

A growth model, gastric evacuation, and body composition in rainbow trout, *Salmo gairdneri* Richardson, 1836

Jon From

Danish Trout Culture Research Station, Brøns, DK-6780 Skærbæk, Denmark

Gorm Rasmussen

Inland Fishery Laboratory, Lysbrogade 52, DK-8600 Silkeborg, Denmark

Abstract

A growth model of fish is formalized. The parameters in the model have been estimated from aquaria experiments with immature rainbow trout fed moist pellets. Different gastric evacuation models are evaluated. The body composition has been analyzed for different feeding regimes and fish sizes. Efficiency of growth in eggs and yolk sac fry has been estimated. Comparisons with other feeds and salmonid species have been made.

Contents

1. Introduction	63
2. Other growth equations	64
2.1. Ivlev's equation	64
2.2. Winberg's equation	64
3. Present model	65
3.1. The anabolic term	66
3.1.1. Feeding	66
3.1.2. Assimilation	67
3.2. The catabolic term	68
3.2.1. (I) Starving catabolism	68
3.2.2. (II) Feeding catabolism	69
3.2.3. Total catabolism	70
3.3. Nitrogen excretion, U	70
3.4. Oxygen consumption $\alpha + k'(T)$	70
3.5. Single fish contra several fish	71
3.6. Comparison with Davis & Warren's equation	71
3.7. The unit used in a growth equation	72
4. Body composition	73
5. Gastric evacuation	73
6. Growth efficiency and yolk sac fry	76
7. Material and methods	76
7.1. Experimental design	76
7.2. Parameter determinations	78
7.2.1. $h(T)$ and m	78
7.2.2. Feeding level experiments $0 < f < 1$	78
7.2.3. Assimilation coefficient, β	78

7.2.3.1.	Energy (COD)	78
7.2.3.2.	Nitrogen	78
7.2.4.	$k(T)$ and n	79
7.2.5.	Nitrogen excretion, U	79
7.2.6.	Total respiration	80
7.2.7.	Size of the weight exponents	80
7.3.	Body composition	80
7.4.	Gastric evacuation	81
7.4.1.	Experiment 1	81
7.4.2.	Experiment 2	81
7.5.	Yolk sac experiments	82
7.5.1.	Experiment 1	82
7.5.2.	Experiment 2	82
7.6.	Analyses	83
7.6.1.	Dry weight	83
7.6.2.	Bomb calorimetry	83
7.6.3.	COD	83
7.6.4.	Lipid	84
7.6.5.	Ash	84
7.6.6.	Nitrogen	85
7.6.7.	NPN	85
7.6.8.	TVN	85
7.6.9.	Carbohydrate	85
7.6.10.	$\text{NH}_3\text{-N}$	86
7.6.11.	Oxygen	86
7.7.	Statistical methods	86
8.	Results and discussion	87
8.1.	The anabolic term, $h(T)$	87
8.2.	Assimilation coefficient, β	90
8.2.1.	Energy (COD)	90
8.2.2.	Nitrogen	93
8.3.	The catabolism of starving fish, $k(T)$	93
8.4.	The $\text{NH}_3\text{-N}$ excretion, $U = U_1 + U_2$	95
8.5.	The oxygen consumption, $\alpha + k'(T)$	97
8.6.	Simulated growth, the growth equation	100
8.6.1.	Energy	100
8.6.2.	Nitrogen	103
8.7.	Body composition	104
8.7.1.	NPN and TVN	104
8.7.2.	Carbohydrate	106
8.7.3.	Protein	107
8.7.4.	Proximate analysis	108
8.8.	Gastric evacuation	115
8.8.1.	Experiment 1	117
8.8.2.	Experiment 2	119
8.8.3.	Use of evacuation model	121
8.9.	Efficiency of growth, yolk sac fry experiments	121
8.9.1.	Experiment 1	121
8.9.2.	Experiment 2	125
9.	Comparative experiments	127
9.1.	Experiments with moist contra dry pellets	127
9.2.	Comparison with brown and brook trout	128
9.3.	Comparison with Pentelow and Elliott	129
10.	References	129
	Appendix	135

The question is, or should be: What amount per day of a given article will be needed to produce a pound of trout within a given time?

Page (1895)

1. Introduction

The pioneering works in fish bioenergetics are e.g. those of: Pütter (1909), Pearse & Achtenberg (1920), Pearse (1924), Hathaway (1927), Pentelow (1939). The four first mentioned authors showed that smaller fish ate more in proportion to their body weight than did the larger individuals of the same species. Further, Hathaway showed that food intake increased with increasing temperature. Pentelow (1939) and Baldwin (1956) extended their experiments to comprise also superoptimal temperatures so they could conclude that the increase in food intake with increasing temperature only reached a certain point beyond which the food intake again decreased. Further they showed that the food conversion ratio (food/fish gain) increased with increasing temperature.

Stauffer (1973) emphasized that a growth model must consider all the factors that might influence growth. He mentioned care, diets, diseases, maturity, photoperiod, ration and feeding frequency, social hierarchy, species and race, swimming activity and exercise, fish size, age and temperature. To this list could of course be added oxygen content of the water. See e.g. Herrmann, Warren & Doudoroff (1962), Adelman & Smith (1970) and Andrews, Murai & Gibbons (1973). However, Swift (1963) and (1964) says that for brown trout, *Salmo trutta* Linné, 1758 and char, *Salvelinus alpinus* (Linné, 1758) oxygen concentration between 50 and 200 per cent air-saturation has little effect on growth rate. But all his fish are fed to satiation without registering the food intake so Swift says nothing about the possible dependence of food conversion on oxygen content. Further, pH, CO₂, various toxic substances as ammonia, nitrite etc. (i.e. water quality) should be mentioned. Parker & Larkin (1959) showed that salinity influenced the growth and that in saltwater male steelhead grew faster than female. Kinne (1960) found that food conversion and growth rate were depending on salinity and temperature. Concerning size hierarchy effect it can be mentioned that Sparre (1976) in a Danish trout-farm found such an effect, but it was so small that it could be ignored. Hathaway (1927) found that moderate changes in illumination produced no perceptible effect on food consumption. Miller (1973) found a photoperiod effect on growth. Further, Gross, Roelofs & Fromm (1965) demonstrated that growth, food consumption, and food conversion efficiency were all influenced by the photoperiod. Björklund (1958) and Anderson (1959) found no relationship between daylength and growth. So that studies on the influence of light on growth have not infrequently resulted in variable, complex, and confusing results, Brett (1979).

Wingfield (1940) investigates the differences in trout growth in hard and soft waters and concludes that such differences may be effected not by differences in the concentration of any specific ion, but by departures from the optimum ionic balance brought about by variations in the relative concentration of any ion present. Concerning growth in chalk streams Edwards, Densem & Russel (1979) find that

in particular the high growth rates of trout in chalk streams may be related almost entirely to the thermal properties of such waters and not to direct effects of calcium.

In summary, Stauffer says: 'any attempt at modelling growth must include the three factors: ration, fish size and temperature, as variables that have the most influence on the growth for a given species and diet.'

2. Other growth equations

2.1. Ivlev's equation

Ivlev (1939) was the first to split up the energy of the food in different terms in an energy budget.

He uses the following equation:

$$Q = Q' + Q_R + Q_t + Q_w + Q_v,$$

where

Q = heat of combustion of devoured food

Q' = heat of combustion of the growth of the organism

Q_R = heat of combustion of the excretions

Q_t = quantity of initial heat generated

Q_w = energy of external work

Q_v = energy of internal work.

However, Ivlev does not (at least not in the English summary) take the trouble to explain the different terms in his budget. Especially his initial or primary heat has been difficult for others to understand. E.g. Winberg (1960) simply denies the existence of primary heat in poikilotherms.

When Ivlev uses his energy budget in practice he makes the simplified assumption that the energy of the external work is approximately 20 per cent of the internal work. This assumption is not (at least not in the English summary) rendered probable in any way.

2.2. Winberg's equation

Winberg (1960) formulated a simple bioenergetic relationship implicitly incorporating temperature and fish size. This relationship has gained wide application and further improvements. Especially Paloheimo & Dickie (1965, 1966a and 1966b) stimulated a lot of work on this subject. E.g. Kerr (1971a, b and c).

The basic equation of Winberg is:

$$\begin{aligned} &\text{Energy of weight increase} + \text{energy of metabolism} \\ &= \text{physiologically useful energy} = 0.8 \text{ times energy of the ration,} \end{aligned}$$

or in letters:

$$P + T = 0.8R.$$

The energy of metabolism T is estimated as twice the energy equivalent of the oxygen consumption of fish at routine level. This idea is based on the following

observations: 'We recall that the computed value was about 1.5 times the expected routine metabolism in the case of the fourth year roach, *Rutilus rutilus* (Linné, 1758) from lake Glubokoe; for second-year carp, *Cyprinus carpio* Linné, 1758 that were feeding intensively and growing rapidly it was 2.5-3 times; for mature verkhovka, *Leucaspilus delineatus* (Heckel, 1843), 2.0-2.8 times; and for young osëtr, *Acipenser güldenstaedti* Brandt, 1833, 1.5-2 times. However, for fingerling wild carp and inconnu, *Stenodus leucichthys* (Güldenstädt, 1772) the calculated values for metabolism were very close to the expected values for routine metabolism'. (Winberg 1960 p. 168-169). The scientific names are added by the present authors. It is surprising that these sparse observations have made Winberg to propose the figure 2 as an universal factor which relates routine metabolism with active metabolism. Winberg gives no physiological explanation for why the active metabolism should be the routine metabolism multiplied by a constant. He ignores that feeding metabolism is physiologically distinct from active metabolism as a fed fish has a higher metabolic rate than a fasting one, even at rest. Further, it is a great simplification to put the physiologically useful energy = 0.8 times the energy of ration, completely independent of fish species, fish size, food object, feeding level, temperature, etc.

In spite of the shortcomings of Winberg's equation Paloheimo & Dickie (1965, 1966a and 1966b) have used it in their three extensive papers. It is Paloheimo & Dickie's 'K-line' that by various authors has attracted most attention. Gross efficiency: $K = (\Delta w/R\Delta t)$, where Δw is growth, R ration, and Δt time. So that $\log K = \log(\Delta w/R\Delta t)$ which is calculated as a function of R . This figure they call the 'K-line'. This relationship has by several authors been called a 'K-line model' and they have devoted much work to it. The only thing this term predicts is that the gross efficiency decreases with increasing ration. This is of course only true for ration sizes higher than optimum ration size, and various authors have spent much time to draw the attention to this, e.g. Warren & Davis (1967); Rafail (1968); Brett, Shelbourn & Shoop (1969); Gerking (1971); Brett & Shelbourn (1975); Elliott (1975b) and (1979); Staples & Nomura (1976), and Huisman (1976).

3. Present model

Growth of a specimen can be considered as the difference between what enters the body and what leaves it: Growth = assimilated part of the food minus the part of food assimilated which gives energy to the different functions of the organism, so that:

$$Growth = In - Out$$

This reflection of growth may be developed and formalized in many ways.

A growth model should be mathematically consistent and applicable to parameter estimations based on relatively simple experimental designs.

The present authors have worked along the lines laid down by Ursin (1967) who elaborated the principles worked out by Pütter (1920). Pütter has growth = $k\lambda^2 - k'\lambda^3$ where k and k' are constants and λ is length. Assuming isometrical growth

Pütter says that the dimension of λ is $G^{1/3}$ where G is weight. This gives: growth = $kaG^{2/3} - k'aG$, where a is a constant. Ursin's growth model fulfils the above mentioned requirements, i.e. it is mathematically consistent and applicable to parameter estimations based on relatively simple experimental designs.

With more or less modifications these ideas have been used by Sparre (1976), Sperber, From & Sparre (1977), Andersen & Ursin (1977), Rasmussen (1977), From & Rasmussen (1979), and Rasmussen & Therkildsen (1979).

The growth model can describe the course of a growth curve according to varying factors, e.g. temperature, ration size and fish size. Further, it may predict e.g. maintenance ration as a function of temperature and fish size; amount of faeces and ammonia from excretions led into recipients from aquaculture systems, and so on.

The basic equation is:

$$dw/dt = H(dR/dt) - K(w_t, H(dR/dt)), \quad (1)$$

where

dw/dt	= weight change per unit time
w_t	= weight of fish to time t , a variable
dR/dt	= weight of food consumed per unit time, feeding rate
$H(dR/dt)$	= the anabolic term ('the build up term')
$K(w_t, H(dR/dt))$	= the catabolic term ('the break down term').

The anabolic term expresses that the quantity absorbed is a function of the quantity eaten. The catabolic term is described by two terms representing (I) the catabolism of a starving fish, and (II) the catabolism resulting from feeding and its subsequent processes.

3.1. The anabolic term

3.1.1. Feeding

The functional coherence is assumed to be valid

$$dR/dt = fh(T)w_t^m, \quad (2)$$

where

$h(T)$	= coefficient of anabolism, temperature dependent
T	= temperature, a variable
m	= exponent of anabolism, a real number
f	= feeding level, a variable
t	= time.

The feeding level is defined as the fraction eaten of the maximum quantity which could be eaten ($0 \leq f \leq 1$). The feeding level for a starving fish is 0, and for a fish eating the maximum ration $f = 1$.

Ursin (1979) describes the coefficient of anabolism as:

$$h(T) = \frac{1}{h_1 \exp(h_2 T) + h_3 \exp(h_4 T)} \quad (3)$$

and says that the expression 'is derived from the Michaelis-Menten expression for the rate of enzymic processes and the Arrhenius equation for the temperature dependence of simple chemical processes' (p.74-75).

According to this expression the feeding rate increases with increasing temperature up to a maximum point beyond which it decreases.

Equation (3) could be substituted by the hyperbolic catenary curve of Janisch (1927). But as Ursin (1967) and Ricker (1979) show, the catenary curve should be used with reservation, because up till now it has not been possible to produce a symmetrical curve based on experiments relating feeding rate and temperature.

Most often, however, only the ascending part of the curve is used, i.e. at temperatures below the maximum feeding rate. (Sperber, From & Sparre 1977) so that an approximation of $h(T)$ can be described as:

$$h(T) = h_1 \exp(h_2 T) \quad (3')$$

From an 'estimating point of view', (3) can be substituted by a purely empirical formula, e.g. a second or better a third order polynomial, see also Stauffer (1973) and Papst, Ayles & Uraiwan (1982). In this it is very simple to estimate the parameters and in practice it gives the same relationship between observed and calculated observations:

$$h(T) = h_1 + h_2 T + h_3 T^2 + h_4 T^3 \quad (3'')$$

From experiments with brown trout Elliott (1975a) presented data which showed that the relationship between dR/dt_{\max} (D_{\max} in Elliott's terminology) and temperature could be adequately described by exponential equations at each temperature in 4 intervals from 3.8°C to 21.7°C. This gives a total of 12 parameters to be estimated. Elliott's data might easily have been incorporated in the present model, see 9.3. and Ursin (1979).

3.1.2. Assimilation

Efficiencies of the absorption of the nutrients in the diet are a fundamental part of dietary formulations (Fänge & Grove 1979) but from a general point of view energy and/or nitrogen assimilation has gained wide application (Brett & Groves 1979). Assimilation, β , can be taken as the fraction of the food which is assimilated. Winberg (1960) states that this fraction is a constant figure, but it is generally realized that the efficiency must be a function of food composition (both quantitatively and qualitatively), feeding level, temperature and maybe fish size (e.g. Smith 1973). That means:

$$\beta = B(f, T, w) \quad (4)$$

Thus the anabolic term becomes:

$$H(dR/dt) = \beta f h(T) w^m \quad (5)$$

Ursin (1967) p.2364 and Sperber, From & Sparre (1977) p.278-279 discuss different possibilities of expressing β . Up to now nobody has proposed a consistent, plausible model for the assimilation of food. In such a model it is very difficult to

estimate the parameters from non-biased experimental data, and the present authors realize that the equations in this paper are purely empirical ones.

In connection with aquaria experiments the total amount of faeces = $(1 - \beta)\Delta R$, will be the quantity which normally is quantitatively determined. At a given fish weight and temperature the amount of faeces is expected to be maximum for $f = 1$ and 0 for $f = 0$, Elliott (1976b).

However, the total amount of faeces are a mixture of non-assimilated food ('true faeces') which are supposed to consist of settleable, suspended and dissolved faeces *plus* different non-reabsorbed residues 'metabolic residues' of body origin, from the intestine (mucosal cells, digestive enzymes, other secretions and microflora), Cho, Slinger & Bayley (1982). I.e. the total amount of determined faeces consists also of a contribution from starving fish.

Therefore, if β is calculated as $1 - (\text{total faeces/food})$ and expressed as a function of f , temperature, and weight, the size of β will be underestimated, depending on the amount of the metabolic residues. Mainly, the settleable faeces will originate from non-assimilated food. In connection with the starvation experiments minute 'settable faeces' were observed, but no attempt to quantify these was made.

The amount of settleable faeces can therefore be described as:

$$\text{Settable faeces} = b_1 f^{b_2} \exp(b_3 T) w^{b_4} \quad (6)$$

(6) expresses that settleable faeces only will occur for $f > 0$. As the suspended and dissolved faeces from a feeding or fed fish cannot be separated analytical in 'true faeces' and 'metabolic residues' this fraction of faeces for $0 \leq f \leq 1$ can best be described as:

$$(\text{Suspended} + \text{dissolved}) \text{ faeces} = b_1 \exp(b_2 f) \exp(b_3 T) w^{b_4} \quad (7)$$

(7) expresses that this fraction of the total amount of faeces has contributions from both starving and feeding fish.

In this way the amount of suspended + dissolved faeces is:

$$(\text{Suspended} + \text{dissolved}) \text{ faeces, } f = 0: b_1 \exp(b_3 T) w^{b_4}, \text{ so that}$$

$$(\text{Suspended} + \text{dissolved}) \text{ faeces, } f > 0: b_1 (\exp(b_2 f) - 1) \exp(b_3 T) w^{b_4} \quad (7')$$

Subsequently for $f > 0$ the total amount of faeces originating from feeding are:

$$\text{Total faeces} = (6) + (7'), \text{ so}$$

$$\beta = 1 - \frac{\text{total faeces}}{f b(T) w^m}$$

Concerning the value of the weight exponents see 7.2.7.

3.2. *The catabolic term.* This consists of the following two terms: (I) + (II).

3.2.1. (I) *Starving catabolism*

The catabolism of a starving fish ($f = 0$).

$$(dw/dt_{\text{starving}}) = k(T) w_i^n,$$

where

$k(T)$ = coefficient of catabolism, temperature dependent.

n = exponent of catabolism, a real number.

$k(T)$ can, in the same way as $h(T)$, be considered as a function of temperature,

$$k(T) = k_1 \exp(k_2 T) \quad (8)$$

As a starving fish has (a) a respiration $k'(T)$, (b) a loss in exfoliated cells $k''(T)$, both from epidermis and the stomach and gut epithelium, and (c) a loss in urine $k'''(T)$, $k(T)$ can be split up in:

$$k(T) = k'(T) + k''(T) + k'''(T), \quad (9)$$

where $k'(T)$ is 'Krogh's respiration curve' (Ege & Krogh 1914, quoted from Ursin (1967) pp. 2395-2397), $k''(T) = b_1 \exp(b_3 T) w^{b_4}$ and $k'''(T) = U_1$ (endogeneous excretion, see 3.4.).

From all the experimental data and references compiled in Brett & Groves (1979), the metabolism of a starving fish is adequately described as an exponential function of temperature up to a certain point when death occurs.

In energy terms

$k(T) = k'(T) + k''(T) + k'''(T)$, where $k'''(T)$ is recalculated from endogenous excretion to energy.

In nitrogen terms

$$k(T) = k''(T) + k'''(T).$$

3.2.2. (II) *Feeding catabolism*

The feeding catabolism assumed to be:

$$A\beta \frac{dR}{dt} \quad (10)$$

where

$$A = \alpha + U_2 \quad (11)$$

where A represents the fraction of the assimilated food producing energy for the catabolic processes resulting from feeding. The value of A depends on the food type and feeding level according to Davis & Warren (1971), and maybe temperature and fish size. This matter is discussed by Brett & Groves (1979) and Jobling (1981a). Apart from the additional energy required for eating α corresponds to what Beamish, Niimi & Lett (1975) call the 'apparent specific dynamic action', measured as oxygen consumption. And U_2 is the energetical loss from the exogenous nitrogen excretion, see 3.4.

In energy terms

$A = \alpha + U_2$, where U_2 is recalculated from exogenous excretion to energy.

In nitrogen terms

$$A = U_2.$$

3.2.3. Total catabolism

(I) + (II) give the total catabolism:

$$K(w_i, H(dR/dt)) = k(T)w_i^n + A\beta dR/dt. \quad (12)$$

Inserting (2) in (12) and then (5) and (12) into (1) gives:

$$dw/dt = (1 - A)\beta f h(T)w_i^m - k(T)w_i^n \quad (13)$$

3.3. Nitrogen excretion, U

The nitrogen excretion U is the sum of the endogenous excretion U_1 , and the exogenous excretion U_2 , i.e. $U = U_1 + U_2$, see also Brett & Groves (1979).

In freshwater fish U will consist of NH_3 , urea and negligible amounts of uric acid, amino acids, and other nitrogen containing compounds. Forster & Goldstein (1969), Goldstein & Forster (1970), and Fischer (1977).

Determination of U_1 on starving fish will be an approximation to the true value of the endogenous nitrogen excretion. The true value will normally be a little lower than the value found for starving fish because these have an increased conversion of protein to fulfil their requirement for energy. See also Brett & Groves (1979).

Determination of U_2 , which represent an energy – and nitrogen loss of the assimilated food, can only be done on basis of determinations of the total nitrogen loss on fed and starved fish, respectively. U_2 is thus determined as $U_2 = U - U_1$. But in practice it will be difficult to separate U_1 and U_2 , see Brett & Groves (1979). The present authors have only determined the *increase* of nitrogen excretion from feeding and not taken into account if this additional nitrogen increase originates from body reserves or/and the food. As the budget is calculated over several days this consideration is unimportant. The nitrogen excretion is analogous to the increase in oxygen consumption after feeding where no distinctions have been made between oxidation of body reserves or/and directly of the food. This matter can only be revealed by using radioactive tracers.

The size of U can be described as:

$$\text{for } f \geq 0: U = \mu_1 \exp(\mu_2 f) \exp(\mu_3 T) w^{\mu_4} \quad (14)$$

in this way:

$$\text{for } f = 0: U_1 = \mu_1 \exp(\mu_3 T) w^{\mu_4} \quad (15)$$

and

$$\text{for } f > 0: U_2 = \mu_1 (\exp(\mu_2 f) - 1) \exp(\mu_3 T) w^{\mu_4}. \quad (16)$$

Nothing indicates that μ_4 should be the same in (15) and (16). But as the size of (15) is smaller than (16) for $f > 0.3$, see Table 8, the error introduced will be insignificant.

Concerning the value of the weight exponents see 7.2.7.

3.4. Oxygen consumption $\alpha + k'(T)$

The oxygen consumption of a fish is considered as the sum of 1) the oxygen consumption $k'(T)$ of a starving fish ($f = 0$) and 2) the oxygen consumption α of a feeding or fed fish ($f > 0$).

The size of $k'(T)$ can be described as:

$$k'(T) = i_1 \exp(i_2 T) w^{i_3}. \quad (17)$$

The oxygen consumption of a feeding or fed fish depends on feeding level, temperature and fish weight, in such a way that $\alpha \rightarrow 0$ for $f \rightarrow 0$ and α is maximum for $f = 1$.

α could best be described as:

$$\alpha = a_1 f^{a_2} \exp(a_3 T) w^{a_4}. \quad (18)$$

But as the total oxygen consumption of a fed or feeding fish not directly can be separated in contributions from α and $k'(T)$, instead we have:

$$\text{Total respiration} = a_1 \exp(a_2 f) \exp(a_3 T) w^{a_4} \quad (19) \simeq (17) + (18)$$

so:

$$\alpha \simeq a_1 (\exp(a_2 f) - 1) \exp(a_3 T) w^{a_4} \quad (20)$$

and

$$k'(T) = i_1 \exp(i_2 T) w^{i_3} \simeq a_1 \exp(a_3 T) w^{a_4} \quad (21)$$

Concerning the size of the weight exponents see 7.2.7.

3.5. *Single fish contra several fish.*

Sperber, From & Sparre (1977) have extended the model to include the influence of number of fish (one or many) as one single fish in one aquarium has a bigger maximum food intake and a smaller starving catabolism than a fish which is in company with one or more other fish. In this paper all the parameters have been determined from experiments with many fish (i.e. $n > 1$). Further, experiments for $f = 1$ have also been carried out with single fish (i.e. $n = 1$).

3.6. *Comparison with Davis & Warren's equation.*

Warren & Davis (1967) propose an equation which resembles Ivlev's in some respects but which has terms that have been defined so as to be independent and measurable. The equation is most known in the notation used in IBP Handbook No. 3, Davis & Warren (1971):

$$C = F + U + \Delta B + R$$

where:

$$R = R_s = R_d + R_a$$

C = energy value of food consumed.

F = energy value of faeces.

U = energy value of materials excreted in the urine or through the gills or skin.

ΔB = total change in energy value of materials of body (growth).

R = total energy of metabolism; this can be subdivided as follows:

R_s = energy equivalent to that released in the course of metabolism of unfed and resting fish (standard metabolism).

