	$\log_{10} K_1$		
1.86	0.391	0.270	−0.408	0.215	
9.92	0.274	0.998	−0.562	0.139	
13.09	0.320	1.117	−0.495	0.167	
19.65	0.284	1.293	−0.547	0.147	
24.63	0.278	1.391	−0.556	0.141	
35.09	0.234	1.545	−0.631	0.116	
45.15	0.199	1.655	−0.701	0.096	*Channa striata*
50.70	0.227	1.705	−0.644	0.112	(see Figure 1)
51.30	0.235	1.710	−0.629	0.116	
57.00	0.208	1.756	−0.682	0.101	
79.80	0.177	1.897	−0.752	0.085	
93.80	0.232	1.972	−0.635	0.115	
107.50	0.157	2.031	−0.804	0.074	
123.80	0.166	2.093	−0.780	0.079	
216	0.247	2.334	−0.607	0.123	
285	0.219	2.455	−0.600	0.107	*Epinephelus guttatus*;
319	0.160	2.504	−0.796	0.076	$\overline{\log_{10} W} = 2.617$;
392	0.153	2.593	−0.815	0.072	$\bar{C} = 0.0894$
424	0.179	2.627	−0.747	0.086	(see Figure 2)
628	0.161	2.798	−0.793	0.076	
647	0.177	2.811	−0.752	0.085	
649	0.187	2.812	−0.728	0.090	
66	0.222	1.820	−0.654	0.109	*Holacanthus bermudensis* (28°C only)[3]
139	0.178	2.143	−0.750	0.085	$\overline{\log_{10} W} = 2.124$
256	−0.258	2.408	not defined	−0.100	$\bar{C} = 0.031$

[1]Mean of starting and end weights.
[2]Growth increment/food intake.
[3]Note that the experiment considered here was conducted with a food which led to deposition of fat, but not of protein (see also Table 2), a consideration that is ignored for the sake of this example.

$$W_t = W_\infty (1 - e^{-K(t-t_0)})^3 \qquad (7)$$

(von Bertalanffy 1938; Beverton and Holt 1957), and where W_t, the weight at time t, is predicted via the constants K, t_0, and W_∞, all three of which are usually estimated from size-at-age data obtained in the field (see Gulland 1983 or Pauly 1984a).

That W_∞ values obtained via Equations (2) and (6) are realistic can be illustrated by means of that part of the data in Table 1 pertaining to *Channa striata* (= *Ophiocephalus striatus*), the "snakehead" or "mudfish" of south and southeast Asia. These data give, when fitted to the traditional model

$$K_1 = 0.482W^{-0.205}. \qquad (8)$$

The same data, when fitted to the new model give

$$K_1 = 1 - (W/1,580)^{0.073}. \qquad (9)$$

(See Figure 1 for both models.) The value of W_∞ = 1,580 g is low for a fish which can reach up to 90 cm in the field (Bardach et al. 1972). However, its growth may have been reduced in laboratory growth experiments conducted by Pandian (1967).

Equation (6) used here to predict W_∞ is extremely sensitive to variability in the data set investigated, and two approaches are discussed to deal with this problem.

The first approach is the appropriate choice of the regression model used. In the example above (Equation (9)), the model used was a Type I (predictive) regression, which is actually inappropriate, given that

1) the $\log_{10} W$ values are not controlled by the experimentator and
2) regression parameters are required, rather than prediction of C values (see Ricker 1973).

The use of a Type II ("functional", or "Geometric Mean") regression appears more appropriate; conversion of a Type I to Type II regression (with parameters a', b') can be performed straightforwardly through

$$b' = b/|r| \qquad (10)$$

and

$$a' = \bar{C} - b' \overline{\log_{10} W} \qquad (11)$$

where r is the correlation coefficient between the C and the $\log_{10} W$ values (Ricker 1973). In the case

of the example here, one obtains with $r = 0.942$ a new model:

$$K_1 = 1 - (W/1,290)^{0.077} \qquad (12)$$

close to that obtained using a Type I regression, due to the high value of r of this example. However, in cases where the fit to the model is poor, the use of a Type II regression can make all the difference between realistic and improbable values of W_∞.

Another approach toward optimal utilization of the properties of the new model (4) is the use of "external" values of asymptotic weight, which will here be coded $W_{(\infty)}$ to differentiate them from values of W_∞ estimated through the model. In such case, β can be estimated from

$$\beta = \bar{C}/(\log_{10} W_{(\infty)} - \overline{\log_{10} W}) \qquad (13)$$

in which $W_{(\infty)}$ is an asymptotic size estimated from other than food conversion and weight data, e.g., from growth data or via the often observed closeness between estimates of asymptotic size and the maximum sizes observed in a given stock (see Pauly 1984a, chapter 4).

These two approaches are illustrated in the example below, which is based on the data in Table 1 pertaining to the grouper *Epinephelus guttatus*. When Equation (6) is interpreted as a Type I regression, these data yield a value of $W_\infty > 12$ kg, which is far too high for a fish known to reach 55 cm at most (Randall 1968). Interpreting Equation (5) as a Type II regression leads to a value of $W_\infty = 3.5$ kg which is realistic, although still not close to the asymptotic weight of 1,880 g estimated by Thompson and Munro (1977). Finally, using the latter figure as an estimate of $W_{(\infty)}$ yields the model

$$K_1 = 1 - (W/1,880)^{0.136} \qquad (14)$$

as a description of the relationship between K_1 and weight in *Epinephelus guttatus* (Fig. 2). The value of β in Equation (14) lies within the 95% confidence interval of the value of $\beta = 0.060$ which generated the first unrealistically high estimate of W_∞.

