

## Maximizing Growth and Growth Efficiency

RICHARD CONDREY AND DEBORAH FULLER  
Coastal Fisheries Institute  
Center for Wetland Resources  
Louisiana State University  
Baton Rouge, Louisiana 70803-7503

### ABSTRACT

Successful mariculture operations, especially where the animals are fed controlled diets, depend in part upon a clear understanding of how the animal uses its food. We will show that the prevailing assumption that an animal uses its diet less efficiently at high, as compared to low, ingestion rates is unfounded. We will develop the argument that the animal is an inherently efficient converter of its diet. Unless some growth-controlling factor in the environment is in a suboptimal concentration, the animal should exhibit maximum growth and maximum growth efficiency at maximum ingestion rate. On the other hand, we will show that because the rate of protein growth and fat deposition may differ, the nutritional composition of the animal may vary with ingestion rate. Finally, we will discuss the implications of our argument in terms of the formulation and testing of diets and in the general design of mariculture operations. Our intention is to alert mariculturists to the growth potential of their animals and to direct their attention to correcting environmental problems which prevent the attainment of maximum growth and growth efficiency.

### INTRODUCTION

We want to replace a common hypothesis which is widely held about the relationship between growth and ingestion. In its place we want to provide you with a clear concept of the simple relationship that seems to apply throughout the animal kingdom and to discuss its exciting consequences for mariculture.

The hypothesis which we want to dispel has been stated in a number of ways, using a variety of mathematical formulas. Basically, it involves the assumption that the feeding animal does not grow as efficiently at high, as compared to low, ingestion rates; or conversely, that maximum growth efficiency is not attained at the maximum ingestion rate (satiation) because of some inefficiency which is inherent in the animal's physiology.

We have failed to find any data set which supports the assumption of the animal as an inherently inefficient converter of diet at high ingestion rates. Rather we have repeatedly found that a simple relationship first proposed by Blackman (1905) describes growth's dependence on ingestion. Simply stated, Blackman kinetics predicts a linear relationship between growth and ingestion from starvation to satiation as long as ingestion is the only growth-controlling parameter which is in a

suboptimal concentration (Fig. 1a). Under this condition, Blackman kinetics also predicts a constant incorporation efficiency at all ingestion rates and a curvilinear increase in growth efficiency from starvation to satiation, with maximum growth efficiency occurring at maximum ingestion rate (Fig. 1b).

If, however, some other growth-controlling factor becomes limiting at an ingestion rate less than satiation, then Blackman kinetics predicts a rectilinear dependence of growth on ingestion (Fig. 1a). In this phase of Blackman kinetics growth is linearly dependent on ingestion until the other growth-controlling factor becomes limiting. Once the other factor limits growth, there is no further increase in growth rate with increasing ingestion. In this case the incorporation efficiency is constant only so long as ingestion limits growth; above this point, the incorporation efficiency declines. Additionally, growth efficiency peaks at an intermediate ingestion rate and then declines as satiation is approached (Fig. 1c). While this pattern (Fig. 1c) is graphically consistent with the concept which we want to dispel - that the animal is inherently less efficient at converting food into tissue at higher, as opposed to lower, ingestion rates - there is one essential difference. With Blackman kinetics, as we propose it, the inefficiency is not inherent with the animal. Rather it results from the suboptimal concentration of some externally derived growth-controlling factor. Under this hypothesis, maximum growth efficiency can be obtained at satiation if all externally derived growth-controlling factors are optimal. Put more simply, if your animals are not exhibiting maximum growth efficiency at maximum growth rate, you - and not they - are "responsible."

We want to briefly discuss how we statistically tested published data sets which have been used to support the hypothesis of the animal as an inefficient converter of diet, review how all of these data support a simple linear dependence of growth on ingestion, and conclude with some generalizations which we feel are relevant to mariculture.

