MEDDELELSER

FRA

DANMARKS

FISKERI- OG HAVUNDERSØGELSER

N.S. Vol. 7, pp. 275–317

O. Sperber, J. From and P. Sparre

A Method to Estimate the Growth Rate of Fishes, as a Funtion of Temperature and Feeding Level, Applied to Rainbow Trout

Published by

The Danish Institute for Fishery and Marine Research

Copenhagen 1977

DK ISSN 0070-3435

The scientific series issued by the Danish Institute for Fishery and Marine Research have appeared under different names. They were started as »Meddelelser fra Kommissionen for Havundersøgelser« in 1904, when they comprised four series viz. »Fiskeri«, »Plankton«, »Hydrografi«, and »Statistik«. Later the name was changed to »Meddelelser fra Kommissionen for Danmarks Fiskeri- og Havundersøgelser«, the four series within this being retained. In 1952 the name was again changed to »Meddelelser fra Danmarks Fiskeri- og Havundersøgelser, New Series«. Into this series merged also »Report of The Danish Biological Station« appearing since 1891.

»Meddelelser« is published and distributed by the Danish Institute for Fishery and Marine Research. The publications appear at irregular intervals and are available on an exchange basis on application to the managing editor Subscription may be sent either to the managing editor or to any international bookseller. Complete list of publications including prices will be furnished on application. All correspondence should be addressed to the managing editor.

Address:

The Danish Institute for Fishery and Marine Research
Charlottenlund Castle
DK 2920 Charlottenlund
Denmark

Bianco Lunos Bogtrykkeri A/S, København

Meddr Danm. Fisk.- og Havunders.		
N.S.	Vol. 7	pp. 275–317

A Method to Estimate the Growth Rate of Fishes, as a Function of Temperature and Feeding Level, Applied to Rainbow Trout

OLE SPERBER, JON FROM* AND PER SPARRE**

CONTENTS

ABSTRACT

Using young rainbow trout (*Salmo gairdneri* Richardson, 1836) estimates of the parameters in a physiological growth equation were provided by aquaria experiments. In connection with a previous paper on production planning of fish farms (Sparre, 1976), it is of paramount importance to solve the following problem: If on a given date, a trout has a given weight, which weight will the trout have obtained at a certain later date, when the temperature of the water has a certain degree and when the trout is given a certain quantity of food?

The main emphasis has been placed on the numerical prediction of growth patterns, rather than on giving physiological or ethological explanations to the observed growth patterns.

* Address: Danish Trout Culture Research Station, Brøns, 6780 Skærbæk, Denmark.
** The Danish Institute for Fishery and Marine Research, Charlottenlund Castle, DK-2920 Charlottenlund, Denmark.

1. INTRODUCTION

The applied model describes growth as the difference of what goes into and what goes out of the body. The fate of the food eaten is decribed as:

(food ration) = (assimilated part of the food) + (undigested part of the food)
(assimilated part of the food) = (production) + (the part of the food assimilated which gives energy to the different functions of the organism)

One possibility is to develop the model along the lines laid down by Warren and Davis (1967) where all terms are measured as energy. The present work consists however of procurements of data for a much less complicated growth model based on wet weight measurements of food and production.

The purpose of the experiments is to develop a growth model applicable for production planning in practical fish farming, (which in Denmark means breeding of rainbow trout) i.e. to solve the following problem: If on a given date, a trout has a given weight, which weight will the trout have obtained at a certain later date, when the temperature of the water has a certain degree and when the trout receives a certain quantity of food?

As we do not consider results obtained in aquaria experiments as being fully valid under pond conditions, these experiments are to be considered as pilot experiments. The next step in the progress will be to design pondbased experiments on the basis of the present work.

The theoretical part of this work is primary a development of an experimental design and a discussion of the mathematics applied in the description of growth. We do not present any new theories on physiology or ethology.

To aid memory all symbols used in the paper are listed in the Appendix.

2. CHOICE OF GROWTH MODEL

Winberg (1956) developed a growth equation which has gained wide application. (E.g. Paloheimo and Dickie, 1965, 1966a and b, and Kerr 1971a and b). The basic energy equation of Winberg is:

(energy of weight increase) + (energy of metabolism) =
(physiologically useful energy) =
0.8 × (energy of ration)

Winberg's energy of metabolism is estimated as the energy equivalent of the oxygen consumption of a comparatively quiet fish, and multiplied by 2 to match the metabolism of a more active feeding fish. To Winberg the metabolic level is a function of activity. He does not appreciate feeding catabolism as physiologically distinct from active metabolism. Contrary to this Ursin, 1967, recognizes feeding catabolism as a mainly physiological event: The fed fish has a higher metabolic rate than the fasting one, even when at rest. The activity necessitated by feeding is pushed into the background, being made proportional with the ration taken.

The present experiments are based on Ursin's model, recognizing feeding catabolism as a mainly physiological event. The basic equation is Ursin's development of Pütter's equation (Pütter, 1920). Pütter's equation is nowadays called "the original Bertalanffy growth equation" (cf. e.g. Weatherley, 1972).

3. URSIN'S GROWTH MODEL

This section gives a concentrated presentation of Ursin's growth model, and parts of it are quotations from his 1967 paper. The basic equation is

$$\frac{dw(\tau)}{d\tau} = \Gamma\left(\frac{dR(\tau)}{d\tau}\right) - G\left(w(\tau), \Gamma\left(\frac{dR(\tau)}{d\tau}\right)\right) \tag{1}$$

$w(\tau)$ = weight at time τ
$dR(\tau)/d\tau$ = weight of food consumed pr time unit.
$\Gamma(dR(\tau)/d\tau)$ = the anabolic term (the "build up term")
$G(w(\tau), \Gamma(dR(\tau)/d\tau))$ = the catabolic term (the "break down term").
Equation (1) expresses that the quantity absorbed is a function of the quantity eaten, whereas the quantity lost is a function of: (I) the size of the fish, because even in a fasting fish every cell must metabolize to remain alive; and (II) of the food absorbed, because digesting and assimilating food require energy. The catabolic term G of equation (1) can be assumed to consist of two additive terms representing: (I) the catabolism of a fasting fish; and (II): the extra catabolism necessitated by feeding partly because mechanical work is involved in eating and digestion, and partly because an extra breakdown is necessary to supply free energy for synthesis of tissue. Fasting catabolism plus feeding catabolism make upp the total catabolism of a fed fish. We assume that fasting catabolism depends on the size of the fish only and that feeding catabolism depends on the quantity of food absorbed only.

A basic assumption underlying this model is that the chemical composition of food and fish does not vary with time.

The anabolic term. The following functional coherence is assumed to be valid

$$dR(\tau)/d\tau = fhw(\tau)^m \tag{2}$$

where f is the *feeding level*, h is the *coefficient of anabolism* and m is the *exponent of anabolism*. The feeding level f is defined as the fraction eaten of the quantity which could possibly be eaten. Thus f is a real number $0 \leqq f \leqq 1$. The feeding level for a starving fish is 0 and a fish eating at the maximum level gets $f = 1$. The food ration corresponding to $f = 1$ is designated $(dR/d\tau)_{\max}$. $f = \xi/\xi_L$ in the notation of Beverton and Holt (1957)* f varying from 0 to 1 corresponds to the food intake $dR/d\tau = f(dR/d\tau)_{\max}$.

The measurement of f involves a measurement of the intricate quantity $(dR/d\tau)_{\max}$. We do not possess a method which provides an objective measurement of the true maximum rate of feeding. Our concept of maximum rate of feeding is closely related to our technique of feeding, the applied equipment, etc. However, whether our measurement of $(dR/d\tau)_{\max}$ actually represents the possible maximum rate of feeding is not the most important aspect. If our measurements constitute a certain percentage, say x %, of the true maximum obtainable rate of feeding at every single experiment, these results are as usable as if we obtained 100 %. If the percentage x, remains constant during all experiments, then the observations are applicable for a prediction of growth under the specific conditions to which this work is limited. And, after all, it is an utopia to think that you can give a growth model, which can be used in every situation.

* Beverton and Holt, 1957 (§ 9.4.3.2.2. page 118) denote by ξ the actual consumption of food per unit of time for a fish of a given size, and by ξ_L the maximum ration a fish of this size would consume. The *intensity of feeding* is then defined as $(\xi_L - \xi)/\xi_L$ and it follows that ξ/ξ_L equals the feeding level.

Let β be the fraction of the food eaten absorbed through the intestinal walls. Then the anabolic term becomes

$$\Gamma(dR(\tau)/d\tau) = \beta dR(\tau)/d\tau = \beta f h w(\tau)^m \tag{3}$$

The quantity absorbed is assumed to be proportional to the absorbing surface (the area of the intestine) which if the fish grows like similar bodies is proportional with $w^{2/3}$. By letting the anabolic exponent be a parameter we do not put such a restriction on growth (cf. Hemmingsen, 1950).

The catabolic term. (1) *The fasting catabolism.* We assume that

$$(dw(\tau)/d\tau)_{\text{fasting}} = -kw(\tau)^n \tag{4}$$

where k is the *catabolism coefficient* and n is the *~~ana~~catabolism exponent.*

Fasting catabolism equals Pütter's catabolic term $-kw$, and is the rate of weight loss of a fish behaving normally. But to put the fasting catabolism $= -kw$, is unsatisfactory because there is evidence from respiration experiments that the fasting catabolism is not usually proportional with weight.

Although catabolic processes are going on all over the body, the necessary oxygen supply has to be introduced through some surface or other, mainly the gills. Appendix XIV, Ursin (1967) refers to experiments which show that the gills do not grow like similar bodies because new units are being added as the fish grows.

(2) *The feeding catabolism.* Let α be the fraction of the food absorbed producing the energy to eat and absorb the food (digestion, assimilation, storage of materials consumed and activity caused by the food intake). The feeding catabolism is assumed to be

$$-\alpha\beta dR(\tau)/d\tau \tag{5}$$

(4) and (5) constitute the total catabolism:

$$-G(w(\tau),\Gamma(dR(\tau))\,d\tau)) = -kw(\tau)^n - \alpha\beta dR(\tau)/d\tau \tag{6}$$

Inserting (3) and (6) into (1) gives Ursin's growth equation

$$dw(\tau)/d\tau = \beta(1-\alpha)fhw(\tau)^m - kw(\tau)^n \tag{7}$$

(formula (7) equals (B8) in Ursin's paper, page 2365).

4. THE RELATION BETWEEN CONSUMPTION AND PRODUCTION

This section deals with the possible feeding level dependence of the factors $\beta(1-\alpha)$ in (7). Write for short

$$L(f) = \beta(f)(1-\alpha(f))$$

Three possibilities are considered

$$L_1(f) = \beta_0(1-C_0 f)(1-\alpha_0) \tag{8.1}$$

$$L_2(f) = \beta_0(1-A_0 f) \tag{8.2}$$

$$L_3(f) = \beta_0(1-C_0 f)(1-A_0 f) = \beta_0(1-(C_0+A_0)f + A_0 C_0 f^2) \tag{8.3}$$

In (8.1) α is assumed to be constant and $\beta = \beta_0(1 - C_0 f)$ is assumed to decrease with increasing f (β_0 and C_0 are constants). Ursin (1967) defines $\beta = 1-\exp(-h_2/f)$

where h_2 is a constant. This expression of β has the same basic properties as (8.1) and (8.1) is chosen because of its simplicity.

In (8.2) it is assumed that β is constant and that α is a function of f: $\alpha = A_0 f$, where A_0 is a constant.

A single pilot experiment to investigate a possible feeding level dependence of β has been carried out. A group of 3 trout were offered maximum ration ($f = 1.0$) and another group of 3 trout were offered a ration corresponding to $f = 0.4$. Each trout had it's own aquarium. Faeces of the two groups were analyzed for kcal/g dry weight (by bomb calorimetry). The values observed were 3.57, 3.66 and 3.66 kcal/g for the trout eating at maximum ration and 2.47, 2.54 and 2.55 kcal/g for the trout eating at $f = 0.4$. The average values 3.63 and 2.52 kcal/g resp. provide a highly significant difference.

In (8.3) both α and β are assumed to be functions of f. As $C_0 < 1$, $A_0 < 1$ and $f \leqq 1$ it is seen that $(C_0 + A_0)f > A_0 C_0 f^2$, so that (8.1) and (8.2) both may be considered as approximations of (8.3).

From the experimental design used in this work it is not possible to compare the three models (8.1), (8.2) and (8.3). Consequently, a common model

$$L(f) = B(1 - Af) \tag{9}$$

is chosen, and (9) may be interpreted as any of the three models. Davis and Warren (1971) consider both $(1 - \alpha)$ and β as decreasing functions of feeding level.

Inserting (9) into (7) gives the growth equation

$$\boxed{dw(\tau)/d\tau = B(1 - Af)fhw(\tau)^m - kw(\tau)^n} \tag{10}$$

So far the progress is in accordance with Ursin. In the next section some new aspects of growth models will be discussed.

5. STOCHASTIC GROWTH EQUATION

In the initial phase of the development we were concerned only about the physiological processes. The purpose was to design experiments from which the parameters of Ursin's deterministic growth model could be estimated, and the calculation of the estimates should be performed by aid of "some regression analysis".

As the experiments were performed various models of regression analysis were developed. It turned out that the estimates were highly dependent on the choice of statistical model. As the confusion in regard to the choice of statistical model grew, also the desire of a more explicit formulation of the assumptions behind the various models increased. These assumptions may be conscious or unconscious. An example of such an apparently unconcious assumption is the Markov assumption. That we made this assumption to growth was realized by an examination of experiments already performed.

The basic problem is the integration of (10). It is necessary to integrate (10) because it is impossible to measure the actual value of $dw/d\tau$. Let $\Delta w = w(\tau_0 + \Delta\tau) - w(\tau_0)$ where Δw and $\Delta\tau$ are large enough to be measured with a reasonable accuracy, say, let $\Delta\tau$ be of the order of magnitude 10 days. Then by integrating (10) formally

$$\frac{\Delta w}{\Delta\tau} = \frac{1}{\Delta\tau}\int_{\tau_0}^{\tau_0+\Delta\tau} \{B(1 - Af)fhw(\tau)^m - kw(\tau)^n\}d\tau \tag{11}$$

The actual growth curve $w(\tau)$ has not been observed. Therefore an approximation to (11) is applied. Let $\bar{w} = (w(\tau_0) + w(\tau_0 + \Delta\tau))/2$, and assume that $w(\tau)$ in a time period of length $\Delta\tau$ is approximately linear. Then

$$\frac{\Delta w}{\Delta \tau} \cong B(1 - Af)fh\bar{w}^m - k\bar{w}^n \tag{12}$$

(12) represents a relation applicable for practical experimental design. (11) represents integration over a relatively short time period. Having estimated the growth parameters on the basis of (12) the next step will be to integrate over a longer time period to obtain the entire growth curve. Thus the integration of (10) plays an important role in the development of a growth curve.

Beverton and Holt (1957), Ursin (1967) and many others consider the integration of (10) as a purely mathematical problem. In our opinion this is not the case.

To facilitate notation, let $H = B(1 - Af)fh$ and $\Psi(w) = Hw^m - kw^n$. In the following f is assumed to be constant. Then (11) can be written

$$w(\tau_1) = w(\tau_0) + \int_{\tau_0}^{\tau_1} \Psi(w(\tau))\,d\tau \tag{13}$$

As a matter of fact, the growth of one fish (or any finite number of fish) is not a deterministic process. In some way (13) must be considered as the mean value of something. The definition of a mean value concept applicable to (13) implies that certain assumptions of the growth process must be done.

To define the stochastic process $\{w(\tau) | \tau \geqq 0\}$ (13) is rewritten

$$w(\tau + d\tau) = w(\tau) + \Psi(w(\tau))\,d\tau + ? \tag{14}$$

where "?" stands for some "stochastic term". Thus the approach is to consider the growth process as a continuous autoregressive sheme. The randomness of the growth is assumed to consist of a number of stochastic terms, each of which is related to the different physiological processes which altogether constitute the growth process. Let these stochastic terms be a family of stochastic processes $Q_1(\tau), Q_2(\tau), \ldots$. Let $Q_i(d\tau) = Q_i(\tau + d\tau) - Q_i(\tau)$. Now (14) becomes:

$$w(\tau + d\tau) = w(\tau) + \Psi(w(\tau))\,d\tau + \sum_i Q_i(d\tau) \tag{15}$$

And formally by integration of (15):

$$w(\tau_1) = w(\tau_0) + \int_{\tau_0}^{\tau_1} \Psi(w(\tau))\,d\tau + \int_{\tau_0}^{\tau_1} \sum_i Q_i(d\tau) \tag{16}$$

The integrals in (16) are stochastic integrals, since the left hand side $w(\tau_1)$ is a stochastic variable. The theory of stochastic integrals is a highly mathematical topic, and will not be discussed in this context. (For a thorough discussion see e.g. Doob (1953), Bartlett (1966) or Cox and Miller (1970)). Only the definition of a stochastic integral shall begiven, since this is what focus on our problems.