MODEL FOR ESTIMATING THE FOOD CONSUMPTION OF FISH POPULATIONS

When feeding experiments have been or can be conducted under conditions similar to those prevailing in the sea (food type, temperature, etc.), the
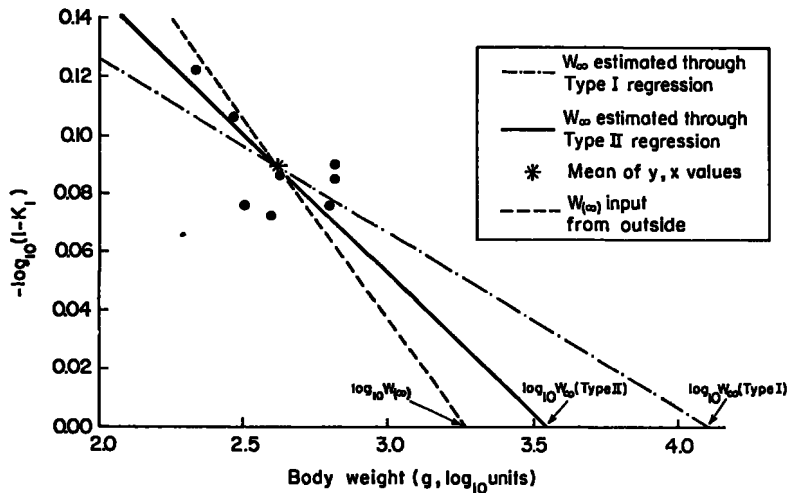
FIGURE 2.—Relationship between gross food conversion efficiency (K_1) and body weight in *Epinephelus guttatus*. Note that a Type I "predictive" regression leads to an overestimation of W_∞ while a Type II "functional" regression leads to a value of W_∞ close to an estimate of W_∞ based on growth data (see text). Based on data in Menzel (1960).

model presented above can be made a part of a model for estimation of food consumption per unit biomass (Q/B), provided a set of growth parameters is also used in which the value of W_∞ or $W_{(\infty)}$ is identical to that estimated from or used to interpret the feeding experiments.

In this case, inserting Equation (8) into Equation (5) leads to

$$K_{1(t)} = 1 - (1 - e^{-K(t-t_0)})^{3\beta} \qquad (15)$$

where $K_{1(t)}$ is the food conversion efficiency of the investigated fish as a function of their age t, and K, t_0, and β are as defined above.

Equation (1) is then rewritten as

$$dq/dt = (dw/dt)/K_{1(t)} \qquad (16)$$

where the "growth increment" is replaced by a growth rate (dw/dt) and the "food ingested" is also expressed as a rate (dq/dt). The growth rate of the fish is then expressd by the first derivative of the VBGF (Equation (7)) or

$$dw/dt = W_\infty\, 3K\, (1 - \exp(-Kr_1))^2 \cdot \exp(-Kr_1) \qquad (17)$$

where $r_1 = t - t_0$. Equations (17) and (15) may be substituted into Equation (16), which is a separable differential equation and may be solved by direct integration. The cumulative food consumption of an individual fish between the age at recruitment (t_r) and the age at which it dies (t_{max}) is thus

$$Q_c = W_\infty\, 3K \int_{t_r}^{t_{max}} \frac{(1 - \exp(-Kr_1))^2 \cdot \exp(-Kr_1)}{1 - (1 - \exp(-Kr_1))^{3\beta}}\, dt. \qquad (18)$$

The food consumption of a population should depend, on the other hand, on the age structure of that population. The simplest way to impose an age structure on a population is to assume exponential decay with instantaneous mortality Z, or

$$N_t = R\, e^{-Z(t-t_r)} \qquad (19)$$

where t_r is the age at recruitment (i.e., the starting age at which Z applies, assuming, if there is any fishery, that $t_r = t_c$, the mean age at first capture), R the number of recruits, and N_t is the number of fish in the population. As the model below assumes a stationary population, the food consumption of the population per unit time can be expressed on a per-recruit basis or

$$\frac{Q}{R} = W_\infty\, 3K$$

$$\int_{t_r}^{t_{max}} \frac{(1 - \exp(-Kr_1))^2 \cdot \exp(-(Kr_1 + Zr_2))}{1 - (1 - \exp(-Kr_1))^{3\beta}}\, dt$$

$$(20)$$

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where $r_2 = t - t_r$.

The biomass per recruit in fish whose growth can be described by Equation (7) is, according to the model of Beverton and Holt (1957; see also Ricker 1975, p. 253):

$$\frac{B}{R} = W_\infty (A_1 + A_2 + A_3 + A_4) \qquad (21)$$

where $A_1 = \dfrac{1 - e^{-Zr_3}}{Z}$

$$A_2 = \frac{-3 \, e^{-Kr_4} \left(1 - e^{-(Z+K)r_3}\right)}{Z + K}$$

$$A_3 = \frac{3 \, e^{-2Kr_4} \left(1 - e^{-(Z+2K)r_3}\right)}{Z + 2K}$$

and

$$A_4 = \frac{- \, e^{-3Kr_4} \left(1 - e^{-(Z+3K)r_3}\right)}{Z + 3K}$$

where $r_3 = t_{max} - t_r$

$r_4 = t_r - t_0.$

This model assumes, as does Equation (20), a stable age distribution.

