

# Food Conversion Efficiency and the von Bertalanffy Growth Function I: A Modification of Pauly's Model

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## Abstract

A simple modification of Pauly's model for relating food conversion efficiency ( $K_1$ ) and body weight is proposed. The key parameter is an index of how efficiently food can be absorbed; the other parameter is related to the surface-limiting growth, an important component of von Bertalanffy's and Pauly's theories of fish growth.

## Introduction

The application of ecosystem models for the understanding and quantification of energy and material fluxes through models such as ECOPATH II (Polovina 1984; Christensen and Pauly 1992) requires reliable estimates of the food consumption of the (fish) species involved.

Since food intake of wild fish generally cannot be observed directly, consumption must be estimated via indirect methods. There are two different sets of methods for the estimation of fish consumption, and both require a combination of field and laboratory observations: (1) either data on mean stomach content in the field are combined with the gastric evacuation pattern observed in laboratory experiments, or (2) the growth observed in the field is combined with laboratory estimates of food or energy requirements.

The second group of methods can be split further into those which attempt to quantify the energy demands of all relevant physiological processes (e.g., growth, routine metabolism, activity metabolism, gonad maturation) separately and those which are based on the measurement of gross food conversion efficiency (Pauly 1986; Silvert and Pauly 1987).

The idea behind the latter approach, which will be focused on in this paper, is simple: fish are fed in the laboratory known amounts of food and the resulting growth is registered. If fish exhibit the same growth in the field, they must have consumed the same amount of food. The accuracy of this method relies mainly on the extent to which the natural conditions with respect to food type, temperature, activity level, gonad production and others are met in the experiments (see Pauly 1986).

The method can be applied in a stepwise fashion to calculate the food consumption for each size group of fish independently. The size-specific estimates are multiplied with the numbers of fish in the different size groups and summed up to give the total food intake of the population.

If, however, conversion efficiencies are to be incorporated into population models, a mathematical representation is required. Commonly power functions have been used to express physiological processes, including conversion efficiency (Paloheimo and Dickie 1966), as a function of body weight:

$$K_1 = a * W^b \quad \dots 1)$$

where a and b are empirical constants with no biological meaning.

Pauly (1986) proposed a different model which has major advantages over the power function model:

$$K_1 = 1 - (W/W_{\infty})^{\beta} \quad \dots 2)$$

where  $W_{\infty}$  is the (mean) asymptotic weight of the fish in the population in question (as also used in the von Bertalanffy Growth Function, or VBGF), and  $\beta$  is an empirical constant.

This model restricts  $K_1$  to a maximum of 1 (for  $W = 0$ ), whereas in the power function  $K_1$  exceeds 1 for  $0 < W_1 < a^{-1/b}$ . Also, when  $W$  equals  $W_{\infty}$ ,  $K_1$  is zero, whereas in the power function, fish above  $W_{\infty}$  are predicted to have a positive conversion efficiency, which is not consistent with the VBGF.

Pauly's model still has two disadvantages:

- 1) The parameter  $\beta$  cannot be interpreted biologically.
- 2) The model implies a  $K_1$  value near 1 when weight is near 0, which is impossible on thermodynamical grounds.

Here, I present a new equation which closely resembles the conversion model proposed by Pauly (1986), but which has parameters that allow a biological interpretation.

## Derivation of the New Model

The basic differential equation expresses the instantaneous rate of weight increase as the result of two different processes with opposite tendencies:

$$dW/dt = \text{anabolism} - \text{catabolism} \quad \dots 3)$$

Anabolism is assumed to be surface dependent, the limiting surface probably being the gill area, restricting the oxygen uptake which is necessary to build up body substances (Pauly 1981). Catabolism is assumed to be proportional to the number of cells, hence to body volume.

If the limiting surface is assumed to grow in proportion to length<sup>2</sup>, and weight in proportion to length<sup>3</sup>, equation (3) can be expressed as

$$dW/dt = EW^{2/3} - kW \quad \dots 4)$$

The model proposed here rests on the assumption that food consumption is proportional at any time, to the anabolism term in equation (4). This assumption is in accordance with the idea of a surface limiting anabolism, if the fish, on the average, do not consume more food than they can metabolize.