R_d = additional energy released in the course of digestion, assimilation, and storage of materials consumed (including specific dynamic action or SDA).

R_a = additional energy released in the course of swimming and other activity.

From (9), (11), and (13)

$$\frac{dw}{dt} = \underbrace{\beta fh(T)w_i^m - k''(T)w_i^n}_{(C - F)} - \underbrace{\alpha \beta fh(T)w_i^m}_{(R_d + R_a)} - \underbrace{(U_2 \beta fh(T)w_i^m + k'''(T)w_i^n)}_U - \underbrace{k'(T)w_i^n}_{R_s}$$

3.7. The unit used in a growth equation

The only terms in which all the quantities can be measured are energy and nitrogen. Sperber, From & Sparre (1977) used units of g body weight (wet), but in this way the 'out' cannot be split up in faeces, excretory products, A, and so on. Further, if wet weight alone is used it must be assumed with Ursin (1967), that the food has the same chemical constitution as the fish. If a model shall be used in connection with fish farming, where pelleted food is used this assumption is clearly not permissible.

Therefore we can write the following balanced equations:

Nitrogen

$$dw/dt = \text{consumed} - \text{faecal} - \text{excreted (exogenous + endogenous)}.$$

Energy

$$dw/dt = \text{consumed} - \text{faecal} - \text{excreted nitrogen (exogenous + endogenous recalculated to energy)} - \text{feeding respiration (recalculated to energy)} - \text{starving respiration (recalculated to energy)}.$$

For energy an appropriate unit is mg oxygen. The only quantity which cannot be measured in this unit is the inorganic matter ($\text{NH}_3\text{-N}$) in the excretory products. In spite of this disadvantage the present authors find mg oxygen to be the most convenient unit. This is due to the fact that in other units e.g. calories it is necessary to use oxycalorific coefficients to convert mg oxygen to cal.

The coefficient used to convert COD (chemical oxygen demand) on dead material is generally accepted to be 3.42 cal/mg oxygen, e.g. Davis & Warren (1971). But the coefficient is varying with the variation in the chemical composition of the organic matter. Ostapenya (1971) gives the following interval 3.33-3.49 cal/mg oxygen, with 3.4 cal/mg oxygen as a mean value. When the oxygen consumption of a living animal shall be converted to calories it is not only necessary to consider the composition of the food but also of the excretory product. Krokhin (1959) uses a coefficient of 3.38 cal/mg oxygen, Davis & Warren (1971) use 3.42 cal/mg oxygen. But Elliott & Davison (1975) say that 3.42 cal/mg oxygen may be applicable to some herbivorous fish but 3.24 cal/mg oxygen is more appropriate for a carnivorous fish that utilizes ammonia as its chief excretory product. For a proteinaceous diet Brafield & Solomon (1972) find a value of 3.20 cal/mg oxygen. All these considerations and inaccuracies are avoided if mg oxygen is used as unit. But here the problem arises that the inorganic material ($\text{NH}_3\text{-N}$) in the excretory product, cannot be measured in this unit. Ammonia can be converted to energy by using a value of 5.94 cal/mg, Elliott & Davison (1975). This figure can then be

converted to mg oxygen by using the factor $1/3.4$ mg oxygen/cal = 0.3 mg oxygen/cal, i.e. X mg $\text{NH}_3\text{-N} = X \cdot 5.94 \cdot 0.3$ mg $\text{O}_2 = X \cdot 1.8$ mg O_2 . The inaccuracy by using these two conversion factors is not important as the fraction of ammonia usually constitutes less than 5% of the ingested food measured as energy. See Table 8.

To estimate the parameters it is only necessary to measure the fish in energy (e.g. mg oxygen by means of COD). But in growth experiments the body composition of the fish is often determined.

4. Body composition

The fish consist of: water + protein + nitrogen extractives + lipid + ash + carbohydrate.

The terms in the relationship can be found from proximate analysis of fish samples, e.g. Beamish, Niimi & Lett (1975).

Often carbohydrate and nitrogen extractives, i.e. the material of non-proteinaceous origin which contains nitrogen (e.g. free amino acids, phosphopeptides and TVN = total volatile nitrogen, mainly ammonia) are excluded from bioenergetics as they are stated to constitute a relatively small part of the fish body, e.g. Elliott (1976a). Data on body constituents can be used to relate lipid, protein, ash, and energy to e.g. body weight, percentage water and so on, which have been done e.g. by Elliott (1976a) and Boëtius & Boëtius (1980). Such relationships can be used to calculate one body component from another component.

Assuming that proteins consist of 16% nitrogen a conversion factor of $100/16 = 6.25$ is used to calculate the amount of protein in the sample from analyzed amount of nitrogen in the sample, e.g. Ostapenya (1971). From equivalents of 5.65 and 9.45 cal/mg e.g. Davis & Warren (1971) of protein and lipid respectively the energy of a sample can be calculated from the amount of protein and lipid. If the total energy content of a sample has been determined together with either protein or lipid the other can be roughly estimated from the relationship:

Total energy cal/mg dry weight (e.g. bombing or COD) = (protein \cdot 5.65 + lipid \cdot 9.45) cal/mg, assuming that the ash does not contribute with any energy (cf. 7.6.2.). Beamish, Niimi & Lett (1975) state that this relationship uncritically has been used without considering the reliability of the conversion factor of nitrogen to protein, and the reliability of the energetical equivalents of protein and lipid.

5. Gastric evacuation

In growth experiments it is important that no stomach and gut content shall interfere with the results of either start and/or final weight. In the gastric evacuation experiments 7.4. it was observed that when the stomach was empty, practically speaking the gut was empty too. Often the gut was empty when little food still was left in the stomach, at the next inspection there could again be small amounts of faeces. In other words: At the time when the stomach nearly is empty the presence of faeces in the gut is irregular. However, should minute amounts of faeces have

been left in the gut when the stomach was empty, these amounts of faeces were so small that they were negligible. That is why the present paper only operates with gastric evacuation and ignores gut evacuation.

Models

Meal size and rate of gastric evacuation have received considerable attention. Barrington (1957), Windell (1967, 1978), Fänge & Grove (1979) and Jobling (1981b) have all gathered the up-to-date knowledge and experimental references. Tseitlin (1980) has proposed a universal equation based on theoretical considerations and literature references. His equation calculates the duration of digestion in hours as a function of temperature, fish weight, and ration as a per cent of fish weight.

Already Pearse & Achtenberg (1920) observed that yellow perch, *Perca flavescens* Mitchill, 1815 approximately halved the time to appearance of faeces after food intake when the temperature was raised about 10°C. This temperature relationship ceases or even reverses at temperatures near the upper physiological limits of the species in question, Gomazhov (1959) and Tyler (1970).

Concerning the influence of meal and/or fish size on the rate of gastric evacuation, this subject has been much discussed in the literature cited. In summary Barrington (1957) suggested that fish digest small meals more rapidly than larger meals, whereas Windell (1978) states (p.174): 'However, the results from many studies do not support this statement and show conclusively that the amount of food evacuated from the stomach per unit time is increased as the size of the meal is increased. Under a normal feeding regime for a meal of normal size most data indicate relatively little effect of meal size on the times to reach 50% and 100% stomach depletion. In rainbow trout, *Salmo gairdneri*, the evacuation of stomach contents was independent of the amount consumed at a single meal except at ration levels below 0.7% body weight.' (On dry weight basis).

Fänge & Grove (1979) say that both statements are true because a larger meal will have a faster digestion rate but a smaller meal will be digested sooner.

Jobling (1981b) discusses the whole matter and from papers where data are available he suggests a volume dependent model of emptying as being most appropriate. He states that the influence of meal- and fish size on gastric emptying are rather conflicting from available data.

A reasonable evacuation model could express, that the rate of stomach evacuation at a given temperature, fish size, food composition, and particle size is a function of the amount of food present in the stomach, so that

$$dV/dt = -aV_t^b, \quad (22)$$

where

dV/dt = rate of stomach evacuation.

a = a constant (instantaneous coefficient) which might be a function of species, temperature, food type and maybe fish size, so that

b = a species specific constant.

V_t = weight (or volume) of the food in the stomach at time t .

If V_t is expressed as fractions (per cent) of the meal size the intricate interference between feeding rate and body size (e.g. a large fish eats relatively less than a smaller fish) can be eliminated. Therefore the stomach evacuation rate's true dependence of fish weight can be examined by testing the instantaneous coefficient for different fish sizes at the same temperature and using the same feed and pellet size.

The exact expressing of dV/dt (22) has been much discussed (e.g. Jobling 1981 b) and depending on the rationale of the physiological considerations (e.g. depending on b) different proposals can be considered. If dV/dt is a constant fraction (per cent) of the food remainder, (22) reduces to

$$dV/dt = -aV_t^1,$$

which integrated gives the *exponential* model for the rate of stomach evacuation.

$$V_t = V_0 e^{-at}, \quad (23)$$

where V_0 is an integration constant which gives the percentual amount of the stomach content for $t = 0$. This model has been used successfully by Elliott (1972).

Another way is to state as Fänge & Grove (1979) that the rate of digestion is proportional to the surface area of the stomach so that (22) gives:

$$dV/dt = -aV_t^{2/3}$$

which integrated gives the *recti-linear* model (Jobling 1981 b) which is linear in the cube root of the stomach content:

$$V_t^{1/3} = V_0^{1/3} - at, \quad (24)$$

where V_0 has the same meaning as in the exponential model.

Hopkins (1966) proposed that the peristaltic contractions in the stomach initiated by the radial gastric distension implies that the circumferential tension so developed is proportional to the radius of the stomach so that (22) becomes

$$dV/dt = -aV_t^{1/2},$$

which integrated gives the *square-root* model (Jobling 1981 b) which is linear in the square root of the stomach content:

$$V_t^{1/2} = V_0^{1/2} - at, \quad (25)$$

where V_0 has the same meaning as before.

All the proposed models can be 'reduced' by putting $V_0 =$ observed stomach content = 100%, for $t = 0$. The relationship between the percentual and the actual amount of stomach content for a given fish size (at constant temperature) can be calculated as:

$$(\text{actual stomach content})_t = (fhw^m/100)(100\exp(-at)) \text{ for the exponential model,}$$

or

$$(\text{actual stomach content})_t^{(1-b)} = (fhw^m/100)^{(1-b)}(V_0^{(1-b)} - at)$$

for the 'recti-linear' or 'square-root' models, depending on b .

6. Growth efficiency and yolk sac fry

In connection with feeding and growth of fish, the terms 'gross efficiency' $K_1 = \Delta w / \Delta R$ or the inverse: 'food conversion ratio' = $\Delta R / \Delta w$, and 'physiologically useful' ration (Brody 1945) $K_2 = \Delta w / (\beta \Delta R)$, are widely used, e.g. Paloheimo & Dickie (1966a & b) and Weatherley (1972). These terms depend, at a given fish weight, temperature, and feeding level on the digestibility of the food (i.e. β) see e.g. Cho & Slinger (1979), and the degree of metabolizability of the assimilated food. This means that highly digestible feed with a low energy loss from excretion and apparent SDA gives a higher K_2 compared to a less physiological balanced feed in relation to nutritional composition. Further, the terms K_1 and K_2 can be evaluated as functions of feeding level, fish weight, and temperature.

We assume that the yolk sac must be considered as the food giving the maximum K_1 . When growth efficiency for yolk sac is compared with growth efficiency for metamorphosized fish it is K_2 for these that has to be compared with K_1 for yolk sac fry, because all the yolk is absorbed, and the amount of yolk sac corresponds to the amount of assimilated food in metamorphosized fish.

When the parameters in the model have been estimated from feeding experiments, K_1 and K_2 can be found and K_2 compared with the efficiency of energy conversion from the yolk of alevins during the stages of growth of fry. In this way the used food can be compared with 'the nature's own food' the yolk.

7. Material and methods

7.1. *Experimental design*

As the Danish trout farm production is based on 10-16 month-old rainbow trout (180-250 g), only sexually immature trout were used in the experiments. These were carried out in 120 liter steel aquaria, supplied with water from the river Brøns. Before entering the aquaria, the water first passed through a filter in order to avoid unregistered food intake. After filtering, the water was led into a 850 liter fibreglass basin where heating, cooling and aeration with atmospheric air took place.

From the basin the water was pumped up into the aquaria which had bottom outlets. The level of oxygen in the inlet of the aquaria was 100% air saturation and the content of the outlets was always more than 80%. Before the start of an experiment, the trout were acclimated to the experimental temperature for at least two weeks. The fish that would not eat, were removed. All the trout used in the experiments were in good condition. Immediately before the start and after the end of an experiment, the trout were starved, in order to weigh the fish with empty stomachs. Experiments were carried out to find the time it took before the stomachs were empty, see 7.4. The aquarium room had a 12 h light-12 h dark photoperiod. Before weighing each trout was anaesthetized with chlorbutolum, and blotted using a wet cloth. The fish were weighed one by one in grammes to the first decimal place. It was tried to obtain fish that not varied more than $\pm 5\%$ from the mean wet weight. The start weight was called $w(0)$ and the weight after n days for

$w(n)$. The periods from the end of feeding to weighing out were as calculated from the experiments with gastric evacuations.

The aquaria were constructed with sloping sides in the bottom to allow for faeces accumulation in tubes placed under the aquaria. All the faeces were collected daily and deep-frozen. At the inlet and the outlet of each aquarium, water pumps were placed, continuously collecting about 2 litres per day. From this daily sample one subsample was deep-frozen and had its content of suspended and dissolved faeces determined after the experiment. Further, one subsample had at once its content of $\text{NH}_3\text{-N}$ determined. The amounts were determined as difference between outlet and inlet.

To avoid the influence of varying diets, moist pellets with constant composition were used as food (Table 1). As the food was not prepared for all the experiments at one time there is some variation in the different batches of food.

Table 1. Composition of moist pellets. At 5°C the fish-oil has been exchanged with codliver-oil.

Saltwater fish	49.5 %	CaHPO_4	0.13 %
Fishmeal	21.5 %	NaCl	0.50 %
Soybean meal	21.0 %	Potassium sorbate	0.19 %
Soylecithin	1.0 %	Raloquin (antioxidant)	0.02 %
Fish-oil	5.1 %	B_1 -vitamin	0.02 %
Alginate	1.0 %	E-vitamin	0.002 %
<i>Mean value</i>		Range	
Dry matter	62.63 %		59.46-62.89
Energetical value	5.45 kcal/g dry weight		5.11- 5.55
Crude protein	52.72 % of dry weight		51.64-56.81
Lipid	10.36 % of dry weight		10.05-10.67
Ash	11.64 % of dry weight		7.62-12.59

All the growth experiments were carried out under different fish size (2.6-411.7 g wet weight) and temperature regimes (5.0-25.6°C) ($\pm 0.1^\circ\text{C}$).

In all the aquaria, all or some of the following calculations have been made for fish samples before and after an experiment: (I) mean weight on basis of wet and dry weight, (II) mean weight, on basis of chemical oxygen demand (COD) using $\text{K}_2\text{Cr}_2\text{O}_7$ as an oxidizing agent. (III) mean weight in kilocalories on the basis of bomb calorimetry using a Gallenkamp ballistic bomb calorimeter CB-370. (IV) mean weight on basis of total nitrogen using the Kjeldahl method, and (V) lipid and ash.

The moist pellets were analysed for: (I) wet weight/individual/day, (II) kilocalories/individual/day, (III) g COD/individual/day, (IV) nitrogen/individual/day, and (V) ash content.

The collected water samples from the inlet and the outlets of the aquaria were analysed for (I) amount of suspended and dissolved organic matter calculated as mg COD/individual/day, (II) total amount of mg $\text{NH}_3\text{-N}$ /individual/day.

Oxygen consumption mg/individual/day was calculated from oxygen measurements in inlet and outlet of the aquaria.

7.2. Parameter determinations

The parameters are determined as described in Statistical Methods, 7.7.

In all cases experiments are carried out under different fish size and temperature regimes.

7.2.1. $h(T)$ and m

The parameters can be estimated on basis of feeding experiments for $f = 1$. The amount of food and gain in fish biomass are registered.

The trout were offered food approximately every hour during the light period. At each feeding, pellets were offered until they were refused twice by the fish.

The parameters of (3), (3') and (3'') are determined on basis of:

dR/dt = weight of food as g consumed per day per fish in units of wet weight, nitrogen or energy.

T = temperature in °C, $T \leq 24.3$ for (3) and (3''), $T \leq 20.1$ for (3')

w = $\frac{1}{2}\{w(0) + w(n)\}$ in g wet weight, nitrogen or energy.

7.2.2. Feeding level experiments $0 < f < 1$

In different aquaria different feeding levels were administered. The change in fish weight implies that we have the problem to predict the daily growth in order to be able to give the fish a constant f throughout the experiment. Based on maximum feeding and starving experiments already carried out, 'guesstimates' of A and β were used to predict the growth curve. After the experiment, the true f was calculated.

7.2.3. Assimilation coefficient, β

7.2.3.1. Energy (COD)

The parameters in (6) and (7) are determined on basis of the daily collected a) setttable faeces and b) water samples:

Settable faeces measured as g COD/fish/day

and

Suspended + dissolved faeces measured as g COD/fish/day

where

f = feeding level calculated on basis of $(dR/dt)/(h(T) w^m)$ in units of g COD, so that

$0 < f \leq 1$ for (6) and $0 \leq f \leq 1$ for (7)

T = temperature in °C, for $T \leq 20.1$

w = $\frac{1}{2}\{w(0) + w(n)\}$ in g COD.

7.2.3.2. Nitrogen

Analogous with the assimilation of the energy in the food, the nitrogen content in the faeces can be estimated as a function of temperature, feeding level, and fish weight. The nitrogen content was only determined for the setttable faeces. The

content is described as:

$$\text{Settable faeces} = b_1 f^{b_2} \exp(b_3 T) w^{b_4} \quad (6)$$

where

settable faeces are measured as g N/fish/day

f = feeding level calculated on basis of $(dR/dt)/(h(T)w^m)$ in units of g N,

where

$$0 < f \leq 1$$

T = temperature in °C for $T \leq 20.1$

$w = \frac{1}{2}\{w(0) + w(n)\}$ in g N.

7.2.4. $k(T)$ and n

The parameters can be estimated from starving fish, $f = 0$:

a. Measurements of biomass changes.

1. Changes of wet weight give biased results if the assumption that the proportions of the body constituents should not change during the starvation is not fulfilled.

2. Changes of weight based on energy from bombing are non-biased but imply that correct oxycalorific coefficients are used if the parameters are included with other terms in the model based on energy from COD.

3. Changes of weight based on energy from COD might be biased depending on the efficiency of the oxidation, see description of the COD method 7.6.3.

b. Measurement of oxygen consumption. The results should correspond to the results from the biomass changes with COD minus $k'''(T)$.

The parameters of $k(T)$ from biomass changes are determined on basis of:

$$dw/dt = \frac{w(0) - w(n)}{\Delta t} \text{ in units of g wet weight, nitrogen or energy from COD}$$

or bombing.

T = temperature in °C, $T \leq 25.6$.

$w = \frac{1}{2}\{w(0) + w(n)\}$ in g wet weight, nitrogen or energy.

The parameters of $k(T)$ from measurements of respiration are determined as described in 7.2.6.

7.2.5. Nitrogen excretion, U

The parameters in (14) are determined on basis of daily collected water samples:

$U = \text{NH}_3\text{-N/fish/day}$ in g N

f = feeding level calculated on basis of $(dR/dt)/h(T)w^m$ calculated in N unit, wet weight unit or energy.

T = temperature in °C, for $T \leq 20.1$

$w = \frac{1}{2}\{w(0) + w(n)\}$ in g N, or g wet weight or g COD

7.2.6. Total respiration

The parameters in (18) are determined on basis of daily oxygen measurements.

Total respiration = oxygen consumption/fish/day in g O₂

f = feeding level, calculated on basis of $(dR/dt)/(h(T)w^m)$,

T = temperature in °C, for $T \leq 20.1$

$w = \frac{1}{2}\{w(0) + w(n)\}$ in g COD or g wet weight.

7.2.7. Size of the weight exponents

The parameters of the weight exponents in the models of β , U and total oxygen consumption are estimated from data both from starving and feeding experiments. This means that weight exponents in both the anabolic and catabolic terms are considered as the same. Nothing indicates that the weight exponents in the two terms are the same and in Bertalanffy (1957) $m = 2/3$ and $n = 1$. This growth model has been used by Beverton & Holt (1957) for commercial marine fish species and the course of growth rate as a function of age is decreasing up to L_∞ (or W_∞). For salmonids Parker & Larkin (1959) and From & Rasmussen (1979) and for european eel *Anguilla anguilla* (Linné, 1758) Rasmussen & Therkildsen (1979) state that the weight exponents in the growth equation can be put equal as a fair approximation. If in fact the weight exponents are different in the anabolic and catabolic terms the estimated values of b_4 , μ_4 , and a_4 can be considered as 'means'.

7.3. Body composition

Except from a very limited number of experiments (some experiments with single fish with $f = 1$) determinations of water content, nitrogen, energy and ash contents (determined as the rest after bombing in the calorimeter) were performed more or less as a standard routine.

A total of 106 samples from temperatures 5, 10, 15, and 20°C were, besides the routine determinations, also analysed for content of lipid and had their ash content determined in a muffle oven. If a fish sample had its nitrogen, lipid, and ash content determined it was found that

$$100\% > 6.25 \cdot N\% + \text{lipid}\% + \text{ash}\%.$$

Further, it was found that the energy of a fish sample found by bombing was less than the energy content found by using the values for energetical content of protein and lipid as mentioned in 4.:

$$\text{Energy of sample (by bombing) cal/g} < 6.25 \cdot N \cdot 5.65 \text{ cal/g} + 9.45 \cdot \text{lipid cal/g}.$$

Therefore it was decided to make some extensions.

33 additional fish samples (besides the above mentioned 106) had their content of water, lipid, nitrogen, ash, and energy per mg dry weight determined in the usual way. The lipid free residue (FFDM = fat free dry material) was quantitatively determined (both the methanol-water phase and the solid phase) and bomb-

ed to find energy content. In this way the residue gave the energetic equivalent of proteins, nitrogen extractives and carbohydrates.

The extracted lipid had also its energetic equivalent determined. Bombing of lipid failed because the Gallenkamp bomb calorimeter demands a relatively large sample (app. 4 kcal), but also on account of the consistence of the lipid. Therefore, the energy determinations were made by the COD method, and a conversion factor of 3.42 cal/mg oxygen, from Warren & Davis (1967), was used.

Further, NPN was found for 35 fish samples, TVN for 11 fish samples and carbohydrate for 24 fish samples.

7.4. Gastric evacuation

7.4.1. Experiment 1

Experiments were carried out at 5.0, 10.0, 15.0, and 20.0°C ($\pm 0.1^\circ\text{C}$) with five different fish sizes at the two lowest temperatures and four different fish sizes at the two other temperatures. A single experiment at 22.0°C and one fish size was also carried out.

The fish were habituated to the experimental conditions as described for the feeding experiments.

After the habituation, during which fish that did not eat were removed, the fish were, depending on the temperature, starved until it was certain that they were empty of food. At 5°C for 14 days, at 10°C for 10 days, at 15°C for 7 days, and at 20°C for 5 days. After this 20 fish from each size group were weighed one by one. From each size group the stomachs were dried together, and the mean dry weight of the stomach ($w(0)$) of each size group was determined.

Then the fish were fed *ad libitum* for two days (fed for 12 hours, then 12 hours darkness and then fed again for 12 hours). After these two days of feeding 10 fish (from each size group) were slaughtered and the total dry weight of the stomachs plus food contents were determined in the way mentioned above. This procedure was repeated with different time intervals (depending on the temperature), until the stomachs were empty. Now, 20 fish (from each size group) were taken and the mean weight of an empty stomach ($w(n)$) of each size group was determined as in the earlier procedure.

As $w(0) \neq w(n)$, although the difference was less than a few per cent the weight of an empty stomach during the evacuating period can be calculated by simple linear interpolation. In this way the weight of the declining food content in the stomach can be calculated from the weighed stomach plus food content minus the estimated weight of an empty stomach (Method 1). The second weighing gave in that way 100% stomach content, and all the following stomach contents were converted to per cent of this first content.

7.4.2. Experiment 2

The experiments just described works with fish eating *ad libitum*. Implicitly the model says that if it takes a fish fed $f = 1$, X hours to reach 50% stomach evacuation, then a fish fed $f = 0.5$ at the same temperature, will have the same amount of

food in the stomach after Y hours, as the fish fed $f = 1$ has after $(X + Y)$ hours. Another way to say it: The instantaneous coefficient a , all other things equal, does not change during the course of stomach emptying.

A single experiment was carried out at 20°C to get some ideas of the possible influence of feeding level on gastric evacuation time. Only one size of fish was used. The fish were as in experiment 1 habituated to the experimental conditions. The weight of the fish and the weight of the stomach were determined as mentioned under experiment 1.

After three days of feeding (in the same way as in experiment 1) with $f = 1.00$ and $f = 0.55$, 10 fish were slaughtered every fourth hour, but now the stomachs were cut up and emptied by means of a pincette and the dry weight of the stomach contents (the food bolus) and the empty stomachs were determined separately (Method 2).

In this way the reliability of the method 1 under experiment 1 can be considered. The food bolus plus the emptied stomach gives the stomach plus content as in experiment 1. But now the effect of different initial feeding levels can be considered under different experimental methods.