Let $Y(\tau)$ be a stochastic process in continuous time and with continuous state space. Let the time interval $[\tau_0, \tau_1]$ be partitioned into a set of disjoint subintervals

$[\tau_0, \tau_1] = [\tau_0, s_1] \cup]s_1, s_2] \cup \ldots \cup]s_{n-1}, \tau_1]$ and let $s_j^* \in]s_{j-1}, s_j]$ and $\Delta_j Y = Y(s_j) - Y(s_{j-1})$.

Let $\Phi(\tau)$ be a function and let

$$U_n = \sum_{j=1}^{n} \Phi(s_j^*)\Delta_j Y$$

If there exists a stochastic variable U so that

$$\lim_{n\to\infty} E\{|U_n - U|^2\} = 0 \tag{17}$$

Φ is said to be *mean square Riemann-Stieltjes integrable* and

$$U = \int_{\tau_0}^{\tau_1} \Phi(s)\, Y(ds)$$

(17) is equivalent to $\lim_{n,m\to\infty} E(U_n U_m) = \mu \geqq 0$ or

$$\lim_{n,m\to\infty} \sum_{i=1}^{n} \sum_{i=1}^{m} \Phi(s_j^*)\Phi(s_i^*) E(\Delta_j Y \Delta_i Y) = \mu \geqq 0 \tag{18}$$

If $Y(\tau)$ is a process with *independent increment*, i.e. if the differences $Y(\tau_1) - Y(\tau_0)$, $Y(\tau_2) - Y(\tau_1), \ldots,$ $Y(\tau_n) - Y(\tau_{n-1})$ are mutually independent where $\tau_0 < \tau_1 < \ldots, < \tau_n$ the condition (18) reduces to

$$\lim_{m\to\infty} \sum_{j=1}^{m} \Phi(s_j^*)^2 E(\Delta_j Y)^2 = \mu \tag{19}$$

(The variable names used in the definition of a stochastic integral are arbitrarily chosen and do not refer to concepts in the foregoing or in the following.)

The next step is to construct a growth process with independent increment satisfying (19). The reason why only processes with independent increment are considered is due to our limited imagination. We are not able to state the properties of a growth process satisfying (17) but not being a process with independent increment.

Let $\sum Q_i = Q_1 + Q_2$ and let the processes P_1 and P_2 be defined by

$$Q_1(d\tau) = Hw(\tau)^m P_1(d\tau) \quad \text{and} \quad Q_2(d\tau) = -kw(\tau)^n P_2(d\tau)$$

P_1 and P_2 are assumed to be independent for all τ. Inserting into (15) gives

$$w(\tau + d\tau) = w(\tau) + Hw(\tau)^m (d\tau + P_1(d\tau)) - kw(\tau)^n (d\tau + P_2(d\tau)) \tag{20}$$

Assume that $w(\tau)$ and $P_i(d\tau)$ are independent for all τ and that all $P_i(\tau)$ have equal distributions. Equation (20) expresses that the randomness of growth is related to consumption and to fasting catabolism, and that the relative variation of these two physiological processes remain constant. Assume $P_i(\tau)$ to be a Poisson process in continuous state space i.e. P_i is a process with events occuring singly in time:

$$P\{P_i(\tau + d\tau) = P_i(\tau)\} = \exp(-\lambda_i d\tau) = 1 - \lambda_i d\tau \quad .i = 1,2.$$

and if an event occurs it is assumed to be normally distributed $(0, \zeta_i)$
$P\{a \leqq P_i(\tau + d\tau) < a + da | P_i(\tau) = b\} =$

$$= \begin{cases} (1 - \lambda_i d\tau) & \text{if } a = b \\ \lambda_i d\tau \dfrac{1}{\sqrt{2\pi\zeta_i}} \exp\left(-\dfrac{a^2}{2\zeta_i}\right) da & \text{if } a \neq b \end{cases} \quad .i = 1,2.$$

Events may be considered as impulses which the fish receives from time to time e.g. the sight of a prey, the sight of a species member, an attack of a parasite, a change in the water quality or the temperature etc. etc. $P_i(d\tau)$ accounts for all events which may result in deviation from the expected growth, and $d\tau$ accounts for the expected growth. Let P' be normally distributed $(0, \zeta_i)$. Then

$$E(\Delta P_i)^2 = \text{VAR}(\Delta P_i) = \text{VAR}((\text{number of events})\, P') \cong \lambda_i \Delta\tau \zeta_i \tag{21}$$

and

$$E(\Delta Q_1)^2 = H^2 E(w(\tau)^{2m})\,\lambda_1 \zeta_1 \Delta\tau$$

if $\Delta\tau$ is small. $E(w(\tau)^{2m})$ is an ordinary Riemann integrable function so the limit

$$\lim_{n\to\infty} \sum_{j=1}^{n} H^2 \lambda_1 \zeta_1 E(w(s_j)^{2m})\,\Delta_j\tau$$

exists.

The question is whether we can accept this process as a reasonable model of growth. The process is a Markov process, which is not in accordance with our intuitive picture of the growth process. The Markov assumption implies that two fish of equal weight at a given time have equal growth characteristic irrespective of how they have obtained their present weight. This is formally stated as

$$P\{w(\tau_n) \leqq w_n \,|\, w(\tau_1) = w_1,\, w(\tau_2) = w_2,\, \ldots,\, w(\tau_{n-1}) = w_{n-1}\} =$$
$$P\{w(\tau_n) = w_n \,|\, w(\tau_{n-1}) = w_{n-1}\} \quad \text{if } \tau_1 < \tau_2 < \ldots < \tau_{n-1} < \tau_n$$

In certain extreme situations this is obviously not fulfilled. Consider two fishes, a and b, with growth curves $w_a(\tau)$ and $w_b(\tau)$ resp. as shown in Figure 1. Assume that the two fishes were offered exactly the same conditions i.e. food rations, water quality etc. Fish a has starved down to weight w_1 and fish b has fed up to weight w_1 in the time period from τ_0 to τ_1. Assume that the time period is long enough to put fish a in a bad condition. In our opinion it is not reasonable to expect the same growth characteristics of the two fishes in the period subsequent to τ_1. Based on a naive consideration the expected growth curves would be as indicated with dotted lines in Figure 1.

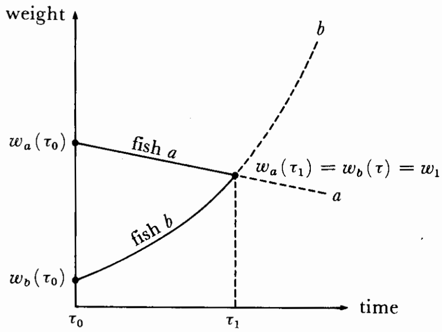


Fig. 1. Hypothetical growth curves to illustrate the Markov-assumption.

This idea could formally be expressed:

$$E\{dP_i(\tau)\,|\,P_i(u)\,;\, u < \tau\} = \left(\int_0^\tau d_i \exp(-r_i u)\, P_i(du)\right) d\tau \;,\; i = 1{,}2. \qquad (22)$$

where $d_i > 0$ and $r_i > 0$ are constants.

Recall that $P_i(du)$ is interpreted as the response from the fish to some impulses received in the period $[u, u+du]$. $\int P_i(du)$ is the sum of these responses to impulses.

If the fish mainly responds positively on the impulses this increases the probability that the response on the next impulse will be positive (positive responses means that $P_i(du) > 0$). $r_i > 0$ means that positive responses to impulses received in the near past count more than those of the farther past.

A process satisfying (22) instead of $E(P_i(d\tau)) = 0$, is not a Markov process and consequently not a process with independent increment.

Thus, we are in the bad position that we want to perform the integration (16) and we want to assume that (22) is valid, and we have realized that these two assumptions together are an absurdity. We are unable to solve this problem. Only on account of convenience we may assume that the integral (16) exists, and that the processes P_1 and P_2 have independent increments.

To visualize the difference between the two types of growth processes (which we denote Markov process and non-Markov process) some computer simulation were carried out.

Both simulations deal with a stock of 100 fish and a growth period of 27 days. The initial weights are uniformly distributed between 25 g and 26 g, i.e. with a mean weight of 25.5 g and a relative standard deviation of 1.13 %. The parameters (ζ_1 and ζ_2 in the Markov process and ζ_1, ζ_2, d_1, d_2, r_1 and r_2 in the non-Markov process) are calibrated so that the final weight distribution in both simulations has a mean of 44.4 g and a relative standard deviation of 6.2 %. The reason for this specific choice of initial and final weight distribution is that such values have been observed in a pond experiment (Sparre, 1976). Thus, it appears that both models are able to provide results which are in accordance with observations. In Fig. 2a and b four computer simulated realizations of each process are shown.

In our opinion it is not obvious from these simulations which type is closest to our intuitive and naive picture of the growth process. And, after all, the problem is not whether "the truth" of growth processes shall be found in the Markov process or in the non-Markov process, but whether the model applied is a reliable approximation.

Concerning the realiability of the Markov assumption it can finally be mentioned that this assumption is in accordance with Winberg (1956) who says: "the metabolic rate of a fish in the course of its individual development changes, in general, only to the degree which corresponds to its increase in size and weight. In other words, age (as such) has no influence on metabolic rate", and with Larkin, Terpenning and Parker (1956) who suggest on basis of their investigations that growth rate of rainbow trout should be related to size independent of age.

We have not considered the genetical differences that probably exist between the individuals of the rainbow trout stock used in the experiments because we think that these differences are of minor importance in relation to the other factors.

Fig. 2a. Simulation of the growth Markov process.

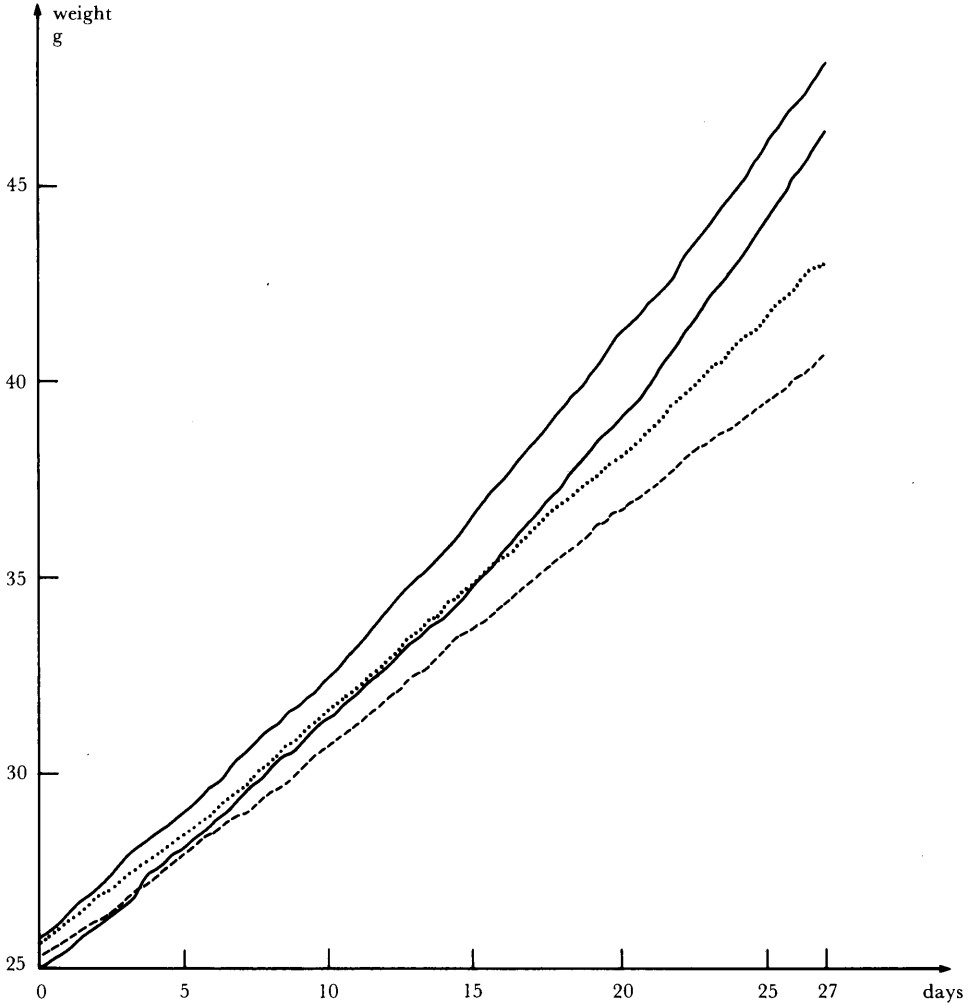


Fig. 2b. Simulation of the growth non-Markov process.

6. THE FORMAL BASIS OF THE EXPERIMENTAL DESIGN

The starting point is formula (20) and the assumption that $P_1(\tau)$ and $P_2(\tau)$ are processes with independent increments and $EP_1 = EP_2 = 0$ for all τ.

All $P_i(\tau)$ are assumed to have the same distribution, and the variance of ΔP_i is assumed to be proportional to $\Delta\tau$, $i = 1,2$.

Then

$$\frac{w(\tau+\Delta\tau)-w(\tau)}{\Delta\tau} = \frac{1}{\Delta\tau}\int_{\tau}^{\tau+\Delta\tau}(Hw(u)^m - kw(u)^n)\,du +$$

$$+\frac{1}{\Delta\tau}\int_{\tau}^{\tau+\Delta\tau}Hw(u)^m P_1(du) - \frac{1}{\Delta\tau}\int_{\tau}^{\tau+\Delta\tau}kw(u)^n P_2(du)$$

Assume that $w(\tau)^m$ and $w(\tau)^n$ are approximately linear in the time period $[\tau, \tau+\Delta\tau]$. Then

$$\Delta w/\Delta\tau = H\bar{w}^m - k\bar{w}^n + H\bar{w}^m\,\Delta P_1/\Delta\tau - k\bar{w}^n\,\Delta P_2/\Delta\tau$$

Let $\varepsilon_1 = 1 + \Delta P_1/\Delta\tau$ and $\varepsilon_2 = 1 + \Delta P_2/\Delta\tau$. Then

$$\Delta w/\Delta\tau = H\bar{w}^m\varepsilon_1 - k\bar{w}^n\varepsilon_2$$

It is seen that $E\varepsilon_1 = E\varepsilon_2 = 1$ and that (cf. 21)

$$\mathrm{VAR}(\varepsilon_i) = \frac{1}{\Delta\tau}\lambda_i\,\zeta_i,\ i = 1,2.$$

Introducing the feeding level:

$$\Delta w/\Delta\tau = B(1-Af)fh\bar{w}^m\varepsilon_1 - k\bar{w}^n\varepsilon_2 \tag{23}$$

And from (2) and (4)

$$(\Delta R/\Delta\tau)_{\max} = h\bar{w}^m\varepsilon_1 \tag{24}$$

$$(\Delta w/\Delta\tau)_{\text{fasting}} = -k\bar{w}^n\varepsilon_2 \tag{25}$$

The three equations (23), (24) and (25) form the basis of the experiments. The parameters to be estimated are A, B, h, k, m and n, and the observations are $\Delta w/\Delta\tau$, $(\Delta R/\Delta\tau)_{\max}$, $(\Delta w/\Delta\tau)_{\text{fasting}}$ and $\bar{w}$.

7. THE INFLUENCE OF THE ENVIRONMENTAL CONDITIONS

So far we have dealt only with what is going on inside the trout. This section deals however, with the relation of the inner processes and the environments. Examples of environmental factors are temperature, variation in temperature, oxygen concentration, density of fishes, food quality, pH, etc. Let $\boldsymbol{E}$ be the environment vector $\boldsymbol{E} = (E_1, E_2, \ldots)$, where each E_i represents an environmental factor. Inserting $\boldsymbol{E}$ the growth equation becomes

$$\Delta w/\Delta\tau = B(\boldsymbol{E})(1-A(\boldsymbol{E})f)fh(\boldsymbol{E})\bar{w}^m\varepsilon_1 - k(\boldsymbol{E})\bar{w}^n\varepsilon_2 \tag{26}$$

At the present stage of the development, only two environmental factors are considered, namely temperature and density of fishes. This does not imply that we consider these as the only important ones, but that our resources are too scanty to support investigations of other factors. Consequently, other environmental factors are assumed to remain constant. In this work $\boldsymbol{E}$ reduces to $\boldsymbol{E} = (t,u)$, where t is the temperature and u is a (0,1)-variable. $u = 0$ indicates that only one trout is used in the experiment and $u = 1$ indicates that more than one trout are used.