Combining Equations (21) and (20) leads to the model for estimating Q/B, which has the form:

$$\frac{Q}{B} = \frac{3K \displaystyle\int_{t_r}^{t_{max}} \dfrac{(1 - \exp(-Kr_1))^2 \cdot \exp(-(Kr_1 + Zr_2))}{1 - (1 - \exp(-Kr_1))^{3\beta}} \, dt}{(A_1 + A_2 + A_3 + A_4)} . \qquad (22)$$

Equation (22) has only 6 parameters (K, t_0, t_r, t_{max}, Z, and β); of these, K and t_0 are estimated from growth data, while t_r and t_{max} can be set more or less arbitrarily (see text below and Figure 3). Total mortality (Z), which is here the equivalent of a production/biomass ratio (see Allen 1971) can be estimated easily, e.g., from length-frequency data and growth parameters (see Pauly 1982, 1984a: chapter 5) and is an input required anyway by the ECOPATH program (Polovina 1984). Thus only β and a "hidden" value of W_∞ applicable to both food experiment and growth data are needed in addition to the easily obtainable parameters required by this model.

APPLICATION EXAMPLE AND SENSITIVITY ANALYSIS OF THE MODEL

In the following application examples, the newly derived model (Equation (22)) is used to compare the food consumption of a tropical carnivore (*Epinephelus guttatus*) with that of a tropical herbivore (*Holacanthus bermudensis*). A list of the parameter values used is given on Table 2.

The solutions of Equation (22), inclusive of the integration of its numerator, were obtained by means of a short BASIC microcomputer program available from me. Note that the integration, which according to Equation (22) should be performed for the interval between two ages (t_r and t_{max}), can be performed for the intervals between two sizes (W_r, W_{max}), the age corresponding to these sizes being estimated from the inverse of Equation (7), i.e.,

$$t = t_0 - ((1/K) (\log_e (1 - W/W_\infty)^{1/3})). \qquad (23)$$

The results, i.e., the values of Q/B, expressed as a percentage on a daily basis are 0.76 for *E. guttatus* and 2.50 for *H. bermudensis*.

A sensitivity analysis of Equation (22) was performed, following the outline in Majkowski (1982). The results are given in Figure 3, which shows that of the six parameters of Equation (22), β is the one which has the strongest impact on the estimates of Q/B, while t_r has the least, the relationships between the importance of these parameters being best summarized by

$$\beta > K > Z \gg t_{max} > t_0 > t_r \qquad (24)$$

These results suggest that, when using this model, most attention should be given to an accurate estimation of β (see below). It should be also noted that β and K have opposite effects on the estimation of Q/B (see Figure 3). Thus, a biased (e.g., high) estimate of W_∞ will be associated with too low values of β and K which partially compensate each other.
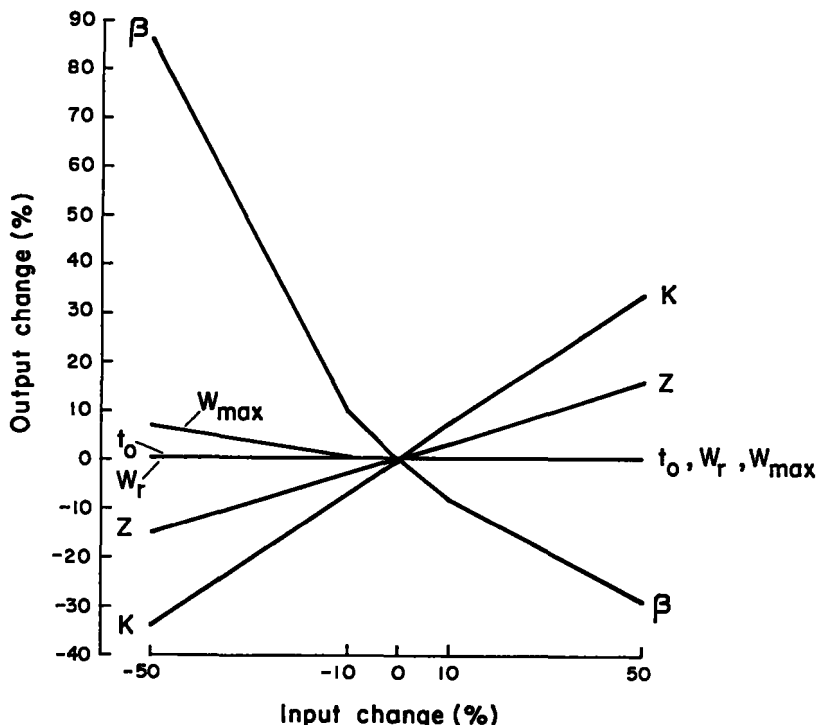
FIGURE 3.—Sensitivity analysis of Equation (22), based on parameter estimates in Table 4 for *Epinephelus guttatus*. Note strong effects of changes in β, intermediate effects of K and Z, and negligible effects of W_{max}, W_r, and t_0.

TABLE 2.—Properties and parameter values of *Epinephelus guttatus* and *Holacanthus bermudensis* relevant to the computation of their food consumption (based on data in Menzel 1958, 1960; See Table 1 and text).

Property/ parameter	Epinephelus guttatus	Holacanthus bermudensis
Asymptotic weight (g)	[1]11,880	[2]800
K (1/yr)	[1]0.24	[3]0.25
t_0 (yr)	[4]−0.2	−0.2
t_r (yr)	[5]0.35	[5]0.45
β	[6]0.136	[2]0.040
Z (1/yr)	[1]0.64	[7]0.72
t_{max} (yr)	[8]12	[8]12
food (in experiments)	fish (*Anchoa, Sardinella* and *Harengula*)	Algae (*Monostroma oxysperma* and *Enteromorpha satina*)

[1]From Thompson and Munro (1977); Z = 0.64 refers to an unfished stock and is thus an estimate of M.
[2]From data in Table 1 and Equation (13).
[3]Based on method in Pauly and Munro (1984) and on growth parameter estimates pertaining to members of the related family Acanthuridae, in Pauly (1978).
[4]Assumed; has little influence on results (see text and Figure 3).
[5]Corresponding to a fish of 1 g with growth parameters W_∞, K, and t_0 as given.
[6]See text and Figure 2.
[7]Based on equation (11) in Pauly (1980), with T = 28°, L_∞ = 30 cm, K = 0.25, and M = Z.
[8]Assumed; has little influence on results (see text and Figure 3).