7.5. Yolk sac experiments

7.5.1. Experiment 1

One large batch of eggs was placed at the river-water temperature, which in mean was 6.9°C (from 3.5°C to 11.5°C).

At hatching the fry were divided and placed at four different temperatures: 9.3°C, 11.4°C, 14.0°C and 17.9°C ($\pm 0.1^\circ\text{C}$). In the room there was light for 12 hours and darkness for 12 hours. During the yolk sac absorption, which took about 240-250 day degrees, 7-8 samples of about 150 alevins were taken from each batch. After complete absorption there was taken one sample from each batch, except at 9.3°C. The alevins were dipped in 96% ethanol for some seconds to harden them. In this way it was easier to dissect away the yolk sac. The dry weights of embryos and yolk sacs were determined. COD determinations were made on the embryos and the yolk sacs. The mg COD content of the alevins was found from the relationship: alevin = embryo + yolk sac.

7.5.2. Experiment 2

The same type of experiment was carried out. But now the eggs were placed at the two following temperatures in the moment they were fertilized: 9.5°C and 14.5°C ($\pm 0.1^\circ\text{C}$). (The temperatures 17.5°C and 20.0°C were tried, but the eggs died after 5 and 3 days, respectively).

One batch of eggs was taken for analysis, just when they were fertilized, before they were placed in water. In trout farming the fertilization take place before the eggs are placed in water.

At each temperature, samples were taken approximately at the following stages of development: Eyed ova, hatching, and a little before complete yolk absorption.

7.6. Analyses

In the following a description of the analyses used will be given.

7.6.1. Dry weight

The fish were minced in a Hobart N-50 mincer. App. 65 g minced fish and 30 g water were then homogenized for 20 min in a MSE homogenizer. App. 5 g of homogenisate was dried at 45°C for 4 days. Before this temperature was chosen 19 fish samples were treated in the following way: From each sample a homogenisate was dried at 45°C for 4 days, and a homogenisate at 105°C for 24 hours. The samples had separately their water content and energy content determined, both by the COD method and by bombcalorimetry. The 19 pairs gave in result, that the samples dried at 45°C had relatively 4.1 % more dry material, 3.4 % more energy (determined by bombcalorimetry) and 2.2 % more energy (determined by the COD method) than the samples dried at 105°C. As the energy content cannot increase, 45°C was selected. The difference between the energy content determined by bombing and COD is attributed to random error. After drying the homogenisate was placed in a dessicator until constant weight, and weighed in grammes to the fourth decimal place. Fourfold determinations were made. Inaccuracy: The range of the single determination within a sample was less than ± 0.5 % of the mean.

App. 50 g moist pellets and app. 50 g water were homogenized for 20 min. Else the same procedure as above.

App. 100 g faeces were homogenized for 20 min. About 25 g homogenisate was taken for determination of dry weight as described above.

7.6.2. Bomb calorimetry

About 600 mg (4 kcal) of the dry samples were bombed in a Gallenkamp CB-70 ballistic bombcalorimeter. There was not corrected for the formation of nitric and sulphuric acids, because according to Lieth (1968) the error caused by formation of acids is less than 0.1 % and is thus within the accuracy limits of the energy determination itself. Further, no correction has been made for the fact that the temperature inside the bomb is high enough to decompose certain salts, because Ostapenya (1971) finds for data in Paine (1966) that the influence of this endothermic decomposition of salts is insignificant at ash contents less than 25 per cent.

Threefold determinations were made. Inaccuracy: The range of the single determination within a sample was less than ± 2 % of the mean.

7.6.3. COD

It is normally accepted (Maciolek 1962) that the COD method only partially oxidize the digestible organic matter so that nitrogen rich compounds should give a relative lower COD content in contrast to material with a higher degree of fat which is regarded to be easier to oxidize.

COD was measured by means of a specially evolved method (Rebsdorf & Therkildsen 1978). The total aqueous solution of the collected organic matter is thoroughly blended for 5 min in an Ultra-Turrax homogenizer (T-45). 20 ml of this

solution is oxidized with a mixture of 5.00 ml 0.05 N potassiumdichromate, 25.0 ml silversulphate-sulphuric acid (10 g Ag_2SO_4 in 1 l conc. H_2SO_4) and 0.2 ml mercurysulphate solution (10 g HgSO_4 in 60 ml H_2O and 20 ml H_2SO_4 (1 + 1) filled up to 100 ml with H_2O) to interfere with the reduction of dichromate from possible chloride in the water. The oxidation takes place at $140^\circ\text{C} \pm 2^\circ\text{C}$ for 1 hour in a Tecator digester 2040. After cooling to room temperature 50 ml demineralized water and 2 drops of ferroin indicator (0.025 M) are added and after further cooling the surplus of dichromate is determined by titrating with 0.025 N ferroammonium sulphate.

The COD method for solid samples was almost the same as for aqueous solutions, but 10.00 ml 1.00 N dichromate and 0.70 N ferroammoniumsulphate were used for a sample of app. 20 mg dry weight.

In both cases, twofold determinations were made. Inaccuracy: The range of the single determination within a sample was less than $\pm 2\%$ of the mean.

7.6.4. *Lipid*

The modification of the Bligh and Dyer method described by Hanson & Olley (1963) was slightly altered. To 2.0-2.5 g of the fish homogenisate (achieved as described above) 5 ml of water was added. Now the total amount of water in the sample was calculated (it was therefore necessary first to have determined the percent of water in the fish) this figure was called x ml. Now, x ml chloroform and $2x$ ml methanol were added. The mixture was homogenized for 2 minutes in the MSE homogenizer. After adding of x ml chloroform and homogenization for 30 seconds, x ml water was added and again homogenization took place for 30 seconds. Finally, the mixture was centrifuged at 3000 rpm for 15 minutes. The upper layer which contained methanol and water was sucked off by means of a water jet pump. The lower layer consisting of chloroform, lipid and fish material was filtered quantitatively through Whatman No. 1 filter paper on a No. 3 Büchner funnel with slight suction. The fish tissue residue was through the same filter paper washed with app. 40 ml chloroform. The filtrate was evaporated by placing it in the draw from a ventilator to the next day. The lipid was placed in a dessicator until constant weight. There were made fourfold determinations. Inaccuracy: The range of the single determination within a sample was less than $\pm 2\%$ of the mean.

7.6.5. *Ash*

Ash was determined in two ways. Either as the rest in the crucible after bombing in the bombcalorimeter, or in a muffle oven. 2 g homogenisate is placed in a crucible at 580°C for 4 hours. In the first method threefold determinations are made, in the second fourfold determinations. Inaccuracy: The range of the single determination within a sample was less than $\pm 3\%$ of the mean. The two different methods were used on 106 samples. The result was: Ash determined as the residue left in the bomb was $94\% \pm 2\%$ of the ash determined in the oven. Whenever an ash value is given in the present paper, the value is found by muffle oven.

7.6.6. *Nitrogen*

Nitrogen was determined on dry material after the Kjeldahl method described in Anon. (1979). Double determinations were made. Inaccuracy: The range of the single determination within a sample was less than $\pm 0.5\%$ of the mean.

7.6.7. *NPN*

In the present study NPN were found for 35 fish samples, in the following way (modified after Mezincesku & Szabo 1936): To 2 g of homogenisate was added 15% trichloro-acetic-acid to make up 100 ml, with filtering after precipitation of proteins. 40 ml of filtrate was determined for N by the Kjeldahl method. Double determinations were made. Inaccuracy: The range of the single determination within a sample was less than $\pm 5\%$ of the mean. Further, at the same 35 fish there were determined: dry weight, energy by bombcalorimetry and total N (for 30 of the fish) on wet material by Kjeldahl's method, to see if NPN were correlated with some of these figures. All the other Kjeldahl determinations in this study have been done on dry weight. But it was the value of NPN compared to the value of total N that was of interest. When N is found on dry samples, a part of the NPN, namely TVN (total volatile nitrogen) has to a greater or lesser extent evaporated under the drying.

7.6.8. *TVN*

TVN was determined for 11 fish samples after a slight modification of the method described by Conway & Byrne (1933): 75 ml water was added to 25 g homogenisate and pH was by 2 N HCl lowered to 5.2. The mixture was slowly heated to 70°C, and then cooled to room temperature and filtered. 2 ml of the filtrate was placed in the outer room of the Conway dish and 2 ml 0.025 N HCl placed in the inner room. 1 ml saturated solution of K_2CO_3 was delivered in the outer room and the lid smeared with vaselin was placed in position. The dish was cautiously tilted to mix the fluids in the outer room. After standing 4-20 hours at room temperature, A.C. Andersen indicator (0.05 g methylblue and 0.10 g methylred in 100 ml absolute alcohol) was added to the inner room, and there was titrated with 0.025 N NaOH. Double determinations were made. Inaccuracy: The range of the single determination within a sample was less than $\pm 1\%$ of the mean.

7.6.9. *Carbohydrate*

Carbohydrate was determined for 24 fish samples after a slight modification of the method described in Ostapenya (1971): To 4-9 mg of finely ground dry material 10 ml of anthrone reagent (0.2 g anthrone, 8 ml absolute ethanol, 30 ml water and 100 ml concentrated sulphuric acid) was added. The mixture was well mixed and heated for 7 minutes in a boiling water bath. The test tubes were immediately cooled and analysed photometrically at 620 nm using a Bausch and Lomb Spectronic 88. The calibration curve was prepared with glucose. Double determinations were made. Inaccuracy: The range of the single determination within a sample was less than $\pm 5\%$ of the mean.

7.6.10. $\text{NH}_3\text{-N}$

This was once a day determined on the water samples which continuously were pumped from the inlet and outlets of the aquaria. The amount was found by means of the indophenol method (Anon. 1973, and Koroleff). For a slightly different method see Scheiner (1976). The inlet was common for all aquaria, and this value was subtracted from the outlet value. Water flow through each aquarium was measured each day by means of a graduated glass and a stop watch. From these observations $\text{NH}_3\text{-N}$ excretion/individual/day was calculated. Double determinations were made for the outlet and fourfold determinations for the inlet. Inaccuracy: The range of the single determination within a sample was less than $\pm 5\%$ of the mean.

7.6.11. *Oxygen*

The content was found either by measuring the partial pressure of oxygen in a water sample by means of a Radiometer pHMII or in later experiments by the Winkler titration. From the water-flow observations oxygen consumption/individual/day was calculated. Continuous measurements of oxygen contents by means of Radiometer TOX40 oxygen transmitters were attempted, but failed because bacterial growth on the probe membranes biased the measurements.

During the first experiments oxygen was measured every 3 or 4 hours (also in the dark period). In this way the frequency of sampling sufficient to determine the 'mean oxygen consumption' for every day could be fixed. Thus, the number of determinations were reduced to 2-3 per day. Double determinations were made. Inaccuracy: The range of the single determination within a sample was less than $\pm 2\%$ of the mean.

7.7. *Statistical methods*

Apart from (3) and (3'') the models in this paper are linear or intrinsically linear in the parameters. The intrinsically linear models (e.g. (3'), (9) and models describing assimilation, respiration, nitrogen excretion) can be transformed into linear forms. Thereafter they can be treated with wellknown statistical methods, e.g. Draper & Smith (1966), Hald (1968). A bias is introduced in the calculated regression equations if the parameters are transformed back to original scale. Therefore to get an unbiased estimation of the dependent variables, $\sigma^2/2$ where σ^2 is residual error variance is added to the estimated transformed parameters before transforming back to the original scale, Beauchamp & Olson (1973), Andersen & Sparre (1975).

Contrary to this, (3) and (3'') are intrinsically non-linear and the parameters have been calculated from the method of linearization, Draper & Smith (1966).

The models are in the form

$$Y = f(\xi, \theta) + \varepsilon \text{ where}$$

$$\xi = (T, w) \text{ i.e. variables}$$

$$\theta = (h_1, h_2, h_3, h_4, m) \text{ i.e. parameters}$$

$$\varepsilon = \text{error term and } \text{var}(\varepsilon) = \sigma^2, \text{ so that } \varepsilon \sim N(0, \sigma^2).$$

The linearization method uses the results of linear least squares in a succession of stages, so that the estimated values of parameters (i.e. guesstimates) are improved

upon in successive iterations. The method consists of carrying out a Taylor series expansion of $f(\xi, \theta)$ about the point θ_0 , where θ_0 is the initial value for the parameters h_1, h_2, h_3, h_4, m and curtails the expansion at the first derivatives so that when θ_0 is close to θ we can approximate:

$$f(\xi, \theta) \approx f(\xi, \theta_0) + \sum_{i=1}^p \left(\frac{\partial f(\xi, \theta)}{\partial \theta_i} \right)_{\theta=\theta_0} \cdot (\theta_i - \theta_{i0})$$

Now we are able to estimate the parameters $(\theta_i - \theta_{i0}), i = 1, \dots, 5$ by ordinary least squares methods. The estimate $\theta_{i'} = (\theta_i - \theta_{i0})$ are replaced in the value of θ_{i0} and the procedure is continued until the solution converges.

True confidence intervals of the estimated parameters cannot be calculated but only confidence regions. But as non-mathematicians the present authors have only evaluated the reliability of the parameters by examining the residuals $\varepsilon = Y_i - \hat{Y}_i, i = 1, \dots, N$ where Y_i is an observation and \hat{Y}_i is the corresponding fitted value obtained by use of the fitted regressions equation, and N is number of aquaria.

The observations have been weighted with \sqrt{n} where n is the number of fish in an aquarium, see Sperber, From & Sparre (1977) in estimating the parameters in the anabolic term and the catabolic term (9) in wet weight, and weighted with \sqrt{n} in (9) where n is the number of fish for chemical analyses of nitrogen and energy in an aquarium. If this number of fish for analyses are different when comparing the start and the end of an experiment the smallest figure has been used as weighting factor. The observations for estimating the parameters of α, β and U have not been weighted.

In the text and the tables the parameters are given together with 95 % confidence limits and multiple correlation coefficient

$$R^2 = \frac{\sum (\gamma_i - \bar{\gamma}) (\hat{\gamma}_i - \bar{\hat{\gamma}})}{\sum (\gamma_i - \bar{\gamma})^2 \sum (\hat{\gamma}_i - \bar{\hat{\gamma}})^2}$$

8. Results and discussion

The data, if not given elsewhere in the paper, are given in the Appendix.

8.1. The anabolic term, $h(T)$

The determination of the parameters in (3), (3') and (3'') are given in Table 2. Fig. 1 shows the daily maximum food intake (wet weight) of a 100 g fish wet weight for the models (3), (3'), and (3'') for several specimen ($n > 1$). In Fig. 24 the same is shown for (3'') for single specimen ($n = 1$). From Fig. 1 it is seen that all three models can be used to calculate the food intake up to 16-17°C. After this temperature (3) and (3'') can be used because they take the decrease in food intake at higher temperatures into consideration.

Fig. 2 shows the calculated curves for $h(T)$ from (3) ($n > 1$). Because different units (g wet weight, g nitrogen, g COD, kcal) are used the $h(T)$ curves differ. E.g. converting g COD to kcal by g COD = 3.42 kcal makes the COD and bombing curves identical.

$h(T)$ increases with increasing temperature and reach a maximum for (3) and (3'') about 20°C for all units (g wet weight, g nitrogen, g COD, kcal), after which $h(T)$ decreases drastically for temperatures beyond 20°C. Depending on the model

Table 2. Parameters of the anabolic term, $h(T)$. All estimates are for several specimens ($n > 1$) except the first column in wet weight which is for single specimen ($n = 1$). Weight of food and fish in g wet, g nitrogen, g COD, and kcal respectively.

Estimate according to (3): $dR/dt = f(h_1 \exp(h_2 T) + h_3 \exp(h_4 T))^{-1} w^m, f = 1$					
Parameter	Wet weight		Nitrogen	COD	Bombing
	$n = 1, N = 58$	$n > 1, N = 54$	$N = 47$	$N = 50$	$N = 48$
h_1	6.1946E-5	1.9916E-3	0.5605	2.9899E-2	8.1970E-3
h_2	0.5017	0.3402	9.9969E-2	0.1875	0.2212
h_3	34.4914	32.0008	40.0003	15.9858	9.6521
h_4	-0.1183	-0.1000	-0.1200	-0.1096	-0.0972
m	0.7527	0.6989	0.6970	0.6351	0.6700
Estimate according to (3'): $dR/dt = f(h_1 \exp(h_2 T)) w^m, f = 1$					
Parameter	Wet weight		Nitrogen	COD	Bombing
	$R^2 = 0.97$ $N = 46$		$R^2 = 0.97$ $N = 44$	$R^2 = 0.96$ $N = 46$	$R^2 = 0.96$ $N = 45$
h_1	0.0343 (+0.0088) (-0.0070)		0.0318 (+0.0045) (-0.0040)	0.0857 (+0.0190) (-0.0159)	0.1266 (+0.0348) (-0.0277)
h_2	0.0752 (±0.112)		0.0755 (±0.0102)	0.0761 (±0.0127)	0.0759 (±0.0122)
m	0.7666 (±0.0544)		0.7246 (±0.0474)	0.6767 (±0.0548)	0.6789 (±0.0538)
Estimate according to (3''): $dR/dt = f(h_1 + h_2 T + h_3 T^2 + h_4 T^3) w^m, f = 1$					
Parameter	Wet weight	Nitrogen	COD	Bombing	
	$N = 54$	$N = 47$	$N = 50$	$N = 48$	
h_1	5.8077E-2	3.3808E-2	0.1745	0.3074	
h_2	-7.2665E-3	-2.3110E-3	-3.1308E-2	-0.0549	
h_3	1.5180E-3	8.6293E-4	4.8213E-3	8.0335E-3	
h_4	-4.4926E-3	-2.6069E-5	-1.3878E-4	-2.2729E-4	
m	0.7162	0.6946	0.6354	0.6292	

and the units used for describing $h(T)$ the parameter m in model (3) varies from 0.64 to 0.70 and in model (3'') from 0.60 to 0.72. The parameters determined in model (3') can be evaluated from a safe statistical view, and here m varies from 0.68 to 0.77. Presuming that the temperature coefficient h_2 and the body-size exponent m are the same for all units the following parameters for (3') are estimated ($R^2 = 0.99$, number of observations = 181):

$$\begin{aligned}
 h_1 \text{ (wet weight)} &= 0.0426_{-0.0047}^{+0.0051} & h_1 \text{ (bombing)} &= 0.1099_{-0.0126}^{+0.0141} \\
 h_1 \text{ (nitrogen)} &= 0.0321_{-0.0026}^{+0.0028} & h_2 &= 0.0757 \pm 0.0054 \\
 h_1 \text{ (COD)} &= 0.0763_{-0.0073}^{+0.0080} & m &= 0.7083 \pm 0.0247
 \end{aligned}$$

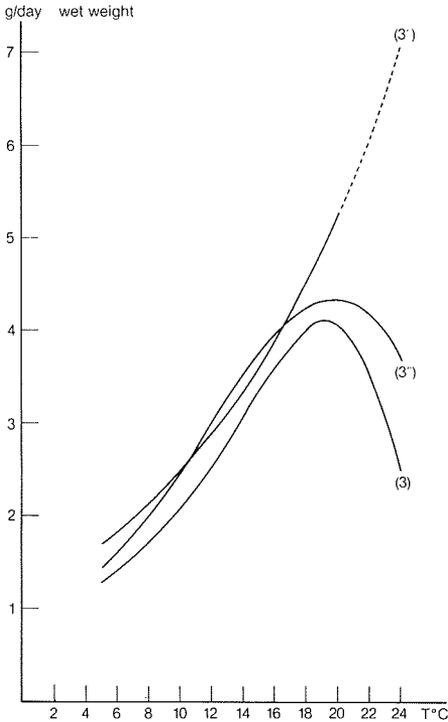


Fig. 1. The daily maximum food intake of moist pellets for a fish of 100 g wet weight. Several specimens ($n > 1$). According to (3), (3'), and (3'').

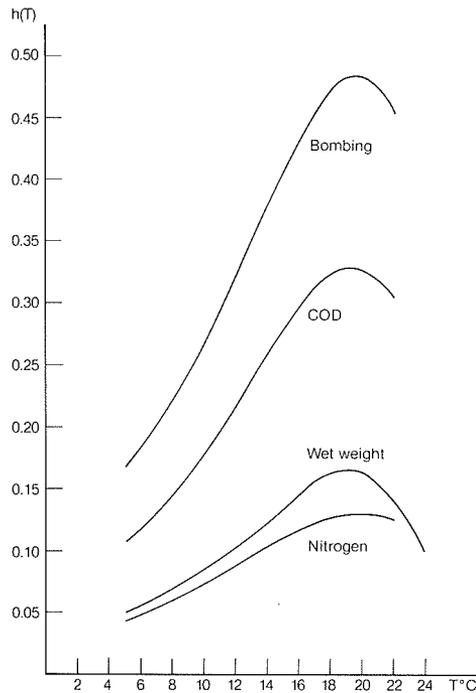


Fig. 2. $h(T)$ for the different units (g wet weight, g nitrogen, g COD, and Kcal) according to (3).

Based on these parameters Fig. 3 is calculated. Again the curves differ because they are calculated for different units (g wet weight, g nitrogen, g COD, kcal).

There are only few determinations of the anabolic parameters for salmonids so the present values can only be compared with few other values. Ursin (1967) finds that generally $m < 2/3$. For brown trout Elliott (1976c) found that m varied from 0.731 to 0.770 (the units are energy based on COD determinations). For rainbow trout Sperber, From & Sparre (1977) found $m = 0.837$ and $h_2 = 0.116$. The confidence interval of this value of m is just overlapping with the confidence interval of the present investigation's value for m for wet weight (Table 2), and probably there is no difference between the two values. However, there is a difference between the values for h_2 and the confidence intervals do not overlap. The parameter values cannot directly be compared because h_1 and h_2 are inversely correlated. Besides, in the two investigations there have been used different kinds of food which gives a difference in the values of h_1 . Further, an explanation of the discrepancy in the two values of h_2 is that Sperber, From & Sparre (1977) only have observations from temperatures up to 16°C, whereas h_2 in the present study have been determined from temperatures up to 20.1°C, after which $h(T)$ decreases.

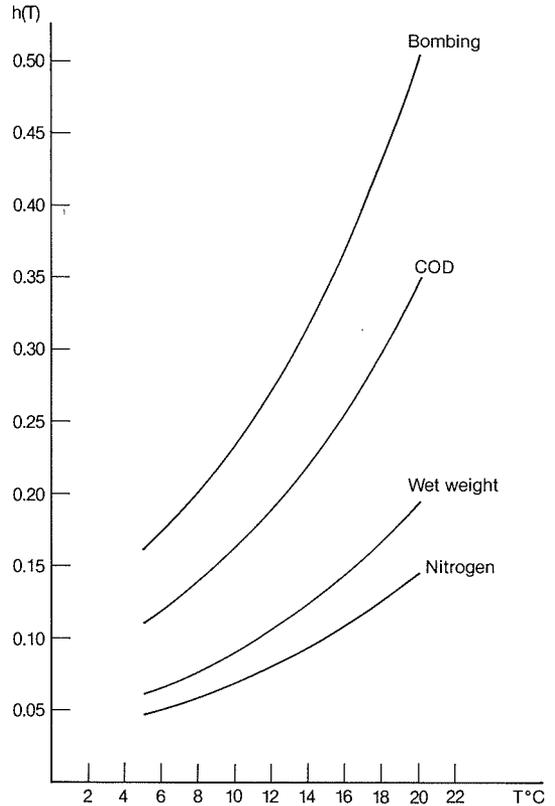


Fig. 3. $h(T)$ for the different units (g wet weight, g nitrogen, g COD, and kcal), according to (3').

This means that the present study includes observations of dR/dt which are smaller than they would have been if calculated with the parameters from Sperber, From & Sparre.

With the present value of h_2 , Q_{10} for temperatures up to 20°C, is 2.13.

8.2. Assimilation coefficient, β

8.2.1. Energy (COD)

The determinations of the parameters in (6) and (7) are given in Table 3. Fig. 4 shows the calculated values of settable faeces, and suspended + dissolved faeces as a function of feeding level for different temperatures. The intercept for $f = 0$ (7) corresponds to the non-reabsorbed metabolic residues.

Fig. 5 shows simulated values of β for different values of f , T , and w .

Few determinations of the assimilation efficiency for fish, particularly for salmonids, have been made. For these the following values can be found in the literature: Winberg (1960) proposed a value of 85% for the assimilation of the food as being generally valid. Job (1960) found a β of 90.3% for brook trout, *Salvelinus fontinalis* (Mitchill, 1815) fed minnows. Brocksen, Davis & Warren

Table 3. Parameters of the anabolic term, assimilation β . Several specimens ($n > 1$). In the table determinations have been done with $b(T)$ found from (3') but determinations with $b(T)$ found from (3) give nearly the same results.

