Food Conversion Efficiency and the von Bertalanffy Growth Function, Part II and Conclusion: Extension of the New Model to the Generalized von Bertalanffy Growth Function

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Abstract

The simple model relating food conversion efficiency (K_1) to body weight derived from the theoretical concepts behind von Bertalanffy's growth model, is extended here in the context of Pauly's generalization of that model. The exponent, which was fixed to 1/3 in the simple model, is in the extended model equivalent to 1-d, with d being the weight exponent of the anabolism term in Pauly's growth model. This makes the model applicable to fish for which the assumptions of the original (special) version of Bertalanffy's growth model are violated.

Introduction

In the first part of this contribution (Temming 1994) I derived a conversion model from the theoretical concepts of the von Bertalanffy growth model. Gross conversion (K_1) was expressed as growth rate divided by consumption rate, where growth rate was taken as in von Bertalanffy's model and consumption rate was assumed to be proportional to the anabolism term. The factor that relates anabolism with consumption was introduced as a model parameter A, defining the fraction of the ingested food that is available for the buildup of body substance. The resulting function took the form

$$K_1 = A \cdot \left(1 - \left(\frac{W_1}{W_\infty} \right)^{\frac{1}{3}} \right) \qquad ...1)$$

Equation (1) is closely related with Pauly's (1986) conversion model, where (A) is fixed to 1 and the exponent β is not predetermined to be 1/3.

Pauly (1981) has demonstrated that von Bertalanffy's assumption of anabolism being proportional to body weight to the power 2/3 can only be taken as a special case and that large and fast-growing fish tend to have higher weight exponents of anabolism than 2/3. For example, this ex-

ponent is about 0.95 in tuna. Pauly (1979, 1981) therefore presented an integrated version of the von Bertalanffy growth model which does not assume isometric growth of the physiologically limiting surface, and which includes a new parameter D, defined as the difference between the allometric exponent, a, of the limiting surface (surface = constant x length^a) and the exponent, b, of the length-weight relationship (weight = constant x length^b). D is related to d according to D = b·(1-d) and d = a/b.

A generalized conversion efficiency model is presented here which is based on the generalized von Bertalanffy growth model (*sensu* Pauly). In addition to this, it will be shown how food consumption can be estimated using either versions of the conversion model. Also, a closed equation can be derived for the calculation of food consumption per time interval, given the special version of the von Bertalanffy growth model.

Derivation of the conversion model from the generalized von Bertalanffy growth model:

$$\frac{dW}{dt} = \text{Anabolism} - \text{Catabolism} = E \cdot W_t^{\chi} - k \cdot W_t \qquad ...2)$$

As in the previous derivation, anabolism is assumed proportional to the consumption rate (dC/dt), with A being the fraction of the ingested food available for the buildup of body substance

$$\frac{dC}{dt} = \frac{1}{A} \cdot E \cdot W^{\chi} \qquad ...3)$$

Now gross conversion efficiency, K_1, is defined as weight gain per food intake in a given time interval. Thus,

$$K_1 = \frac{dW/dt}{dC/dt} = \frac{E \cdot W_t^{\chi} - k \cdot W_t}{(1/A) \cdot E \cdot W_t^{\chi}} \qquad ...4)$$

The constants E and k can be replaced by an expression based on the parameters commonly used in the VBGF

$$E = 3 \cdot K \cdot W_\infty^{D/b} \text{ and } k = 3 \cdot K \text{ giving}$$

$$K_1 = \frac{3 \cdot K \cdot W_\infty^{\%} \cdot W_t^{\%} - 3 \cdot K \cdot W_t}{(1/A) \cdot 3 \cdot K \cdot W_\infty^{\%} \cdot W_t^{\%}} \qquad ...5)$$

$$K_1 = A \cdot \frac{3 \cdot K \cdot W_t^{\%} \cdot \left(W_\infty^{\%} \cdot W_t^{\%}\right)}{3 \cdot K \cdot W_t^{\%} \cdot W_\infty^{\%}} = A \cdot \frac{W_\infty^{\%} - W_t^{\%}}{W_\infty^{\%}} \qquad \text{or}$$

$$K_1 = A \cdot \left(1 - \left(\frac{W_t}{W_\infty}\right)^{\%}\right) \qquad ...6)$$

Note that equation (6) simplifies to equation (1) if a = 2 and b = 3 (with D = b-a) as in the special VBGF.