#### Statistical Approach

We used a very simple and straightforward statistical approach. First, we plot the data as growth versus ingestion and test for the significance of the quadratic term. If the quadratic is not significant, then a linear model, consistent with the simplest form of Blackman kinetics, applies. If the quadratic term is significant then we transform the data using the procedures suggested by Lineweaver and Burk (1934) to examine enzyme kinetics for an indication of the underlying mechanism. We do this because all of the models used to describe growth's dependence on ingestion can be derived as part of a family of equations which describe enzyme kinetics. When Blackman kinetics applies, for example, we assume that growth is at least limited by a sequence of enzymatic reactions which have widely separated rate-limiting steps. As such, intermediate products build up and the effect of diffusion is not critical to

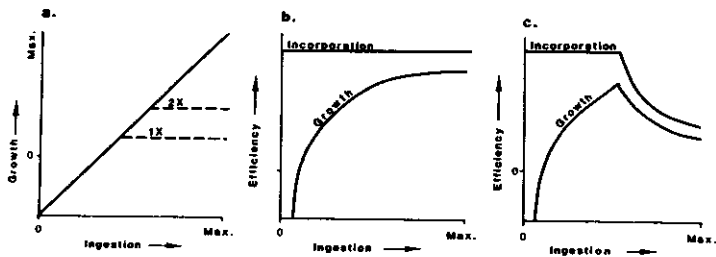


Figure 1. Expected dependence of growth, growth efficiency and assimilation efficiency on ingestion for cases where Blackman kinetics applies. The solid line in panel a shows the expected linear dependence of growth on ingestion when growth is the only growth-controlling parameter limiting growth. The dotted lines in panel a show the abrupt shift in growth's dependence on ingestion when the concentration (1x, 2x) of some other growth-controlling factor limits growth. Panel b shows the expected dependence of the efficiencies of growth and incorporation on ingestion when the linear form of Blackman kinetics applies, while panel c shows the patterns expected when the rectilinear form applies.

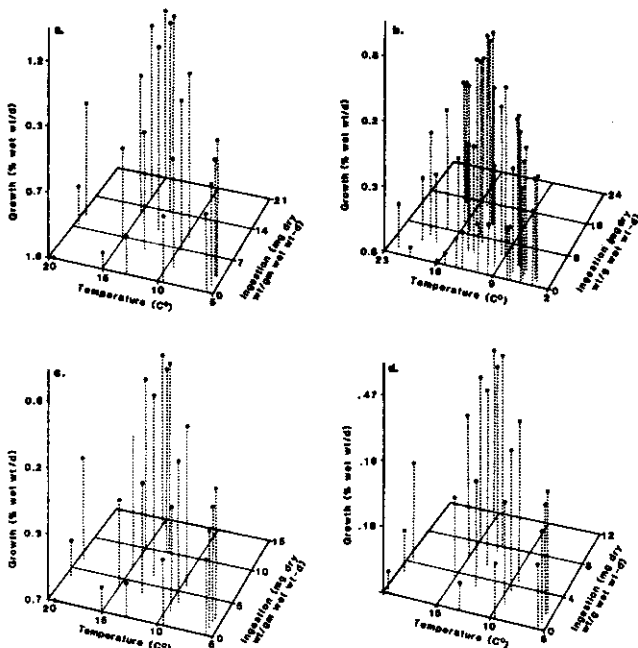


Figure 2. The dependence of growth of brown trout (*Salmo trutta*) on temperature, ingestion and initial body weight: (a) ~12 g wet wt, (b) ~50 g wet wt, (c) ~90 g wet wt, and (d) ~250 g wet wt. (data from Elliott 1975a, b).

end-product formation (Dabes et al., 1973).

Once transformed, we examine how Blackman kinetics fits the data as compared to Monod kinetics (Monod, 1942). We use Monod kinetics in the comparison because it is the antithesis of Blackman kinetics in that Monod kinetics predicts that growth is controlled by a single rate-limiting reaction.

#### DISCUSSION

We found eighteen published data sets with sufficient information to test the fit of Blackman kinetics (Condrey, 1982; Kausch and Ballion-Cusamano, 1976). All eighteen are consistent with Blackman kinetics. Of the eighteen cases, two are consistent with the rectilinear form of Blackman kinetics and sixteen are consistent with a simple linear relationship between the growth response and ingestion. Ten of these sixteen cases contained data on animals at satiation and are, therefore, consistent with the hypothesis that maximum growth rate and maximum growth efficiency can be attained at maximum ingestion rate. Several of these are classic studies in fish nutrition. For example, they include Dawes (1931a, b) data on plaice fed differing levels of mussel and Gerking's (1955) data on the bluegill fed mealworm larvae.