QUANTITIES OTHER THAN Q/B ALSO ESTIMATED BY THE MODEL

In addition to estimating Q/B, the model presented above can be used to obtain other useful quantities; namely, 1) maintenance ration and related information, and 2) trophic efficiency.

Although there are differences between authors, maintenance ration is usually defined as the food used by fish to just maintain their weight at some "routine" level of activity. Usually, maintenance ration is estimated by feeding fish over a wide range of rations and determining by interpolation the ration generating neither weight gains nor losses (Jones 1976).

The model presented here allows the estimation of maintenance ration (even if fish have been fed constant rations) through extrapolation of weight-specific estimates of Q/B, such as presented in Figure 4 to the size W_∞, i.e., to the size at which, by definition, all food consumed by a fish is used for maintenance. In the case of the feeding data on *E. guttatus* analyzed here, an estimate of daily main-
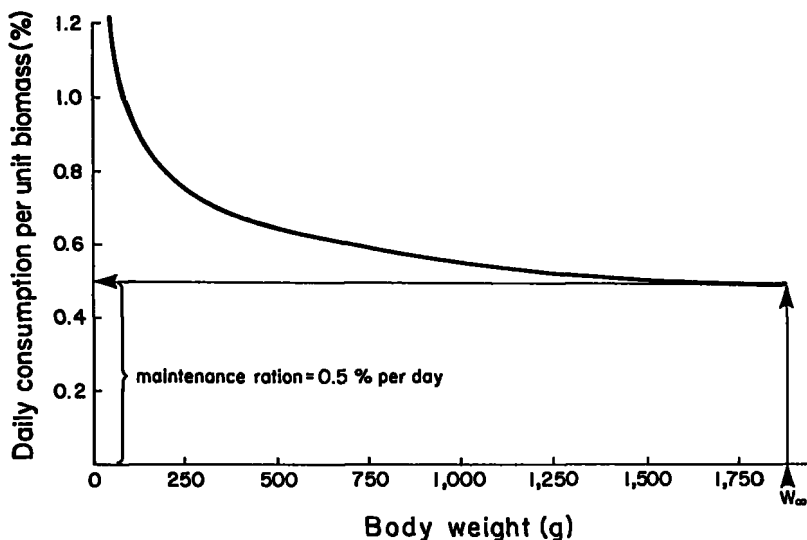
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FIGURE 4.—Size-specific estimates of food consumption per unit biomass in *Epinephelus guttatus*, as obtained by integrating Equation (22) over narrow ranges of weight, then plotting the resulting Q/B estimates against the midranges of the weights. Note definition of maintenance ration as "Q/B at W_∞".

tenance ration of 0.5% body weight per day is obtained (Fig. 4), while the corresponding value for *H. bermudensis* is 1.73%.

Using the computed output of Equation (22) one can also obtain an estimate of population trophic efficiency (E_T) from

$$E_T = Z \cdot (B/Q) \qquad (25)$$

which expresses production per unit food consumed, production being expressed here as total mortality (i.e., production/biomass ratio) times biomass (Allen 1971).

For *E. guttatus*, the estimated value of trophic efficiency is $E_T = 0.23$, i.e., slightly less than one quarter of the fish food eaten by a population of *E. guttatus* is turned into production. The corresponding value for *H. bermudensis* is $E_T = 0.08$, which is low, as should be expected in an herbivore.

ACCOUNTING FOR MULTIFACTOR EFFECTS ON K_1

Experimental data allowing for the estimation of values of W_∞ and β corresponding exactly to those to be expected in nature cannot be obtained, since no experimental design can account for all the environmental factors likely to affect the food conver-

sion of fishes in nature. Among the factors which can be experimentally accounted for are

1) ration size (Paloheimo and Dickie 1966; but see Condrey 1982),
2) type of food (see below),
3) temperature (Menzel 1958, Taylor 1958, Kinne 1960, and see below),
4) salinity (Kinne 1960).

Also, "internal states" affecting food conversion efficiency, such as the sex of the fish, previous thermal history, and stress undergone during an experiment, can be accounted for given a suitable experimental design.

One method of incorporating some of these factors into a linear form of the basic model (Equation (5)) is to extend the model into a multiple regression of the form

$$C = a - \beta \log_{10} W + b_1 V_1 + b_2 V_2 \ldots b_n V_n \qquad (26)$$

in which V_1, V_2, and V_n are factors which affect C ($= -\log_{10}(1 - K_1)$) after the effect of weight on C has been accounted for.

For example,

$$C = 0.363 - 0.0419W - 0.0116T$$

$$+ 0.0156S + 0.0488M \qquad (27)$$

is derived from the results of experiments conducted with dab (*Limanda limanda*) by Pandian (1970, figs. 5, 6)[4] in which the type of food, M (0 = herring meat, 1 = cod meat), and sex, S (0 = ♂, 1 = ♀), and the temperature, T (in °C) were reported in addition to the weight, W (in g and $\log_{10}$ units).

This model permits exact tests on the effects of each factor (Table 3), and permits adjusting parameter values (W_∞, β) so that they relate to conditions resembling those occurring in nature.