How to estimate consumption per individual for a given time interval based on the VBGF and K_1

An equation for the estimation of the consumption per time interval can be derived from equation (3), if W_t is substituted by the corresponding function of time, in this case the generalized VBGF

$$W_t = W_\infty \cdot \left(1 - e^{-\frac{3 \cdot D}{b} \cdot K \cdot (t - t_0)}\right)^{b/D} \qquad ...7)$$

substituting in equation (3) and replacing E in equation (3) with conventional parameters of the VBGF gives

$$\frac{dC}{dt} = \frac{1}{A} \cdot 3 \cdot K \cdot W_\infty^{\%} \cdot \left(W_\infty \cdot \left(1 - e^{-\frac{3 \cdot D}{b} \cdot K \cdot (t - t_0)}\right)^{\%}\right)^{\%} \qquad ...8)$$

which simplifies to

$$\frac{dC}{dt} = \frac{1}{A} \cdot 3 \cdot K \cdot W_\infty \cdot \left(1 - e^{-\frac{3 \cdot D}{b} \cdot K \cdot (t - t_0)}\right)^{\%} \qquad ...9)$$

Equation (9) can be integrated numerically within limits t_1 and t_2 to give the consumption of an individual fish between ages t_1 and t_2. If, however, parameters "a" and "b" are set to the values of the special VBGF (with a = 2, b = 3, and D = b-a = 1), equation (9) simplifies to (10), for which an explicit, or "closed" solution can be derived through integration

$$\frac{dC}{dt} = \frac{1}{A} \cdot 3 \cdot K \cdot W_\infty \cdot \left(1 - e^{-K \cdot (t - t_0)}\right)^2 \qquad ...10)$$

$$C_t = \int \frac{1}{A} \cdot 3 \cdot K \cdot W_\infty \cdot \left(1 - e^{-K \cdot (t - t_0)}\right)^2$$

$$C_t = \frac{3}{A} \cdot W_\infty \cdot \left(-\frac{1}{2} \cdot e^{-2 \cdot K \cdot (t - t_0)} + 2 \cdot e^{-K \cdot (t - t_0)} + K \cdot (t - t_0)\right) \qquad ...11)$$

Consumption of an individual fish between ages t_1 and t_2 can now directly be computed by subtracting

$$C_{t_1 - t_2} = C_{t_2} - C_{t_1}.$$

Application examples

1) *Megalops cyprinoides*. The data on conversion efficiency for different weights are from Pandian (1967). The general conversion model (6) has been fitted to the data (Pandian's Table 3) by means of nonlinear regression (Marquart algorithm in SPSS for Windows). All three parameters and their lower and upper asymptotic 95%-limits have been estimated from the data:

A = 0.6 (-0.68/1.88);
W_∞ = 2,308 g (-11926/16543);
and D/b = 0.15, r^2 = 0.69
(-0.54/0.85).

Although the estimates seem reasonable, it is obvious from the wide confidence limits that one cannot obtain statistically reliable estimates just from a set of 14 data pairs on conversion efficiency and weight.