Once we began to look for simplicity we found it nearly everywhere. Rather than seeing different patterns with different organisms, we found no apparent phylogenetic effect. We found a linear dependence of chordate, arthropod, and molluscan predators on arthropod, molluscan, algal and formulated diets. Where we had data on animals fed differing diets we sometimes found that one diet supported a greater growth rate and a higher growth efficiency than the other diet, but this difference was not necessarily phylogenetic. For example, we found that euphausiid shrimp grew just as efficiently on an algal diet as they did on one of *artemia nauplii*; while the copepod *Calanus helgolandicus* grew more efficiently on the diatom than the *Thalassiosira fluviatilis* than on the dinoflagellate *Gymnodinium splendens*.

We found that rising temperatures tended to increase the maintenance metabolism rate and the maximum ingestion rate, while decreasing the growth efficiency. The result was that maximum growth rate and maximum growth efficiency were attained at satiation when animals (rainbow and brook trout) were raised at a temperature which was at the upper end of their tolerance range, but below their lethal limit (e.g., Fig. 2).

We found that the rates of production of metabolic wastes were also linearly related to ingestion. For example, we found a linear dependence of nitrogen excretion on ingestion for brook and rainbow trout from starvation to satiation. Or, with bream larvae feeding on a water flea, we found that absorption of food across the gut, assimilation of food into tissue, and respiration and defecation of ingested diet are linear functions of the ingestion rate.

Twelve of the eighteen data sets had been used by other authors to describe more complex models. These models included

the Paloheimo and Dickie (1966) model,

$$\log (G 100/I) = - a - b \cdot R$$

where R is the ingestion rate beginning at some level greater than that supporting maintenance and a and b are constants; Reeve's (1963) hypothesis of intermediate ingestion rates at which growth efficiency is maximized; the use by Corner et al (1963) of a Monod type equation,

$$G = [a I - I_m] / [b + (I - I_m)],$$

where  $I_m$  is the maintenance ingestion rate: and Paulson's (1980) power curve;

$$E = a \cdot 10^{(I b_1 + T b_2) W^{b_3}}$$

where E is excretion, T is temperature, W is weight and a,  $b_1$ ,  $b_2$ , and  $b_3$  are constants. None of these data sets supported anything other than a simple linear relationship between growth and ingestion, from levels of ingestion near or at starvation to levels near or at satiation. Indeed, eight of these studies contained data at satiation levels of ingestion and as such were consistent with the hypothesis that maximum growth rate and maximum growth efficiency can be attained at the maximum ingestion rate.

#### SUMMARY

We are not the only people to draw straight lines through growth rate data. Indeed, though it is not well recognized, Blackman kinetics has been shown to apply to the relationship between growth and ingestion for a number of higher animals, including chicken (e.g., Fisher, 1980) and rats (Morgan, 1981), as well as to microbes (Condrey and Fuller, 1985). The clear nature of this commonality allows us to propose the following general concept of a feeding animal from a mariculture viewpoint.

Given that no other growth-controlling factor is in suboptimal concentration, the mariculturist can expect a linear dependence of growth on ingestion from starvation to satiation. The magnitude of the incorporation efficiency and of the maximum growth attained should be a function of several parameters which are under experimental control. These include the diet's composition and palatability and the genetic potential of the animal. Diets can be selected through a series of comparative tests in which growth is measured at various ingestion rates ranging from starvation to satiation. Since the animal can be expected to exhibit different (but linear) rates of fat and protein growth as functions of ingestion rate and diet composition, the mariculturist may elect to strive for the production of some optimum body composition rather than for a maximum rate of growth. However, this level is more readily estimated if the mariculturist views the inherent relationship

between growth and ingestion as linear rather than curvilinear.

A similar argument applies to efforts to select a genetically superior animal in terms of growth and yield. If the mariculturist can establish a set of environmental conditions which will support maximum growth rate, then the genetic selection of potential brood stock is facilitated by feeding candidates at satiation - since under these conditions the animals should exhibit their genetic potential for both maximum growth and growth efficiency.

In conclusion, we feel that by expecting a linear relationship between growth and ingestion, the mariculturist can develop methods to maximize his yield and yield efficiency by using the simple rule of thumb "If maximum growth efficiency is not reached at maximum ingestion rate then something in the animal's environment needs attention."

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