Then, W_∞ is estimated—at least in principle—from

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[4]A table listing all values extracted from figures 5 and 6 in Pandian (1970) is included in the document mentioned in footnote 1, and will be supplied on request by me.

$$W_\infty = \text{antilog}_{10} \, (1/\beta) \, (a + b_1V_1 + b_2V_2 \ldots b_nV_n).$$

(28)

This equation implies that there is, for every combination of V_1, V_2, ... V_n values, a corresponding value of W_∞. This is reasonable, as it confirms that W_∞ is environmentally controlled (Taylor 1958; Pauly 1981, 1984b). W_∞-values obtained through Equation (31) will generally be reliable—as was the case with the one-factor model (4)—only when a wide range of weights are included, variability is low, and the correct statistical model is used.

As a first approach toward an improved statistical model, one could conceive of a geometric mean multiple regression which, in analogy to a simple geometric mean regression, would be derived from the geometric mean of the parameters of a series of multiple regressions. This approach would involve, in the case of $n + 1$ variables (= $Y, Y_1, Y_2, \ldots Y_n$) in the following steps:

1) Compute the parameters of $n + 1$ Type I multiple regressions, where each regression (j) has another variable as dependent variable (i.e., Y, then $Y_1, Y_2, \ldots$ to Y_n; see $j = 1$ to 5 in Table 4).

2) Solve each of the j equations for the "real" dependent variable ($Y = C$, see $j = 6$ to 10 in Table 4).

3) Compute the geometric mean of each partial regression coefficient from

$$b_i{}' = (b_{1j} \cdot b_{2j} \cdot \ldots . b_{nj})^{1/n}.$$

(29)

4) Compute the intercept of the new Type II

TABLE 3.—Details of a Type I multiple regression to quantify the effects of some factors on the food conversion efficiency of dab (*Limanda limanda*) (see text footnote 3).

Source of variation	Degrees of freedom	Sum of squares	Mean squares
Regression	4	0.0813	0.0203
Residual	57	0.0516	0.0009
Total	61	0.1329	

$F_{(4,57)}$	22.465	$P < 0.001$	

multiple correlation = 0.7822
R^2 = 0.6119
Corrected R^2 = 0.5846
Standard error = 0.0301

Variable	Coefficient	t	SE	P
Weight	−0.041869	−3.926	0.0107	<0.001
Temp	−0.011584	−7.362	0.0016	<0.001
Sex	0.015635	1.982	0.0079	0.049
Meat	0.048840	5.301	0.0092	<0.001
Constant	0.363416	—	—	—

TABLE 4. Estimation of parameters in a "mixed" multiple regression (see also text).

j	Dependent variable	Constant ("a")		Independent variables and partial regression coefficients[1]							Remarks and R^2
1	C	= 0.363	−0.0419	W	−0.016	T	+0.0156	S	+0.0488	M	0.585
2	W	= 3.52	−5.08	C	−0.0820	T	+0.0693	S	+0.300	M	0.199
3	T	= 23.1	−2.45	W	−42.1	C	+1.07	S	+1.94	M	0.490
4	S	= −1.30	+0.151	W	+0.0780	T	+4.13	C	−0.285	M	0.035
5	M	= −2.32	+0.341	W	+0.0739	T	−0.149	S	+6.76	C	0.295
6	C	= 0.363	−0.419	W	−0.0116	T	+0.0156	S	+0.0488	M	—
7	C	= 0.693	−0.197	W	−0.0161	T	+0.0136	S	+0.0591	M	—
8	C	= 0.549	−0.0582	W	−0.0238	T	+0.0254	S	+0.0461	M	—
9	C	= −0.315	−0.0366	W	−0.0189	T	+0.242	S	+0.0690	M	not used,
10	C	= −0.345	−0.0504	W	−0.0109	T	+0.0220	S	+0.148	M	see text

mean partial regression coefficients: b_j = −0.0783   −0.0164   +0.0175   +0.0510
(for j = 6-8)

| 11 | 0.1564 = a' − (0.0.83 · 1.738) − (0.164 · 13.32) + (0.0175 · 0.581) + (0.051 · 0.226) | | | | | | | | | | |
| 12 | C | = 0.4892 | −0.0783 | W | −0.0164 | T | +0.0175 | S | +0.051 | M | final result |

[1]Note that body weight (W) is here expressed in $\log_{10}$ units.

multiple regression from

$$a' = \bar{Y} - (b_1'\bar{Y}_1 + b_2'\bar{Y}_2 \ldots + b_n'\bar{Y}_n) \qquad (30)$$

where the $\bar{Y}_i$ are the means of the Y_i-values and b_i' the geometric mean partial regression coefficients.

This method cannot be used here without modification because in most cases the multiple regression is "mixed" (Raasch 1983), consisting of variables which can be expected to generate normally distributed residuals when used as dependent variables (here: C, W, T) as well as "dummy" or binary variables (S, M) which cannot generate normally distributed residuals when they are used as dependent variables.

As might be seen in Table 4, the use of dummy variables as "dependent" variables generates unstable interrelationships between the remaining variables, making the computation of meaningful mean partial regression coefficients impossible.

The best solution here seems to omit for the computation of the mean regression coefficient those multiple regressions which have binary variables as "dependent" variables; Table 4 illustrates this approach.

The mixed model so obtained is

$$C = 0.489 - 0.0738W - 0.0164T + 0.0175S$$

$$+ 0.0151M \qquad (31)$$

which corresponds to the standard model

$$C' = 0.62W' - 0.90T' + 0.19S' + 0.46M' \qquad (32)$$

in which the original variables C, W, T, S, and M are expressed in standard deviation units and in which the slopes (= path coefficients, see Li 1975) allow for comparing the effects of W, T, S, and M on C. These variables suggest that with regards to their impact on C,

$$T > W > M \gg S. \qquad (33)$$

See Li (1975) for further inferences based on path coefficients.