Parameter	Estimate		
	Settable faeces according to (6); $b_1 f^{b_2} \exp(b_3 T) w^{b_4}$		Susp. + dissolved faeces according to (7): $b_1 \exp(b_2 f) \exp(b_3 T) w^{b_4}$
	g COD/individual/day w in g COD $R^2 = 0.89, N = 136$	g N/individual/day w in g N $R^2 = 0.88, N = 130$	g COD/individual/day w in g COD $R^2 = 0.47, N = 153$
b_1	$0.0162 \begin{pmatrix} +0.0061 \\ -0.0044 \end{pmatrix}$	$2.0471E-3 \begin{pmatrix} +0.5756E-3 \\ -0.4524E-3 \end{pmatrix}$	$1.1861E-2 \begin{pmatrix} +0.9409E-2 \\ -0.5289E-2 \end{pmatrix}$
b_2	$1.4259 (\pm 0.1428)$	$1.6006 (\pm 0.1532)$	$1.1057 (\pm 0.4508)$
b_3	$0.0577 (\pm 0.0139)$	$0.0663 (\pm 0.0157)$	$0.0808 (\pm 0.0294)$
b_4	$0.5471 (\pm 0.0730)$	$0.6215 (\pm 0.0874)$	$0.5499 (\pm 0.0157)$

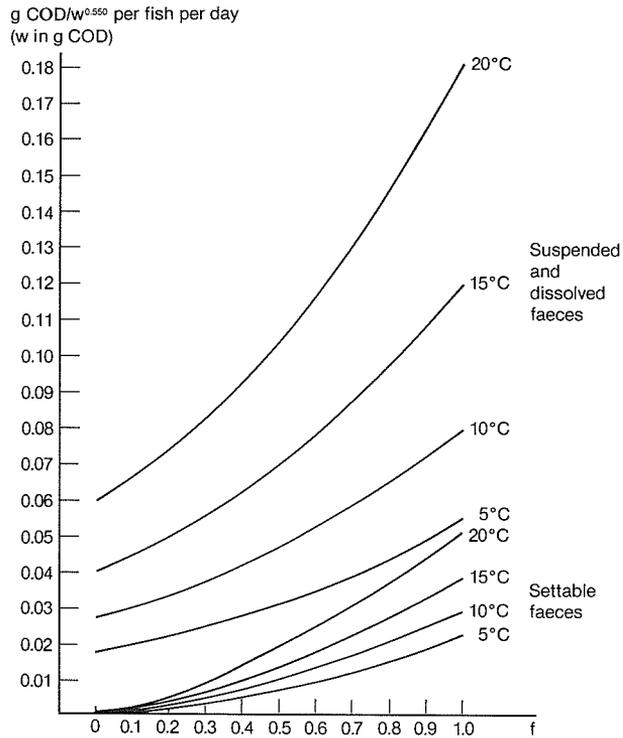


Fig. 4. Calculated curves for settable (6) and suspended + dissolved faeces (7) as a function of feeding level at 5, 10, 15, and 20°C.

(1968) found that under-yearling cutthroat trout, *Salmo clarki* Richardson, 1836 assimilated 85.6% of the food at 10°C. Averett (1969) found that juvenile coho salmon, *Oncorhynchus kisutch* (Walbaum, 1792) at a food intake from 10 cal/kcal fish and up to 110 cal/kcal fish per day assimilated app. 85% independent of

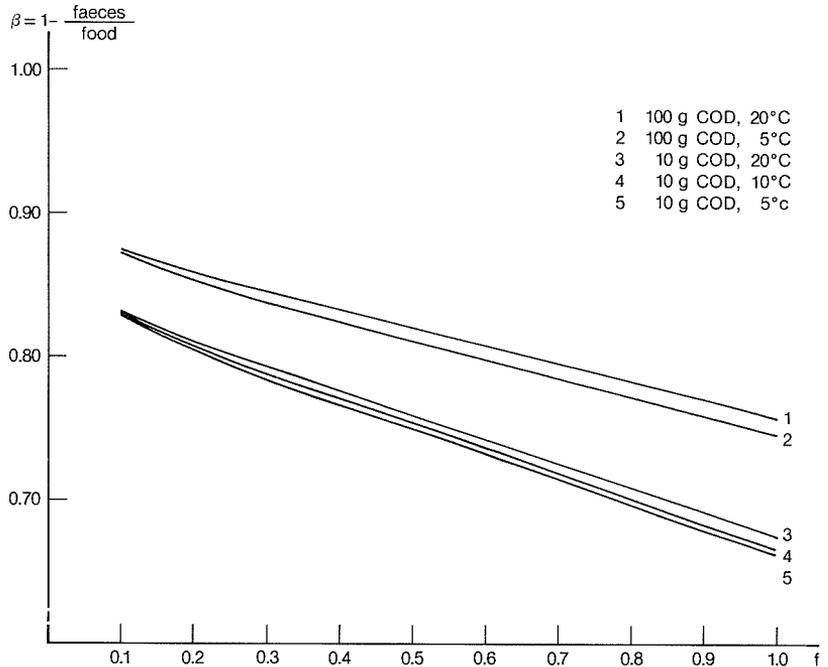


Fig. 5. Calculated values of the assimilation coefficient β for different values of f , T , and w .

temperature, whereas an additional food intake up to 220 cal/kcal fish per day would decrease the assimilation to app. 60%.

Brocksen & Bugge (1974) investigated the effect of temperature on β for rainbow trout at 15 g wet weight. At 5°C, β was 72% increasing up to 84% at 20°C. Elliott (1976b) claimed that β for brown trout, was independent of fish size, but dependent on feeding level and temperature so that the assimilation is increasing with increasing temperature for compensating an increasing energy demand, and assimilation is falling with increasing feeding level.

Ursin (1967) makes β in general dependent only on feeding level in such a way that for $f \rightarrow 0$, $\beta \rightarrow 100\%$. Sperber, From & Sparre (1977) determined for rainbow trout (73.4 – 119.0 g wet weight) a β of 62.1% independent of fish weight, feeding level and temperature. But because of the method they used to estimate the parameters it was not possible to determine β and A independently of each other.

In the above mentioned references natural food items have been used. Contrary to this Cho, Bayley & Slinger (1976) for rainbow trout (96–145 g wet weight) use food pellets of a given composition and find a β of 70% when the food contained 40% dietary protein and 15% dietary lipid (commercially formulated), 78% when the food contained 40% dietary protein and 25% dietary lipid, and 85% when the food contained 60% dietary protein and 15% dietary lipid. Cho, Slinger & Bayley (1982) say that the commercially formulated diets for salmonids are assimilated with efficiencies from 60% to 90% depending on the composition.

The assimilation efficiency in the present investigation increases with decreasing feeding level at a given temperature and fish weight in accordance with Ursin (1967) and Elliott (1976b).

An increase in temperature at a given feeding level and fish size has negligible effect on β , and this is in accordance with Averett (1969) but contrary to Brocksen & Bugge (1974) and Elliott (1976b). Fish weight has, contrary to Gerking (1952) (for protein), Menzel (1960), Pandian (1967) and Elliott (1976b) who all found that β was independent of fish weight, an effect on β in such a way that a bigger fish assimilates more effectively than a smaller one. This has, except for Smith (1973) apparently not earlier been described in the literature. This correlation between w and β cause the weight exponents in (6) and (7) to be less than the weight exponents in (3').

8.2.2. Nitrogen

The determinations of the parameters in (6) are given in Table 3. In contrast to the assimilation of energy few determinations of the size of faecal-N by salmonids have been made. Morgulis (1918) found that faecal-N for brook trout fed with oxheart and liver constituted 2.5-5.5% of the nitrogen content in food. Nose (1967) found that rainbow trout fed with fish meal and casein lost 8 and 1% respectively of the nitrogen from the food in the faeces. However, a few investigations on this matter, have been done on other fish species by Birkett (1969), Atherton & Aitken (1970) and Beamish (1971). All authors found that faecal-N constituted insignificant amounts and up to app. 10% of the nitrogen content of the food.

The present investigation finds that at a given temperature and fish weight the assimilation of nitrogen measured in settable faeces increases with decreasing feeding level (e.g. from 95% to 99% at 10°C).

An increase in temperature at a given feeding level and fish weight increases the assimilation very slightly and a bigger fish has only a slightly better assimilation of nitrogen than a smaller fish at the same feeding level.

Apparently there is a reasonable accordance between the present results and the informations in the literature. But as described in 8.6.2. it is argued that the total assimilation of nitrogen in the present paper is over-estimated. Probably because the nitrogen content in the suspended and dissolved faeces have not been taken into account, as it was done for β calculated for energy (COD).

8.3. The catabolism of starving fish, $k(T)$

The determinations of the parameters in (8) (from biomass changes) are given in Table 4.

Provided that k_2 and m are the same for all units the following parameters for (8) are found ($R^2 = 0.93$, number of observations = 221):

$$\begin{array}{ll}
 k_1 \text{ (wet weight)} = 0.004077 \begin{array}{l} -0.001100 \\ +0.001487 \end{array} & k_1 \text{ (bombing)} = 0.009615 \begin{array}{l} -0.000308 \\ +0.000282 \end{array} \\
 k_1 \text{ (nitrogen)} = 0.001647 \begin{array}{l} -0.000330 \\ +0.000405 \end{array} & k_2 = 0.0907 \pm 0.0100 \\
 k_1 \text{ (COD)} = 0.008014 \begin{array}{l} -0.002035 \\ +0.002691 \end{array} & n = 0.7719 \pm 0.0671
 \end{array}$$

Table 4. Parameters of catabolism, $k(T)$. Several specimens ($n > 1$). Weight of fish in g wet, g nitrogen, g COD, and kcal, respectively.

Parameter	Estimate according to (8): $dw/dt = k_1 \exp(k_2 T) w^n$			
	Wet weight $R^2 = 0.97, N = 91$	Nitrogen $R^2 = 0.63, N = 39$	COD $R^2 = 0.73, N = 37$	Bombing $R^2 = 0.77, N = 54$
k_1	0.00370 (+0.001401) (-0.001030)	0.001359 (+0.001000) (-0.000602)	0.008464 (+0.008179) (-0.004264)	0.005481 (+0.006495) (-0.003008)
k_2	0.0875 (± 0.0104)	0.1260 (± 0.0427)	0.0911 (± 0.0372)	0.0883 (± 0.0197)
n	0.7688 (± 0.0697)	0.5850 (± 0.2320)	0.7751 (± 0.1907)	0.9296 (± 0.1725)

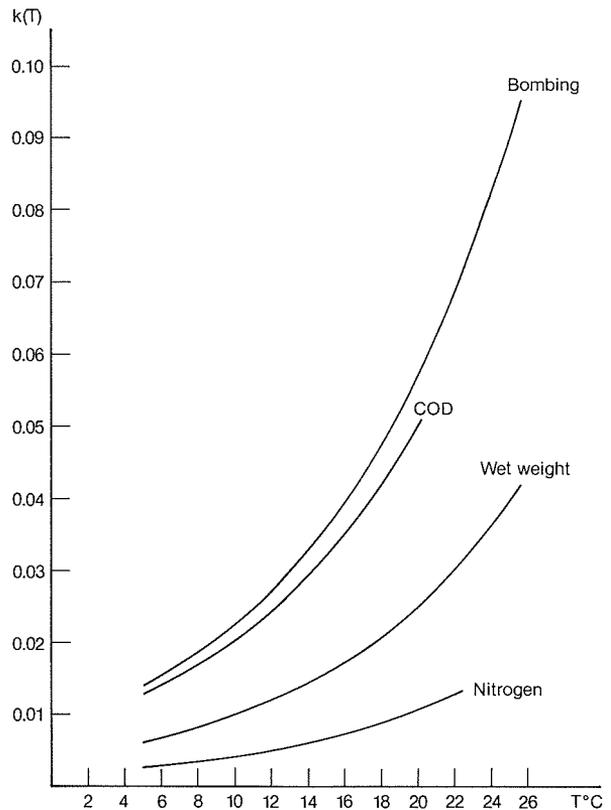


Fig. 6. $k(T)$ for the different units (g wet weight, g nitrogen, g COD, and kcal), according to (8).

Fig. 6 shows $k(T)$ calculated on basis of these parameter values.

Again the curves are not identical because different units are used. $k(T)$ increases with increasing temperature, and there is no basis for believing that $k(T)$ will reach a maximum, and then decrease beyond this, as proposed by Ursin (1967 & 1979).

k_1 (wet weight), k_2 and n can be compared with values in Sperber, From & Sparre (1977) which have: 0.00330, 0.101, and 0.740 respectively. The parameter

values for nitrogen and energy cannot immediately be compared with other investigations.

$k_2 = 0.0920$ gives a $Q_{10} = 2.51$ which is slightly above the value 2.3 given for Q_{10} by Brett & Groves (1979) for standard metabolism. But in the present study Q_{10} varies from 2.20 to 2.86 when k_2 is varying from 0.0789 to 0.1051 which is the confidence interval.

Winberg (1960) proposes that $n = 0.81$ for salmonids, Ursin (1967) proposes $n = 5/6$ as a common estimate, whereas Brett & Groves (1979) claim that $n = 0.86 \pm 0.03$ (S.E.) is more correct for fish in general. The value in the present study is generally speaking in accordance with the mentioned authors.

8.4. The NH_3 -N excretion, $U = U_1 + U_2$

The parameter determination of (14) is given in Table 5. In Fig. 7 the calculated values of NH_3 -N excretion as a function of feeding level at different temperatures are shown. The intercept for $f = 0$ corresponds to the endogenous excretion U_1 .

Independent of fish size and temperature U_2/U varies from 0% for $f = 0$ and up to 88.5% for $f = 1$.

At a given temperature the exogenous excretion constitutes an increasing amount of the nitrogen content of the food, with increasing f , however in such a way that a bigger fish excretes a little more than a smaller fish. As examples can be given:

Temp. °C	Fish weight in g N	Feeding level	$U_2/\Delta R$ % in nitrogen units
10.0	0.25 (~10 g wet)	0.1	7.1
		0.5	11.4
		1.0	22.5
	2.5 (~100 g wet)	0.1	7.4
		0.5	11.9
		1.0	23.5
20.0	0.25 (~10 g wet)	0.1	10.0
		0.5	16.1
		1.0	35.9
	2.5 (~100 g wet)	0.1	10.4
		0.5	16.8
		1.0	37.4

It is difficult to compare these results with other investigations on nitrogen excretion in rainbow trout because published results of the endogenous NH_3 -N excretion are calculated on basis of wet weight of fish, apart from Elliott (1976b) who converts all his values for food ration, fish weight and excretion to energy. In Table 5 the determinations of the parameters in (14) are given for the same set of data, and here the weight of the fish also are given in wet weight. In practical fish farming the last mentioned will be of interest. But now problems will arise when comparing these results with others, because differences in the nitrogen contents of the fish will cause different rates of endogenous NH_3 -N excretion. In the summary

Table 5. Parameters of catabolism, U . Several specimens ($n > 1$). In the table determinations have been done with $h(T)$ found from (3') but determinations with $h(T)$ found from (3) give nearly the same results.

Parameter	Estimate according to (14): $U = \mu_1 \exp(\mu_2 f) \exp(\mu_3 T) w^{\mu_4}$		
	w in g nitrogen $R^2 = 0.81, N = 164$	w in g wet weight $R^2 = 0.80, N = 166$	w in g COD $R^2 = 0.80, N = 164$
μ_1	$6.7462E-4 \begin{pmatrix} +3.6408E-4 \\ -1.6523E-4 \end{pmatrix}$	$3.7614E-5 \begin{pmatrix} +3.3934E-5 \\ -1.0301E-5 \end{pmatrix}$	$1.2766E-4 \begin{pmatrix} +0.4173E-4 \\ -0.5032E-4 \end{pmatrix}$
μ_2	$2.1660 (\pm 0.2883)$	$2.1558 (\pm 0.2934)$	$2.1320 (\pm 0.3031)$
μ_3	$0.1099 (\pm 0.0187)$	$0.1103 (\pm 0.0190)$	$0.1112 (\pm 0.0196)$
μ_4	$0.7429 (\pm 0.1041)$	$0.7385 (\pm 0.1083)$	$0.6572 (\pm 0.1027)$

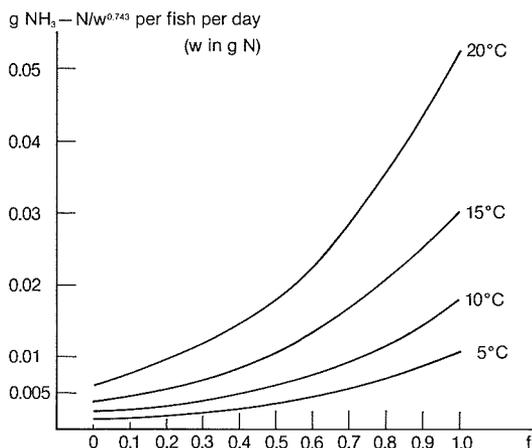


Fig. 7. $\text{NH}_3\text{-N}$ excretion as a function of f at 5, 10, 15, and 20°C.

below the present results are compared with $\text{NH}_3\text{-N}$ in mg/kg fish wet weight/day on basis of informations about fish size and temperature. Fromm (1963) calculates for starving rainbow trout on 129 g wet weight at 13°C an excretion of 75 mg N/kg/day. Under the same conditions the parameters from (14) give 43 mg N/kg/day. Nightingale (1974) calculates for starving rainbow trout on 900 g wet weight at 10, 15 and 20°C an excretion of 31, 55, and 85 mg N/kg/day, respectively. From (14) the excretion is calculated to be: 18, 32 and 56 mg N/kg/day, respectively. The $\text{NH}_3\text{-N}$ excretion for starving fish in the present study is underestimated with 60% (57.3-65.9), compared with Fromm (1963) and Nightingale (1974). The difference is probably caused by differences in origin and state of nutrition of the fish in the present and mentioned studies.

As mentioned only $\text{NH}_3\text{-N}$ was measured. No determination of urea-N was performed, but this constitutes from 21% to 25% of the total endogenous nitrogen excretion (Brett & Groves 1979) in salmonids. Brett & Zala (1975) could not demonstrate any raise of urea-N in the exogenous nitrogen excretion of sockeye salmon, *Oncorhynchus nerka* Walbaum (1792), but a marked raise in $\text{NH}_3\text{-N}$ was shown following feeding. Further, Love (1980) says that ammonia is the chief compound deriving from exogenous nitrogen and that the rate of its excretion

contrary to urea increases after feeding. So it is seen that the error introduced by only measuring $\text{NH}_3\text{-N}$ is biggest for starving fish. Elliott (1976b) found that $\text{NH}_3\text{-N}$ constituted app. 90% of $\text{NH}_3\text{-N}$ and urea-N for both starving and fed or feeding fish. Burrows (1964) found that $\text{NH}_3\text{-N}$ constituted an increasing amount under unfavourable conditions.

U_2 is analogous to the increase in oxygen consumption caused by food handling. $U_2/\Delta R$ increases by a factor about 3 when f goes from 0.1 to 1. Whereas $\alpha/\Delta R$ only rises by a factor about 2. One of the explanations might be that the nitrogen excretion is underestimated at low feeding levels but not at higher feeding levels. This will make the increase in nitrogen excretion bigger than the increase in oxygen consumption which not is underestimated at low feeding levels.

8.5. The oxygen consumption, $\alpha + k'(T)$

The determination of the parameters in (17) and (19) are given in Table 6 & 7, respectively. In Fig. 8, the calculated values for total respiration of fish as a function of feeding level, are shown for different temperatures. In Fig. 9 the calculated values of α in proportion to total respiration, assimilated, and ingested food are shown for different values of feeding level, temperature and fish weight.

Table 6. Parameters of catabolism, $k'(T)$ starving respiration. Several specimens ($n > 1$).

Parameter	Estimate according to (17): $k'(T) = i_1 \exp(i_2 T) w^{i_3}$	
	w in g COD $R^2 = 0.75, N = 16$	w in g wet weight $R^2 = 0.83, N = 25$
i_1	$4.1246\text{E-}3 \begin{pmatrix} +1.2831\text{E-}3 \\ -1.0036\text{E-}3 \end{pmatrix}$	$1.0989\text{E-}3 \begin{pmatrix} +2.0449\text{E-}3 \\ -0.71829\text{E-}3 \end{pmatrix}$
i_2	$0.1774 (\pm 0.0347)$	$0.1003 (\pm 0.0369)$
i_3	$0.5764 (\pm 0.2584)$	$0.8845 (\pm 0.2714)$

Table 7. Parameters of catabolism, α feeding respiration. Several specimens ($n > 1$). In the table determinations have been done with $b(T)$ found from (3') but determinations with $b(T)$ found from (3) give nearly the same results.

Parameter	Estimate according to (19): Total respiration = $a_1 \exp(a_2 f) \exp(a_3 T) w^{a_4}$	
	w in g COD $R^2 = 0.88, N = 122$	w in g wet weight $R^2 = 0.89, N = 144$
a_1	$6.2374\text{E-}3 \begin{pmatrix} +1.6684 \\ -1.3208 \end{pmatrix}$	$2.2287\text{E-}3 \begin{pmatrix} +0.7354\text{E-}3 \\ -0.5542\text{E-}3 \end{pmatrix}$
a_2	$1.0885 (\pm 0.2065)$	$1.0249 (\pm 0.1880)$
a_3	$0.0769 (\pm 0.0109)$	$0.0785 (\pm 0.0102)$
a_4	$0.7030 (\pm 0.0677)$	$0.7930 (\pm 0.0662)$

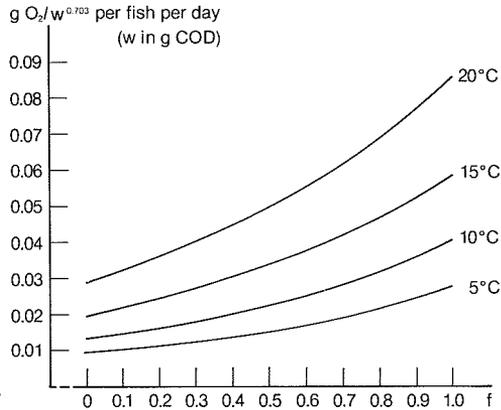


Fig. 8. Total respiration as a function of f at 5, 10, 15, and 20°C.

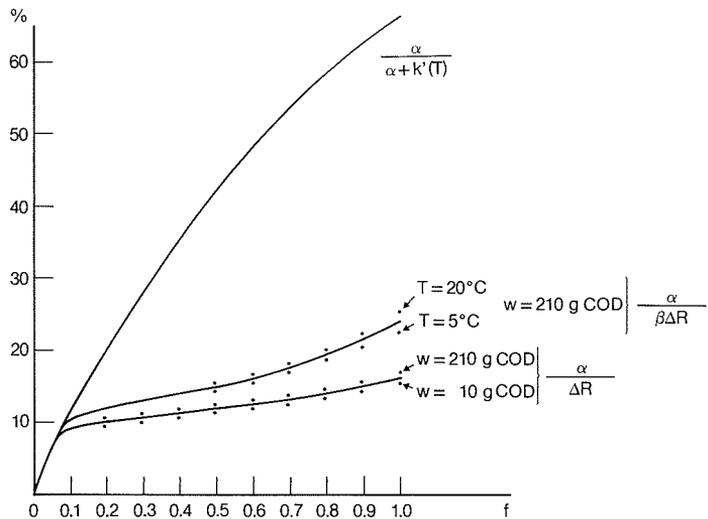


Fig. 9. α in proportion to total respiration, assimilated, and ingested food.

The literature about oxygen consumption of fish is enormous, and there can among others be referred to Winberg (1960), Doudoroff & Shumway (1970), Fry (1971), Brett (1979), and Brett & Groves (1979) for references.

Winberg (1960) was the first to give parameter values for calculation of the oxygen consumption of starving and feeding or fed fish, respectively. The 'routine metabolism' in Winberg (1960) corresponds to $k'(T)$ in the present paper. As comparison can for example be calculated, with the figures given by Winberg, that the respiration at 20°C for a 10 g and 100 g (wet weight) fish, will be 65 and 409 mg O₂ per fish per day, respectively. For starving fish with the values of the parameters in (17) and (19) for wet weight the values for (17) are: 63 and 480 mg O₂ per fish per day, and for (19) (for $f = 0$): 67 and 413 mg O₂ per fish per day. The accordance between Winberg's values and the values of the present investigation is good. For feeding or fed fish at the same temperature and sizes as the above mentioned

the total respiration calculated with Winberg's parameters are 130 and 820 mg O₂ per fish per day, that is a doubling of the respiration. With the parameter values calculated from (19) the mentioned oxygen consumptions correspond to a feeding level of 0.65 for the fish of 10 g wet weight and a feeding level of 0.67 for the fish of 100 g wet weight. The routine metabolism in Winberg (1960) is calculated on basis of an incredible amount of earlier published data, and it would be peculiar if the results of the present study had not been in accordance with Winberg's predictions. In Fig. 9 is shown how many per cent α constitutes of the total respiration and of the ingested and assimilated food (units of COD). Independent of fish weight and temperature α constitutes from 0% at $f = 0$ to 66.3% of the total respiration at $f = 1$, calculated on basis of (19). of course, at $f = 0$, α constitutes 0% of the food, for $f = 0.1$ about 9-10%, and raises to 15-16% for $f = 1.0$, slightly dependent on fish weight and temperature. Though the absolute values of α for $f = 0.1$ is app. 5% of α for $f = 1.0$, α 's share of the food is varying only with a factor 2 for f growing from 0.1 to 1. α 's share of the assimilated food, $\beta(dR/dt)$ constitutes a decreasing amount with increasing fish weight but is nearly independent of temperature (for $f = 0.1$ app. 11% of $\beta(dR/dt)$, for $f = 1$ app. 24%).