The temperature dependence is introduced as follows:

$$A(t) = A \text{ (constant)} \tag{27.1}$$

$$B(t) = B \text{ (constant)} \tag{27.2}$$

$$h(t) = h_1 \exp(h_2 t) \tag{27.3}$$

$$k(t) = k_1 \exp(k_2 t) \tag{27.4}$$

Due to Warren and Davis (1967) it could be expected that optimal temperatures of A and B existed, i.e. temperatures which minimize A and maximize B. However, from experiments we have the impression that the temperature dependence of A and B are of minor importance (no statistical significant differences were observed). 27.1 and 27.2 are to be considered as the simplest reasonable approximations.

The expressions of h and k are valid only in a limited temperature interval. Obviously the temperature dependence of $\Delta w/\Delta\tau$ should be a curve with a maximum as shown by Brett *et al.* (1969). However, in the temperature interval applied to these experiments the exponential curves fit well. For most practical purposes (i.e. in the case of Danish fish farming) the temperature varies from 0°–20° C and within this interval the exponential curve is considered as a reasonable approximation. (For a discussion of temperature dependence of growth see e.g. Ursin (1967), Brett *et al.* (1969) and Elliot (1975 *a* and *b*)).

Let N be the number of fish in the aquarium and let

$$u(N) = \begin{cases} 1 \text{ if } N > 1 \\ 0 \text{ if } N = 1 \end{cases}$$

and $s(N) = 1 - u(N)$. The density dependence of growth is introduced as:

$$h_1(N) = u(N)h_1'' + s(N)h_1' \text{ and } k_1(N) = u(N)k_1'' + s(N)k_1' \tag{28}$$

where h_1'', h_1', k_1'' and k_1' are constants.

Thus, one fish alone in an aquarium is assumed to behave different from another fish which is in company with one or more other fish. This model is due to the fact that such an effect was observed in the case of fasting catabolism. Again, the expressions (28) are to be considered as the simplest imperical models which take into account the experimental facts.

8. THE GROWTH EQUATION

Inserting (27) and (28) into (26) the growth equation gets its final form

$$\begin{aligned} \frac{\Delta w}{\Delta \tau} &= B(1 - Af)f(u(N)h_1'' + s(N)h_1')\exp(h_2 t)\bar{w}^m \varepsilon_1 \\ &- (u(N)k_1'' + s(N)\, k_1')\exp(k_2 t)\bar{w}^n \varepsilon_2 \end{aligned} \tag{29}$$

$\Delta\tau$: time in days. $\Delta\tau = \tau_2 - \tau_1$ where τ_1 = starting time and τ_2 = end time of the experimental period.

t: temperature in degrees Celsius.

f: feeding level (pure number). t and f are assumed to remain constant during the $\Delta\tau$ days.

A, B: (pure numbers). Three possible interpretations of A and B are given in section 4.

Δw: weight alteration in grammes. $\Delta w = w(\tau_2) - w(\tau_1)$.

$\bar{w}$: mean weight in grammes. $\bar{w} = (w(\tau_1) + w(\tau_2))/2$.

n: catabolism exponent (pure number).

m: anabolism exponent (pure number).

$\mathcal{N}$: the number of trout in the aquarium. $\mathcal{N}$ remains constant within each experiment.

u: $u(\mathcal{N}) = 1$ if $\mathcal{N} > 1$ and $u(\mathcal{N}) = 0$ if $\mathcal{N} = 1$. (pure number).

s: $s(\mathcal{N}) = 1 - u(\mathcal{N})$. (pure number).

h_1'', h_1', h_2: $(u(\mathcal{N})h_1'' + s(\mathcal{N})h_1')\exp(h_2 t)$ anabolism coefficient. (h_1'' and h_1' g^{1-m}/day and h_2 degrees C^{-1}).

k_1'', k_1', k_2: $(u(\mathcal{N})k_1'' + s(\mathcal{N})k_1')\exp(k_2 t)$ catabolism coefficient. (k_1'' and k_1' g^{1-n}/day and k_2 degrees C^{-1}).

$\varepsilon_1, \varepsilon_2$: stochastic terms. $E\varepsilon_1 = E\varepsilon_2 = 1$. (pure numbers).

9. MATERIAL AND METHODS

As the Danish trout farm production is based on 10–16 months old rainbow trout (*Salmo gairdneri*) (portion size, 180-250 g) only immature trout were used in the experiments.

The experiments were carried out in ten 100 liters steel aquaria, supplied with water from a brook. Before entering the aquaria the water first passed through a wood-wool filter and then through a sand and gravel filter. The filtering was done in order to remove prey from the water to avoid an unregistered food intake. After the filtering the water was led into a 500 liter fibre glass bassin where heating, cooling and aeration with atmospheric air took place. The level of dissolved oxygen was between 90 % and 100 % of air saturation (measured at inlet and outlet of the aquaria). From the bassin the water were pumped up into the aquaria and from there it ran back to the brook. The water flow through the aquaria was from 1.5 to 2 l/min.

Before the start of an experiment the trout were acclimated to the experimental temperature for at least one week. Only weight (not age) was registered. However, to make it probable that only immature trout were used all animals were less that 18 months old.

The aquaria room was lit-up for 12 hours and dark for 12 hours. Before weighing, each trout was anesthetized with chlorbutolum, and blotted using a wet cloth.

A determination of the parameters consists of three experiments:

I. Determination of h_1'', h_1', h_2 and m.

II. Determination of k_1'', k_1', k_2 and n.

III. Determination of A and B.

9.1 EXPERIMENT I. MAXIMUM FEEDING

Experiment I is based on (24)

$$\left(\frac{\Delta R}{\Delta \tau}\right)_{\max} = h(\mathcal{N}, t)\bar{w}^m \varepsilon_1 = (u(\mathcal{N})h_1'' + s(\mathcal{N})h_1')\exp(h_2 t)\bar{w}^m \varepsilon_1$$

or by taking logarithms

$$\log \left(\frac{\Delta R}{\Delta \tau}\right)_{\max} = \log\ (u(\mathcal{N})h_1'' + s(\mathcal{N})h_1') + h_2 t + m \log \bar{w} + \log \varepsilon_1 \tag{30}$$

The following indices are used:

- j: index of temperature
- v: index of $\mathcal{N}$ (one or many)
- i: index of aquarium

Let

$\mathcal{J}_v$ = the number of different temperatures considered at density v.

$\mathcal{N}_{vij}$ = the number of trout in aquarium i at temperature no. j and density v. ($\mathcal{N}_{1ij} = 1$ and $\mathcal{N}_{2ij} > 1$).

t_{vj} = temperature at experiment j at density v.

$\mathcal{Z}_{vij} = \log\left(\frac{\Delta R}{\Delta \tau}\right)_{\max}$ = log max rate of feeding at density v, in aquarium i and temperature t_{vj}. If $v = 2, \Delta R/\Delta\tau$ is the mean value $\mathcal{N}_{2ij}^{-1}\sum\left(\frac{\Delta R}{\Delta \tau}\right)_{\max}$ of the $\mathcal{N}_{2ij}$ trout.

M_{vj} = the number of aquaria used at temperature t_{vj} at density v.

$W_{vij} = \log \bar{w}$ = log mean weight at density v in aquarium i at temperature t_{vj}. If $v = 2, \bar{w}$ is the mean value $\mathcal{N}_{2ij}^{-1}\sum \bar{w}$ of the $\mathcal{N}_{2ij}$ trout.

$\Delta_{vij} = \log \varepsilon_1 - E(\log \varepsilon_1)$.

Then (30) can be rewritten

$$\mathcal{Z}_{vij} = (\log[u(\mathcal{N}_{vij})h_1'' + s(\mathcal{N}_{vij})h_1'] + E(\log \varepsilon_1)) + h_2 t_{vj} + mW_{vij} + \Delta_{vij} \tag{31}$$

$v = 1, 2.\ j = 1, 2, \ldots, \mathcal{J}_v.\ i = 1, 2, \ldots, M_{vj}$.

As $E\Delta_{vij} = 0$ an ordinary linear regression model can be applied to (31). The design matrix, the procedure of estimation and the tests are discussed in the Appendix.

The following measurements were performed:

$\Delta\tau_{vij}$: growth period (Starting time = 0)

ΔR_{vij}: food ration

t_{vj}: temperature

$w_{vij}(0)$: initial weight

$w_{vij}(\Delta\tau)$: final weight

$\mathcal{N}_{vij}$: number of trout

$v = 1, 2.\ j = 1, 2, \ldots, \mathcal{J}_v.\ i = 1, 2, \ldots, M_{vj}$.

All trout used in the experiments were in good condition, i.e. well fed and free of diseases. Immediately before the start of the experiment the trout were starved, so that the weight $w_{vij}(0)$ is the weight of a fish with empty stomach and gut.

As food fresh sprat (*Sprattus sprattus*) and various sand eels (*Ammodytes sensu latiore*) were used. These species are among the most commonly used food fish in Danish trout farms. The food fishes were cut into pieces of suitable size so that they could easily be swallowed by the trout. The trout have been offered food approximately every hour during the 12 hours when light was on in the aquaria room. At every feeding the trout were offered pieces of food until they refused twice to eat. The food not eaten was picked up again. The trout ate two to four times a day at a temperature of about 8° C and four to six times a day at a temperature of about 16° C.

At the end of the growth period the trout were starved so that $w_{vij}(\Delta\tau)$ was the weight of a trout with empty stomach and gut. The time elapsing before this emptying had taken place was approximately 65 hours at 8° C and 35 hours at 16° C. As it is rather difficult to make a precise estimate of the minimum time needed by the trout to empty its stomach and gut, we had the possibilities of weighing with a certain residual stomach and gut content or of weighing the trout after the stomach and gut were emptied and after a certain time of fasting catabolism. The last mentioned possibility was chosen, i. e. the weight was measured after a few hours of fasting catabolism. Anyhow, the error introduced is negligible compared to other sources of uncertainty.

The choice of the number of days $\Delta\tau$ is problematic. If $\Delta\tau$ is large it is more likely that $\Delta w/\Delta\tau$ will take a value we can accept as a fair estimate of the mean differential coefficient $E\{\dot{w}(\Delta\tau/2)\}$. (The differential coefficient is defined as the stochastic variable $\dot{w}(u)$ satisfying $\lim_{du\to 0} E\{|(w(u+du)-w(u))/du-\dot{w}(u)|^2\}=0$). On the other hand, the approximation $\bar{w}^n\Delta\tau=\int_0^{\Delta\tau} w(u)^n du$ is expected to be more inaccurate as $\Delta\tau$ grows. So far it has been impossible to assess the remainder terms in the approximations, since this implies a thorough knowledge of the stochastic growth process.

In the case $v=2$, the N_{2ij} trout were selected to obtain fishes of approximately equal initial weight.

9.2 Experiment II. Fasting catabolism

This experiment is based on (25)

$$\left(\frac{\Delta w}{\Delta\tau}\right)_{\text{fasting}} = -k(N,t)\,\bar{w}^n\varepsilon_2 = -(u(N)k_1''+s(N)k_1')\exp(k_2t)\,\bar{w}^n\varepsilon_2$$

From a mathematical point of view this model is equivalent to the model of $(\Delta R/\Delta\tau)_{\max}$ described in the foregoing section. Except that no feeding took place the experimental design is identical to that of experiment I. In this case another difficulty in the choice of $\Delta\tau$ arises, which is due to the fact that fish starving for a longer period will change their chemical composition considerably (cf. Brett *et. al.*, 1969).

9.3 Experiment III. Determination of A and B. Feeding level experiment.

This experiment is baseed on (23)

$$\left(\frac{\Delta w}{\Delta\tau}\right)_f = B(1-Af)fh\bar{w}^m\varepsilon_1 - k\bar{w}^n\varepsilon_2$$

Inserting (24) and (25) gives

$$\left(\frac{\Delta w}{\Delta\tau}\right)_f + k\bar{w}^n = B(1-Af)\left(\frac{\Delta R}{\Delta\tau}\right)_f - k\bar{w}^n(\varepsilon_2-1) = B\left(\frac{\Delta R}{\Delta\tau}\right)_f - BA\left(f\left(\frac{\Delta R}{\Delta\tau}\right)_f\right) + \varepsilon_3 \quad (32)$$

where $\varepsilon_3 = -k\bar{w}^n(\varepsilon_2-1)$.

In this experiment only the case $v = 1$ is considered, i.e. the density dependence of A and B is not tested. Even if A and B are assumed to be temperature independent the experiment was performed at different temperatures in order to test this hypothesis.

Since we want to measure $(\Delta w/\Delta \tau)_f$ as a function of f (or $\Delta R/\Delta \tau$), experiment III has to be more complicated than I and II. This implies that $\bar{w}$ must be kept constant for several trout eating at different feeding levels. The reason for this is that when $\bar{w}$ is a constant, B and BA can be estimated as ordinary linear regression, coefficients. Assume that k and n are known parameters (known from experiment II). Then $k\bar{w}^n$ can be considered as a constant. Let

$Y_{ij} = (\Delta w/\Delta \tau) + k\bar{w}^n$ = net production rate of trout i (or aquarium i) at temperature t_j.
$D_{1ij} = (\Delta R/\Delta \tau)$ = ration per time unit of trout i at temperature t_j.
$D_{2ij} = f(\Delta R/\Delta \tau)$ = (feeding level) × (ration per time unit)

Let $\mu_{1j} = B$ and $\mu_{2j} = -AB$. Then (32) may be rewritten

$$Y_{ji} = \mu_{1j} D_{1ij} + \mu_{2j} D_{2ij} + \varepsilon_3 \tag{33}$$

As $E\varepsilon_3 = 0$ (33) is a linear regression model for each temperature t_j. Having estimated μ_{1j} and μ_{2j} for various temperatures and having tested the temperature independence of μ_1 and μ_2, a pooled estimate of μ_1 and μ_2 can be obtained by reducing (33) to

$$Y_i = \mu_1 D_{1i} + \mu_2 D_{2i} + \varepsilon_3 \tag{34}$$

The statistical aspects are discussed in the Appendix.

Now the only problem left is how to keep $\bar{w}$ constant. Consider an experiment at constant temperature and let the number of trout be M. Let the subscripts be chosen so that

$$w_1(0) > w_2(0) >, \ldots, > w_M(0)$$

and let the corresponding feeding levels be $f_1, f_2, \ldots, f_M$. We want to determine f_i so that

$$(w_i(0) + w_i(f_i, \Delta \tau))/2 = \bar{w} \text{ (constant) for all } i.$$

Obviously $f_1 < f_2 <, \ldots, < f_M$, but a numerical estimate of f_i can only be obtained if you know the growth parameters, and this is why experiment III is problematic. Assume that the parameters h_1', h_2, m, k_1', k_2 and n are known from experiment I and II and that "guesstimates" of A and B are present. Then a guesstimate of f_i can be obtained by solving the equation $dw_i/d\tau = B(1 - Af_i)f_i h w_i^m - k w_i^n$ with respect to f_i. That means that you determine f_i so that the solution of the differential equation pass through the two points $(0, w_i(0))$ and $(\Delta \tau, 2\bar{w} - w_i(0))$. If $m \neq n$ some numerical method must be applied, if $m = n$ the solution is

$$w_i(\Delta \tau) = \{w_i(0)^{1-n} + (1-n)[B(1 - Af_i)f_i h - k]\Delta \tau\}^{1/(1-n)}$$

From $\Delta R_i = f_i h \bar{w}^m \Delta \tau$ the food ration is estimated.

The first time when experiment III is carried out very rough estimates of A and B must be used, but the next time you run the experiment estimates of A and B will be available, and every time a new replicate experiment is performed the estimates of A and B will be improved.

The following measurements were performed:

$\Delta \tau_{ij}$: growth period (starting time = 0)
ΔR_{ij}: food ration

t_j: temperature
$w_{ij}(0)$: initial weight
$w_{ij}(\Delta\tau)$: final weight

$j = 1,2,\ldots,J.\quad i = 1,2,\ldots,M_j.$

The experimental procedure is as in experiment I, except that only one trout is offered maximum feeding level at each temperature. The reason why only a single trout is used is that feeding of several trout in one aquarium at an approximately equal feeding level less that 1.0 is very difficult.

10. RESULTS

10.1 Experiment I. h_1', h_1'', h_2 and m

The direct observations are given in Table 1.1.