In the southern North Sea in late summer-early autumn, *Limanda limanda* experiences temperatures usually ranging between 10° and 20°C (Lee 1972). Solving Equation (31) for $T = 18$°C, the highest temperature in Pandian's experiments (i.e., assuming the higher late summer-early autumn temperatures limit W_∞) leads to estimates of $W_\infty =$

500 g for the females and 298 g for the males, compared with the values of 756 and 149 g obtained by Lee (1972) on the basis of growth studies.

Estimating values of β that are wholly compatible with the latter estimates of W_∞ is straightforward, however, since it consists of solving Equation (31) for $T = 18$°C, $M = 0$, and the appropriate value of S, based on the equation

$$\beta = 1/\log W_{(\infty)} (a + b_1'V_1 + b_2'V_2 \ldots b_n'V_n) \quad (34)$$

In the present case, this leads to β values of 0.073 and 0.089 for females and male dab, respectively. The "average" relationship (if such exists) between food conversion efficiency and body weight in female dab fed herring meat is thus

$$K_1 = 1 - (W/756)^{0.073} \qquad (35)$$

while for males it is

$$K_1 = 1 - (W/149)^{0.089} \qquad (36)$$

with both values of β within the 95% confidence interval of the first estimate of β (in Equation (27), see Table 3).

DISCUSSION

The model presented here for the computation of Q/B is not meant to compete against the more sophisticated models whose authors were cited above. Rather, it was presented as a mean of linking up the results of feeding experiments with elements of the theory of fishing such that inferences can be made on the food consumption of fish populations which 1) do not invoke untenable assumptions, 2) make maximum use of available data, and 3) do not require extensive field sampling.

A distinct feature of the method is that it does not require sequential slaughtering of fish for the estimation of their stomach evacuation rate, nor field sampling of fish stomachs, which may be of relevance when certain valuable fishes are considered (e.g., coral reef fishes in underwater natural parks).

Several colleagues who reviewed a draft version of this paper suggested that Equation (4) should incorporate an upper limit for K_1 smaller than unity. This model would have the form

$$K_1 = K_{1max} - (W/W_\infty)^{\beta_m} \qquad (37)$$

with parameters W_∞ and β_m identical and analogous respectively to those in Equation (4) and a value of

K_{1max} to be estimated independently prior to fitting Equation (37) to data.

Data do exist which justify setting the upper limit of K_1 at or near unity. They pertain to fish embryos, whose gross conversion efficiency can be defined by

$$K_1 = \frac{W_h}{W_e - W_y} \qquad (38)$$

where W_h is the larval weight at hatching, W_e the egg weight, and W_y is the weight of the yolk sac at hatching. Values of K_1 as high as 0.93 have been reported using this approach (From and Rasmussen 1984), extending further toward unity the range of K_1 values reported by earlier authors, e.g., 0.85 in *Solea solea* (Flüchter and Pandian 1968), 0.79 in *Sardinops caerulea* (Lasker 1962), and 0.74 in *Clupea harengus* (Blaxter and Hempel 1966).

Thus, for a wet weight of 0.5 mg corresponding to a spherical egg of 1 mm diameter, one obtains, using Equation (14) for *E. guttatus*, a value of K_1 = 0.87 which is within the range of K_1 values given above. This example is not meant to suggest that K_1 values pertaining to large fish should be used in combination with the model presented here to "estimate" K_1 in eggs or larvae. Rather, it is meant to illustrate the contention that, of the possible choices of an upper bound for K_1 in Equation (4), the one selected here has the feature of making the model robust, particularly with respect to high values of K_1 and extrapolations toward low values of W.

Apart from β, the key elements of the model (isometric von Bertalanffy growth, constant exponential decay, steady-state population) are all parts of other, widely used models. Thus, whether estimates of Q/B obtained by this model are considered "realistic" or not will depend almost entirely on the value of β used for the computation.

There are several ways of reducing the uncertainty associated with β. The following may need special consideration:

1) Feeding experiments used to estimate β could be run so as to mimic as closely as possible the crucial properties of the habitat in which the population occurs whose Q/B value is estimated, inclusive of seasonally oscillating factors.

2) Further research and study should lead to the identification of anatomical, physiological, and ecological properties of fish correlating with their most common value of β.

3) An additional parameter could be added to account for fish reproduction, which is not explicitly considered in Equation (22).

Little needs to be said about item 1 which should be obvious since (except in the context of aquaculture) feeding and growth experiments are conducted in order to draw inferences on wild populations. With regards to item 2, it suffices to mention that relative gill area (= gill surface area/body weight), which appears to a large extent to control food conversion efficiency (Pauly 1981, 1984b), should be a prime candidate for correlational studies. Item 3 could cause Q/B values obtained by the model presented here to substantially underestimate actual food consumption, were it not for three circumstances which produce opposite tendencies:

a) The assumption that the energy needed by fish to develop gonads is taken from the energy otherwise available for growth may not apply (Iles 1974; Pauly 1984b). Rather, the reduction of activity occurring in some maturing fish may more than compensate for the energy cost of gonad development (Koch and Wieser 1983).

b) Growth parameters are usually computed using size data from fish whose gonads have not been removed, thus accounting for at least a fraction of the food converted into gonad tissue. When the value of Z used in the model is high, this fraction will be large because the contribution of the older fish to the overall estimate of Q/B will be small.

c) Experimental fish are usually stressed and therefore have lower conversion efficiencies than fish in nature, even though they may spend little energy on food capture (see Edwards et al. 1971). This effect leads to low values of β and hence high estimates of Q/B.