Brocksen, Davis & Warren (1968) found for cutthroat trout fed with invertebrates that α constituted about 36% of the food (app. 42% of the assimilated food). As α was found as a difference, the value is probably a little overestimated. Averett (1969) is normally considered to be the first that determined α (called SDA by Averett) for salmonids (for other fish species Saunders (1963) was the first), as an independent element in the energy budget. The oxygen consumption was by Averett converted to calories, using an oxycalorific coefficient of 3.42 cal/mg O₂. He found that even fish that get a 'sub-maintenance ration have a cost of food handling', and 'at high consumption rates and high temperatures, SDA ranged from 10.7 to 17.3% of the value of the food assimilated. At low rations it was usually less'.

Brett & Groves (1979) sum up the data for determinations of feeding metabolism, and conclude that the ratio of feeding metabolic rate to routine metabolism can be put equal to 1.7 ± 0.4 (standard deviation). However, this ratio will depend on feeding level, and a ratio of 1.7 is in the present investigation achieved for $f = 0.5$, and for $f = 1$ the ratio is maximum and 2. Further, the feeding metabolic rate increases with increasing intake of food and increasing temperature at a given fish size.

α determined on basis of oxygen consumptions in connection with food intake, as done in the present investigation, is not an expression of the true 'heat increment'. Smith, Rumsey & Scott (1978a & b) are probably the only in the literature who have determined the heat increment by determining the direct energy loss in connection with the physiological handling of the food, independent of the activity associated with this. However, the major part of the heat increment constitutes in Smith, Rumsey & Scott (1978a & b) only a few per cent of the food, but as artificial food compositions were used, it is difficult to directly compare these results with others, see Brett & Groves (1979).

A strength by measuring α as oxygen consumption is, besides from the problem with a correct oxycalorific coefficient, see Solomon & Brafield (1972) and Elliott

& Davison (1975), that an enhanced activity in connection with an increased food intake merely results in an increased oxygen consumption, which can be measured with relatively simple technical facilities (as long as the energy consumption does not come from anaerobic processes).

If the oxygen consumption at enhanced respiration in connection with and caused by increased food intake can be used as an indicator for α , then the present results can be compared with results in e.g. Brett & Groves (1979). Here it is claimed on account of oxygen measurements that apparent SDA constitutes 12-16% of the food, which is in accordance with the results of the present investigations. Cho, Bayley & Slinger (1976) found that the ration, for rainbow trout fed with pellets, varied from 8 to 12% and Miura, Suzuki, Nagoshi & Yamamura (1976) found that the ratio for biwamasu salmon, *Oncorhynchus rhodorus* Jordan & McGregor, 1925 varied from 9.5-25.9%, (18.9 in mean) and of the assimilated food the ratio varied from 11.9-32.3% (23.3 in mean).

8.6. Simulated growth, the growth equation

8.6.1. Energy

The growth equation can now be written down as follows on basis of COD measurements:

$$dw/dt = \text{food} - \text{faeces (caused by food)} - \text{feeding catabolism} - \text{exogenous excretion} - \text{starving catabolism.}$$

The suspended + dissolved faeces caused by food are described by (7) whereas the settable faeces can be described by (6).

The starving catabolism can either have been measured as biomass changes or as: $k'(T) + k''(T) + k'''(T)$. Measured as biomass changes the starving catabolism is probably encumbered with the smallest defectives as the other possibility has an uncertainty as a sum of three times as many uncertainties. As an example the difference can be shown:

		$dw/dt =$ $k'(T) + k''(T) + k'''(T)$ g COD	$dw/dt =$ biomass changes g COD
5°C	$w = 10$ g COD	-0.1115	-0.0795
	$w = 100$ g COD	-0.4691	-0.4738
10°C	$w = 10$ g COD	-0.1661	-0.1254
	$w = 100$ g COD	-0.6987	-0.7472
15°C	$w = 10$ g COD	-0.2478	-0.1978
	$w = 100$ g COD	-1.0415	-1.1783
20°C	$w = 10$ g COD	-0.3697	-0.3199
	$w = 100$ g COD	-1.5540	-1.8581

It is seen that the difference between the two different methods to determine the starving catabolism is biggest for the fish of 10 g COD (or ≈ 30 g wet weight) and smaller for the bigger fish.

The parameter values found can be inserted in the single terms of the growth equation and the course of growth can be simulated by numerical integration of the growth equation, where $w(0)$ is start weight and where the observed temperature ($T \leq 20.1$) and feeding level enter as variables.

Though the differences were small, the growth equation calculated with starving catabolism measured as biomass changes gave the best agreement between observed and calculated final weight, $w(n)$:

Number of observations	=	178
Mean difference	=	0.55 %
Mean $w(n)$ observed	=	35.66 g COD
Mean $w(n)$ calculated	=	35.19 g COD
Residual error variance	=	28.581

where

$$\text{Mean difference} = \Sigma \frac{w(n) \text{ observed} - w(n) \text{ calculated}}{w(n) \text{ observed}} \times \frac{100\%}{\text{no. of observations}}$$

$$\text{Residual error variance} = \frac{\Sigma (w(n) \text{ observed} - w(n) \text{ calculated})^2}{\text{no. of observations}}$$

Based on COD the growth equation can be written down as ($T \leq 20.1$):

$$\begin{aligned} dw/dt = & f \cdot 0.085 \cdot \exp(0.0761 \cdot T) \cdot w^{0.6767} - 0.011861 \cdot [\exp(1.1057 \cdot f) - \\ & 1] \cdot \exp(0.0808 \cdot T) \cdot w^{0.5499} - 0.0162 \cdot f^{1.4259} \cdot \exp(0.0577 \cdot T) \cdot \\ & w^{0.5471} - 0.006237 \cdot [\exp(1.0885 \cdot f) - 1] \cdot \exp(0.0769 \cdot T) \cdot w^{0.7030} \\ & - 1.8 \cdot 1.2766\text{E-}4 \cdot [\exp(2.132 \cdot f) - 1] \cdot \exp(0.1112 \cdot T) \cdot w^{0.6572} \\ & - 0.008464 \cdot \exp(0.0911 \cdot T) \cdot w^{0.7751} \end{aligned}$$

The growth equation set up can among other things be used to simulate a course of growth where temperature and feeding level enter as variables. It can also be used to construct an energy budget which shows how much the single terms relatively constitute of, e.g. the food. Examples are shown in Table 8.

In Fig. 10 dw/dR is shown as a function of feeding level for different temperatures for a fish of 10 and 100 g COD respectively. $dw/dR = 0$ corresponds to $f = f_{\text{maintenance}}$, which for a given fish weight increases a little with temperature.

When dw/dR is maximum, the fish, from a purely energetical consideration, have the most effective utilization of the food, (dw/dR) ≈ 0.40 at 5°C and ≈ 0.33 at 20°C.

It appears from Fig. 10 that dw/dR for low values of f at a given temperature is smaller for the smallest fish. For $f \approx 0.75$ the bigger fish has a better utilization of food than the smaller fish at a given temperature. The picture is the same for other

Table 8. Energy budget at different feeding levels.

<i>f</i>	ΔR g COD	Per cent of ΔR							$k(T)$ biomass changes dw/dt	
		Defecation		Excretion		Respiration				
		Settable faeces	Susp. + diss. faeces	U urine	U_2 exo- gen	α	$k'(T)$			
$T = 5^\circ\text{C}, w = 10 \text{ g COD}$										
0.1	0.0596	4.80	12.37	4.59	0.9	8.73	77.64	133.50	-60.50	
0.2	0.1191	6.45	13.09	2.85	1.0	9.44	38.82	66.76	3.26	
0.3	0.1787	7.66	13.87	2.36	1.1	9.99	25.88	44.51	22.87	
0.4	0.2382	8.66	14.71	2.20	1.3	10.59	19.41	33.38	31.36	
0.5	0.2978	9.52	15.62	2.18	1.4	11.23	15.53	26.71	35.52	
0.6	0.3573	10.29	16.60	2.26	1.6	11.92	12.94	22.25	37.34	
0.7	0.4169	10.99	17.66	2.41	1.9	12.67	11.09	19.08	37.70	
0.8	0.4765	11.63	18.81	2.61	2.2	13.48	9.70	16.69	37.19	
0.9	0.5360	13.23	20.05	2.89	2.5	14.35	8.63	14.84	36.03	
1.0	0.5956	12.79	21.39	3.23	2.9	15.29	7.76	13.35	34.28	
$T = 20^\circ\text{C}, w = 10 \text{ g COD}$										
0.1	0.1865	3.64	13.27	7.62	1.5	9.04	78.57	167.20	-94.65	
0.2	0.3730	4.89	14.05	4.73	1.7	9.55	39.29	83.60	-13.79	
0.3	0.5595	5.81	14.89	3.92	1.9	10.11	26.19	55.74	11.55	
0.4	0.7460	6.57	15.79	3.65	2.1	10.72	19.64	41.80	23.02	
0.5	0.9225	7.23	16.76	3.63	2.4	11.37	15.71	33.44	28.80	
0.6	1.1190	7.81	17.82	3.75	2.7	12.07	13.10	27.87	31.73	
0.7	1.3055	8.34	18.95	3.99	3.1	12.82	11.22	23.89	32.90	
0.8	1.4920	8.83	20.18	4.34	3.6	13.64	9.82	20.90	32.85	
0.9	1.6785	9.28	21.51	4.79	4.1	14.52	8.73	18.58	32.01	
1.0	1.8650	9.71	22.95	5.36	4.7	15.48	7.86	16.72	30.44	

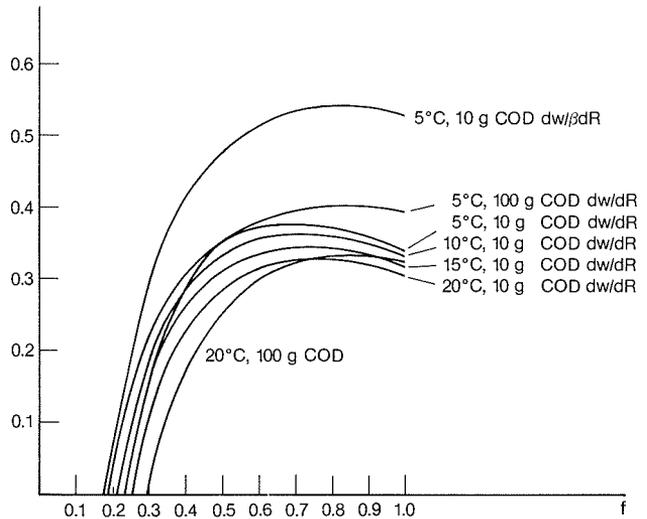


Fig. 10. dw/dR as a function of f for fish of 10 and 100 g COD at different temperatures. Further, $dw/\beta dR$ is shown at 5°C for a fish of 10 g COD.

fish sizes in such a way that the interception between the curves for the two given fish sizes is for $f \approx 0.55$ at 5°C .

This result is hardly due to fortuitousness in the parameter determinations alone, because the *observed* values of dw/dR for $f = 1.0$ and $f = 0.4$ (0.35-0.45) respectively were in excellent agreement with values calculated with the parameter values in the model.

In the literature it has been discussed whether dw/dR is size-dependent and it is often claimed that dw/dR is decreasing with increasing fish size. Paloheimo & Dickie (1966b) conclude that the relationship between $\log K = \log\{\Delta w/(R\Delta t)\}$ and R is adequately described by a linear equation. This equation expresses growth as a function of rations independent of body weight. Warren & Doudoroff (1971) comment on Paloheimo & Dickie and simply state that large fish do tend to grow with less efficiency than small fish. But they give no evidence for this. Brett & Groves (1979) claim that there is a decreasing conversion efficiency accompanying increasing size and say that the relationship is apparent in the studies of Kinne (1960). However, from Kinne's table 13 is seen that at 15 and 20°C it is the biggest fish that have the highest gross efficiency whereas it is opposite at 25, 30 and 35°C .

On basis of the above references and the present investigation it is the opinion of the present authors that it is not a natural law that dw/dR has to decrease with increasing fish size. Instead of presupposing any relationship between dw/dR and fish size or age it would be more profitable to carry out controlled feeding experiments to determine the parameters of the terms in a growth equation. Particularly the sizes of the weight exponents in the anabolic terms in relation to the weight exponents in the catabolic terms. When it is observed that the growth rate decreases as a function of age, e.g. Beverton & Holt (1957), it might be a true physiological fact. But it can also be an effect of spawning. Here a high loss of biomass has to be compensated before additional growth take place, e.g. Ursin (1979). The physiologically growth parameters cannot be deduced from age/length-data. It might be possible that controlled aquaria experiments with e.g. sexually immature cod will show a non-decreasing growth rate until maturing takes place.

8.6.2. Nitrogen

$$dw/dt = \text{food} - \text{faeces} - \text{excretion (endogenous + exogenous)}.$$

Only the settable faeces were collected, why dw/dR will be overestimated. From the assumption that the relation between settable and suspended + dissolved faeces is dependent on f in the same way as it was for COD, the balance can with guesstimates simulate a course of growth. The guesstimates are changed until there is a reasonable accordance between observed and calculated values for $w(n)$ for nitrogen.

Number of observations	= 177
Mean differences	= -0.03 %
Mean $w(n)$ observed	= 2.0810 g N
Mean $w(n)$ calculated	= 2.1199 g N
Residual error variance	= 0.1659.

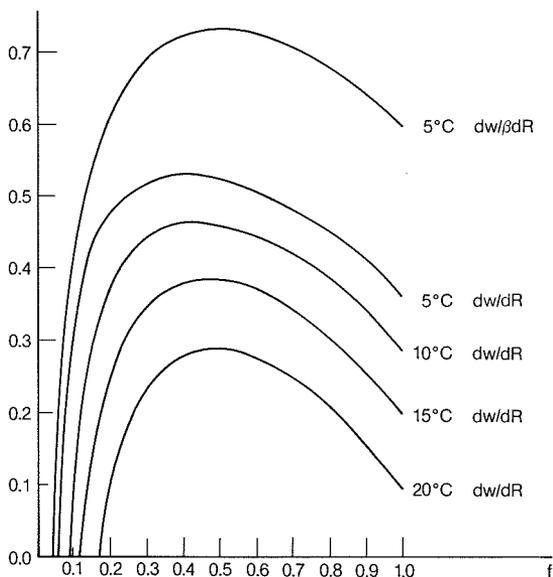


Fig. 11. dw/dR as a function of f for fish of 3.25 g N at different temperatures. Further, $dw/\beta dR$ is shown at 5°C for a fish of same size.

Based on nitrogen the growth equation can be written down as ($T \leq 20.1$):

$$dw/dt = f \cdot 0.0318 \cdot \exp(0.0755 \cdot T) \cdot w^{0.7246} - 0.005531 \cdot [\exp(1.1057 \cdot f) - 1] \cdot \exp(0.0912 \cdot T) \cdot w^{0.6215} - 0.002047 \cdot f^{1.6006} \cdot \exp(0.0663 \cdot T) \cdot w^{0.6215} - 6.7462E-4 \cdot [\exp(2.166 \cdot f) - 1] \cdot \exp(0.1099 \cdot T) \cdot w^{0.7429} - 0.001359 \cdot \exp(0.1260 \cdot T) \cdot w^{0.5850}$$

dw/dR for an average fish, 3.25 g N at 5, 10, 15, and 20°C is shown in Fig. 11. Here the same considerations as in Fig. 10 about the values of dw/dR are valid.

A more correct determination of the growth equation based on nitrogen will require quantitatively nitrogen determinations in the outlet water with its N-containing suspended + dissolved faeces and other nitrogen containing excretion products.

8.7. Body composition

8.7.1. NPN and TVN

The total nitrogen content, usually determined by the Kjeldahl method, consists of NPN (non-protein nitrogen) and PN (protein nitrogen).

NPN can be converted to nitrogen extractives if the N content in these is known, and PN can be converted to protein if the N content in protein is known.

The results for NPN and TVN are shown in Table 9.

From the table it is seen that the amount of NPN is small, 0.12% of wet weight and 0.46% of dry weight. Concerning the amount of NPN, Niimi (1972a) states

Table 9. Amount of NPN and TVN in fish samples.

Wet weight, g	% dry material	kcal/g dry	% of wet weight		
			NPN	Total N	TVN
27.9	23.36	5.27	0.108	2.52	0.037
29.1	21.74	4.70	0.083	2.59	
30.2	23.80	5.06	0.156	2.64	
39.6	28.04	6.03	0.054		
43.0	21.88	4.77	0.046	2.62	
51.1	24.24	5.52	0.121	2.64	
54.3	22.00	4.68	0.114	2.68	0.027
58.4	24.95	5.46	0.141	2.59	
61.1	24.08	6.44	0.076	2.56	
62.5	24.11	5.33	0.070	2.68	
67.5	23.90	5.19	0.068	2.60	
73.3	25.94	5.79	0.072	2.65	0.020
74.2	24.74	5.20	0.189	2.71	
86.6	24.54	5.58	0.077	2.70	0.017
89.9	24.56	5.59	0.076		
94.7	25.06	5.60	0.094	2.68	0.022
96.7	26.70	5.77	0.067	2.75	
97.3	25.50	5.63	0.066		
108.4	26.08	5.46	0.079	2.60	
111.0	25.89	5.51	0.089	2.66	
111.2	23.72	5.93	0.088	2.74	
112.2	29.16	5.75	0.051	2.73	0.024
113.3	23.71	5.71	0.119	2.65	0.019
118.4	24.88	5.21	0.183		
119.8	25.38	5.26	0.220	2.82	
125.5	23.66	6.34	0.047	2.68	
137.3	27.74	5.98	0.142	2.69	
148.4	23.93	5.33	0.248		
151.9	26.49	5.78	0.169	2.83	
155.0	24.61	5.65	0.079	2.74	0.022
155.1	25.64	5.55	0.129	2.84	
174.0	25.85	5.56	0.086	2.74	0.019
180.6	25.83	5.49	0.221	2.86	
182.4	26.72	5.78			
192.6	27.21	5.82	0.184	2.80	
209.8	25.66	5.38	0.206	2.83	0.033
222.4	27.88	5.71			0.016

that the level decreased with increasing body weight for fish between 100 and 900 g. Our analyses gave the opposite: that a bigger fish had a bigger amount of NPN in % of total N, than a smaller fish. The relationship can be expressed:

$$Y = 2.9 (\pm 1.4) + 0.049 (\pm 0.047) X, \text{ where } X \text{ is body dry weight (g) and } Y \text{ the per cent NPN of total N.}$$

The present results are in accordance with the general assumption that the amount of NPN for bioenergetic purposes is negligible. For salmonids the following results

can be mentioned: Duncan & Tarr (1958) found 0.4-0.5 % of wet weight in muscles for migrating sockeye salmon, Brett, Shelbourn & Shoop (1969) found also for sockeye salmon 0.05 % wet weight for whole fish. Lukton & Olcott (1958) mention 0.38 % of wet weight in muscles from rainbow trout, Cowey & Parrey (1963) found 0.20 % and 0.28 % wet weight in the muscles of parr and smolt of Atlantic salmon, *Salmo salar* Linné, 1758, respectively, For brown trout whole fish, Elliott (1976a) found a value of 0.2 % of dry weight (app. 0.05 % of wet weight).

A part of NPN is called TVN (total volatile nitrogen). In very fresh fish it consists almost wholly of ammonia, Shewan (1951). In Table 9 it is seen that TVN constitutes 0.023 % of wet weight (0.095 % dry weight).

8.7.2. Carbohydrate

The results are shown in Table 10.

It is seen that the amount of carbohydrate is small 0.26 % of wet weight and 0.94 % of dry weight.

Determination of carbohydrate contents has not usually been made in connection with fish bioenergetics. Craig (1977) found for perch, *Perca fluviatilis* Linné, 1758, the following values for carbohydrate: 0.134 % wet (0.595 % dry) on tissues and 0.508 % wet (2.398 % dry) for ovaries and 0.268 % wet (1.350 % dry) for testes. Niimi & Beamish (1974) found for largemouth bass, *Micropterus salmoides* (Lacépède, 1802) the amounts of lipid, protein, ash, and non-proteinaceous materials and say that these materials accounted for 92-98 % of the dry weight. All values were adjusted to 98 % of dry weight, the other 2 % assigned to carbohydrate (0.5 % of wet weight). Burt (1961) found 0.20 % carbohydrate on wet weight basis in muscles of cod, *Gadus morhua* Linné, 1758. Brett, Shelbourn & Shoop (1969) cite Vinogradov (1953) and Black (1958) for saying that carbohydrate does not amount to more than 0.5 % of body wet weight.

Table 10. Amount of carbohydrate in fish samples.

Wet weight, g	% dry material	% carbohydrate of wet weight	Wet weight, g	% dry material	% carbohydrate of wet weight
59.1	25.41	0.23	101.7	26.83	0.28
59.9	25.85	0.20	102.4	26.08	0.37
64.1	27.19	0.31	104.5	26.13	0.24
65.8	25.73	0.19	113.2	27.04	0.29
67.3	27.92	0.33	116.4	28.29	0.22
69.2	26.27	0.23	116.7	27.56	0.23
71.4	25.92	0.12	117.0	26.62	0.39
72.0	25.99	0.15	121.6	26.14	0.39
76.0	27.25	0.30	133.5	30.87	0.26
81.1	26.33	0.18	143.6	28.27	0.22
92.5	27.17	0.22	157.4	30.80	0.26
98.3	26.14	0.27	347.0	32.00	0.36

8.7.3. *Protein*

The amount of protein is nearly always determined from the amount of nitrogen (found by the Kjeldahl method) multiplied by 6.25 (called crude protein) as it is assumed that nitrogen constitute 16% of protein. As Kirk (1947) says: 'It is a fact that the analyst rarely knows with certainty the correct conversion factor to use for any given protein which he is analysing. Since the nitrogen content of individual proteins may vary from about 14 to 19%, it is evident that analysis of protein mixtures of unknown composition may be determined only approximately by use of any empirical factor which has not been carefully determined for the particular system'. As long as the factor 6.25 uncritically is used it is the opinion of the present authors that it has no meaning to discuss the error introduced by neglecting NPN. It would be of more interest to determine the conversion factor between N and the considered protein better.

In the literature the following values for the conversion factor between nitrogen and protein can be found:

- 6.41 on horse serum-albumins, Adair & Robinson (1930).
- 6.024 on myosin in muscle proteins from dog, ox cheek, chicken, fish, and lobster, Bailey (1937).
- 6.56 on egg albumin, pepsin and β -lactoglobulin, Chibnall, Rees & Williams (1943).
- 6.53 on casein, Jonnard (1945).
- 6.08 (5.91-6.80) on muscle proteins in haddock, lemonsole, and dogfish, Subba Rao (1948).
- 6.07 (6.02-6.17) on muscle proteins in haddock and herring, Nottingham (1952).
- 6.26, 6.32 and 6.25 for whole brook trout, wild, hatchery 1, and hatchery 2, respectively. The values are calculated from values for the amino-acid composition from Block (1959) given in Love (1970), table 9, p. 54.

As 6.25 is commonly used and probably as good as many other values, it is chosen in the present study. Another reason is that the value for the only whole salmonid found in the literature by the authors (brook trout, Love 1970, p. 54) is very near to 6.25.

The value of the conversion factor could be found if the conversion factor between NPN and nitrogen extractives were known together with the content of ash, lipid, carbohydrate, and N, in which case we would have:

Ash + lipid + carbohydrate + NPN \times conversion factor + protein N \times X = total and X could be found. But the problem is to find the conversion factor between NPN and nitrogen extractives. The only information in the literature about the composition of the nitrogen extractives, the present authors know, is Kjosbakken (1970). His table 12, p. 61 gives the composition of nitrogen extractives in light

muscle for herring, *Clupea harengus* Linné, 1758 in December and March, respectively, for capelin, *Mallotus villosus* (Müller, 1776) in April and November, respectively, and for mackerel, *Scomber scombrus* Linné, 1758 in April.

If IMP, inosine and hypoxanthine which only occur in stored and not in fresh fish are excluded the values for the conversion factor between NPN and nitrogen extractives are: 4.20, 4.06, 4.24, 4.39, and 4.00. (In average: $\text{NPN} \times 4.18 = \text{nitrogen extractives}$). Further, if trimethylamineoxide which only occur in salt-water fish is excluded, the following values are found: 3.99, 3.83, 3.88, 4.04, and 3.86 (in average: $\text{NPN} \times 3.92 = \text{nitrogen extractives}$). So it seems that a conversion factor of 4 is a fairly good guess.

If this value is used in the present study a value of app. 6.6 is found as conversion factor between protein N and protein. This value (bigger than 6.25) is probably due to a lipid extraction which likely not is 100% effective, pp. 111 & 112.

Therefore, the values for protein in the paper (if else not is stated) are Kjeldahl $\text{N} \times 6.25$ (crude protein).

8.7.4. Proximate analysis

The data from 106 observations relating water content, crude protein, lipid, ash, and energy are shown in Figs 12-14 and given in Table 11 and the Appendix.

Fig. 12 relates the contents of crude protein, lipid, and ash as a function of percentage water.

From Fig. 13 which relates the energetic content per g wet weight as a function of water content it can be deduced that the energetic content per g dry weight is not the same if we take for instance:

70 % water	6.09 kcal per g dry weight		
75 %	5.63	—	—
80 %	4.92	—	—

The relationship is a non-linear regression, so the body constituents with different energetical values must change in different proportions with changing water content.

It seems therefore profitable to delimit the effect of water as has been done in Fig. 14 which relates protein, lipid and ash as mg per g dry weight to the energetical content per g dry weight determined by bombing using the same 106 set of data.