2) *Thunnus thynnus*. The data on K_1 vs weight were taken from Palomares (1987) and were originally based on Fig. 37 in Vincent (1981). The conversion model is fitted in three different ways: (i) with all parameters free as in example 1, (ii) with W_∞ fixed at the value estimated from growth data using the VBGF and D/b fixed to 1/3 and (iii) with W_∞ fixed at the value estimated from growth data using the generalized VBGF with a = 2.7 and b = 3 and with D/b fixed at 0.1 (Fig. 1). In cases (ii) and (iii) only parameter
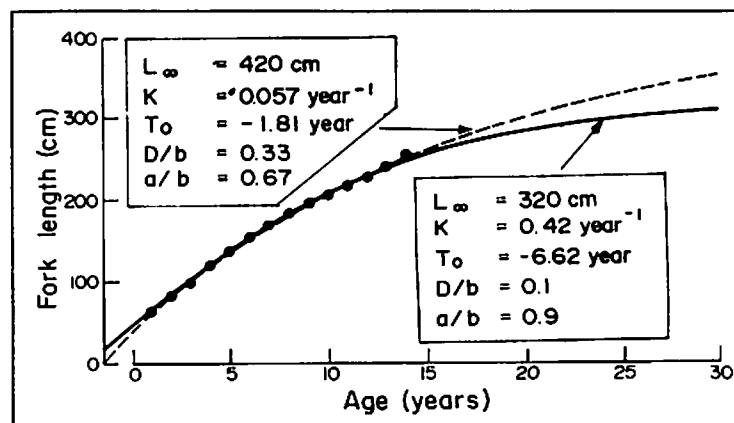

Fig. 1. *The generalized (solid line) and special (dotted line) versions of the VBGF, fitted to length-at-age data of bluefin tuna Thunnus thynnus (data from Hohendorf 1966, based on Sella 1929).*

A was estimated. Growth parameters for the special (D/b = 0.33) and the generalized (D/b = 0.1) version of the VBGF were estimated by means of nonlinear regression from data of Sella (1929) as given in Hohendorf (1966):

D/b = 0.33;
L_∞ = 420 (365/476);
K = 0.057 (0.045/0.070);
t_0 = -1.81 (-2.18/-1.43);
D/b = 0.1;
L_∞ = 320 (298/342);
K = 0.42 (0.36/0.48);
and t_0 = -6.62 (-7.52/-5.72)

where the values in brackets are the upper and lower 95% confidence limits.

The explained variance was very similar in both regressions, r^2 being 0.9989 in the special case and 0.9985 in the generalized case (L_∞ is given in cm, K in year^{-1} and t_0 in years). L_∞ was converted into W_∞ according to $W = 0.000017 \cdot L^3$ (Palomares 1987), giving 1,265 kg and 557 kg, respectively. Parameter estimates for the conversion models are given in Table 1 and Fig. 2. Although the conversion data comprise only 10 observations of fish between 0.4 and 27 kg, the generalized model (with parameters W_∞ and D/b fixed) fits the data better than the standard model ($r^2 = 0.85$ vs $r^2 = 0.55$).

Based on the estimates of A for both conversion models and the corresponding growth parameters W_∞ and D/b, equations (11) and (9) have been applied to calculate consumption per age group. Equation (9) was integrated numerically. The results are given in Fig. 3. It is obvious that differences between the model results are minor within the age range covered by the conversion experiments. If, however, the models are used to extrapolate beyond this range, the deviations between the predictions of the two models increase substantially.

portant consideration, however, because the growth model type must be related to the type of conversion model. Furthermore, since the quality (with regard to weight range and number of observations) of the conversion data is usually low, and since the choice of the version of the VBGF also determines the exponent D/b in equation (6), it will be possible in most practical cases to estimate only parameter A from the conversion data (see below).

Table 1. Parameter estimates of the conversion efficiency model fitted to data of *Thunnus thynnus*.