However, only a certain fraction of the food consumed is available for the buildup of body substance in the sense of equation (4). The factor determining this fraction will be named A (with 0 < A < 1). Consumption rate can then be expressed as

$$dC/dt = 1/A EW^{2/3} \quad \dots 5)$$

Gross conversion efficiency K<sub>1</sub> is defined as weight increase per food intake in a given time interval. Thus,

$$K_1 = \frac{dW/dt}{dC/dt} = \frac{EW^{2/3} - kW}{1/A EW^{2/3}} \quad \dots 6)$$

The original parameters E and k can be substituted by expressions of those parameters used commonly in the VBGF, which leads to

$$E = 3 KW_{\infty}^{1/3} \text{ and } k = 3K.$$

Thus,

$$K_1 = \frac{3 KW_{\infty}^{1/3} W^{2/3} - 3 KW}{1/A 3KW_{\infty}^{1/3} W^{2/3}} \quad \dots 7)$$

$$K_1 = \frac{A3 KW_{\infty}^{1/3} W^{2/3}}{3KW_{\infty}^{1/3} W^{2/3}} - \frac{A3KW}{3KW_{\infty}^{1/3} W^{2/3}} \quad \dots 8)$$

and

$$K_1 = A(1 - (W/W_{\infty})^{1/3}) \quad \dots 9)$$

It will be noted that equation (9) relates to equation (2) through  $\beta = 2/3$  if  $A = 1$ .

All parameters of the new model have a clear biological interpretation:

- 1) The exponent (previously  $\beta$ ) of the weight term is defined as one minus the exponent of the anabolism term in the differential form of the VBGF (equation 3).
- 2)  $W_{\infty}$  is the asymptotic weight of the VBGF, as in Pauly's model.
- 3) The parameter A quantifies the fraction of the ingested food that is available for the buildup of body substance (anabolism). It will be highly dependent on the

chemical composition of food. Thanks to this new parameter the curve is no longer forced through the point  $K_1 = 1$  at  $W = 0$ .


I suggest that the nitrogen content of the food be used to obtain an independent estimate of A, as this has been shown to be strongly correlated with absorption efficiency (Pandian and Marian 1985).

## Discussion

I am well aware that gill surface area does not usually grow in proportion to length<sup>2</sup>, and that body weight does not necessarily increase with length<sup>3</sup>, i.e., that gill surface and body growth are usually not isometric (see also Pauly 1981).

The advantages of the isometry assumption (which may still be tenable for practical curve fitting over a small range of sizes) is that it allows the derivation of a closed form equation (not presented here) for estimating relative food consumption (Q/B in Pauly 1986) thus obviating the need for an integration when computing food consumption, as in the model of Pauly (1986).

Extending the model proposed here to account for allometry, and thus making it compatible with the generalized VBGF *sensu* Pauly (1981, 1984) is rather straightforward, and results in the exponent of equation (9) being equivalent to 1-d, with d being the exponent linking in fishes, gill area and body weight (0.50 < d < 0.95, Pauly 1981).

The main point here, though, is that the interpretation of A will not change, i.e., it will continue to be related to food absorption efficiency, i.e., to food nitrogen contents. 

## References

- Christensen, V. and D. Pauly. 1992. ECOPATH II - A software for balancing steady-state ecosystem models and calculating network characteristics. *Ecol. Modelling* 61:169-185.
- 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(8):1209-1248.
- Pandian, T.J. and M.P. Marian. 1985. Nitrogen content of food as an index of absorption efficiency in fishes. *Mar. Biol.* 85:301-311.
- Pauly, D. 1981. The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. *Meeresforschung/Rep. Mar. Res.* 28(4):251-282.
- Pauly, D. 1984. Fish population dynamics in tropical waters: a manual for use with programmable calculators. *ICLARM Stud. Rev.* 8, 325 p.
- Pauly, D. 1986. A simple method for estimating the food consumption of fish populations from growth data and food conversion experiments. *US Fish. Bull.* 84(4):827-842.
- Polovina, J.J. 1984. Model of a coral reef ecosystem I. The ECOPATH II model and its application to French Frigate Shoals. *Coral Reefs* 3(1): 1-11.
- Silvert, W. and D. Pauly. 1987. On the compatibility of a new expression for gross conversion efficiency with the von Bertalanffy growth equation. *US Fish. Bull.* 85(1):139-140.

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