The total amount in a sample of dry weight (i.e. crude protein + lipid + ash), Fig. 14 can be equated as:

$$\text{mg per g dry weight} = 1122.24 - 30.64 \times \text{kcal per g dry weight.}$$

Testing the hypothesis $H_0: \beta_0 = 1000, \beta_1 = 0$ gives the F -statistic = 498 (1,106) so H_0 is not accepted, so there is an increasing divergence between the expected 1000 mg/g dry weight when the kcal/g dry weight increases.

From the following it is seen that taking NPN and carbohydrate in consideration will in fact not change the value of the missing part:

$$\text{Total\% (dry)} = \text{ash\%} + \text{lipid\%} + \text{carbohydrate\%} + \text{N\%} \times 6.25 + \text{NPN\%} \times 4$$

where the conversion factor 4 between NPN and nitrogen extractives is calculated from Kjosbakken (1970) as mentioned above. As an example the following values

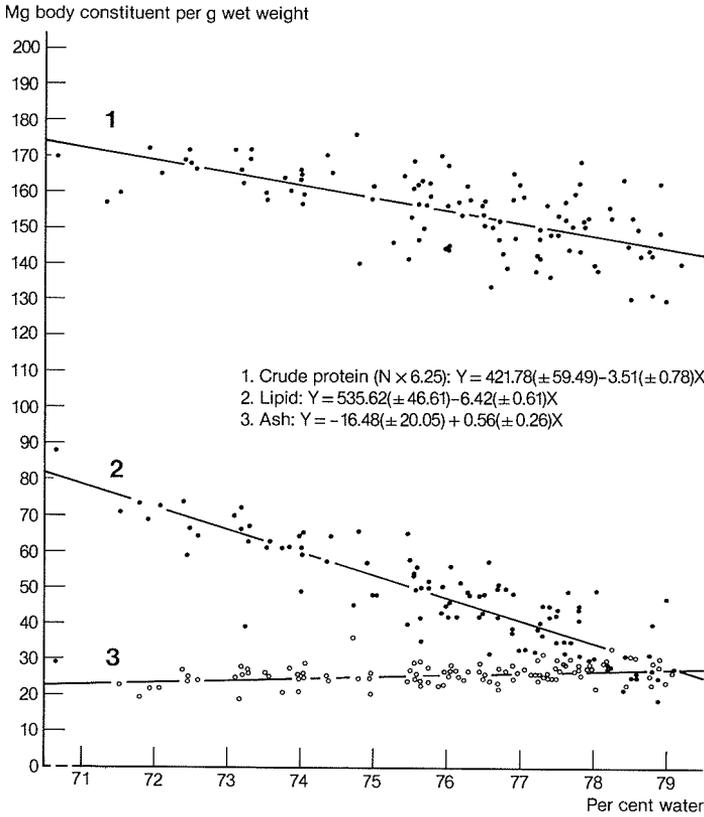


Fig. 12. The amount of crude protein, lipid, and ash as a function of per cent water.

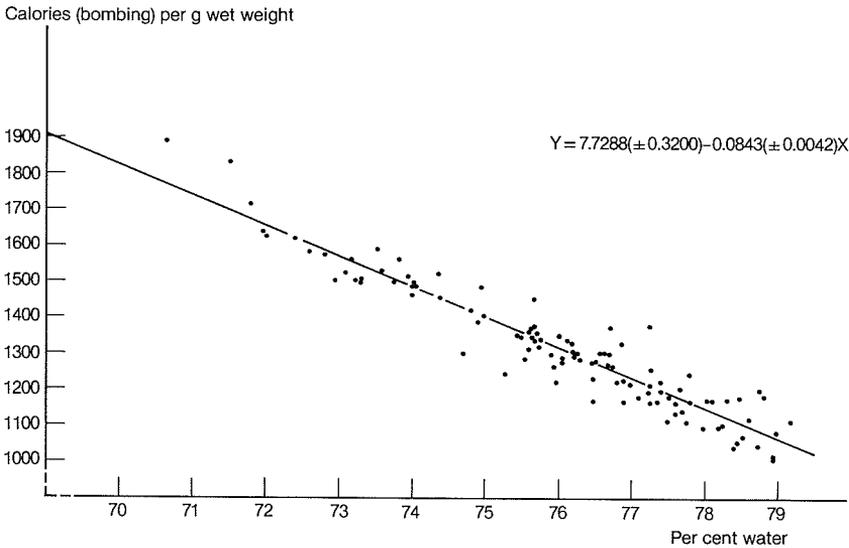
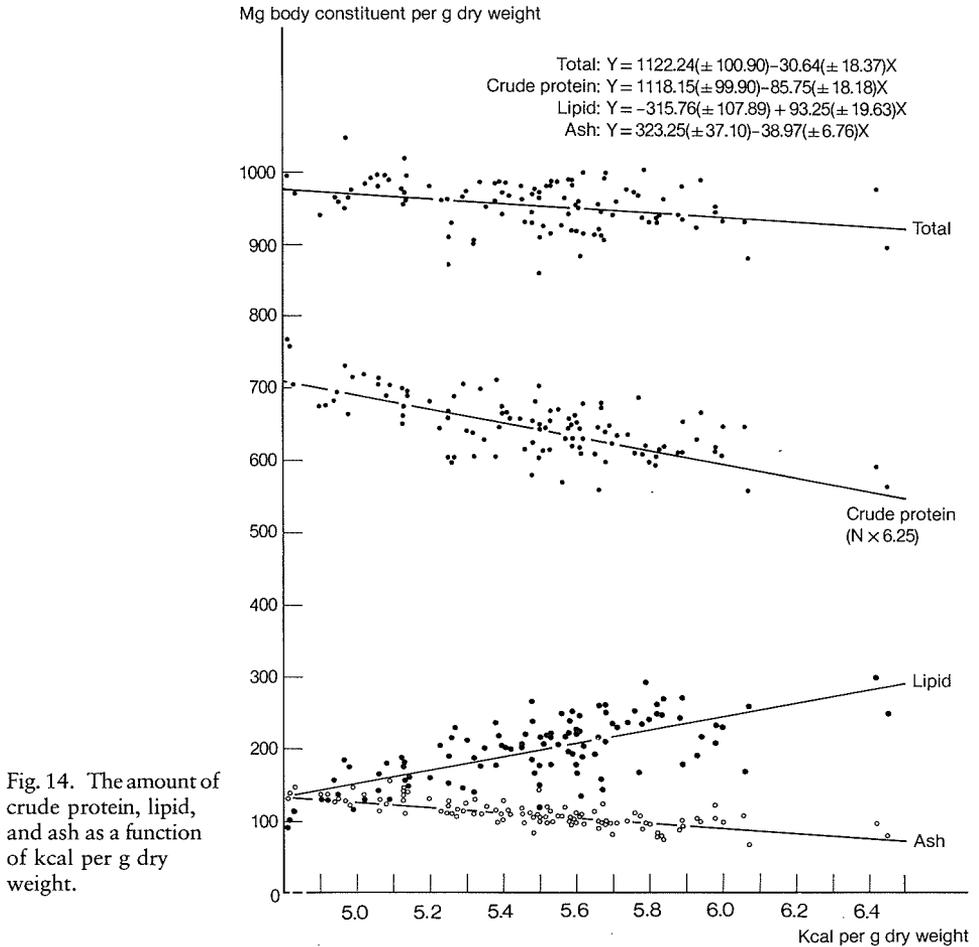


Fig. 13. The energetical content of the fish as a function of per cent water.



can be taken (NPN and carbohydrate are the mean values, and the other values are found from Fig. 14 for 5.35 kcal/g):

$$\text{Total\%} = 11.48\% + 18.31\% + 0.94\% + 10.09 \times 6.25\% + 0.46 \times 4\% = 95.63\%$$

If NPN and carbohydrate are not considered we will get:

$$\text{Total\%} = 11.48\% + 18.31\% + 10.55 \times 6.25\% = 95.73\%.$$

It is not considered probable that the determinations of nitrogen and ash are biased. The Kjeldahl technique was all times tested with ammonium chloride as a standard and proved to be 100% effective. Thus it can be stated that (a) the method of lipid extraction is biased giving substantially too low values or/and (b) the converting factor of 6.25 is too low. From Fig. 14 it can be seen that the more

Table 11. Amount of lipid and ash. In the table some of the values for $w(0)$ are the same for different aquaria. This is shown by *. The ash is determined in muffle oven. Ser/aqu means series and aquarium number. This figure enables one to find the other informations about the fish in the Appendix.

Ser/ aqu	$w(0)$		$w(n)$		Ser/ aqu	$w(0)$		$w(n)$	
	Lipid, % dry weight	Ash, % dry weight	Lipid, % dry weight	Ash, % dry weight		Lipid, % dry weight	Ash, % dry weight	Lipid, % dry weight	Ash, % dry weight
11.01*	16.92	10.68	20.55	12.12	12.16	21.54	9.00	23.31	8.04
11.02*	16.92	10.68	17.92	10.25	13.01	21.79	11.78	22.22	10.68
11.03*	16.92	10.68	19.19	11.34	13.02	20.24	11.56	14.25	13.14
11.04*	16.92	10.68	15.07	12.06	13.03*	13.06	15.40	15.79	13.11
11.05*	16.73	10.72	11.71	14.37	13.04*	13.06	15.40	11.78	14.39
11.06*	16.73	10.72	16.63	9.88	13.05	14.38	11.51	9.19	13.45
11.07*	16.73	10.72	18.96	10.50	13.06	21.60	9.87	20.54	10.21
11.08*	16.73	10.72	23.02	9.79	13.07*	19.87	11.11	21.84	11.86
11.10	29.88	9.85	25.98	7.88	13.08*	19.87	11.11	13.30	13.01
11.11*	26.05	6.84	23.54	8.72	13.09	21.63	10.63	18.80	11.29
11.12*	26.05	6.84	23.33	10.55	13.11	21.57	11.88	11.75	12.54
11.13*	22.42	9.98	24.84	8.01	13.12	25.12	9.92	29.13	9.26
11.14*	22.42	9.98	24.23	8.65	13.14	18.86	10.70	14.53	10.68
11.15*	22.42	9.98	24.56	8.21	13.15	26.87	7.23	24.82	9.33
11.16*	22.42	9.98	18.89	9.54	13.16	22.56	9.80	17.93	9.67
12.01	21.00	9.60	20.46	11.55	14.02	15.73	13.67	17.71	12.19
12.02	18.44	10.54	20.52	10.77	14.03	14.48	12.12	20.07	12.10
12.03	22.87	10.53	25.10	11.03	14.04	13.13	13.54	18.91	11.20
12.04	13.84	12.44	16.14	13.81	14.05	10.18	13.74	16.36	11.51
12.05	20.21	11.93	17.56	11.27	14.06	18.53	12.78	23.71	10.94
12.06	16.49	10.77	17.65	10.98	14.07	11.56	14.40	23.60	11.53
12.07	19.35	10.08	14.30	9.82	14.08	15.73	12.40	12.90	13.65
12.08	23.99	9.28	24.67	10.30	14.09*	13.50	13.00	20.31	11.35
12.09	20.65	10.41	20.05	11.31	14.10	21.07	12.29	26.58	8.23
12.10	17.63	9.82	13.51	10.43	14.11	17.77	13.19	18.59	10.89
12.11	21.91	9.66	22.23	11.75	14.12	18.00	14.24	17.87	12.43
12.12	24.67	7.81	26.03	9.41	14.13	21.53	11.82	26.01	9.96
12.13	17.73	11.48	22.35	11.53	14.14*	13.87	12.87	24.54	10.76
12.14	22.87	9.51	23.68	10.05	14.15*	13.50	13.00	12.94	13.40
12.15	26.93	9.64	23.78	10.11	14.16*	13.87	12.87	14.71	11.81

lipid a fish contains the higher is the amount missing. Therefore, the conclusion must be that the lipid extraction is not 100 % effective. If the missing part should be exclusively explained by a conversion factor higher than 6.25 it should be expected that the missing part would be lower the lower the protein content was. But from Fig. 14 it is seen that the opposite is the case.

Even that the amount of protein and lipid found by analysis is less than the theoretical amount (Fig. 14), the calculated energy content from: protein \times 5.65 kcal/g + lipid \times 9.45 kcal/g is a little higher than the observed values from bombing, or in other words: The conversion factors of 5.65 and/or 9.45 for protein and lipid, respectively are not correct.

The additional analyses carried out to determine the energetical content of fat and of FFDM – ash (fat free dry material – ash) gave as a result, (number of analyzed fish: 33):

	Range
<i>w</i> (wet weight):	0.4 -871.2 g
% dry matter:	16.36- 33.23
% ash (dry):	5.30- 15.03
% lipid (dry):	7.79- 37.82
Theoretical protein % = 100 % – (ash + lipid) %:	71.55 ± 1.42
(FFDM – ash) % dry:	68.94 ± 1.47
N % × 6.25 (dry):	68.72 ± 1.60
kcal/g FFDM (ash free) (dry) bombing:	5.45 ± 0.12
kcal/g lipid (dry) COD:	8.46 ± 0.21
kcal/g fish (dry) bombing:	5.57 ± 0.11
(Lipid × 8.46 + Theoretical protein × 5.45) kcal/g (dry):	5.42 ± 0.10
(Lipid × 8.46 + Theoretical protein × 5.65) kcal/g (dry):	5.56 ± 0.09
(Lipid × 9.45 + Theoretical protein × 5.45) kcal/g (dry):	5.62 ± 0.11
(Lipid × 9.45 + Theoretical protein × 5.65) kcal/g (dry):	5.76 ± 0.11

It is seen that using the factors 8.46 kcal/g lipid and 5.65 kcal/g protein gives a calculated energy content (5.56 ± 0.09) which is nearly the same as the value found by bombing (5.57 ± 0.11). This is in accordance with Craig (1977) and Craig, Kenley & Talling (1978) who for lipid by bombing found 8.49 kcal/g and who assumed that the theoretical 5.65 kcal/g is correct for protein. As the COD method gives nearly 100 % oxidation for fat, Maciolek (1962) and Rebsdorf & Therkildsen (1978) it is seen that there is agreement between the two values (8.46 and 8.49 kcal/g) found for lipid.

It can be mentioned that using the two factors 8.46 and 5.65 on the figures for proximate composition given in Rottiers & Tucker (1982) gives good agreement with their energy values found by bombing. Niimi (1972b) found 8.508 kcal/g lipid and 4.893 kcal/g ash free FFDM.

Finally, it can be mentioned that it will not help to consider NPN and carbohydrate when finding the energy content, because the energy content of the nitrogen extractives is not known.

On p. 111 it was suggested that the lipid extraction was not 100 % effective and therefore the more lipid a fish contained the higher was the missing part. If this is the case than the energetical value of the FFDM should be higher at a higher lipid content in the fish because of the lipid still present in the FFDM. This was examined for the 33 fish samples and the relationship between % lipid in the fish (dry) and kcal/g FFDM ash free can be expressed:

$$Y = 4.97 (\pm 0.344) + 0.02 (\pm 0.0183) X$$

where $X = \% \text{ lipid (dry)}$ and $Y = \text{kcal/g FFDM ash free}$. So this shows indeed that the higher the fat content of the fish is, the higher is the energetical value in the FFDM (ash free).

During the experimental period it was observed that the energetical content of a sample determined by the COD method divided with the energetical content from the bombing method of the same sample was less than unity and decreased with increasing energy content. A purely empirical relationship describes this course for 404 fish samples where both bombing and COD were carried out.

Energy (COD) = β_1 kcal + β_2 kcal², where kcal comes from the bombing method.

$$\frac{\text{g COD} \cdot 3.42 \text{ kcal/g}}{\text{Bombing kcal}} = 1.0924(\pm 0.0532) - 3.2148\text{E}-2(\pm 0.9343\text{E}-3) \cdot \text{kcal}$$

which as a 'rule-of-thumb' gives:

$$\text{energy (COD)} \sim 91 \% \text{ energy (bombing)}.$$

It is seen from the relationship between bombing and the COD method that the higher the energetical value is, the smaller is the kcal found by the COD method compared with the kcal found by bombing. This could appear to be contradictory to what is mentioned in 7.6.3. that the COD method is more efficient for fat than for nitrogen rich compounds. But our result could be explained by the fact that the total calories found by taking mg COD multiplied by a constant for nitrogen-containing samples do not compare directly with bomb calorimeter results, Maciolek (1962).

It is of interest to find the different body constituents, kcal/g and dry matter from as simple measurements as possible. The wet weight alone is not enough, it is also necessary to know f . Or said in another way: A fish that is starved to a wet weight of e.g. 100 g has not the same composition as a fish that is fed to a wet weight of 100 g, and a fish which has achieved the wet weight by getting, e.g. $f = 0.5$ has not the same composition as the fish that achieved the weight by getting, e.g. $f = 1$.

If wet weight and f are known the following relationship can be used to find kcal/g wet:

$$\text{kcal/g wet weight} = 1.1820(\pm 0.0341) + 0.2062(\pm 0.0580)f + 1.1253\text{E}-3(\pm 1.5846\text{E}-4)w(n)$$

where f = feeding level and $w(n)$ = wet weight in g. Number of observations = 202.

To find kcal/g dry weight the following relationship can be used (the same observations as above):

$$\text{kcal/g dry weight} = 5.2913(\pm 0.0735) + 0.4143(\pm 0.1251)f + 1.6541\text{E}-3(\pm 3.415\text{E}-4)w(n)$$

where f = feeding level and $w(n)$ = wet weight in g.

If the previous history i.e. the feeding level of the fish not is known, the kcal/g dry weight can be found from the relative simple determination of dry weight in the following way:

$$\text{kcal/g dry weight} = 3.0051(\pm 0.4366) + 10.4634(\pm 1.9054) \frac{\% \text{ dry matter}}{100} + 8.1502\text{E}-4(\pm 6.28\text{E}-4)w$$

where w = dry weight in g. Number of observations = 404.

Even more simple than the determination of dry matter is to measure the length of the fish. From this the condition factor $k = w/L^3$ can be found. If this figure together with the wet weight is known, kcal/g wet weight can be found from the following expression:

$$\text{kcal/g wet weight} = 1.3171 \left(\begin{matrix} -0.0160 \\ +0.0353 \end{matrix} \right) k^{0.78(\pm 0.21)}$$

where k = condition factor. Number of observations = 157.

Table 12a-d. Stomach content in per cent. Fish were fed *ad libitum* for two days until $t = 0$, where feeding ceased.

a. 5°C.						c. 15°C.				
Time (hours)	Wet weight of fish, g					Time (hours)	Wet weight of fish, g			
	12.3	23.4	36.7	48.3	66.9		5.2	14.6	40.6	66.4
0	100	100	100	100	100	0	100	100	100	100
22	67.18	78.25	70.45	59.92	81.38	6	98.88	78.66	88.06	93.70
44	43.32	56.82	54.10	75.23	44.24	12	71.99	55.35	59.50	49.61
66	20.92	38.64	45.96	21.99	19.98	18	29.69	44.47	34.25	34.59
91	35.00	10.22	17.33	17.32	10.01	24.5	41.29	26.03	38.61	29.77
116	11.85	10.04	6.38	5.40	11.45	36	27.20	23.26	15.02	18.35
140	4.72	4.63	11.43	8.56	13.82	43.5	10.60	15.77	10.83	14.40
167.5	2.61	2.65	5.21	2.57	2.13	51	17.94	13.15	18.93	5.50
190	1.43	3.27	1.29	2.08	1.43	60	8.86	10.41	4.45	9.31
213	1.56	0.17	1.43	1.75	—	68	4.69	4.50	5.37	9.35
						75	5.89	2.56	1.95	5.53
						84	3.42	1.55	0.64	2.91
						92	0.99	1.65	2.05	2.06
						98.5	1.87	0.88	1.42	1.39
						109.5	0.61	—	—	—
b. 10°C.						d. 20°C.				
Time (hours)	Wet weight of fish, g					Time (hours)	Wet weight of fish, g			
	11.6	22.3	27.5	46.1	71.7		3.9	10.3	30.5	78.8
0	100	100	100	100	100	0	100	100	100	100
9	70.39	61.20	91.19	83.19	70.87	4	—	83.42	85.61	48.47
18	48.57	46.96	68.47	38.48	45.72	8	78.26	63.11	78.91	91.69
28.5	42.88	38.83	54.21	40.62	40.28	12	42.61	51.77	37.69	—
44.5	32.43	12.48	16.59	11.41	42.84	16	43.14	27.04	24.04	36.16
52.5	30.10	18.79	10.88	12.50	14.39	20	34.45	37.12	35.06	24.80
66.5	11.09	15.71	9.42	10.15	7.60	24	24.30	22.83	19.87	—
79	14.31	6.35	7.37	8.84	6.93	28	18.47	27.93	16.13	20.09
91	7.80	7.03	4.79	7.26	3.76	32	21.45	23.56	—	11.87
102	8.80	2.77	4.99	4.56	5.57	36	11.92	18.27	13.92	7.74
114.5	3.52	2.51	9.09	4.34	7.73	44	4.68	9.01	7.03	8.43
127	2.86	3.20	3.66	1.03	5.50	52	2.63	3.86	4.90	2.78
140	1.59	1.37	3.79	3.01	2.86	60	—	3.38	—	—
152	—	—	1.99	1.40	0.02	68	—	2.10	—	—

Table 13a & b. 20°C. Stomach content in per cent. Fish fed $f = 1.00$ and $f = 0.55$ for three days until $t = 0$, where feeding ceased.

a. Method 1.			b. Method 2		
Time (hours)	Wet weight 29.5 g $f = 1.00$	Wet weight 28.3 g $f = 0.55$	Time (hours)	Wet weight 29.5 g $f = 1.00$	Wet weight 28.3 g $f = 0.55$
0	100	100	0	100	100
4	66.22	62.60	4	60.60	44.54
8	43.69	17.79	8	38.78	15.05
12	36.91	14.85	12	31.91	18.82
16	25.70	6.52	16	18.47	9.70
20	15.73	6.41	20	8.32	3.16
24	10.74	3.40	24	6.66	3.03
28	12.32	11.87	28	2.82	1.23
32	9.76	0.68	32	2.14	1.16
36	9.11	3.78	36	1.28	1.51
40	4.65	1.16	40	0.68	0.97

To find kcal/g dry weight (from the same observations) the following equation is used:

$$\text{kcal/g dry weight} = 5.4707 \left(\begin{matrix} -0.5288 \\ +0.5848 \end{matrix} \right) k^{0.29(\pm 0.10)}$$

where k = condition factor.

If the % of dry matter is known, the percentages of crude protein (total N \times 6.25), lipid, and ash can be found from Fig. 12. Fig. 13 shows the relationship between kcal/g wet weight and percentage of water for the same analytical data as in Fig. 12. All the other experimental data where lipid were not determined fit into the presented limited number of data.

8.8. Gastric evacuation

Table 12 gives the stomach content as per cent of the first content for time $t = 0$, and as a function of time t for the experimental temperatures and fish sizes in experiment 1. The results from experiment 2 are given in Table 13.

There is no immediate cognition that the relative decrease of stomach content should be dependent on fish size.

But, this possible dependence on stomach evacuation rate on fish size has been included in the model and the hypothesis has been tested by analysis of variance. In all conditions (i.e. the three models (24), (25), (26) with four temperatures and a total of 18 different fish sizes) the F -ratios did not exceed the F ($f_1, f_2, 1 - \alpha$, $\alpha = 0.05$) distribution. It was therefore concluded that possibly there was no dependence on relative stomach evacuation rates on body weight.

8.8.1. Experiment 1

All the experimental data have been incorporated in the mentioned 'stomach evacuation models' (24), (25), (26) and the estimated parameters without any fish size dependence are presented in Tables 14, 15, 16.

In all cases the 'square root model' (26) describes least satisfactorily the relationship between model and experimental data. The 'exponential model' (24) has the inherent weakness that theoretically the stomach content approaches to zero at infinite time whereas the 'recti-linear model' (25) with the present experimental data is far from 100% at $t = 0$.

The 'exponential model' fits the data very well in most instances, at least during the phase of effective digestion, in which about 90% of the original food portion is evacuated from the stomach.

In most instances it is not profitable to reduce the evacuation models to a course with start exactly at 100%, i.e. the known stomach content at $t = 0$, as the residual error variance increases considerably. Because this increase is least for the exponential evacuation model this model has been chosen as the best.

As an example the results from 15°C are presented in Figs 15, 16, and 17 together with experimental data and calculated lines of regressions for all three evacuation models. Though the residuals deviate more systematically for the 'recti-linear' and 'square-root models' all three models predict e.g., the duration of evacuation to 5% of the original content to app. 65 hours.

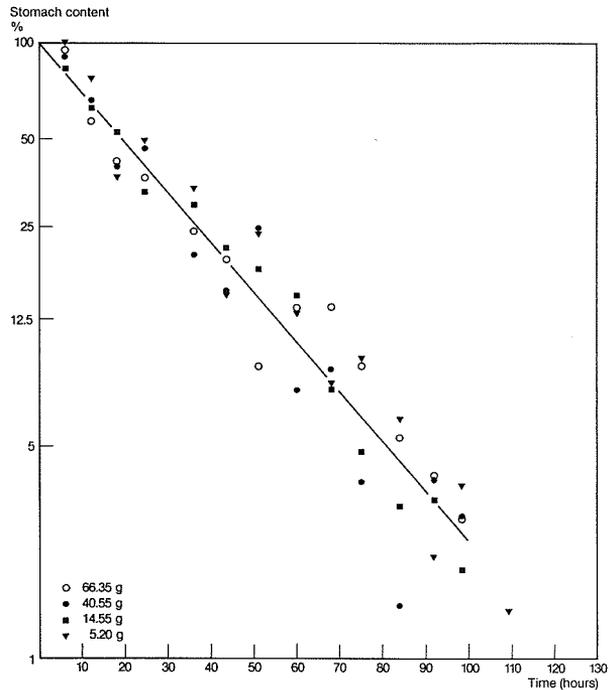


Fig. 15. Exponential gastric evacuation according to (23) at 15°C.