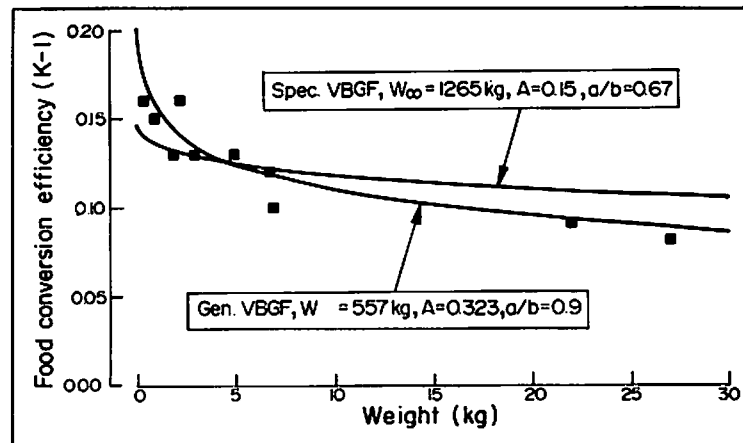| Method/model	Estimates and 95% conf. limits	D/b	W_∞ (kg)	A	r^2
All parameters estimated	Estimate	0.262	187	0.201	0.865
	upper	-0.298	-299	0.037	
	lower	0.822	973	0.367	
W_∞ and D/b fixed special VBGF	Estimate	[0.33]	[1,265]	0.15	0.545
	upper	fixed	fixed	0.134	
	lower			0.166	
W_∞ and D/b fixed general VBGF	Estimate	[0.1]	[557]	0.323	0.854
	upper	fixed	fixed	0.303	
	lower			0.342	

Fig. 2. *Fit of two different conversion models to data from Vincent (1981) on gross conversion efficiency of Thunnus thynnus.*
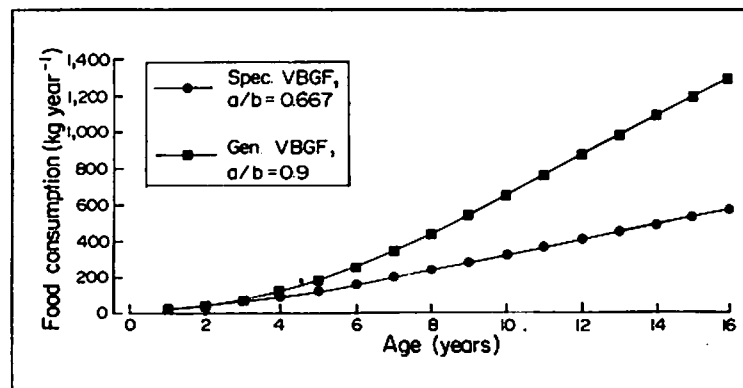

Fig. 3. *Consumption of Thunnus thynnus in kg·year⁻¹ by age group, as estimated with two different versions of the conversion model. Note that little deviation occurs between model predictions in the age range that was covered by the conversion experiments (approximately, ages 0-4).*

Discussion

How to apply the new model

It is obvious from the analysis presented here for the two sets of experimental data that reliable estimates (with narrow confidence limits) of the three model parameters cannot be obtained from data sets comprising some 10 to 15 observations and/or covering only a limited size range of experimental fish. But since the majority of the available data sets are comparable to the two examples presented here with regard to the number of fish and the investigated size range, there is a need to predefine at least one of the model parameters from other sources of information. If growth data are available, W_∞ can easily be taken from a fit of the VBGF to the data. Which version of the VBGF is applied to the data becomes an im-

Choice of the appropriate version of the VBGF

Following Pauly's (1981) line of arguments, the gills are the most likely candidates for the physiologically limiting surface in von Bertalanffy's growth model. Thus, the allometric exponent of gill growth can be taken also as the allometric exponent of anabolism. Food consumption and oxygen uptake are linked directly, if it is assumed that fish do not ingest more food, on average, than can be metabolized aerobically. There is supporting evidence for this link between food intake and oxygen uptake (summarized in Pauly 1981). Hence, the allometric exponent of food consumption is identical with that of anabolism and gill growth. Pauly (1981), following De Jager and Dekkers (1975) also argued that the allometric weight exponent of routine metabolism simply reflects the allometric exponent of gill growth. Based on this, he established a significant regression of the allometric exponents (both gill growth and routine metabolism exponents combined) on the logarithm of the maximum weight of the species. Thus, it should be possible to estimate the allometric exponent of anabolism from three different approaches: 1) from gill area measurements, 2) from routine metabolism measurements or 3) from information of maximum weights in a population. Since non-oxidative catabolism is always proportional to body weight, it is not necessary to estimate its exponent from other sources. Therefore the model type is determined, once the anabolism exponent is estimated. Since the majority of metabolic exponents are larger than 0.67 (because most fish get larger than guppies, from which $d \approx 0.67$), the generalized version of the VBGF will have to be used in most cases. Independent estimates of the consumption/anabolism exponent could also be derived from experiments on maximum food intake. Maximum food intake is usually considered as a power function of fish weight; its exponent should thus be identical with the allometric exponent of anabolism.