Indices v	j	i	Number N_{vij}	Temp. t_{vj}	Time $\Delta\tau_{vij}$	Initial weight $w_{vij}(0)$	Final weight $w_{vij}(\Delta\tau)$	Total ration $R_{vij}(\Delta\tau)$
1	1	1	1	3.5	14.2	67.6	77.3	27.4
1	1	2	1	3.5	14.2	177.1	196.3	47.2
1	1	3	1	3.5	14.2	277.4	302.4	71.7
1	2	1	1	5.7	19.4	16.1	23.1	20.3
1	2	2	1	5.7	26.0	42.0	59.8	48.5
1	2	3	1	5.7	26.0	57.0	89.7	87.9
1	2	4	1	5.7	26.0	82.6	119.4	94.4
1	2	5	1	5.7	26.0	117.5	169.5	120.5
1	3	1	1	7.6	7.3	62.3	72.0	27.2
1	3	2	1	7.6	7.3	101.8	115.6	32.7
1	3	3	1	7.6	7.3	161.6	188.7	65.2
1	3	4	1	7.6	7.3	266.2	298.4	83.8
1	4	1	1	10.0	17.0	21.4	35.8	37.1
1	4	2	1	10.0	15.2	80.4	119.3	95.7
1	4	3	1	10.0	15.2	132.3	193.2	146.0
1	4	4	1	10.0	17.0	164.3	244.8	171.8
1	5	1	1	14.5	15.0	43.4	86.9	112.0
1	5	2	1	14.5	15.0	87.8	147.0	152.3
1	5	3	1	14.5	15.0	96.2	164.9	178.6
1	5	4	1	14.5	15.0	132.4	233.2	236.8
1	5	5	1	14.5	15.0	202.2	323.5	320.0
1	5	6	1	14.5	15.0	251.0	379.9	370.9
1	6	1	1	16.0	9.0	32.8	43.1	38.7
1	6	2	1	16.0	9.0	112.9	158.4	138.4
1	6	3	1	16.0	9.0	194.3	256.5	200.5
1	6	4	1	16.0	9.0	209.6	270.6	205.3
1	6	5	1	16.0	9.0	211.5	279.5	210.3
1	6	6	1	16.0	9.0	242.9	311.8	195.9
2	1	1	8	3.5	8.0	91.6	97.2	17.5
2	1	2	2	3.5	14.2	98.0	109.6	32.9
2	1	3	2	3.5	14.2	147.8	167.9	51.8
2	2	1	3	7.6	7.3	99.5	111.2	30.4
2	2	2	2	7.6	7.3	144.4	163.6	48.4
2	2	3	2	7.6	7.3	253.5	278.0	70.2
2	3	1	19	16.0	9.0	31.9	42.9	39.4
2	3	2	3	16.0	9.0	104.6	140.1	111.2

Table 1.1.

Using the procedure of calculations described in the Appendix, the following estimates were obtained:

	Estimate	95 % confidence interval
h_1'	.0385	.0290 – .0509
h_1''	.0339	.0263 – .0437
h_2	.116	.109 – .122
m	.837	.786 – .887

Table 1.2.

The standard deviations and the correlation coefficients are given in Table 1.3.

	$\log(h_1')$	$\log(h_1'')$	h_2	m
$\log(h_1')$	.14			
$\log(h''_1)$	.97	.13		
h_2	−.54	−.57	.0033	
m	−.96	−.95	−.34	.025

Table 1.3.

Residual error variance $\sigma^2 = .13$ and the multiple correlation coefficient $\varrho = .99$. The correlation between observed and calculated values of $\sqrt{N}\log(\Delta R/\Delta\tau)_{\max}$ is shown in Figure 3. $\sqrt{N}\log(\Delta R/\Delta\tau)$ is chosen because the linear regression analysis was carried out on these figures (cf. Appendix).

Let H designate hypothesis and let $F(H,a,b)$ represents the Fisher distribution on a, b degrees of freedom. If $F(H, a, b)$ is less than the 95 percent fractile, the hypothesis H is accepted. Two hypotheses were tested:

$H1$: m independent of temperature.

$H2$: $\log(h_1') = \log(h_1'')$. (density independence).

$H1$: Two values m_1 and m_2 of the anabolism exponent were considered. The estimation of m_1 was based on observations at temperatures less than or equal to 10° C and m_2 was estimated from observations taken at temperatures greater than 10° C. Formally $H1$ is stated as $m_1 = m_2$. The actual values are $m_1 = .847$ and $m_2 = .825$. The F-statistic is $F(H1, 1, 32) = 1.45$, so $H1$ is accepted.

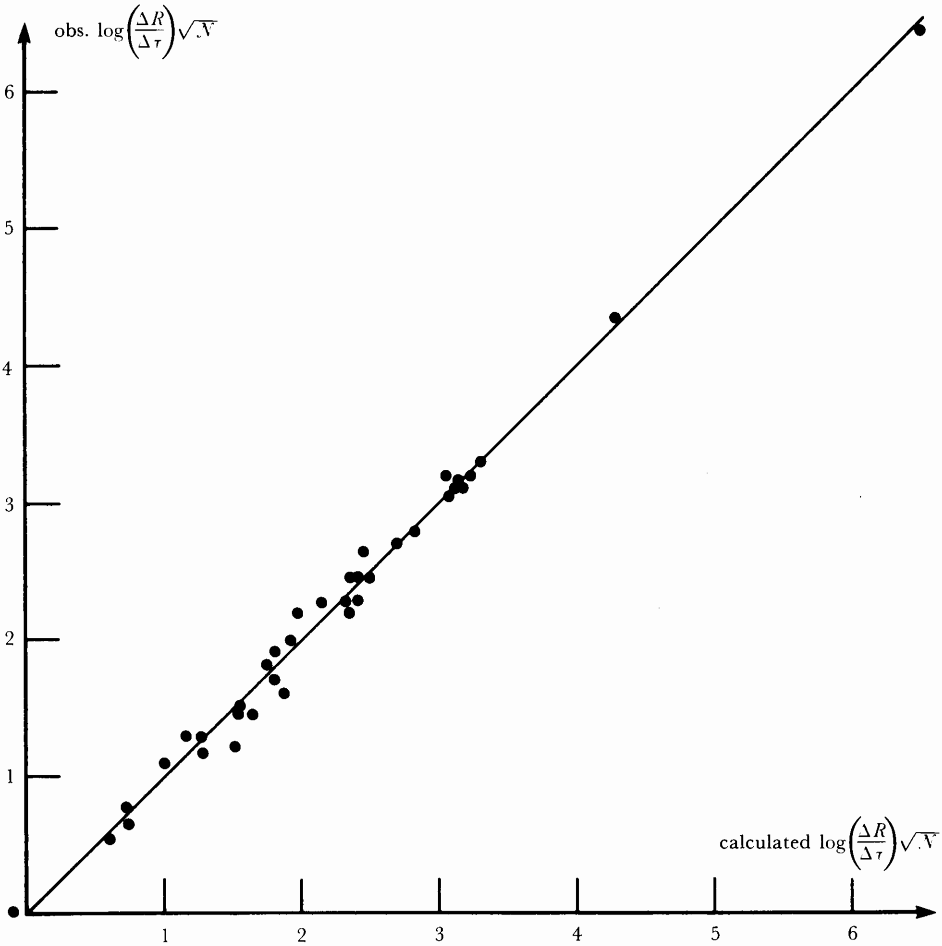


Fig. 3. Correlation between observed and calculated values in the linear regression analysis applied to the maximum feeding experiments.

$H2$: The F-statistic is $F(H2, 1, 33) = 12.2$ which corresponds to the 99.9 % fractile, so $H2$ is not accepted.

The calculations of the F-statistics are described in the Appendix.

10.2 Experiment II. k_1', k_1'', k_2 and n

The direct observations are given in Table 1.2.

Indices v	j	i	Number N_{vij}	Temp. t_{vj}	Time $\Delta\tau_{vij}$	Initial weight $w_{vij}(0)$	Final weight $w_{vij}(\Delta\tau)$
1	1	1	1	3.7	28.7	69.8	67.6
1	1	2	1	3.7	28.7	110.9	107.2
1	1	3	1	3.7	28.7	181.1	177.1
1	1	4	1	3.7	28.7	286.0	277.4
1	1	5	1	3.7	28.7	289.9	283.9
1	2	1	1	5.7	31.2	22.5	21.7
1	2	2	1	5.7	31.2	42.1	40.8
1	2	3	1	5.7	31.2	66.9	65.8
1	2	4	1	5.7	31.2	74.1	72.3
1	2	5	1	5.7	31.2	300.5	291.7
1	2	6	1	5.7	31.2	320.2	315.6
1	3	1	1	6.8	21.0	5.2	5.1
1	3	2	1	6.8	21.0	7.9	7.6
1	3	3	1	6.8	21.0	12.1	12.0
1	3	4	1	6.8	21.0	24.0	22.0
1	3	5	1	6.8	21.0	38.0	36.5
1	3	6	1	6.8	21.0	79.7	74.8
1	3	7	1	6.8	21.0	112.7	109.2
1	3	8	1	6.8	21.0	135.8	134.3
1	3	9	1	6.8	21.0	166.1	160.5
1	3	10	1	6.8	21.0	409.2	404.8
1	4	1	1	7.8	12.0	23.4	22.5
1	4	2	1	7.8	12.0	43.3	42.1
1	4	3	1	7.8	12.0	68.6	66.9
1	4	4	1	7.8	12.0	76.6	74.1
1	4	5	1	7.8	12.0	305.2	300.5
1	4	6	1	7.8	12.0	326.9	320.2
1	5	1	1	8.1	18.0	13.8	13.4
1	5	2	1	8.1	18.0	42.6	40.0
1	5	3	1	8.1	18.0	58.0	53.7
1	5	4	1	8.1	18.0	75.3	72.3
1	5	5	1	8.1	18.0	165.2	162.2
1	6	1	1	8.7	20.0	5.1	4.7
1	6	2	1	8.7	20.0	9.7	8.9
1	6	3	1	8.7	20.0	14.3	12.0
1	6	4	1	8.7	20.0	19.1	16.5
1	6	5	1	8.7	20.0	51.2	48.0
1	6	6	1	8.7	20.0	72.4	67.0
1	6	7	1	8.7	20.0	100.1	92.6
1	6	8	1	8.7	20.0	123.1	120.2
1	6	9	1	8.7	20.0	286.2	282.5
1	7	1	1	10.0	20.9	24.7	22.9
1	7	2	1	10.0	20.9	44.8	42.7
1	7	3	1	10.0	20.9	72.6	70.9
1	7	4	1	10.0	20.9	78.2	75.8
1	7	5	1	10.0	9.1	99.7	97.2
1	7	6	1	10.0	9.1	100.0	97.5
1	7	7	1	10.0	20.9	306.5	298.7
1	7	8	1	10.0	20.9	327.6	312.4
1	8	1	1	12.0	14.0	16.4	15.2
1	8	2	1	12.0	13.0	58.5	56.8
1	8	3	1	12.0	13.0	93.5	91.0
1	8	4	1	12.0	14.0	182.8	171.0
1	8	5	1	12.0	14.0	225.4	218.2

Table 1.2. (cont. on next page).

(continued)

Indices			Number	Temp.	Time	Initial weight	Final weight
v	j	i	N_{vij}	t_{vj}	$\Delta\tau_{vij}$	$w_{vij}(0)$	$w_{vij}(\Delta\tau)$
1	9	1	1	13.5	14.0	56.3	54.4
1	9	2	1	13.5	14.0	60.3	57.1
1	9	3	1	13.5	14.0	60.6	57.8
1	9	4	1	13.5	14.0	61.0	58.1
1	9	5	1	13.5	14.0	61.0	58.5
1	9	6	1	13.5	14.0	63.6	61.3
1	9	7	1	13.5	14.0	63.7	61.7
1	9	8	1	13.5	14.0	64.6	61.4
1	9	9	1	13.5	14.0	68.2	66.0
1	10	1	1	20.4	4.5	14.8	14.3
1	10	2	1	20.4	4.6	44.1	43.0
1	10	3	1	20.4	4.6	74.1	72.7
1	10	4	1	20.4	4.6	181.3	178.9
1	10	5	1	20.4	4.6	245.7	236.8
2	1	1	3	3.7	28.7	106.6	101.2
2	1	2	2	3.7	28.7	153.2	147.8
2	2	1	100	8.1	18.0	13.8	12.7
2	2	2	35	8.1	18.0	42.6	40.7
2	2	3	27	8.1	18.0	58.0	54.7
2	2	4	22	8.1	18.0	75.3	71.6
2	2	5	10	8.1	18.0	165.2	158.0
2	3	1	20	12.0	13.0	57.6	55.0
2	3	2	15	12.0	13.0	93.5	88.7
2	3	3	9	12.0	14.0	185.2	176.7
2	3	4	7	12.0	14.0	227.1	218.8
2	4	1	8	13.5	14.0	60.0	54.5
2	5	1	82	20.4	4.6	12.5	11.7
2	5	2	23	20.4	4.6	42.4	39.9
2	5	3	18	20.4	4.6	74.4	70.9
2	5	4	5	20.4	4.5	246.2	238.5

Table 1.2.

The procedure of estimation and testing is identical to that of the foregoing section. The following estimates were obtained:

	Estimate	95 % confidence interval
k_1'	.00207	.00155 – .00277
k_1''	.00330	.00258 – .00421
k_2	.101	.091 – .110
n	.740	.685 – .794

Table 2.2.

The standard deviations and the correlation coefficients are:

	$\log(k_1')$	$\log(k_1'')$	k_2	n
$\log(k_1')$	.15			
$\log(k_1'')$	.86	.12		
k_2	−.43	−.61	.0048	
n	−.84	−.84	.15	.027

Table 2.3.

Residual error variance $\sigma^2 = .30$ and multiple corr. coeff. $\varrho = .99$.

The correlation between observed and calculated values of log $((\Delta w/\Delta\tau)_{fasting})\sqrt{N}$ is shown in Figure 4.

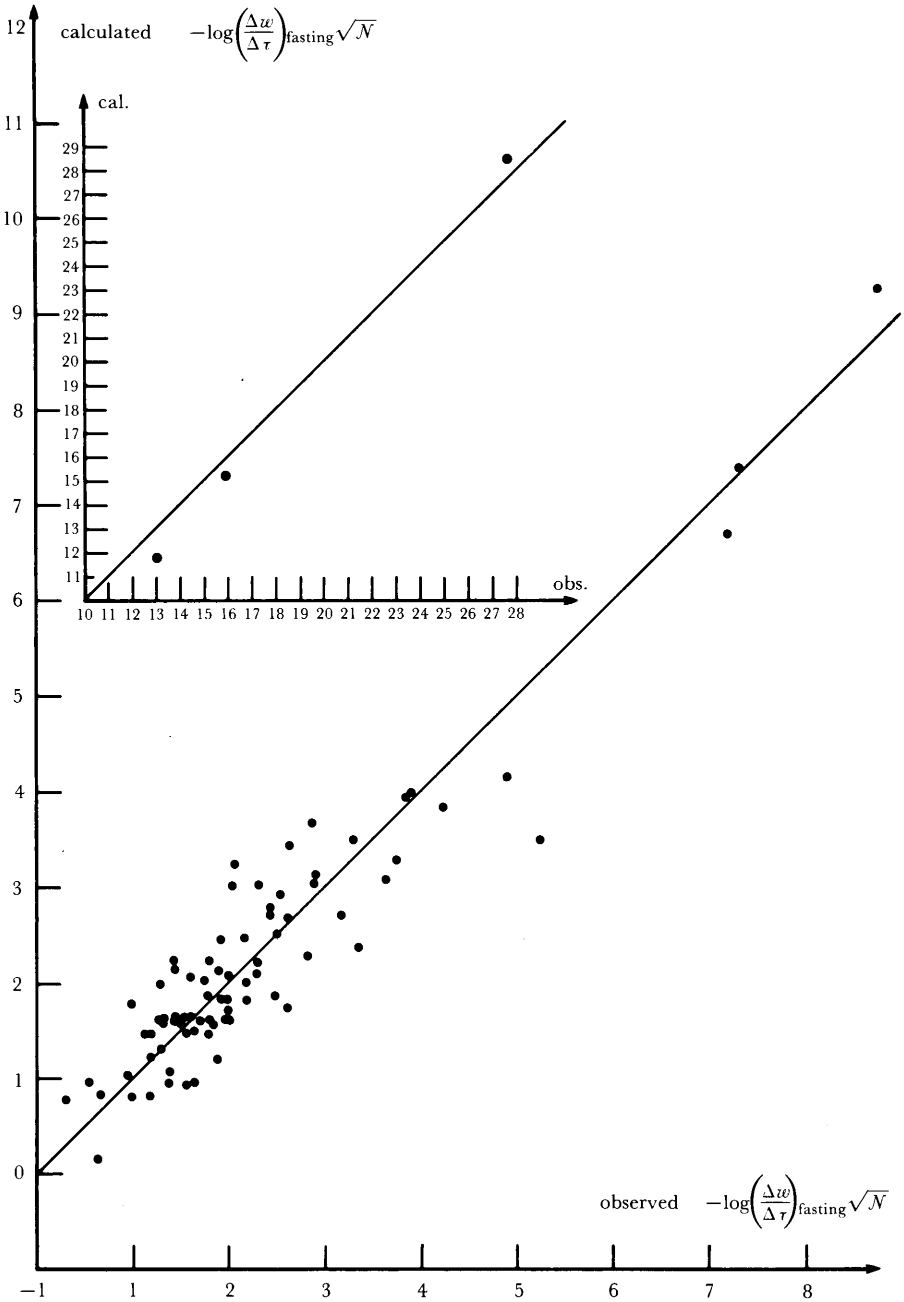


Fig. 4. Correlation between observed and calculated values in the linear regression analysis applied to the fasting catabolism experiments.