	Parameter	Estimate	R ²	N
5°C	log V ₀	4.7785 (±0.2316)	0.92	49
	a ₁	0.0220 (±0.0019)		
	a ₂	0.0208 (±0.0011)	0.90	44
10°C	log V ₀	4.4745 (±0.2812)	0.82	68
	a ₁	0.0288 (±0.0033)		
	a ₂	0.0301 (±0.0019)	0.82	63
15°C	log V ₀	4.6197 (±1690)	0.95	57
	a ₁	0.0448 (±0.0029)		
	a ₂	0.0446 (±0.0016)	0.95	53
20°C	log V ₀	4.6117 (±0.1350)	0.94	46
	a ₁	0.0601 (±0.0044)		
	a ₂	0.0607 (±0.0029)	0.94	42

Table 14. Parameters in the exponential model (23):
 $V_t = V_0 \exp(-a_1 t)$;
 $V_t = 100 \exp(-a_2 t)$.

	Parameter	Estimate	R ²	N
5°C	V ₀ ^{1/3}	4.5249 (±0.2286)	0.89	49
	a	0.0181 (±0.0019)		
10°C	V ₀ ^{1/3}	4.0612 (±0.1785)	0.87	68
	a	0.0220 (±0.0021)		
15°C	V ₀ ^{1/3}	4.2367 (±0.1548)	0.93	57
	a	0.0350 (±0.0026)		
20°C	V ₀ ^{1/3}	4.3422 (±0.1617)	0.92	46
	a	0.0543 (±0.0053)		

Table 15. Parameters in the rectangular model (24): $V_t^{1/3} = V_0^{1/3} - at$.

	Parameter	Estimate	R ²	N
5°C	V ₀ ^{1/2}	8.9620 (±0.5047)	0.90	49
	a	0.0425 (±0.0041)		
10°C	V ₀ ^{1/2}	8.0615 (±0.4974)	0.84	49
	a	0.0538 (±0.0059)		
15°C	V ₀ ^{1/2}	8.4769 (±0.4769)	0.89	57
	a	0.0846 (±0.0081)		
20°C	V ₀ ^{1/2}	8.8637 (±0.4684)	0.88	46
	a	0.1386 (±0.0153)		

Table 16. Parameters in the square-root model (25): $V_t^{1/2} = V_0^{1/2} - at$.

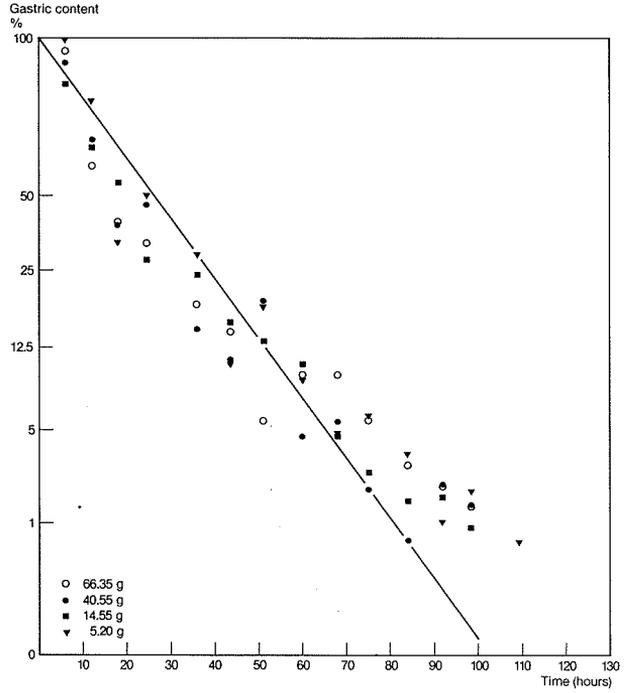


Fig. 16. Rectilinear gastric evacuation according to (24) at 15°C.

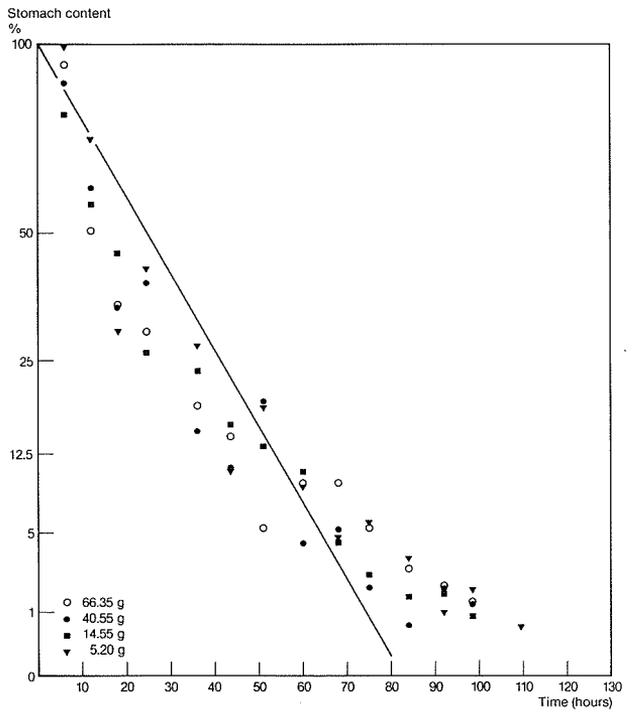


Fig. 17. Square root evacuation according to (25) at 15°C.

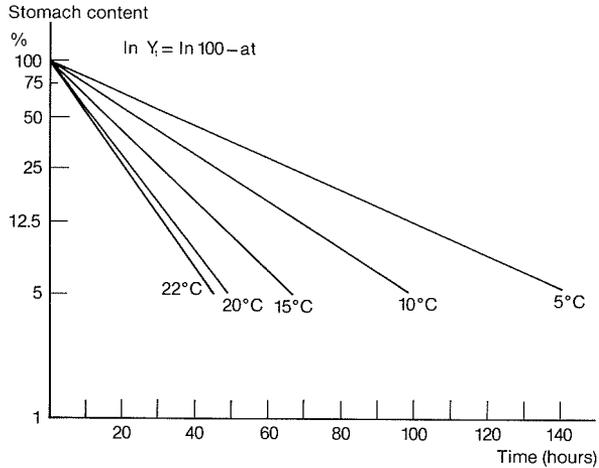


Fig. 18. Calculated regressions for the 'exponential evacuation model' at 5, 10, 15, 20, and 22°C.

In Fig. 18 the calculated regressions at all four experimental temperatures for the 'exponential evacuation model' together with a single experiment with fish size about 36 g at 22°C are presented. The data might indicate that the relationship between temperature T and the constant a with the presented type of food and temperature regime can be described as:

$$a = 0.0057 T^{0.7639}, R^2 = 0.97$$

so that (23) can be expanded to:

$$V_t = V_0 \cdot \exp(-0.0057 \cdot T^{0.76} \cdot t)$$

or with actual stomach content depending of body size 'incorporated'.

$$(\text{actual stomach content})_t = \text{Ration} \cdot \exp(-0.0057 \cdot T^{0.76} \cdot t)$$

8.8.2. Experiment 2

The results are presented in Table 12. Table 17 shows that, disregarding the data from the experiment for $f=1$ with method 1, the values of the instantaneous coefficient a not are statistically different from each other at the different tempera-

Table 17. Parameters in $V_t = 100 \exp(-a_2 t)$ and $T = 20^\circ\text{C}$, Method 1 & 2.

		Para- meter	Estimate	R ²	N
Method 1	$f = 1$	a_2	0.0851(±0.0062)	1.00	10
	$f = 0.55$	a_2	0.1375(±0.0218)	0.94	10
Method 2	$f = 1$	a_2	0.1175(±0.0090)	1.00	10
	$f = 0.55$	a_2	0.1573(±0.0151)	0.98	10

tures. Therefore it is reasonable to conclude that the specimen does not adapt to a special value of the constant a during for example a feeding level experiment.

The relative lower rate of stomach evacuation for $f = 1$ using method 1 might be explained in the following way: The stomachs in method 2 are not completely emptied and thus the contents are underestimated. This is also suggested by the fact that when the content is determined to zero, the weight of the empty stomach is surprisingly high.

Further, in method 1 the problem is to decide when the stomach is empty. It is easy to increase arbitrary the time of the experiment in excess of the time it takes to empty the stomach. In this way the weight of the empty stomach will be too low because a starving catabolism has occurred. In this way the weight of the empty stomach will be underestimated and thereby the stomach content will be overestimated and in this way the gastric evacuation rate will be too slow.

From the results it is concluded that gastric evacuation rates determined by emptying the stomach and then analyse the content are too high.

8.8.3. *Use of evacuation model*

The results from the evacuation experiments can be tested on the feeding experiments. The experiments at 5°C were performed during about one month. The rations for each day are presented in Fig. 19. Three different aquaria with approximately the same start weight but different feeding levels are showed. The fig. gives the actual rations given each day per aquarium with the calculated stomach content. The calculations have been done under the assumption that the daily ration at $f = 1$ is consumed during a single meal.

The assumption slightly overestimates the calculated stomach content compared with the actual stomach content because feeding several times per day at $f = 1$ makes the actual amount of evacuated food as high as possible so that the actual stomach content is lower and vice versa. Nevertheless, it can be seen from the figure that the fish eat relatively much in the start at $f = 1$ and thereafter the daily ration decreases for a couple of days after which the food intake oscillates strongly around the mean ration.

Contrary to this the calculated stomach content stabilizes to a higher degree around a slight trend of increase accompanying the increase in body size (and stomach size). During the period between the last ration and weighing of the fish the stomach content decreases very quickly to a level app. 5% of the original stomach content. This last figure can be calculated to be an approximate amount present in the stomach at weighing after each experiment. The feeding level fish on the other hand are much more stabilized in their stomach content which rises in accordance with an increase in stomach capacity which depends on fish size.

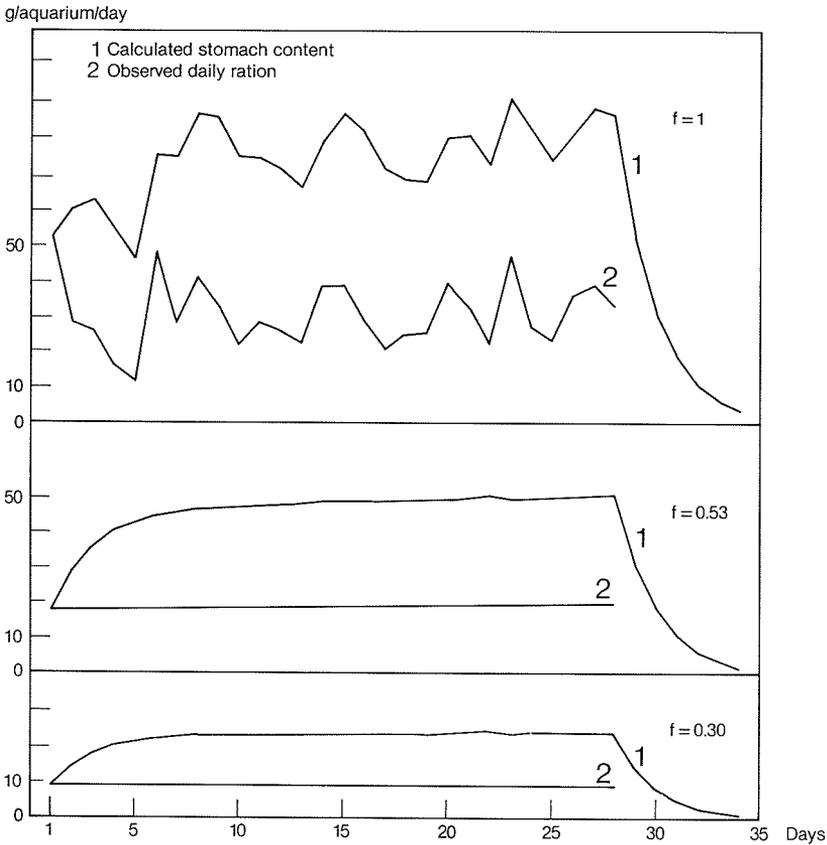


Fig. 19. Daily ration and calculated stomach content for three aquaria given three different feeding levels at 5°C.

8.9. Efficiency of growth, yolk sac fry experiments

8.9.1. Experiment 1

The results are given in Table 18. Figs 20-23 show the development of alevin.

The gross conversion efficiency $K_1 = K_2$ (cf. remarks in 6) is found by dividing the increase in energy of the embryo by the decrease in yolk sac, i.e.

$$K_1 = \frac{\text{embryo}(t=n) - \text{embryo}(t=0)}{\text{yolk sac}(t=0)} \times 100\%,$$

where embryo and yolk sac ($t=0$ & n) are dry weight or mg oxygen used in the COD of the embryos and yolk sacs at time of hatching and complete absorption of the yolk sac, respectively. K_1 is given in Table 19.

The values of K_1 suggest that gross efficiency grows with temperature up to a maximum and then decreases. If this is true then it is in accordance with Marr (1966) and Ryland & Nichols (1967).

Table 18. Development of alevin at 9.3, 11.4, 14.0, and 17.9°C.

Temperature	Time in hours	Wet weight of embryo in mg	Dry weight of embryo in mg	mg COD in embryo	Wet weight of yolk sac in mg	Dry weight of yolk sac in mg	mg COD in yolk sac	mg COD in alevin
9.3°C	0	25.6	4.7	7.34	46.1	17.1	28.64	35.98
	52.5	41.7	6.9	10.56	44.3	15.9	26.46	37.02
	167	85.1	9.7	15.58	36.2	10.5	17.16	32.74
	190	62.4	10.2	16.44	30.7	11.4	19.47	35.91
	406	102.9	15.3	22.79	18.0	5.6	9.72	32.51
	501.5	102.4	16.2	24.80	8.3	2.0	3.56	28.36
	622.25	127.1	17.4	26.82	0	0	0	26.82
11.4°C	0	25.6	4.7	7.34	46.1	17.1	28.64	35.98
	47.5	43.6	6.1	10.15	45.9	16.1	27.13	37.28
	190	72.7	12.7	21.33	22.1	8.3	15.38	36.71
	243.5	90.7	12.6	19.16	18.9	7.1	15.23	34.39
	308.5	119.6	15.5	23.6	17.6	5.1	8.95	32.55
	412.8	111.2	16.4	24.56	8.0	1.4	2.50	27.06
	501.5	124.3	17.7	27.06	0	0	0	27.06
622.25	101.6	15.1	21.52	0	0	0	21.52	
14.0°C	0	25.6	4.7	7.34	46.1	17.1	28.64	35.98
	26	33.3	6.8	11.08	39.8	15.9	27.32	38.41
	47.5	48.2	6.1	9.50	48.5	16.5	27.82	37.32
	97.5	56.1	8.4	13.28	39.8	13.8	23.97	37.25
	190	86.4	14.9	22.84	14.8	5.7	9.47	32.31
	243.5	105.7	16.9	26.51	10.9	3.4	5.95	32.46
	308.5	129.7	16.8	25.65	8.2	1.9	3.45	29.10
412.8	128.3	18.0	27.86	0	0	0	27.86	
501.5	96.5	15.0	22.99	0	0	0	22.99	
17.9°C	0	25.6	4.7	7.34	46.1	17.1	28.64	35.98
	26	36.4	6.8	10.85	38.9	14.8	24.42	35.27
	52.5	44.3	7.4	11.82	37.3	14.1	24.82	36.64
	95.7	67.1	9.0	13.96	38.8	12.5	21.65	35.61
	142.5	67.3	11.2	17.29	28.6	6.9	11.59	28.88
	190	94.0	14.5	21.17	13.1	4.4	7.40	28.57
	243.5	100.8	16.6	25.29	10.0	2.0	3.31	28.60
308.5		17.4	25.42	0	0	0	25.42	
412.8		11.7	16.04	0	0	0	16.04	

Temp. °C	K ₁ per cent	
	Energy	Dry weight
9.3	68	74
11.4	69	76
14.0	72	78
17.9	63	74

Table 19. K₁ on energy and dry weight basis.

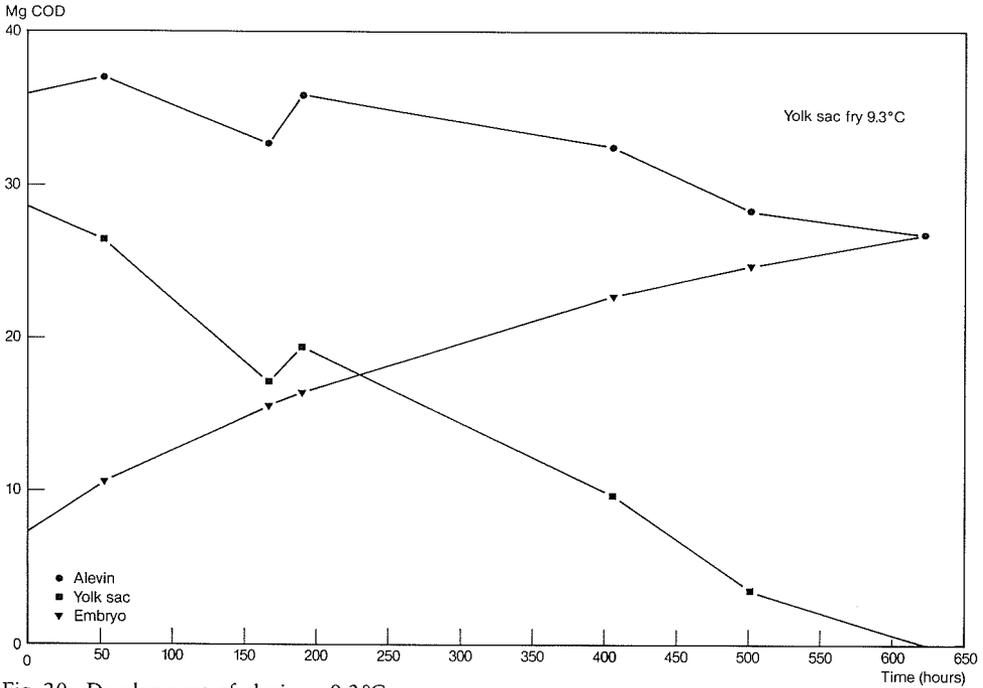


Fig. 20. Development of alevin at 9.3°C.

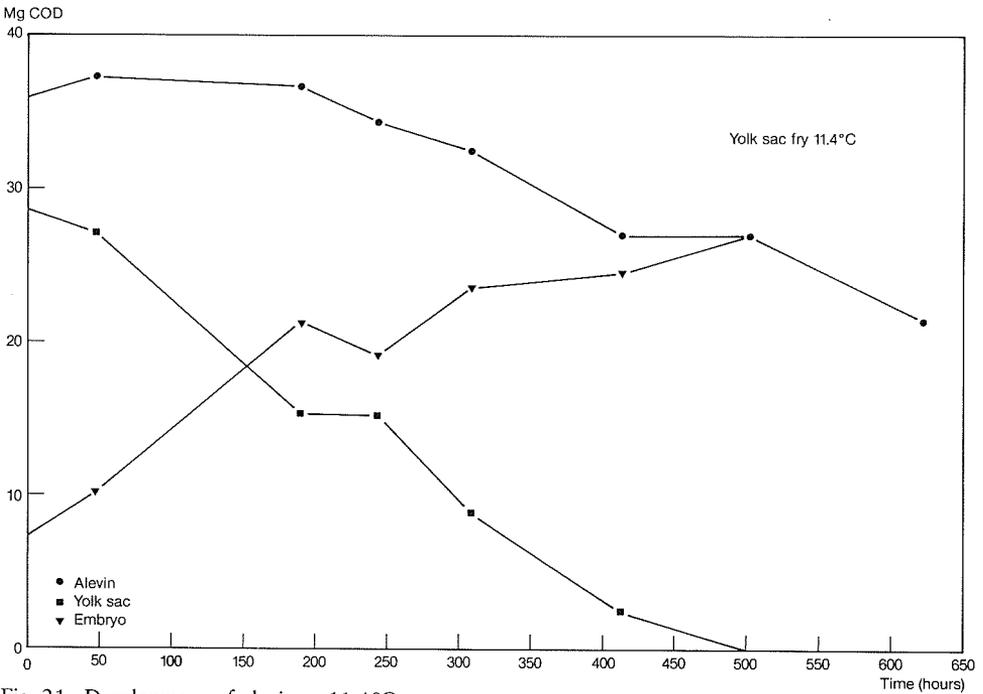


Fig. 21. Development of alevin at 11.4°C.

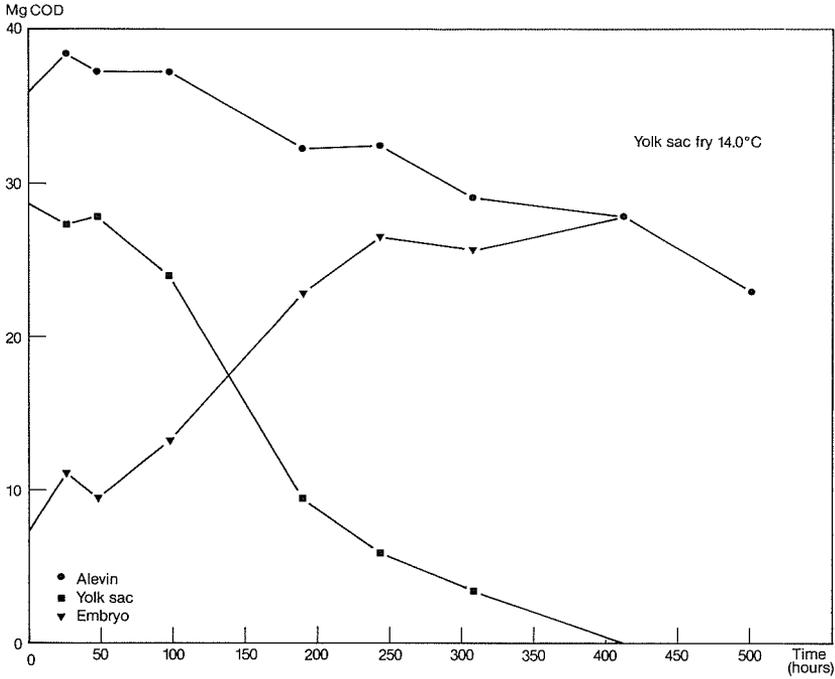


Fig. 22. Development of alevin at 14.0°C.

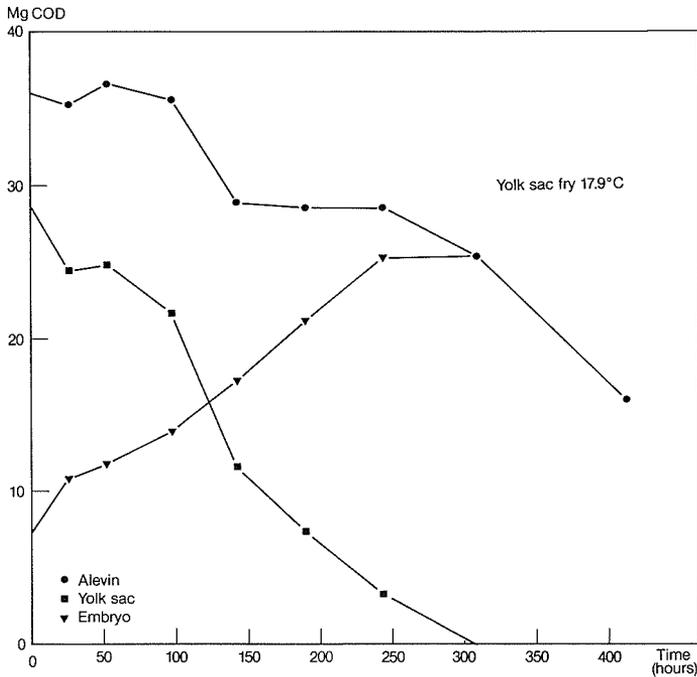


Fig. 23. Development of alevin at 17.9°C.

8.9.2. *Experiment 2*

The results are given in Table 20.

Table 20. Gross efficiency in eggs and alevins.

Temperature °C	COD in mg					K ₁ in %	
	At fertilization eggs	Eyed ova eggs	At hatching		At complete yolk absorption alevin	For eggs	For alevin
			Embryos	Yolk sac			
9.5	40.11	39.60	7.72	31.79	30.62	93	72
14.5	40.11	40.37	9.65	29.74	29.64	93	67

Gross efficiency for eggs is found from:

$$K_1 = \frac{\text{Embryo at hatching}}{\text{Eggs at fertilization} - \text{yolk sac at hatching}}$$

where the different figures are measured as mg COD.

K₁ for alevins is found as in experiment 1.

From the experiment it is possible to compare K₁ for two different stages of the development: from fertilization to hatching and in the course of yolk absorption. The results have not been pooled with the data for experiment 1, because experiment 2 only is carried out for two temperatures. But it is seen that the value from experiment 2 is in reasonable agreement with experiment 1. It is seen that K₁ for eggs is 0.93. As

$$K_1 = 1 - \left(A + \frac{\text{Fasting catabolism}}{\text{Eggs at fertilization} - \text{eggs at hatching}} \right) = 1 - \text{loss},$$

it can be deduced that the loss of eggs is very low compared with the loss of alevin.