Because of these factors, the values of Q/B obtained by the method proposed here may lack a downward bias.

ACKNOWLEDGMENTS

LITERATURE CITED

ALLEN, K. R.
1971. Relation between production and biomass. J. Fish.

Res. Board Can. 28:1573-1581.

ANDERSEN, K. P.
1982. An interpretation of the stomach contents of fish in relation to prey abundance. Dana 2:1-50.

ARMSTRONG, D. W., J. R. G. HISLOP, A. P. ROBB, AND M. A. BROWN.
1983. A preliminary report on the analysis of whiting stomachs collected during the 1981 North Sea Stomach Sampling Project. ICES. Doc. C.M. 1983/G:59.

BARDACH, J. E., J. H. RYTHER, AND W. O. MCLARNEY.
1972. Aquaculture: the farming and husbandry of freshwater and marine organisms. Wiley-Inter-Science, N.Y., 868 p.

BERTALANFFY, L. VON.
1938. A quantitative theory of organic growth (Inquiries on growth laws. II). Hum. Biol. 10:181-213.

BEVERTON, R. J. H., AND S. J. HOLT.
1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish Food (G.B.) Ser. II, Vol. 19, 533 p.

BLAXTER, J. H. S., AND G. HEMPEL.
1966. Utilization of yolk by herring larvae. J. Mar. Biol. Assoc. U.K. 46:219-234.

CONDREY, R. E.
1982. Ingestion-limited growth of aquatic animals: the case for Blackman kinetics. Can. J. Fish. Aquat. Sci. 39:1585-1595.

DAAN, N.
1973. A quantitative analysis of the food intake of North Sea cod, (Gadus morhua). Neth. J. Sea Res. 6:479-517.
1983. Analysis of the cod data collected during the 1981 stomach sampling project. ICES Doc. C.M. 1983/G:61.

EDWARDS, R. R. C., J. H. S. BLAXTER, U. K. GOPALAN, C. V. MATHEW, AND D. M. FINLAYSON.
1971. Feeding, metabolism, and growth of tropical flatfish. J. Exp. Mar. Biol. Ecol. 6:279-300.

FLÜCHTER, J., AND T. J. PANDIAN.
1968. Rate and efficiency of yolk utilization in developing eggs of the sole Solea solea. Helgol. Wiss. Meeresunters. 18:53-60.

FROM, J., AND G. RASMUSSEN.
1984. A growth model, gastric evacuation and body composition in rainbow trout, Salmo gairdneri Richardson 1836. Dana 3:61-139.

GULLAND, J. A.
1983. Fish stock assessment: a manual of basic methods. John Wiley and Sons, N.Y., 223 p.

ILES, T. D.
1974. The tactics and strategy of growth in fishes. In F. R. Harden-Jones (editor), Sea fisheries research, p. 331-345. Elek Sci. Books, Ltd., Lond., 511 p.

IVLEV, V. S.
1939. Balance of energy in carps. [In Russ.] Zool. Zh. 18: 303-318.
1966. The biological productivity of waters. J. Fish. Res. Board Can. 23(11):1727-1759. W. E. Ricker (transl.).

JONES, R.
1976. Growth of fishes. In D. H. Cushing and J. J. Walsh (editors), The ecology of the seas, p. 251-279. Blackwell Scientific Publications, Oxford.

KINNE, O.
1960. Growth, food intake, and food conversion in a euryplastic fish exposed to different temperatures and salinities. Physiol. Zoöl. 33:288-317.

KOCH, F., AND W. WIESER.
1983. Partitioning of energy in fish: can reduction of swimming activity compensate for the cost of production? J. Exp. Biol. 107:141-146.

LASKER, R.
1962. Efficiency and rate of yolk utilization by developing embryos and larvae of the Pacific sardine Sardinops caerulea (Girard). J. Fish. Res. Board Can. 19:867-875.

LEE, C. K. G.
1972. The biology and population dynamics of the common dab Limanda limanda (L.) in the North Sea. Ph.D. Thesis, Univ. East Anglia.

LI, C. C.
1975. Path analysis: a primer. The Boxwood Press, Pacific Grove, CA, 347 p.

MAJKOWSKI, J.
1982. Usefulness and applicability of sensitivity analysis in a multispecies approach to fisheries management. In D. Pauly and G. I. Murphy (editors), Theory and management of tropical fisheries, p. 149-165. ICLARM Conf. Proc. 9, 360 p.

MAJKOWSKI, J., AND W. S. HEARNS.
1984. Comparison of three methods for estimating the food intake of a fish. Can. J. Fish. Aquat. Sci. 41:212-215.

MENZEL, D. W.
1958. Utilization of algae for growth by the Angelfish Holacanthus bermudensis. J. Cons. Int. Explor. Mer 24:308-313.
1960. Utilization of food by a Bermuda reef fish, Epinephelus guttatus. J. Cons. Int. Explor. Mer 25:216-222.

PALOHEIMO, J. E., AND L. M. DICKIE.
1966. Food and growth of fishes. III. Relations among food, body size, and growth efficiency. J. Fish. Res. Board Can. 23:1209-1248.

PANDIAN, T. J.
1967. Intake, digestion, absorption and conversion of food in the fishes Megalops cyprinoides and Ophiocephalus striatus. Mar. Biol. (Berl.) 1:16-32.
1970. Intake and conversion of food in the fish Limanda limanda exposed to different temperatures. Mar. Biol. (Berl.) 5:1-17.