Two hypotheses were tested:

$H1$: n independent of temperature.

$H2$: $\log(k_1') = \log(k_1'')$ (density independence).

The values of n were equal in the two cases $t > 10°$ C and $t \leq 10°$ C, so $H1$ is accepted. The F-statistic for $H2$ is $F(H2, 1, 80) = 38.3$ which corresponds to the 99.99 % fractile, so $H2$ is not accepted.

10.3 Experiment III. A and B. Feeding Level Experiment.

The direct observations are given in Table 3.1.

Indices j	Indices i	Temp. t_j	Time $\Delta\tau_{ij}$	Initial weight $w_{ij}(0)$	Final weight $w_{ij}(\Delta\tau)$	Total ration ΔR_{ij}	Feeding level = $\frac{\Delta R_{ij}}{\Delta R_{1i}}$	$\bar{w}$
1	1	5.7	26.0	57.0	89.7	87.9	1.00	73.4
1	2	5.7	26.0	63.1	89.0	52.8	.60	76.1
1	3	5.7	26.0	66.9	86.8	39.4	.45	76.9
1	4	5.7	26.0	68.9	85.6	32.4	.37	77.3
1	5	5.7	26.0	74.3	78.0	13.5	.15	76.2
1	6	5.7	26.0	75.8	73.4	8.1	.09	74.6
2	1	10.0	15.2	80.4	119.3	95.7	1.00	99.9
2	2	10.0	15.2	82.5	116.4	69.1	.72	99.5
2	3	10.0	15.2	88.6	108.1	38.8	.41	98.4
2	4	10.0	15.2	92.7	102.2	25.6	.27	97.5
2	5	10.0	15.2	95.5	100.0	19.2	.20	97.8
2	6	10.0	15.2	98.0	100.5	10.5	.11	99.3
3	1	14.5	15.0	87.8	147.0	152.3	1.00	117.4
3	2	14.5	15.0	90.8	145.1	129.6	.86	118.0
3	3	14.5	15.1	92.1	145.9	118.7	.78	119.0
3	4	14.5	15.1	109.3	121.8	42.3	.28	115.6
3	5	14.5	15.0	114.3	121.9	27.6	.18	118.1

Table 3.1.

The initial estimation is based on (33), i.e. to each temperature a pair of parameters $(\alpha_{1j}, \alpha_{2j}) = (B_j, (AB)_j), j = 1,2,3$ are calculated (as described in the Appendix). The results are:

Temp.	Parameter	Estimate	95 % confidence interval
	A_1	.414	.052 – 1.203 *
5.7	$\mu_{11} = B_1$	.718	.469 – .968
	A_2	.283	.052 – .659 *
10.0	$\mu_{12} = B_2$	.646	.503 – .789
	A_3	.219	.027 – .530 *
14.5	$\mu_{13} = B_3$	.580	.460 – .670
5.7	$\mu_{21} = -(AB)_1$	.297	−.003 – .598
10.0	$\mu_{22} = -(AB)_2$	.183	.015 – .351
14.5	$\mu_{23} = -(AB)_3$	.127	−.009 – .263

Table 3.2.

* Fiducial limits (see Appendix).

The relative standard deviation and the correlation coefficients are:

	B_1	$-(AB)_1$	B_2	$-(AB)_2$	B_3	$-(AB)_3$
B_1	15.8 %					
$-(AB)_1$	.94	46.0 %				
B_2	0	0	10.0 %			
$-(AB)_2$	0	0	.95	41.8 %		
B_3	0	0	0	0	9.4 %	
$-(AB)_3$	0	0	0	0	.98	48.5 %

Table 3.3.

The hypothesis of temperature independence of A and B is stated as:

$$H3: \mu_{11} = \mu_{12} = \mu_{13} \text{ and } \mu_{21} = \mu_{22} = \mu_{23}.$$

The F-statistic is $F(H3, 4, 11) = .53$ so $H3$ is accepted.

Under $H3$ estimates of μ_1 and μ_2, based on (34) are calculated

	Estimate	95 % confidence interval
B	.621	.543 – .699
A	.273	.130 – .461 (*)
$-AB$	.170	.080 – .259

(*) Fiducial limits (see App.)

Table 3.4.

Relative standard deviations and the correlation coefficient are:

	B	$-AB$
B	5.9 %	
$-AB$	.98	24.7 %

Table 3.5.

The correlation between observed and calculated values are shown in Fig. 5.

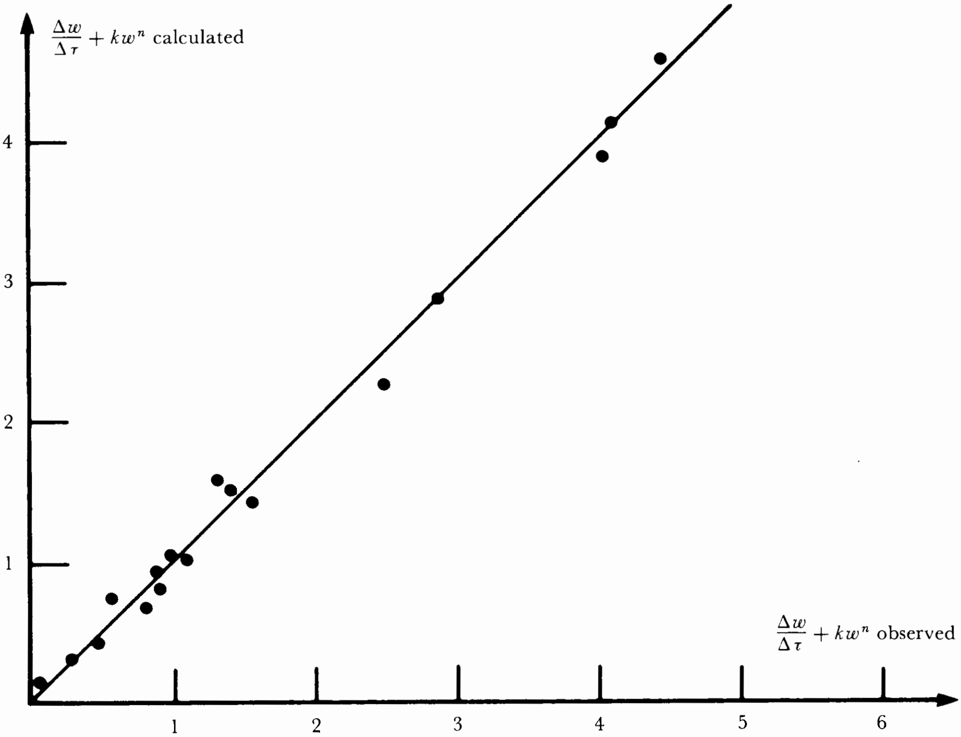


Fig. 5. Correlation between observed and calculated values in the linear regression analysis applied to the feeding level experiments.

10.4 Examples of growth curves

Assume that the growth process is differentiable at every time τ i.e. assume that for every τ there exists a random variable $\dot{w}(\tau)$ so that

$$\lim_{\Delta\tau\to 0}\left\{E\left|\frac{w(\tau+\Delta\tau)-w(\tau)}{\Delta\tau}-\dot{w}(\tau)\right|^2\right\}=0$$

Assume further that for all τ

$$E\dot{w}(\tau) = B(1-Af)fh(Ew(\tau))^m - k(Ew(\tau))^n$$

i.e. it is assumed that $E(w^m) = (Ew)^m$ and $E(w^n) = (Ew)^n$. To assess the reasonableness of these approximations, we need to state the distributional properties of $w(\tau)$ given $w(0)$. From pond experiments it is known that $w(\tau)$ given $w(0)$ is approximately log normally distributed for large values of τ. For relatively small values of τ, $w(\tau)$ can be approximated by a normal distribution. No direct aqaria observations are available. Let us assume that $w(\tau)$ is log normally distributed, then $w(\tau)^m$ is also log normally distributed with

$$Ew^m = (Ew)^m \exp((m^2-m)\,\mathrm{VAR}(\log w)/2)$$

If we approximate m and n by .8 we get $Ew^m = (Ew)^m \exp(-.08\,\mathrm{VAR}\,(\log w))$. Depending on τ, VAR ($\log w$) varies from 0 to at most .5, when τ varies from 0 to 12 months, (no direct aquaria observations are available) and the error factor exp ($-.08\,\mathrm{VAR}\,(\log w)$) varies from 1.0 to .96.
Then the mean growth curve $\bar{W}(\tau) = Ew(\tau)$ is the solution of the ordinary differential equation

$$d\bar{W}/d\tau = B(1-Af)fh\bar{W}(\tau)^m - k\bar{W}(\tau)^n \tag{35}$$

Inserting the estimates the differential equation becomes

$$\boxed{\begin{aligned} d\bar{W}/d\tau = {} & .62(1-.27f)f\Big(u(\mathcal{N}).034 + s(\mathcal{N}).039\Big)\exp(.116t)\,\bar{W}(\tau)^{.84} \\ & -\Big(u(\mathcal{N}).0033 + s(\mathcal{N}).0021\Big)\exp(.101t)\,\bar{W}(\tau)^{.74} \end{aligned}} \tag{36}$$

In Fig. 6 solutions of (36) are shown corresponding to various values of f, $\mathcal{N}$ and t. f, $\mathcal{N}$ and t remain constant for every single mean growth curve in Fig. 6.

11. DISCUSSION

The experimental design is based on a rather speculative model, a certain type of an autoregressive scheme. This model was constructed to allow for application of a linear approach to the procedure af parameter estimation. The model was developed primaryly to fulfill our desire of a consistent mathematical model, from which the experiments could be designed. It turned out that we were forced to make certain non-evident assumptions on growth in order to obtain both a consistent mathematical model and an experimentally applicable model. It is possible to test the assumption of independent weight increment by experiment, but to our knowledge no such experiments have been carried out.

The mathematical problems involved in a description of growth appeared to be of a rather profound nature, and in this paper it has been given only a very superficial and incomplete treatment. Unfortunately we are unable to give references to papers discussing the physiological growth equation from a mathematical point of view, and we do not feel capable to go any deeper into the investigation of the mathematical problems. On the other hand we feel that the randomness of growth is so dominating that growth cannot be described in a reasonable way by means of a deterministic model. Further in the case of average growth of a great number of fish it is necessary to specify the underlying state space, if you want to estimate the parameters from single realizations.

To us, from a naive point of view, it seems unreasonable to describe an extremely complicated process as growth by aid of a simple mathematical equation as e.g. the von Bertalanffy equation.

Another open question is how to perform an objective measurement of the feeding level, i.e. a method which is independent of who actually performs the feeding experiments. We have no guaranty that the values of $(\Delta R/\Delta\tau)_{\max}$ obtained in the present work represent the actual maximum food intake of each individual. The definition of f in the case of many trout in one aquarium is problematic (cf. Sparre, 1976). In the present work it is assumed that no food competition takes place in the case of maximum feeding, so that feeding level 1 means that each specimen eats the maximum

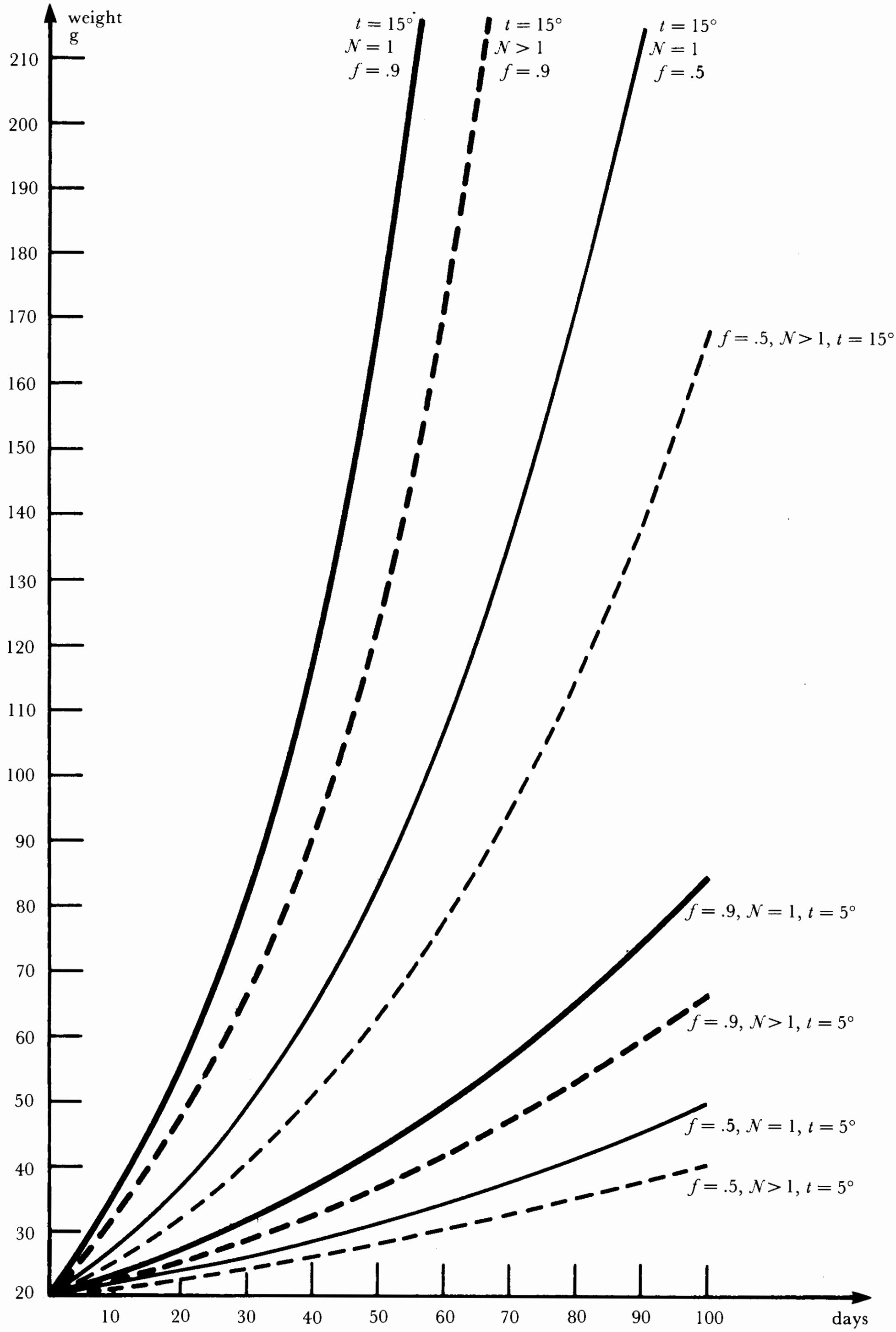


Fig. 6. Hypotehtical mean growth curves. (Solutions of equation (36)).

ration per time unit. In our opinion it is nearly impossible to feed several trout in one aquarium so that every trout gets the same feeding level if this is less than 1.

In the von Bertalanffy equation $m = 2/3$ and $n = 1$. Hemmingsen (1960) found $n = .75 \pm .015$ and Parker and Larkin (1959) cite various authors indicating that metabolic rate increases approximately as the .73 power of weight, but since these results do not include temperature dependence they are not immediately comparable to our results.

We found that $(m,n) = (.84, .74)$ which is significantly different from the usual Bertalanffy parameters $(2/3,1)$. It is a generally accepted hypothesis that $m > n$ for most animal groups, because in that case weight has an asymptotic limitation $W\infty = (B(1-Af)fh/k)^{1/(n-m)}$. The estimates $(m,n) = (.84, .74)$ indicates that $w(\tau) \rightarrow \infty$ for $\tau \rightarrow \infty$ for rainbow trout, if the growth characteristics for adult trout were equal to those of immature trout. But as the growth patterns for adult trout differs greatly from those of young trout the finding of $m > n$ is not unreasonable. It is customary roughly to estimate the weight loss due to spawning to be 20 %. (When the trout has to migrate up from and down to the sea the loss will be approx. 40 %). It is well known that salmonid fishes grow rapidly to a relatively large size and for their size have a very short lifespan (cf. Beverton and Holt, 1959). The two latter factors prevent the trout from growing to an infinitely large size, even if $m > n$, for mature trout.