Experimental design for conversion experiments

The model requires estimates of the gross conversion K_1, ideally covering a wide range of weights for the species investigated. The problem is that the magnitude of K_1 depends on the size of the experimental meal, especially when the daily meals are close to the maintenance ration. The best approach would be to feed the experimental fish a daily ration equal to the amount which these fish would take in their natural environment. However, the daily meal in the sea is unknown (it is in fact the main output of this approach). The second best strategy seems to be *ad libitum* feeding, assuming that the fish are not food-limited in their environment. In either case, the fish must be kept under experimental conditions which closely resemble the natural conditions, especially with regard to diet composition, temperature and activity level.

The interpretation of parameter A

Parameter A quantifies the fraction of the ingested food that is available for the buildup of body substance. In the first part of this contribution (Temming 1994), I suggested that the nitrogen content of the food could be used to obtain an independent estimate of A, because it is strongly correlated with absorption efficiency (Pandian and Marian 1985). However, the extremely low values of A estimated for the tuna example indicate that other processes also contribute to the magnitude of A. Going back to the generalized VBGF (Pauly 1981), it can be stated that the 'catabolic' processes behind this model refer only to the non-oxidative breakdown of proteins down to the level of amino-acids. Therefore all processes which require oxygen are integrated under the 'anabolism' term. These processes are mainly (1) maintenance (blood circulation, osmotic work, breathing, etc.), (2) activity (swimming, foraging, etc.) and (3) digestion. Thus, parameter A, which relates food consumption and anabolism, can be considered as a transfer efficiency, defining the fraction of the total food energy that is finally available for the synthesis of new body material, after some fraction of the total food energy has been lost as feces (absorption efficiency *sensu* Pandian and Marian 1985) and some fraction has been used up for maintenance, swimming and digestion. Therefore, parameter A is probably not a good candidate for *a priori* estimation and it should - as done in the tuna example - preferably be estimated from the conversion data with b/D and W_∞ estimated from growth data.

Plausibility check of the consumption estimates derived for *Thunnus thynnus*

No estimates of food consumption in *T. thynnus* appear to be available apart from the study in Palomares (1987), summarized in Palomares and Pauly (1989). However, the yellowfin tuna, *Thunnus albacares*, is well studied with regard to bioenergetics and consumption (Kitchell et al. 1978; Olson 1981), and the estimates derived here for *Thunnus thynnus* can at least be compared with estimates for yellowfin tuna of the same size. Olson (1981) has estimated consumption based on stomach content samples and evacuation rates for four age classes of yellowfin tuna; his results are summarized in Table 2 together with results for *Thunnus thynnus* from this study. The estimates derived in this study are generally of the same order of magnitude as those given by Olson (1981), but for comparable length classes, the estimates for *Thunnus thynnus* amount to only 60% of the estimates for *Thunnus albacares*. Olson has compared his stomach content-based estimates with the results of a bioenergetic approach, which predicts for age classes 1 and 2 slightly higher, and for age classes 3 and 4 very similar consumption rates, if energetic costs for activity are assumed to be equal to the energetic costs of maintenance. He has also applied a more

Table 2. Comparison of consumption estimates of yellowfin and bluefin tuna by age group.