PAULY, D.
1978. A preliminary compilation of fish length growth parameters. Ber. Inst. f. Meeresk., Univ. Kiel No. 55, 200 p.
1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer 39:175-192.
1981. The relationship between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. Meeresforschung 28:251-282.
1982. Studying single-species dynamics in a tropical multispecies context. In D. Pauly and G. I. Murphy (editors), Theory and management of tropical fisheries, p. 33-70. ICLARM Conf. Proc. 9, Manila, 360 p.
1984a. Fish population dynamics in tropical waters: a manual for use with programmable calculators. ICLARM Studies and Reviews 8, Manila, 325 p.
1984b. A mechanism for the juvenile-to-adult transition in fishes. J. Cons. Int. Explor. Mer 41:280-284.

PAULY, D., AND J. L. MUNRO.
1984. Once more on the comparison of growth in fish and invertebrates. Fishbyte 2(1):21.

PENNINGTON, M.
1984. Estimating the average food consumption by fish in the field from the stomach contents data. I.C.E.S., Doc. C.M. 1984/H:28.

POLOVINA, J. J.
1984. Model of a coral reef ecosystem. I. The ECOPATH model and its application to French Frigate Shoals. Coral Reefs 3:1-11.

RANDALL, J. E.
  1968. Caribbean Reef Fishes. T.F.H. Publications, Neptune City, NJ, 318 p.
RASCH, D. (editor)
  1983. Biometrie: Einführung in die Biostatistik. VEB Dtsch. Landwirtschaftsverlag, Berl., 276 p.
RICE, J. A., J. E. BRECK, S. M. BARTELL, AND J. F. KITCHELL.
  1983. Evaluating the constraints of temperature, activity and consumption on growth of largemouth bass. Environ. Biol. Fishes 9:263-275.
RICKER, W. E.
  1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.
  1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.
SPRUGEL, D. G.
  1983. Correcting for bias in log-transformed allometric equa-

tions. Ecology 64:209-210.
STEWART, D. J., D. WEININGER, D. V. ROTTIERS, AND T. A. EDSALL.
  1983. An energetics model for lake trout, Salvelinus namay-cush: application to the Lake Michigan population. Can. J. Fish. Aquat. Sci. 40:681-698.
TAYLOR, C. C.
  1958. Cod growth and temperature. J. Cons. Int. Explor. Mer 23:366-370.
THOMPSON, R., AND J. L. MUNRO.
  1977. Aspects of the biology and ecology of Caribbean reef fishes: Serranidae (hinds and groupers). J. Fish. Biol. 12: 115-146.
URSIN, E.
  1967. A mathematical model of some aspects of fish growth, respiration, and mortality. J. Fish. Res. Board Can. 24: 2355-2453.

APPENDIX

List of symbols used in model development and illustration

A_1-A_4 — terms used in computation of biomass per recruit (Equation (21))

a — multiplicative term in equation linking K_1 and body weight (Equation (3))
— intercept of a Type I (multiple) linear regression

a' — intercept of a Type II (multiple) linear regression

b — slope of a Type I linear regression
— exponent in equation linking K_1 and body weight

b_c — slope of a Type I multiple linear regression

b' — slope of a Type II linear regression

b_i' — slope of a Type II multiple linear regression

B — biomass (under equilibrium condition)

β — exponent in model linking K_1 and body weight (Equation (4))

β_m — similar to β, but estimated jointly with K_{1max} (Equation (37))

C — $(-\log_{10}(1 - K_1))$

C' — same as C, but expressed in standard deviation units

dq/dt — rate of food consumption

dw/dt — rate of growth in weight

E_T — trophic efficiency, i.e., production by population/food consumption by population

i — counter for number of variables in a multiple regression

j — counter for number of multiple regressions

K — constant in VBGF

K_1 — gross conversion efficienty (Equation (1))

K_{1max} — hypothetical upper limit for K_1 (with $K_{1max} < 1$) (Equation (37))

M — instantaneous rate of natural mortality
— a dummy variable expressing food type (Equation (27))

M' — a dummy variable expressing food type in standard deviation units

n — number of partial regression coefficient used in computing a given value of b_i'

N — number of fish in population (Equation (19))

Q — food consumption of a population (per unit time)

Q/B — food consumption per unit biomass of an age-structured animal population

Q_c — cumulative food consumed by a single fish between ages t_r and t_{max} (Equation (22))

R — number of recruits (Equation (19))

r — product moment correlation coefficient

S — a dummy variable expressing sex

S' — a dummy variable expressing sex in standard deviation units

t — age

t_c — mean age at first capture (in an exploited stock)

t_0 — a parameter of the VBGF expressing the theoretical age at size zero

t_{max} — maximum age considered (= longevity)

t_r — mean age at recruitment to the part of the population considered when computing Q/B

T — temperature in °C

T' — temperature in °C, expressed in standard deviation units (Equation (32))

V_i — any variable beyond W which affects K_1

VBGF — the von Bertalanffy growth function

W — body weight (in log units in some cases)

W' — body weight (in $\log_{10}$ units), expressed in standard deviation units

W_c — weight of a fish egg

W_h — weight of a fish at hatching (yolk sac excluded)

W_{max} — body weight corresponding to t_{max}

W_r — body weight corresponding to t_r

W_t — mean weight at age t

W_y — yolk sac weight in a newly hatched fish

W_∞ — asymptotic weight in the VBGF or in new model (Equation (4))

$W_{(\infty)}$ — an estimate of asymptotic weight obtained indirectly (i.e., from data of a type different than those in model using value of $W_{(\infty)}$

Y_i — any variable included in a multiple regression

Z — instantaneous rate of mortality (= P/B ratio)