11.1 Maximum rate of feeding

To describe maximum rate of feeding Elliott, 1975 a and b, applied the model

$$D = A_D W^{b_1} \exp(b_3 T)$$

where W is live weight of the trout (W g) (*Salmo trutta* L.), D is the maximum dry weight of food (D mg) and T is temperature (T C°). As food *Gammarus pulex* L. was used. W varied from 9 g to 302 g. Elliott's model equals the equation $(R/\Delta\tau)_{max} = h_1' \exp(h_2 t)\, \bar{w}^{\varepsilon_1}$ (cf. section 9.1).

He found values of A_D, b_1 and b_3 in three distinct temperature ranges and the results were:

Temperature	A_D	b_1	b_3
3.8 – 6.6	.654	.762 ± .027	.418 ± .035
6.6 – 13.3	3.384	.759 ± .023	.171 ± .012
13.3 – 18.4	5.956	.767 ± .041	.126 ± .031

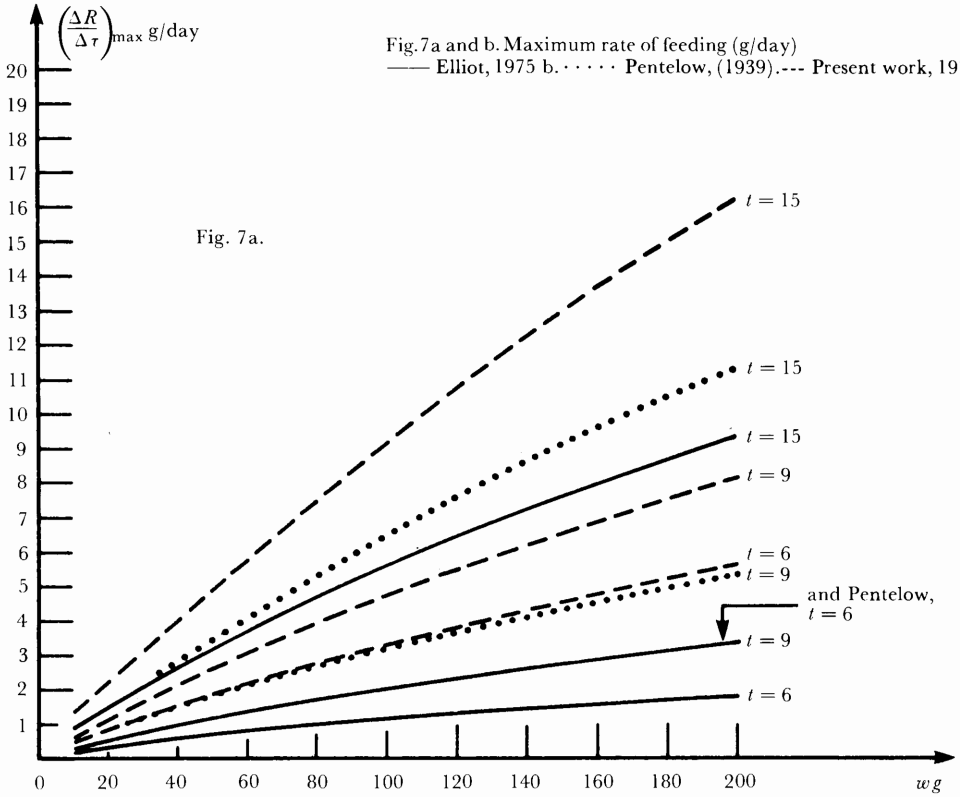
To convert Elliott's results to units comparable to our results A_D is multiplied by .004, i.e. it is assumed that 1 g live weight of trout corresponds to 1/4 g dry weight of *Gammarus*.

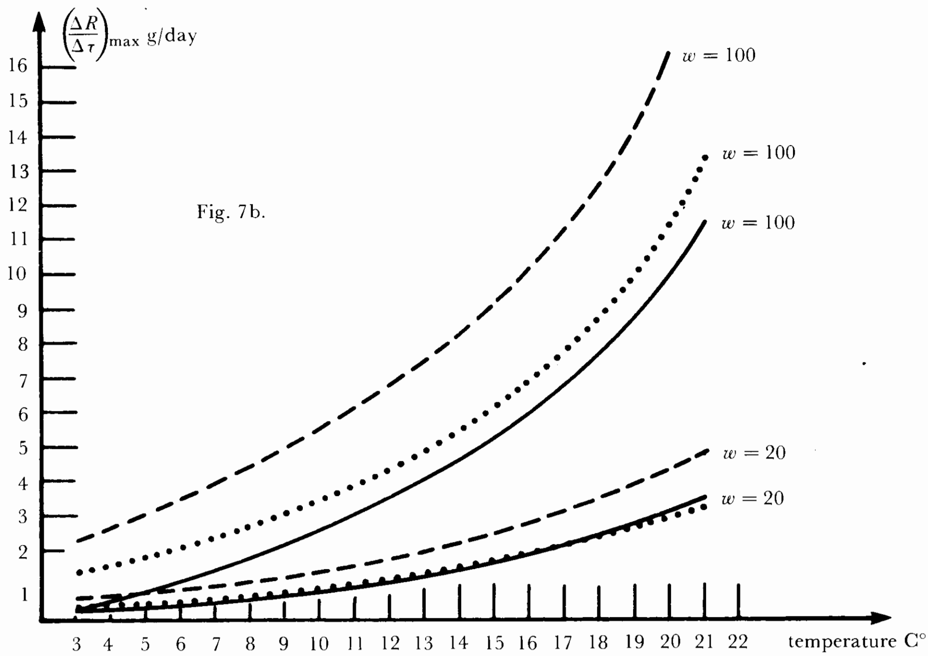
Pentelow (1939) carried out maximum feeding experiments with 9 brown trout. The number of observations were 84 at 19 different temperatures (3.3° C–19.4° C). As food *Gammarus pulex* was used. Using his data to estimate the parameters in the model applied in the present work, the result is:

	Estimate	95 % confidence limits
h_1'	.0171	.0135 – .0216
h_2	.127	.106 – .147
m	.867	.787 – .947

In Figs. 7a and 7b comparisons of the results from Elliott, Pentelow, and the present work are shown.

Fig. 7a and b. Maximum rate of feeding (g/day)
—— Elliot, 1975 b. · · · · · Pentelow, (1939).--- Present work, 1977.





11.2 Fasting catabolism

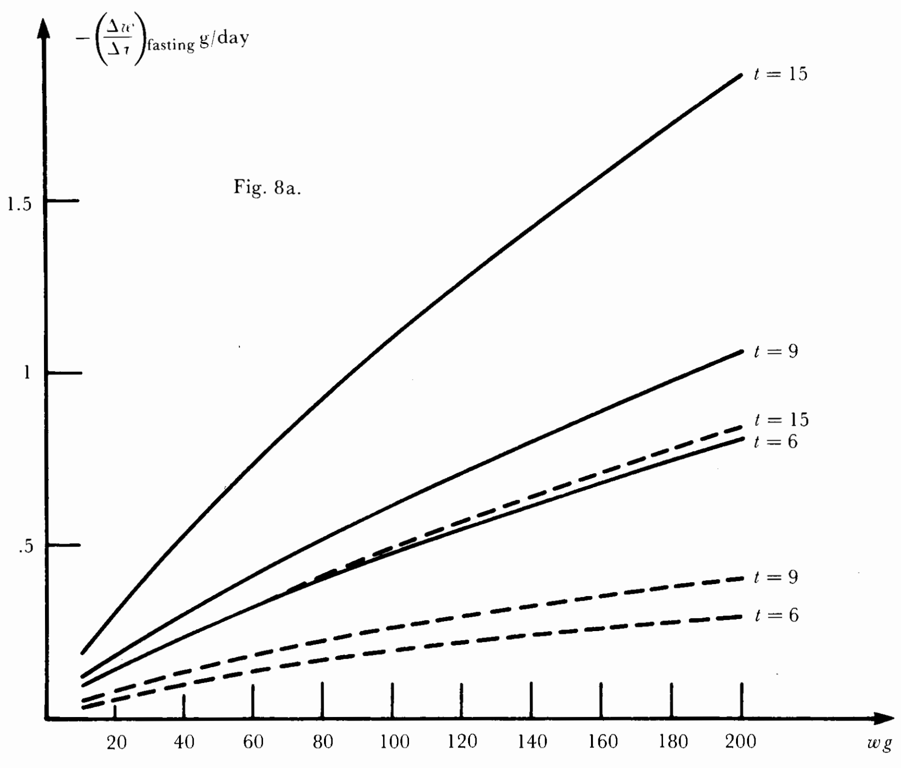
Pentelow (1939) made 77 observations at 10 different temperatures (2.8° C–15.6° C) on the weight loss in starving brown trout (*Salmo trutta* L.). In some of the aquaria there was a single trout and in others there were more than one. As there is no clearly difference between these two categories, we have taken Pentelow's data together in the estimation of the parameters in the model applied in the present work.

Pentelow's result is:

	Estimate	95 % confidence limits
k_1	.00830	.00503 – .0137
k_2	.0918	.0693 – .114
n	.759	.593 – .925

In Figs. 8a and 8b comparisons of Pentelow's results and the present work are shown.

The bigger fasting catabolism of the trout in Pentelow's experiment can be due to the fact that some of his fish probably not having been empty for food. As Pentelow says: "The fish were taken direct from the stock pond, and no information on how recently they have fed was obtained. Some, therefore, probably had food in their stomachs, whilst others were already empty."



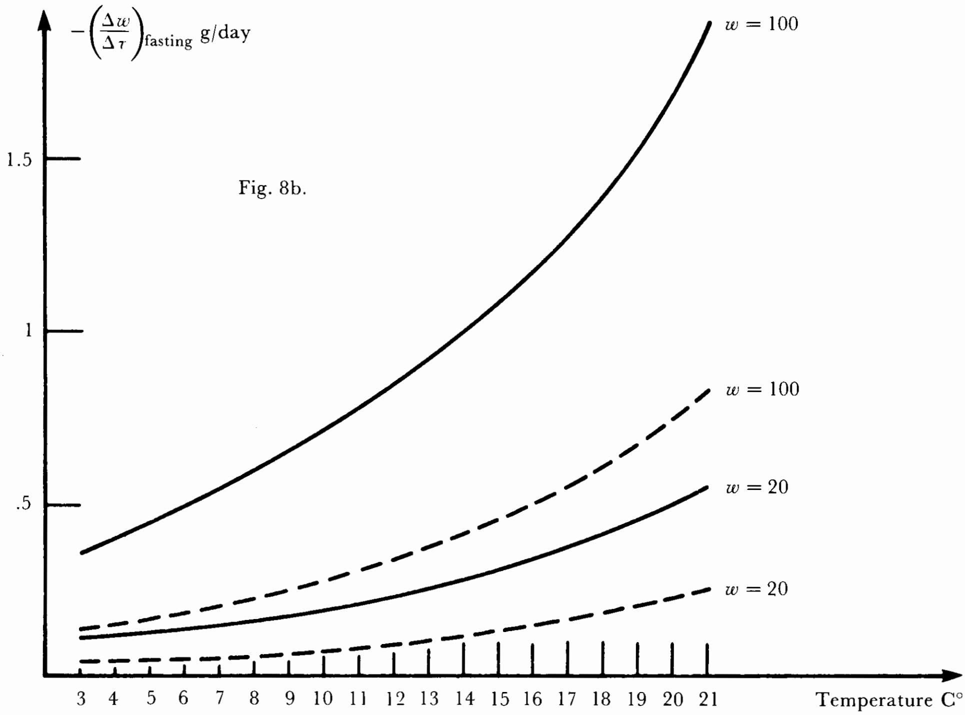


Fig. 8a and b. Fasting catabolism (g/day). —— Pentelov, 1939. - - - - Present work, $N > 1$.

11.3 Maintenance ration

Several authors, e.g. Pentelow (1939), Brown (1957), Paloheimo & Dickie (1966a), Ursin (1967), and Brett *et al.* (1969), emphasize the maintenance ration, i.e. the ration allowing the fish just to maintain its weight.

If we in (10) put $\frac{dw(\tau)}{d\tau} = 0$ and solve the equation for f, we get $f_{\text{maintenance}}$. From (2) we can also determine $\left(\frac{dR(\tau)}{d\tau}\right)_{\text{maintenance}}$.

$$f_{\text{maint}} = \frac{1 \pm \sqrt{1 - 4Ak_1 \exp((k_2 - h_2)t)\, w^{n-m}/(Bh_1)}}{2A}$$

$$(dR(\tau)/d\tau)_{\text{maint}} = f_{\text{maint}}\, h_1 \exp(h_2 t)\, w^m$$

Each of the equations have two solutions because we consider the assimilation efficiency as a decreasing function of f. (See section 4). But as $f \leqq 1$, only one pair of the two solutions have a meaning.

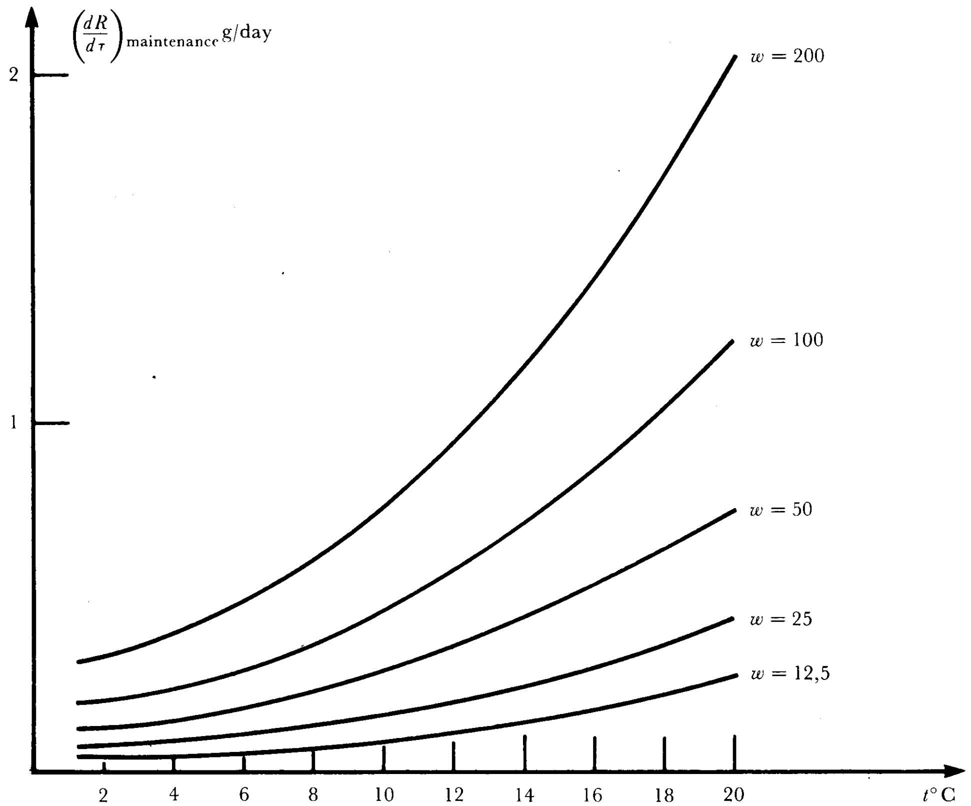


Fig. 9a. Maintenance ration, $N > 1$.