Study		Method	Age group 1	2	3	4
Yellowfin tuna	length range (cm)		30-55	55-88	85-122	122-160
Olson 1981	consumption (kg·fish⁻¹·year⁻¹)	stomach contents	32	75	168	512
Bluefin tuna	length range (cm)		40-62	62-83	83-103	103-121
This study	consumption (kg·fish⁻¹·year⁻¹)	spec. VBGF	22	43	69	98
		gen. VBGF	21	43	76	121

realistic calculation of the energy cost of activity based on measurements of swimming speeds in the sea, which gives consumption estimates for age class 1 slightly below, and for age class 2 comparable to the simple bioenergetic approach. From age 3 onwards, the consumption estimates of the improved bioenergetic approach increasingly exceed those of the simple model, indicating that the cost of swimming for age 4 tuna is even higher than twice the cost of maintenance. Compared with this, our estimates seem to be quite low. However, Kitchell et al. (1978) have ·estimated gross conversion efficiencies from bioenergetic balances for 1-kg skipjack tuna of only 9.6%, if fish swim at their minimum swimming speed. This value decreases further, down to 5.3% and 3.7%, if costs for swimming are assumed to be equal to or twice the cost of maintenance, respectively. The bluefin tuna data from Vincent (1981), which have been used here, give a gross conversion efficiency of 15% for a 1-kg bluefin tuna. This comparatively high value might reflect, apart from species-specific differences and food type effects, a low mean swimming speed during the experiments. This would imply that consumption estimates derived from these conversion efficiencies are underestimates of the real values. But it must not be overlooked, on the other hand, that K_1 values decrease with increasing weight until they become zero at W_{∞}, and that a 1-kg skipjack is much closer to its W_{∞} of 25 kg than is a 1-kg bluefin tuna, which has a W_{∞} of more than 300 kg. This could also at least partly explain the high K_1 of the 1-kg bluefin tuna.

References

De Jager, S. and W.J. Dekkers. 1975. Relations between gill structure and activity in fish. Neth. J. Zool. 25:276-308.

Hohendorf, K. 1966. Eine Diskussion der von Bertalanffy Funktion und ihre Anwendung zur Charakterisierung des Wachstums von Fischen. Kiel. Meeresforsch. 22:70-94.

Kitchell, J.F., W.H. Neill, A.E. Dizon and J.J. Magnuson. 1978. Bioenergetic spectra of skipjack and yellowfin tunas, p. 357-368. In G.D. Sharp and A.E. Dizon (eds.) The physiological ecology of tunas. Academic Press, New York.

Olson, R.J. 1981. Feeding and energetic studies of yellowfin tuna, food for ecological thought. ICCAT Coll. Tec. Vol. Scient. Pap. XVII(2):444-457.

Palomares, M.L.D. 1987. Comparative studies on the food consumption of marine fishes with emphasis on species occurring in the Philippines. University of the Philippines, Quezon City, Philippines. 107 p. MS thesis.

Palomares, M.L.D. and D. Pauly. 1989. A multiple regression model for predicting the food consumption of marine fish populations. Aust. J. Mar. Freshwat. Res. 40(3):259-284.

Pandian, T.J. 1967. Intake, digestion and conversion of food in the fishes Megalops cyprinoides and Ophiocephalus striatus. Mar. Biol. 1:16-32.

Pandian, T.J. and M.P. Marian. 1985. Nitrogen content of food as an index of the absorption efficiency in fishes. Mar. Biol. 85:301-311.

Pauly, D. 1979. Gill size and temperature as governing factors in fish growth: a generalization of von Bertalanffy's growth formula. Ber. Inst. Meereskd. 63, 156 p.

Pauly, D. 1981. The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. Meeresforschung 28(4):251-282.

Pauly, D. 1986. A simple method for estimating the food consumption of fish populations from growth data and conversion experiments. US Fish. Bull. 84(4):827-842.

Sella, M. 1929. Migrazioni e habitat del tonno (Thunnus thynnus) studiati col metodo degli ami, con osservazioni su l'accrescimento, etc. Mem. R. Comm. Talassog. 156:1-24.

Temming, A. 1994. Food conversion efficiency and the von Bertalanffy growth function I: a modification of Pauly's model. Naga, ICLARM Q. 17(1):38-39.

Vincent, P. 1981. L'elevage du thon rouge: experiences japonaises. Centre National pour l'Exploration des Océans. Rapp. Sci. Tech. 47, 71 p.

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