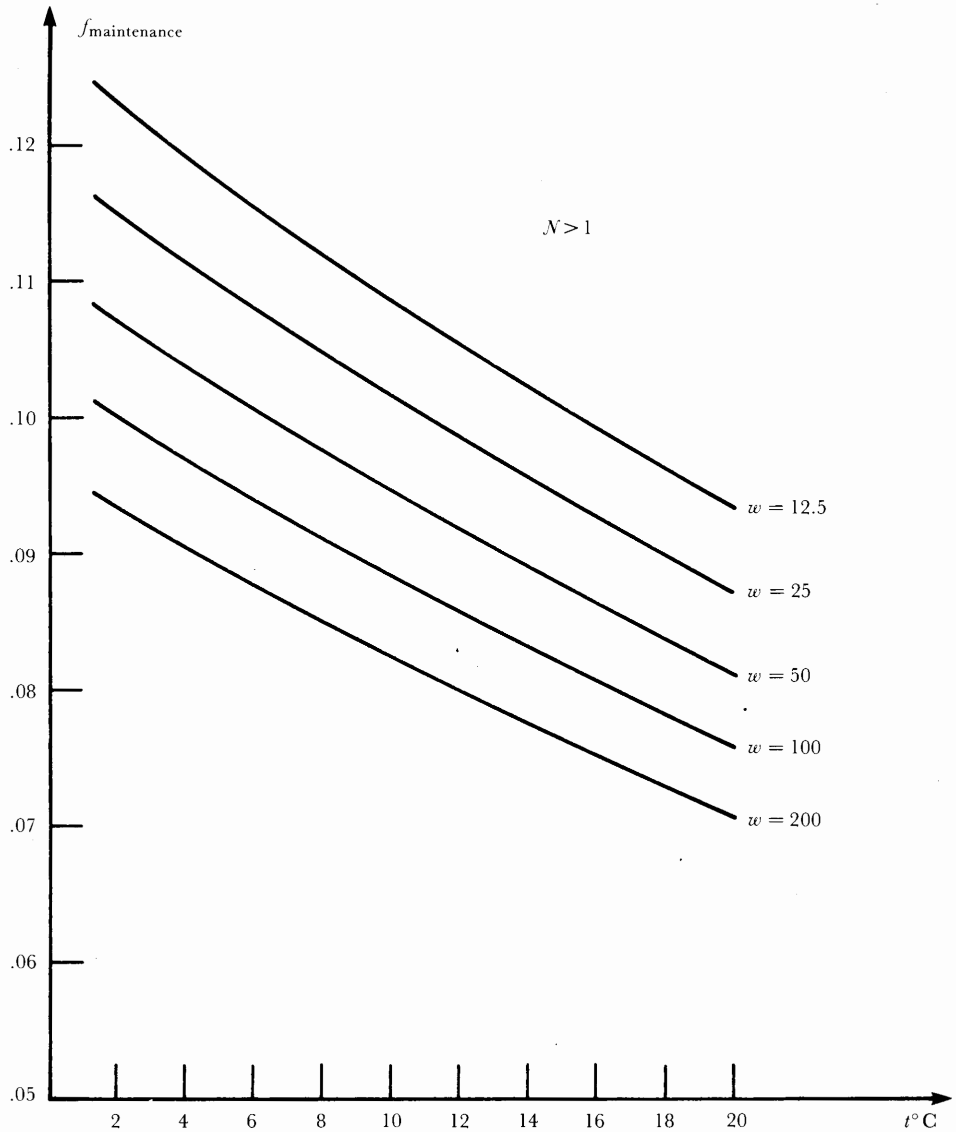


Fig. 9b. Maintenance feeding level, $N > 1$.

11.4 FOOD CONVERSION RATIO

In the context of production planning the food conversion ratio $U(f, \bar{W}, t) = dR/d\bar{W}$ is an important figure. Usually it is desirable to minimize U. U is derived from (35) and (2)

$$dR/d\bar{W} = \frac{f}{B(1-Af)f - (k_1''/h_1'')\exp((k_2-h_2)t)\bar{W}^{n-m}}$$

in the case $N > 1$. Inserting the estimates

$$U(f, \bar{W}, t) = \frac{f}{.62(1-.27f)f - .085\exp(-.015t)\bar{W}^{-.10}}$$

thus U will be a slightly decreasing function of temperature and weight, under the hypothesis that $k_2 < h_2$ and $m > n$. Due to the uncertainties of the estimates of parameters and to the stochastic terms ε_1 and ε_2, the expression of U is to be considered only as an indication of the functional coherence between U and f, W, t and we do not feel that it would be reasonable to draw any conclusion about optimal combinations of f, W and t. In Figure 10 examples of U as a function of f are shown. Figure 10 indicates that the concept of optimal combinations of f, W and t might be of minor importance, when feeding levels greater that .3 are considered. This topic was discussed by Brett *et al.* (1969), but it is difficult to compare their results to those of the present work, since Brett *et al.* express the food eaten per day as a percentage of the weight of the fish and pay little attention to this percentage decreasing with an increase in the weight of the fish (cf. Elliott, 1975 b, Table 8.).

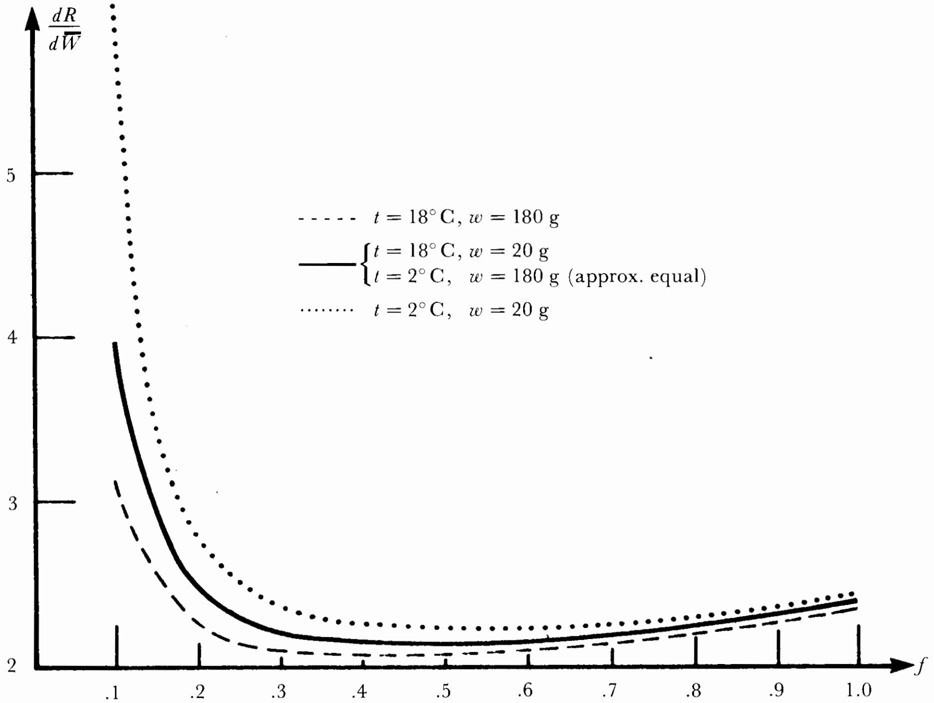


Fig. 10. Food conversion ratio.

11.5 Density dependence

Shlaifer (1938) has shown that in a given volume of water an isolated goldfish consumes more oxygen and has a higher rate of locomotor activity than does each fish in a group of four. Further he showed that in a given volume of water each goldfish in a group of two consumes the same amount of oxygen and has the same rate of locomotor activity as does each fish in a group of four. This finding indicates that the split up into the two categories "one" and "many" is adequate without any grading of the concept "many". (However this was done mainly for the sake of convenience).

In contrast with the findings of Shlaifer we found that in one aquarium one single trout has a lower fasting catabolism than each trout in a group of more than one. This difference is quite understandable if one looks at the ethology for goldfish and rainbow trout. The goldfish is a gregarious species whereas the rainbow trout in freshwater is a solitary species. When the goldfish is alone it displays appetitive behaviour consisting of orientation movements. And the consummatory act, which would bring the appetitive behaviour to an end, is that of being a member in a fish school. See e.g. Hemmings (1966) for the gregarious species roach, *Rutilus rutilus* (L). For the rainbow trout it is opposite. As a member of a school the trout will display orientation movements, and the consummatory act is that of being alone.

We found that many trout eat less per individual than a single trout. Since one of the results of territorial behaviour is to prevent an overexploitation of the living space, for exemple through overgrazing (see e.g. Wynne-Edwards (1962)) our findings can be explained in the following way: When the territorium, as in the aquarium, is broken down it is conceivable that the fishes have a built-in mechanism which prevent overgrazing by inhibiting food intake. The stimulus for this mechanism should then be a species member.

REFERENCES

Barlett, M. S. (1966). *An introduction to stochastic processes with special reference to methods and applications.* Cambridge University Press.

Beverton, R. J. H & S. J. Holt (1957). On the dynamics of exploited fish populations. *Fishery Invest., Lond. Ser. II. vol. XX.*

Beverton, R. J. H. & S. J. Holt (1959). A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. *Ciba Found. Coll. Ageing, 5:* 142–180.

Brett, J. R., J. E. Shelbourn, & C. T. Shoop (1969). Growth rate and body composition of fingerling sockeye salmon. *Oncorhynchus nerka,* in relation to temperature and ration size. *J. Fish. Res. Bd. Canada 26(9):* 2363–2397.

Brown, M. E. (1957). Experimental studies of growth. Chapter IX in *The physiology of fishes:* 361–398. *Brown, M. E.* (ed.). Academic Press.

Cox, D. R. & H. D. Miller (1970). *The theory of stochastic processes.* Methuen & Co Ltd.

Davis, G. E. & C. E. Warren (1971). Estimation of food consumption rates. *Methods for assessment of fish production in fresh waters:* 227–248. *Ricker, W. E.* (ed.). Blackwell, Oxford.

Doob, J. L. (1953). *Stochastic Processes.* John Wiley & Sons, Inc.

Elliot, J. M. (1975a). Weight of food and time required to satiate brown trout, *Salmo trutta* L. *Freshwater Biology,* Vol. 5, No. 1, February 1975. pp: 51–64.

Elliott, J. M. (1975b). Number of meals in a day, maximum weight of food consumed in a day and maximum rate of feeding for brown trout, *Salmo trutta* L. *Freshwater Biology.* Vol. 5, No. 3, June 1975. pp: 287–303.

Hemmings, C. C. (1966). The mechanism of orientation of roach, *Rutilus rutilus* L in an odour gradient. *J. Exptl. Biol. 45:* 465-474.

Hemmingsen, A M. (1950). The relation of standard (basal) energy metabolism to total fresh weight of living organisms. *Rept. Steno Mem. Hosp. IV:* 7–58.

Hemmingsen, A. M. (1960). Energy metabolism as related to body size and respiratory surfaces, and its evolution. *Rept. Steno Mem. Hosp. IX(II):* 7–110.

Kerr, S. R. (1971a): Analysis of laboratory experiments on growth efficiency of fishes. *J. Fish. Res. Bd. Canada 28(6):* 801–808.

Kerr, S. R. (1971b). Prediction of fish growth efficiency in nature. *Ibid:* 809–814.

Larkin, P. A., J. G. Terpenning, & R. R. Parker (1956). Size as a determinant of growth rate in rainbow trout, *Salmo gairdneri. Trans. Amer. Fish. Soc. 1957:* 84–96.

Paloheimo, J. E. & L. M. Dickie (1965). Food and growth of fishes. I. A growth curve derived from experimental data. *J. Fish. Res. Bd. Canada 22(2):* 521–542.

Paloheimo, J. E. & L. M. Dickie (1966a). Food and growth of fishes II. Effects of food and temperature on the relation between metabolism and body weight. *J. Fish. Res. Bd. Canada 23(6): 869–908.*

Paloheimo, J. E. & L. M. Dickie (1966b). Food and growth of fishes. III. Relations among food, body size, and growth efficiency. *J. Fish. Res. Bd. Canada 23(8):* 1209–1248.

Parker, R. R. & P. A. Larkin (1959). A concept of growth in fishes *J. Fish. Res. Bd. Canada 16(5):* 721–745.

Pentelow, F. T. K. (1939). The relation between growth and food consumption in the brown trout (*Salmo trutta*). *J. Exp. Biol.,* 16(4): 446–473.

Pütter, A. (1920). Studien über physiologische Åhnlichkeit. VI. Wachstumsähnlichkeiten. *Pflügers Arch. Ges. Physiol. 180:* 298–340.

Shlaifer, A. (1938). Studies in mass physiology: effect of numbers upon the oxygen consumption and locomotor activity of *Carassius auratus. Physiol. Zool. XI(4):* 408–424.

Sparre, P. (1976). A markovian decision process applied to optimization of production planning in fish farming. *Meddr Danm. Fisk. Havunders. N. S. Vol. 7.* pp: 111–197

Ursin, E. (1967). A mathematical model of some aspects of fish growth, respiration and mortality. *J. Fish. Res. Bd. Canada 24(11):* 2355–2453.

Warren, C. E. & G. E. Davis (1967). Laboratory studies on the feeding, bioenergetics, and growth of fish. *The biological basis of freshwater fish production:* 175–213. *Gerking, S. D.* (ed). Blackwell, Oxford.

Weatherley, A. H. (1972). *Growth and ecology of fish populations.* Academic Press.

Winberg, G. G. (1956). Rate of metabolism and food requirements of fishes. *Fish. Res. Bd. Canada Transl. Ser. 194* (1960).

Wynne-Edwards, V. C. (1962). *Animal dipersion in relation to social behaviour.* Oliver & Boyd.

APPENDIX

This Appendix describes the statistical method applied to the growth experiments. Topics treated in textbooks of statistic (e.g. Rao, 1973 or Searle, 1971) are given a very brief discussion. The purpose is to give information sufficient for the reader to se through all manipulations of the observations.

THE LINEAR MODEL OF FULL RANK

This section deals with a general description of the applied method. The variable names are arbitrarily chosen and do not refer to concepts defined in the foregoing.

All estimations and tests are based on the linear model of full rank

$$z_i = \beta_1 r_{1i} + \beta_2 r_{2i} + \ldots + \beta_k r_{ik} + \varepsilon_i, \; i = 1,2,\ldots,n. \tag{1}$$

or in matrix notation

$$\boldsymbol{Z} = \boldsymbol{R\beta} + \boldsymbol{\varepsilon} \tag{2}$$

z_i, $i = 1,2,\ldots,n$ are random variable (dependent variables), r_{ij}, $i = 1,2,\ldots,n.\ j = 1,2,\ldots,k.$ are numbers fixed in advance by the observer (independent variables) and ε_i, $i = 1,2,\ldots,n$ are stochastic terms with $E\varepsilon_i = 0$ for all i. The variance-covariance matrix for the ε_i's is designed $\boldsymbol{V}$. $\beta_j, j = 1,2,\ldots,k$ are the parameters to be estimated. Let $\hat{\beta}_j$ designate the estimate of β_j. Then

$$\hat{\boldsymbol{\beta}} = (\boldsymbol{R}'\boldsymbol{V}^{-1}\boldsymbol{R})^{-1}\boldsymbol{R}'\boldsymbol{V}^{-1}\boldsymbol{Z} \tag{3}$$

To facilitate notation let $\boldsymbol{X} = \boldsymbol{V}^{-1/2}\boldsymbol{R}$ and $\boldsymbol{y} = \boldsymbol{V}^{-1/2}\boldsymbol{Z}$. Then (3) becomes

$$\hat{\boldsymbol{\beta}} = (\boldsymbol{X}'\boldsymbol{X})^{-1}\boldsymbol{X}'\boldsymbol{y} \tag{4}$$

$\boldsymbol{y}$ and $\hat{\boldsymbol{y}}$ are designated observed and calculated values resp.

$$\hat{y}_i = \hat{\beta}_1 x_{i1} + \hat{\beta}_2 x_{i2} + \ldots + \hat{\beta}_k x_{ik}$$

The multiple correlation coefficient is

$$\varrho^2 = \frac{(\boldsymbol{y}'\hat{\boldsymbol{y}})^2}{\boldsymbol{y}'\boldsymbol{y}(\hat{\boldsymbol{y}}'\hat{\boldsymbol{y}})}$$

The residual error variance is estimated by

$$\hat{\sigma}^2 = \frac{(\boldsymbol{y}-\hat{\boldsymbol{y}})'(\boldsymbol{y}-\hat{\boldsymbol{y}})}{n-k}$$

The confidence interval of β_i is given by $\hat{\beta}_i - \hat{\sigma} t_{n-k}\sqrt{v_{ii}}$ and $\hat{\beta}_i + \hat{\sigma} t_{n-k}\sqrt{v_{ii}}$ where t_{n-k} is the 97.5 % fractile of the t-distribution on $n-k$ degrees of freedom, and v_{ii} is the i'th diagonal element of $(\boldsymbol{X}'\boldsymbol{X})^{-1}$.

$\boldsymbol{X}$ or $\boldsymbol{R}$ are the *design matrices*.

The variance-covariance matrix of $\hat{\boldsymbol{\beta}}$ is $\hat{\sigma}^2(\boldsymbol{X}'\boldsymbol{X})^{-1}$.

The general linear hypothesis is stated as

$$H\colon \boldsymbol{K}'\boldsymbol{\beta} = \boldsymbol{m}$$

where $\boldsymbol{K}'$ is a $(s \times k)$-matrix with rank s and $\boldsymbol{m}$ is a vector of order s. The F-statistic for testing the hypothesis H is

$$F(H,s,n-k) = \frac{1}{s\hat{\sigma}^2}(\boldsymbol{K}'\hat{\boldsymbol{\beta}} - \boldsymbol{m})'(\boldsymbol{K}'(\boldsymbol{X}'\boldsymbol{X})^{-1}\boldsymbol{K})^{-1}(\boldsymbol{K}'\hat{\boldsymbol{\beta}} - \boldsymbol{m})$$

Experiment I.

The notation is that of section 9.1. The experiment is based on

$$z_{vij} = a_1' s(N_{vij}) + a_1'' u(N_{vij}) + h_2 t_{vj} + (S(t_{vj}) m_1 + (1 - S(t_{vj}) m_2) W_{vij} + \Delta_{vij}$$

where

$$S(t_{vj}) = \begin{cases} 1 \text{ if } t_{vj} \leqq 10 \\ 0 \text{ if } t_{vj} > 10 \end{cases}$$

$a_1'' = \log h_1'' + E \log \varepsilon_1$ and $a_1' = \log h_1' + E \log \varepsilon_1$. The equation corresponding to (2) are shown in Figure 1. Assume that $\text{VAR}(\Delta_{1ij}) = \sigma^2$ for all i, j, $\text{VAR}(\Delta_{2ij}) = \sigma^2/N_{2ij}$ for all i, j and that $\text{COV}(\Delta_{vij}, \Delta_{abc}) = 0$ if $(v, i, j) \neq (a, b, c)$. Then the matrix $\boldsymbol{V}$ is defined. The hypothesis $m_1 = m_2$ is stated as

$$H1: \{0\ 0\ 0\ 1\ -1\}\boldsymbol{\beta} = \{0\}\ ; \quad \boldsymbol{\beta}' = (a_1', a_1'', h_2, m_1, m_2)$$

$$\boldsymbol{Z} = \left\{ \begin{array}{ccccc}
1 & 0 & t_{11} & W_{111} & 0 \\
1 & 0 & t_{11} & W_{121} & 0 \\
\vdots & \vdots & \vdots & \vdots & \vdots \\
1 & 0 & t_{11} & W_{1M_{11}1} & 0 \\
\hline
1 & 0 & t_{12} & W_{112} & 0 \\
\vdots & \vdots & \vdots & \vdots & \vdots \\
1 & 0 & t_{12} & W_{1M_{12}2} & 0 \\
\hline
\bullet & \bullet & \bullet & \bullet & \bullet \\
\bullet & \bullet & \bullet & \bullet & \bullet \\
\bullet & \bullet & \bullet & \bullet & \bullet \\
\bullet & \bullet & \bullet & \bullet & \bullet \\
\hline
1 & 0 & t_{1J_1} & 0 & W_{11J_1} \\
\vdots & \vdots & \vdots & \vdots & \vdots \\
1 & 0 & t_{1J_1} & 0 & W_{1M_{1J_1}J_1} \\
\hline
0 & 1 & t_{21} & W_{211} & 0 \\
\vdots & \vdots & \vdots & \vdots & \vdots \\
0 & 1 & t_{21} & W_{2M_{21}1} & 0 \\
\hline
0 & 1 & t_{22} & W_{212} & 0 \\
\vdots & \vdots & \vdots & \vdots & \vdots \\
0 & 1 & t_{22} & W_{2M_{22}2} & 0 \\
\hline
\bullet & \bullet & \bullet & \bullet & \bullet \\
\bullet & \bullet & \bullet & \bullet & \bullet \\
\bullet & \bullet & \bullet & \bullet & \bullet \\
\bullet & \bullet & \bullet & \bullet & \bullet \\
\hline
0 & 1 & t_{2J_2} & 0 & W_{21J_2} \\
0 & 1 & t_{2J_2} & 0 & W_{22J_2} \\
\vdots & \vdots & \vdots & \vdots & \vdots \\
0 & 1 & t_{2J_2} & 0 & W_{2M_{2J_2}J_2}
\end{array} \right\}
\left\{ \begin{array}{c} a_1' \\ a_2'' \\ h_2 \\ m_1 \\ m_2 \end{array} \right\} + \boldsymbol{\Delta}
\quad \begin{array}{l} \} \ t \leqq 10°\text{C} \\ \} \ t > 10°\text{C} \\ \} \ t \leqq 10°\text{C} \\ \} \ t > 10°\text{C} \end{array}$$

or $\boldsymbol{Z} = \boldsymbol{R}\boldsymbol{\beta} + \boldsymbol{\Delta}$

Figure 1.

Under the hypothesis $H1$ the matrix $\boldsymbol{R}$ reduces to a $(J_1 + J_2) \times 4$ matrix, and the hypothesis $\log h_1' = \log h_1''$ is stated as

$$H2: \{1, -1, 0, 0\} \boldsymbol{\beta} = \{0\} \; ; \quad \boldsymbol{\beta}' = (a_1', a_1'', h_2, m)$$

Assume ε_1 to be log-normally distributed ($E\varepsilon_1 = 1$ and $\text{VAR}(\varepsilon_1) = \lambda_1 \zeta_1 / \Delta\tau$). Then $\log \varepsilon_1$ is normally distributed $(-\sigma^2/2, \sigma^2)$ where $\sigma^2 = \log(1 + \lambda_1 \zeta_1 / \Delta\tau)$. Thus, $E \log \varepsilon_1 = -\sigma^2/2$. That σ^2 is dependent on $\Delta\tau$, introduces new problems, especially concerning the tests. But due to the general intricacy of the choice of $\Delta\tau$, this has been ignored (cf. section 9.1). Consider the case $v = 1$ and let

$$\hat{\mathcal{Z}}_{1ij} = \hat{a}_1' + \hat{h}_2 t_{1j} + \hat{m} W_{1ij}$$

where $\hat{a}_1'$, $\hat{h}_2$ and $\hat{m}$ are the least squares estimates. $\hat{\mathcal{Z}}_{1ij}$ is biased since

$$E(\exp \hat{\mathcal{Z}}_{1ij}) \neq h_1' \exp(h_2 t_{1j}) \bar{w}_{vij}^m$$

which follows from

$$E(\exp \hat{\mathcal{Z}}_{1ij}) = \exp(E\hat{\mathcal{Z}}_{1ij} + \text{VAR}(\hat{\mathcal{Z}}_{1ij})/2) = h_1' \exp(h_2 t_{1j}) w_{1ij}^m \exp(-\sigma^2/2 + \text{VAR}(\hat{\mathcal{Z}}_{1ij})/2)$$

Thus, if the estimate $\tilde{a}_1' = \hat{a}_1' + \sigma^2/2 - \text{VAR}(\hat{\mathcal{Z}}_{1ij})/2$ is applied

$$\hat{\mathcal{Z}}_{1ij} = \tilde{a}_1' + \hat{h}_2 t_{1j} + \hat{m} W_{1ij}$$

will be unbiased. As $\text{VAR}(\hat{\mathcal{Z}}_{1ij})$ depends on the independent variables the mean value of $\text{VAR}(\hat{\mathcal{Z}}_{1ij})$, $j = 1, 2, \ldots, J_1$. $i = 1, 2, \ldots, M_{1j}$, is used as an approximation.

Experiment III

The experiment is based on $Y_{ji} = \mu_{ij} D_{1ij} + \mu_{2j} D_{2ij} + \varepsilon_3$ (cf. 9.3). In the case $j = 3$ the equation in matrix notation is

$$\boldsymbol{Y} = \begin{Bmatrix} D_{111} & D_{211} & 0 & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ D_{1M_11} & D_{2M_11} & 0 & 0 & 0 & 0 \\ 0 & 0 & D_{112} & D_{212} & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & D_{1M_22} & D_{2M_22} & 0 & 0 \\ 0 & 0 & 0 & 0 & D_{113} & D_{213} \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & 0 & D_{1M_33} & D_{2M_33} \end{Bmatrix} \cdot \begin{Bmatrix} \mu_{11} \\ \mu_{21} \\ \mu_{12} \\ \mu_{22} \\ \mu_{13} \\ \mu_{23} \end{Bmatrix} + \varepsilon_3$$

The hypothesis $\mu_{11} = \mu_{12} = \mu_{13}$ and $\mu_{21} = \mu_{22} = \mu_{23}$ is stated as

$$\begin{Bmatrix} 1 & 0 & -1 & 0 & 0 & 0 \\ 0 & 1 & 0 & -1 & 0 & 0 \\ 0 & 0 & 1 & 0 & -1 & 0 \\ 0 & 0 & 0 & 1 & 0 & -1 \end{Bmatrix} \begin{Bmatrix} \mu_{11} \\ \mu_{21} \\ \mu_{12} \\ \mu_{22} \\ \mu_{13} \\ \mu_{23} \end{Bmatrix} = \begin{Bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{Bmatrix}$$

A is estimated by $\hat{A} = \hat{\mu}_{2j} / \hat{\mu}_{1j}$. The usual 95 % confidence interval of A is not defined, so Fieller's theorem (cf. Finney, 1952) is applied to determine the *fiducial limits*.

REFERENCES

Finney, D. J., (1952). *Statistical Methods in Biological assay.* Charles Griffin & Company Ltd. London.
Rao, C. R., (1973). *Linear Statistical Inference and its Applications.* John Wiley & Sons.
Searle, S. R., (1971). *Linear Models.* John Wiley & Sons.

INDEX OF SYMBOLS

Variable names used in definitions of mathematical concepts (the text written in brevier types) are excluded from the index. Numbers in brackets refer to sections.

Roman letters:

A_0: see $L(f)$. (4).

A: A constant in the equation $L(f) = B(1 - Af)$ (the factor $\beta(1-\alpha)$ considered as a function of f). Three alternative interpretations of A and B are given:
1) $B = \beta_0(1-\alpha_0)$ and $A = C_0$ in $L_1(f) = \beta_0(1 - C_0 f)(1-\alpha_0)$.
2) $B = \beta_0$ and $A = A_0$ in $L_2(f) = \beta_0(1 - A_0 f)$.
3) $B = \beta_0$ and $A = C_0 + A_0$ in $L_3(f) = \beta_0(1 - (C_0 + A_0)f + A_0 C_0 f^2)$, where the term $A_0 C_0 f^2$ is ignored). (4).

B: A constant in the general expression for $\beta(1-\alpha)$. See A. (4).

C_0: See $L(f)$. (4).

d_1, d_2: Parameters in the processes P_1 and P_2 defined as a non-Markov process. (5).

D_{1ij}: $(\Delta R/\Delta \tau)$ and $D_{2ij} = f(\Delta R/\Delta \tau)$ for trout i at temperature t_j. (9.3).

$\boldsymbol{E}$: $(E_1, E_2, \ldots..)$ environment vector. (7).

f: feeding level. (3).

F: $F(H, a, b)$ is the F-statistic on a, b degrees of freedom for the hypothesis H.

G: $G(w(\tau), \Gamma(dR/d\tau))$ is the catabolic term in the general growth equation. (3).

h: coefficient of anabolism. (3).

H: $H = B(1 - Af)fh$. (5).

h_1, h_2: $h(t) = h_1 \exp(h_2 t)$, where $t =$ temperature. (7).

h_1', h_1'': $h_1 = h_1'' u(N) + h_1' s(N)$, where $N =$ number of trout. (7).

J_v: the number of different temperatures considered at density v. (9.1).

k: catabolism coefficient. (3).

k_1, k_2: $k(t) = k_1 \exp(k_2 t)$, where $t =$ temperature. (7).

k_1', k_1'': $k_1 = k_1'' u(N) + k_1' s(N)$, where $N =$ number of trout. (7).

L: $L(f)$ is the factor $\beta(1-\alpha)$ considered as a function of feeding level. Three alternatives are considered:
$L_1(f) = \beta_0(1 - C_0 f)(1-\alpha_0)$ (α constant, $\beta = \beta_0(1 - C_0 f)$
$L_2(f) = \beta_0(1 - A_0 f)$ (β constant, $\alpha = (1 - A_0 f)$)
$L_3(f) = \beta_0(1 - C_0 f)(1 - A_0 f)$ ($\alpha = (1 - A_0 f)$, $\beta = \beta_0(1 - C_0 f)$)
α_0, β_0, A_0 and C_0 are constants. (4).
The equation $L(f) = B(1 - Af)$ where A and B are constants is a common expression for L_1 and L_2 and an approximation of L_3. (4).

m: exponent of anabolism. (3).

m_1, m_2: exponent of anabolism for temperatures $\leqq 10°C$ and $> 10°C$ resp. (10.1).

M_{vj}: number of aquaria used at density v and at temperature t_{vj}. (9.1).

n: exponent of catabolism. (3).

N_{vij}: number of trout at density v in aquarium i and at temperature t_{vj}. (9.1).

$P_1(\tau)$: the stochastic process related to consumption, accounting for the deviation from the expected consumption. (5).

$P_2(\tau)$: the stochastic process related to fasting catabolism, accounting for the deviation from expected fasting catabolism. (5).

$Q_i(\tau)$: the family of stochastic processes, which constitutes the total random variation from the average growth, $i = 1, 2, \ldots\ldots$ (5).

$R(\tau)$: wet weight of food consumed until time τ. (3).

$(dR/d\tau)_{\max}$: maximum rate of feeding. (3).

r_1, r_2: parameters in the processes P_1 and P_2, defined as non-Markov processes. (5).

$\boldsymbol{R}$: design matrix in the linear model. (App.)

$s(N)$: $s(N) = 1$ if $N > 1$ and else 0, where N = number of trout. (7).

$S(t)$: $S(t) = 1$ if $t \leqq 10$ and else 0, where t = temperature. (App.)

t: temperature (°C).

t_{vj}: temperature at experiment j at density v. (9.1).

$u(N)$: $u(N) = 0$ if $N > 1$ and else 1, where N = number of trout. (7).

$U(f, \bar{W}, t)$: $dR/d\bar{W}$, expected food conversion ratio. (1.4).

$\boldsymbol{V}$: the variance-covariance matrix of the dependent variables. (App.).

$w(\tau)$: live weight of the trout at time τ. (3).

$(dw/d\tau)_{\text{fasting}}$: rate of weight decrease for a fasting trout. (3).

$\bar{w}$: $\bar{w} = (w(\tau + \Delta\tau) + w(\tau))/2$. (5).

W_{vij}: $W_{vij} = \log \bar{w}$ at density v in aquarium i at temperature t_{vj}. If $v = 2$, $\bar{w}$ is the mean value of the N_{2ij} trout. (9.1).

$\dot{w}(\tau)$: stochastic differential coefficient of $w(\tau)$. (9.1).

$\bar{W}(\tau)$: $\bar{W}(\tau) = Ew(\tau)$. (10.4).

W_∞: $W_\infty = (B(1-Af)fh/k)^{1/(n-m)}$. (11).

Y_{ij}: $(\Delta w/\Delta\tau) + k\bar{w}^n$ for trout i at temperature t_j. (9.3).

Z_{vij}: $\log(\Delta R/\Delta\tau)_{\max}$ at density v in aquarium i at temperature t_{vj}. If $v = 2 (\Delta R/\Delta\tau)_{\max}$ is the mean value of the N_{2ij} trout. (9.1).

Greek letters:

α:	the fraction of the food absorbed producing the energy to absorb the food. (3).
α_0:	see $L(f)$. (4).
β:	the fraction of the food eaten absorbed. (3).
β_0:	see $L(f)$. (4).
$\boldsymbol{\beta}$:	the set of parameters in the linear model. (App.)
$\Gamma(dR/d\tau)$:	anabolic term in the general growth equation. (3).
Δw:	$\Delta w = w(\Delta\tau + \tau) - w(\tau)$ where $\Delta\tau$ is a non-infinitesimal time interval. (5).
Δ_{vij}:	$\log\varepsilon_1 - E\log\varepsilon_1$ (the stochastic term in experiment I) at density v in aquarium i and at temperature t_{vj}. (9.3).
$\varepsilon_1, \varepsilon_2$:	$\varepsilon_1 = 1 + \Delta P_1/\Delta\tau$ and $\varepsilon_2 = 1 + \Delta P_2/\Delta\tau$. (2).
ε_3:	$\varepsilon_3 = -k\bar{w}^n(\varepsilon_2 - 1)$. The stochastic term in experiment III. (9.1).
ζ_1, ζ_2:	parameters in the processes P_1 and P_2. (5).
λ_1, λ_2:	parameters in the processes P_1 and P_2. (5).
μ_{ij}:	$\mu_{1j} = B$ and $\mu_{2j} = -AB$ at temperature t_j. (9.3).
ϱ:	multiple correlation coefficient. (App.)
σ^2:	residual error variance. (App.)
τ:	time in days. (3).
$\Psi(w)$:	$\Psi(w) = Hw^m - kw^n$. (5).