If the fasting catabolism of the alevin was known A could be found from: $K_1 = 1 - (A + (\text{fasting catabolism}/\text{yolk sac at hatching}))$. But, as it not with the present technique is possible to measure the fasting catabolism for yolk sac fry (they are never starving as they constantly are feeding on the yolk sac), it would be enchanting to assume that the fasting catabolism in yolk sac fry can be put equal to the fasting catabolism for bigger fish, as found from the other experiments. Indeed, this was done but gave as result that the final weight of the alevin with completely absorbed yolk contained more energy than yolk + embryo at hatching. The conclusion must be that yolk sac fry has a considerable less starving catabolism than bigger fish. The question now arises: For how small fish is the fasting catabolism found in the other starving experiments valid? In experiment 1 at 11.4, 14.0, and 17.9°C the measurements were carried on after complete absorption of the yolk. If we calculate the weight of the alevin at the final observation from the weight in the last but one observation by means of the values for $k(T)$ found in the experiments for bigger fish, we can compare these values with the observed. The mean weights

are: 11.4°C, calculated 20.74 mg COD, observed 21.52 mg COD, 14.0°C, calculated 21.75 mg COD, observed 22.99 mg COD, and 17.9°C, calculated 16.64 mg COD, observed 16.04 mg COD. These sparse observations suggest that yolk sac fry have a considerably less starving catabolism than metamorphosed fish, and that it is just at metamorphosation that the drastic raise in starving catabolism occurs. Further, the starving catabolism for newly metamorphosed fish can be described by the same value of $k(T)$ as for bigger fish (at least up to 250 g wet weight).

The values for K_1 can be compared with values from other investigations on salmonids. Smith (1946) determined energy values in embryo and yolk sac for rainbow trout at 10°C. From his table 4 gross efficiency based on *energy* is found to be 44%. (It is assumed that the correct value in Smith's column 6 should be 8316 and not 9316 as stated in his table.).

Still from table 4 in Smith (1946) the following K_1 (10°C) based on *dry weight* is found: 53%. Also based on *dry weight* fig. 3 in Hayes & Pelluet (1945) gives the following values for Atlantic salmon:

K_1 (9.3°C): 49 %
 K_1 (11.4°C): 52 %
 K_1 (14.0°C): 56 %

For brown trout Gray (1926) found based on *dry weight* K_1 (10°C) = 63%. Also for brown trout Wood (1932) finds based on *dry weight*:

K_1 (3°C) = 54 %
 K_1 (7°C) = K_1 (12°C) = 63 %.

As pointed out by Marr (1966) it is difficult to compare the results of different authors because they measure the K_1 for different stages in the development from fertilization to complete yolk absorption. Marr considered the gross efficiency of growth between the 15 and 80 per cent stages of development. Stage of development he defines as (dry weight of embryo/dry weight of alevin) × 100%. He has calculated the gross efficiency between 15 and 80% stages of development for Gray (1926) and Smith (1946) and finds based on *dry weight*:

Gray (1926): K_1 = 71% for brown trout reared at 10°C.
 Smith (1946): K_1 = 68% for rainbow trout reared at 10°C.
 Marr (1966): K_1 = 70% for Atlantic salmon reared at 10°C.

Temp. °C	K_1 per cent	
	Energy	Dry weight
9.3	74	84
11.4	75	85
14.0	84	89
17.9	68	78

Table 21. K_1 between 20 and 80% stages of development.

In the present study it is from Table 18 seen that the stage of development at hatching is 20% based on energy and 22% based on dry weight. By interpolating in the tables the Table 21 can be set up.

9. Comparative experiments

9.1. Experiments with moist contra dry pellets

In order to reveal whether the growth equation found with moist pellets also was valid with other types of food (calculated on energy basis), comparative experiments with moist and dry pellets were carried out. The amount of energy in fish and food was found by the COD method. The results are shown in Table 22. From the experiments with $f = 1$, $h(T)$ was found for moist and dry pellets respectively at 10.0, 15.0, and 20.0°C. The – in this way – found three pairs of $h(T)$ were compared, and there was no difference. A students t -test gave $t = -1.03$, degrees of freedom = 4. With the value of $h(T)$ found, the feeding levels were calculated for the other experiments. The start weight ($w(0)$) was inserted in the growth equation with the parameter values found from (3') and the calculated values for final

Table 22. Comparison between observed and calculated growth with dry and moist pellets as food.

	Temp. °C	f	Δt day	$w(o)$ g COD	$w(n)$ obs. g COD	$w(n)$ calc. g COD	Diff. %	Number of fish
D.P.	10.0	0.08	16	12.469	11.167	11.069	0.9	40
	10.0	0.15	16	12.453	12.250	11.843	3.3	40
	10.0	0.22	16	12.312	12.471	12.515	-0.4	40
	10.0	0.29	16	12.442	13.179	13.386	-1.6	40
	10.0	1.00	16	12.253	18.421	18.924	-2.7	40
M.P.	10.0	1.00	16	12.445	17.591	19.188	-9.1	40
D.P.	15.0	0.23	10	15.374	15.095	15.426	-2.2	27
	15.0	0.45	10	15.366	17.686	17.784	-0.6	27
	15.0	0.67	10	15.294	19.573	19.784	-1.1	27
	15.0	1.00	10	15.308	21.930	22.021	-0.4	27
M.P.	15.0	1.00	10	15.454	22.888	22.212	3.0	27
D.P.	20.0	0.16	8	8.876	8.589	8.184	4.7	25
	20.0	0.29	8	8.972	10.380	9.439	9.1	25
	20.0	0.46	8	8.908	11.142	10.795	5.4	25
	20.0	1.00	8	8.972	14.036	14.190	-1.1	25
M.P.	20.0	1.00	8	8.858	14.392	14.028	2.5	25

Number of obs = 16 Residual error variance = 0.3275
Mean difference = 0.61% D.P. = Dry pellets
Mean $w(n)$ observed = 15.07 g COD M.P. = Moist pellets
Mean $w(n)$ calculated = 15.05 g COD

weight ($w(n)$) were compared with the observed values. From the table it is seen that the growth equation found by means of moist pellets predicts the values for $w(n)$ achieved with dry pellets as food. Or said in other words: The parameter values (from (3')) in the growth equation are valid for the two different kinds of food (on energy basis). The moist pellets used had 63.36% dry matter and 5.93 kcal/g dry weight and dry pellets had 91.92% dry matter and 5.37 kcal/g dry weight. I.e. 1 g dry pellets corresponds to 1.31 g moist pellets in energy.

9.2. Comparison with brown and brook trout

Besides the experiments with rainbow trout some sparse feeding experiments with brown trout and brook trout were performed during the investigation.

There was used domesticated fish of the two species, and they were fed with moist pellets at $f = 1$, and there was one fish ($n = 1$) in each aquarium. The fish were fed in a temperature regime from 15.0 to 21.8°C. The total number of aquaria were 15 for brown trout and 16 for brook trout.

The observations were fitted to second degrees polynomia. The calculated curve of the feeding rate of a 100 g fish is shown in Fig. 24. This calculated curve can be compared with the feeding rate for rainbow trout of same size for $n = 1$ (single fish) and $n > 1$ (several fish) respectively.

The curves on Fig. 24 suggest that the optimum temperature for brown and brook trout is about 17.5°C which is a little higher than the optimum found for brown trout from Pentelow's and Elliott's data (see 9.3). But the difference can probably be ascribed to random error.

However, it can be read from the figure that rainbow trout eat app. 25 % more than the two other species, and have a maximum about 20°C.

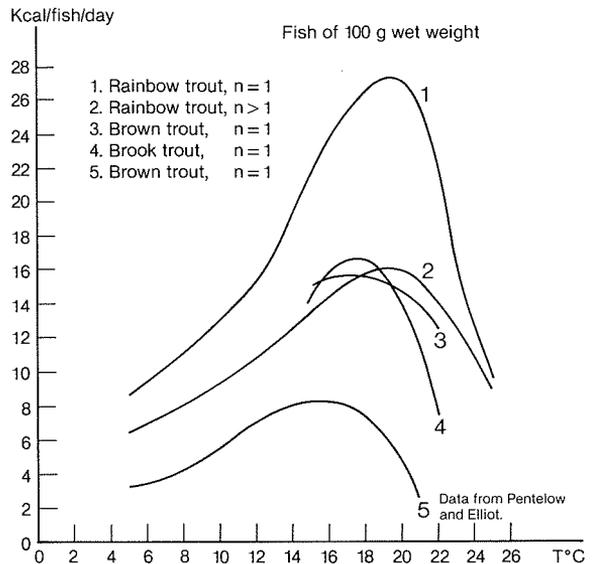


Fig. 24. The maximum daily kcal intake for a fish of 100 g wet weight. Curves 1-4: present study. Curve 5: Data from Pentelow and Elliott.

9.3. Comparison with Pentelow and Elliott

The experiments with moist contra dry pellets, 9.1., Grove, Loizides & Nott (1978), and Bromley & Smart (1981) show that fish compensate for a food with lower energetical value by eating more in grammes. However, the difference in food in these studies has been minor both in respect to chemical composition and energetical value. It could be stated that this compensation only is possible up to a certain difference in food compositions. Pentelow (1939) and Elliott (1975a) describe maximum feeding experiments ($f = 1$) with single fish per aquarium ($n = 1$) for brown trout fed *Gammarus pulex* (Linné, 1758). Elliott (1972) finds the dry matter to be app. 24% and Elliott (1976c) states that the energetical content is about 4.4 kcal/g dry weight for *Gammarus*. The composition of moist pellets can be seen in Table 1.

Comparison between the food intake of brown trout fed moist pellets in the present study was made with the food intake of brown trout fed *Gammarus* by Pentelow and Elliott. This comparison makes it possible to see if the fish are able to ingest the same amount of energy, when they are fed food types with very different composition.

Pentelow's and Elliott's data are fitted to (3'') and the feeding rate for a 100 g fish is shown as curve 5 in Fig. 24. The food intake for brown trout increases with the temperature and reach a maximum about 15-16°C in accordance with the results in Elliott (1975a), and the food intake ceases at app. 21°C. Curve 3 and 5 show that the feeding rates are different when the fish are fed so different food types as moist pellets and *Gammarus* sp.

10. References

- Adair, G.S. & M.E. Robinson, 1930: The specific refraction increments of serum-albumin and serum-globulin. – *Biochem. J.* 24: 993-1010.
- Adelman, I.R. & L.L. Smith, 1970: Effect of oxygen on growth and food conversion efficiency of northern pike. – *Prog. Fish Cult.* 32: 93-96.
- Andersen, K.P. & P.Sparre, 1975: User's manual. Linear regression analysis applied to the model $Z = \gamma V^\beta$. – Danish Institute for Fisheries and Marine Research. Mimeogr.
- Andersen, K.P. & E. Ursin, 1977: A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. – *Meddr. Danm. Fisk.- og Havunders.* N.S. 7: 319-435.
- Anderson, R.O., 1959: The influence of season and temperature on growth of the bluegill, *Lepomis macrochirus* (Rafinesque). – Ph.D. Thesis, Univ. of Michigan, Ann. Arbor.
- Andrews, J.W., T. Murai & G. Gibbons, 1973: The influence of dissolved oxygen on the growth of channel catfish. – *Trans Amer. Fish. Soc.* 102(4): 835-838.
- Anon., 1973: Limnologisk metodik (Limnological methodology) (In Danish). – Freshwater Laboratory, University of Copenhagen, Akademisk Forlag.
- Anon., 1979: Determination of Kjeldahl nitrogen content by using the Kjeltex system I. – In: Tecator Manual.
- Atherton, W.D. & A. Aitken, 1970: Growth, nitrogen metabolism and fat metabolism in *Salmo gairdneri* Rich. – *Comp. Biochem. Physiol.* 36: 719-747.
- Averett, R., 1969: Influence of temperature on energy and material utilization by juvenile coho salmon. – Ph. D. Thesis, Oregon State University, Corvallis Oregon.

- Bailey, K., 1937: Composition of the myosins and myogen of skeletal muscle. – *Biochem. J.* 31: 1406-1413.
- Baldwin, N.S., 1956: Food consumption and growth of brook trout at different temperatures. – *Trans. Amer. Fish. Soc.* 86: 323-328.
- Barrington, E.J.W., 1957: The alimentary canal and digestion. – In: M.E. Brown (ed.): *The physiology of fishes*. Vol. 1, pp.109-161. Academic Press.
- Beamish, F.W.H., 1971: Ration size and digestion in largemouth bass, *Micropterus salmoides* Lacépède. – *Can. J. Zool.* 50: 153-164.
- Beamish, F.W.H., A.J. Niimi & P.F.K.P. Lett, 1975: Bioenergetics of teleost fishes: Environmental influences. – In L. Bolis, H.P. Maddrell & K. Schmidt-Nielsen (eds): *Comparative Physiology - Functional Aspects of Structural Materials*, pp.187-209. North Holland Publishing Company, Amsterdam.
- Beauchamp, J.J. & J.S. Olson, 1973: Corrections for bias in regression estimates after logarithmic transformation. – *Ecology* 54(6): 1403-1407.
- Bertalanffy, von L., 1957: Quantitative laws in metabolism and growth. – *Quarter. Rev. Biol.* 32(3): 217-231.
- Beverton, R.J.H. & S.J. Holt, 1957: On the dynamics of exploited fish populations. – *Fishery Invest.*, Lond. Ser. II Vol. XX.
- Birkett, L., 1969: The nitrogen balance in plaice, sole and perch. – *J. Exp. Biol.* 50: 375-386.
- Björklund, R.G., 1958: The biological function of the thyroid and the effect of length of day on growth and maturation of goldfish, *Carassius auratus* Linn. – Ph. D. Thesis, Univ. of Michigan, Ann. Arbor.
- Black, E.C., 1958: Energy stores and metabolism in relation to muscular activity in fishes. – In P.A. Larkin (ed.): *The investigation of Fish-Power Problems*. H.R. MacMillan lectures in fisheries, Univ. of British Columbia, Vancouver, B.C.
- Block, J.R., 1959: The approximate amino acid composition of wild and hatchery trout (*Salvelinus fontinalis*) and some of their principal foods (*Gammarus* and *Hexagenia bilineata*). – *Contr. Boyce Thomson Inst. Pl. Pes.* 20: 103-105.
- Boëtius, I. & J. Boëtius, 1980: Experimental maturation of female silver eels, *Anguilla anguilla*. Estimates of fecundity and energy reserves for migration and spawning. – *Dana* 1: 1-28.
- Brafield, A.E. & D.J. Solomon, 1972: Oxy-calorific coefficients for animals respiring nitrogenous substrates. – *Comp. Biochem. Physiol.* 43A: 837-841.
- Brett, J.R., 1979: Environmental factors and growth. – In W.S. Hoar, D.J. Randall & J.R. Brett (eds): *Fish Physiology* Vol. VIII, Bioenergetics and Growth, pp. 599-675. Academic Press.
- 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): 2353-2394.
- Brett, J.R. & J.E. Shelbourn, 1975: Growth rate of young sockeye salmon, *Oncorhynchus nerka*, in relation to fish size and ration level. – *J. Fish. Res. Bd. Canada* 32: 2103-2110.
- Brett, J.R. & C.A. Zala, 1975: Daily pattern of nitrogen excretion and oxygen consumption of sockeye salmon (*Oncorhynchus nerka*) under controlled conditions. – *J. Fish. Res. Bd. Canada* 32: 2479-2486.
- Brett, J.R. & T.D.D. Groves, 1979: Physiological energetics. – In W.S. Hoar, D.J. Randall & J.R. Brett (eds): *Fish Physiology*. Vol. VIII, Bioenergetics and Growth, pp. 280-352. Academic Press.
- Brocksen, R.W., G.E. Davis & C.E. Warren, 1968: Competition, food consumption and production of sculpins and trout in laboratory stream communities. – *Journ. Wildl. Mgmt.* 32: 51-75.
- Brocksen, R.W. & J.P. Bugge, 1974: Preliminary investigations on the influence of temperature on food assimilation by rainbow trout *Salmo gairdneri* Richardson. – *J. Fish. Biol.* 6: 93-97.
- Brody, S., 1945: Bioenergetics and Growth. – Reinhold.
- Bromley, P.J. & G. Smart, 1981: The effect of the major food categories on growth, composition and food conversion in rainbow trout (*Salmo gairdneri* Richardson). – *Aquaculture* 23: 325-336.
- Burrows, R.E., 1964: Effects of accumulated excretory products on hatchery-reared salmonids. – *Res. Rep. U.S. Fish. Wildl. Serv.* 66.
- Burt, J.R., 1961: Free sugars and sugar phosphates in muscle of chillstored aquarium cod (*Gadus callarias*). – *J. Food. Sci.* 26: 462-468.

- Chibnall, A.C., M.W. Rees & E.R. Williams, 1943: The total nitrogen content of egg albumin and other proteins. – *Biochem. J.* 37: 354-359.
- Cho, C.Y., H.S. Bayley & S.J. Slinger, 1976: Energy metabolism in growing rainbow trout: Partition of dietary energy in high protein and high fat diets. – In M. Vermorel (ed.): *Energy Metabolism of Farm Animals*, pp. 299-302. 7th Symp., Vichy, EAAP 19.
- Cho, C.Y. & S.J. Slinger, 1979: Apparent digestibility measurements in feed stuffs for rainbow trout. In J.E. Halver & K. Tiews (eds): *Proc. World Symp. on Finfish Nutrition and Fishfeed Technology*, Hamburg 20-23 June, 1978. Vol. II, pp. 239-247. Heenemann.
- Cho, C.Y., S.J. Slinger & H.S. Bayley, 1982: Bioenergetics of salmonid fishes: Energy intake, expenditure and productivity. – *Comp. Biochem. Physiol.* 73B(1): 25-41.
- Conway, E.J. & A. Byrne, 1933: Micro-determination of ammonia. – *Biochem. J.* 27: 419-429.
- Cowey, C.B. & G. Parry, 1963: The non-protein nitrogenous, constituents of the muscle of parr and smolt stages of the Atlantic salmon (*Salmo salar*). – *Comp. Biochem. Physiol.* 8: 47-51.
- Craig, J.F., 1977: The body composition of adult perch, *Perca fluviatilis* in Windermere, with reference to seasonal changes and reproduction. – *J. Anim. Ecol.* 46: 617-632.
- Craig, J.F., M.J. Kenley & J.F. Talling, 1978: Comparative estimations of the energy content of fish tissue from bomb calorimetry, wet oxidation and proximate analysis. – *Freshwat. Biol.* 8: 585-590.
- Davis, G.E. & C.E. Warren, 1971: Estimation of food consumption rates. – In W.E. Ricker (ed.): *IBP Handbook No. 3. Methods for Assessment of Fish Production in Fresh Waters*, pp. 227-248. Blackwell Scientific Publications (2. ed.).
- Doudoroff, P. & D.L. Shumway, 1970: Dissolved oxygen requirements for freshwater fishes. – *FAO Fish. Tech. Pap.* 86.
- Draper, N.R. & H. Smith, 1966: *Applied regression analysis*. – John Wiley & Sons, Inc.
- Duncan, D.W. & H.L.A. Tarr, 1958: Biochemical studies on sockeye salmon during spawning migration. III. Changes in the protein and non-protein nitrogen fractions in muscles of migrating sockeye salmon. – *Can. J. Biochem. Physiol.* 36: 799-803.
- Edwards, R.W., J.W. Densen & P.A. Russel, 1979: An assessment of the importance of temperature as a factor controlling the growth of brown trout in streams. – *J. Anim. Ecol.* 48: 501-507.
- Ege, R. & A. Krogh, 1914: On the relation between the temperature and the respiratory exchange in fishes. – *Int. Revue Gesamten Hydrobiologie und Hydrographie VII*: 48-55.
- Elliott, J.M., 1972: Rates of gastric evacuation in brown trout, *Salmo trutta* L. – *Freshwat. Biol.* 2: 1-18.
- Elliott, J.M., 1975a: The growth rate of brown trout (*Salmo trutta* L.) fed on maximum rations. – *J. Anim. Ecol.* 44: 805-821.
- Elliott, J.M., 1975b: The growth rate of brown trout (*Salmo trutta* L.) fed on reduced rations. – *J. Anim. Ecol.* 44: 823-842.
- Elliott, J.M., 1976a: Body composition of brown trout (*Salmo trutta* L.) in relation to temperature and ration size. – *J. Anim. Ecol.* 45: 273-289.
- Elliott, J.M., 1976b: Energy losses in the waste products of brown trout (*Salmo trutta* L.). – *J. Anim. Ecol.* 45: 561-580.
- Elliott, J.M., 1976c: The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. – *J. Anim. Ecol.* 45: 923-948.
- Elliott, J.M., 1979: Energetics of freshwater teleosts. – *Symp. zool. Soc. Lond.* 44: 29-61.
- Elliott, J.M. & W. Davison, 1975: Energy equivalents of oxygen consumption in animal energetics. – *Oecologia (Berl.)* 19: 195-201.
- Fänge, R. & D. Grove, 1979: Digestion. – In W.S. Hoar, D.J. Randall & J.R. Brett (eds): *Fish Physiology*. Vol. VIII. Bioenergetics and Growth, pp. 161-260. Academic Press.
- Fischer, Z., 1977: Some remarks on nitrogen excretion by fish. – *Pol. Arch. Hydrobiol.* 24(3): 355-360.
- Forster, R.P. & L. Goldstein, 1969: Formation of excretory products. – In W.S. Hoar & D.J. Randall (eds): *Fish Physiology*. Vol. I. Excretion, Ionic Regulation, and Metabolism, pp. 313-350. Academic Press.
- From, J. & G. Rasmussen, 1979: Growth modelling for use in trout production planning. – In J.E. Halver & K. Tiews (eds): *Proc. World Symp. on Finfish Nutrition and Fishfeed Technology*, Hamburg 20-23 June, 1978. Vol. II, pp. 591-605. Heenemann.

- Fromm, P.O., 1963: Studies on renal and extra-renal excretion in a freshwater teleost, *Salmo gairdneri*. – Comp. Biochem. Physiol. 10: 121-128.
- Fry, F.E.J., 1971: The effect of environmental factors on the physiology of fish. – In W.S. Hoar & D.J. Randall (eds): Fish Physiology. Vol. VI, Environmental Relations and Behavior, pp. 1-98. Academic Press.
- Gerking, S.D., 1952: The protein metabolism of sunfishes of different ages. – Physiol. Zool. 25: 358-372.
- Gerking, S.D., 1971: Influence of rate of feeding and body weight on protein metabolism of bluegill sunfish. – Physiol. Zool. 44: 9-19.
- Goldstein, L. & R.P. Forster, 1970: Nitrogen metabolism in fishes. – In Comparative Biochemistry of Nitrogen Metabolism. Vol. 2, The Vertebrates, pp. 495-518.
- Gomazhov, O.A., 1959: Effect of temperature on digestion of the burbot, *Lota lota*. (In Russian) – Byull. Inst. Biol. Vodokhran., Akad. Nauk SSSR 5: 26-28.
- Gray, J., 1926: The growth of fish. I. The relationship between embryo and yolk in *Salmo fario*. – J. Exptl. Biol. 4: 215-225.
- Gross, W.L., E.W. Roelofs & P.O. Fromm, 1965: Influence of photoperiod on growth of green sunfish *Lepomis cyanellus*. – J. Fish. Res. Bd. Canada 22(6): 1379-1386.
- Grove, D.J., L.G. Loizides & J. Nott, 1978: Satiation amount, frequency of feeding and gastric emptying rate in *Salmo gairdneri*. – J. Fish. Biol. 12: 507-516.
- Hald, A., 1968: Statistiske metoder (Statistical Methods). (In Danish). Akademisk Forlag.
- Hanson, S.W.F. & J. Olley, 1963: Application of the Bligh and Dyer method of lipid extraction to tissue homogenates. – Biochem. J. 89(3): 101-102.
- Hathaway, E.S., 1927: The relation of temperature to the quantity of food consumed by fishes. – Ecology VIII(4): 428-435.
- Hayes, F.R. & D. Pelluet, 1945: The effect of temperature on the growth and efficiency of yolk conversion in the salmon embryo. – Canadian Journal of Research 23 sec. D(2): 7-15.
- Herrmann, R.B., C.E. Warren & P. Doudoroff, 1962: Influence of oxygen concentration on the growth of juvenile coho salmon. – Trans. Amer. Fish. Soc. 91(2): 155-167.
- Hopkins, A., 1966: The pattern of gastric emptying: A new view of old results. – J. Physiol. 182: 144-149.
- Huismann, E.A., 1976: Food conversion efficiencies at maintenance and production levels for carp, *Cyprinus carpio* L., and rainbow trout *Salmo gairdneri* Richardson. – Aquaculture 9: 259-273.
- Ivlev, V.S., 1939: Energetičeskij balans karpov. (Energy balance of carps). (In Russian with English summary.) – Zool. Zh. 18: 308-318.
- Janisch, E., 1927: Das Exponentialgesetz als Grundlage einer Vergleichenden Biologie. – Abhandl. Z. Theorie Org. Entwicklungsmech. 2: 1-371.
- Job, S.V., 1960: Growth and calorific approximation in the speckled trout (*Salvelinus fontinalis*). – Indian J. Fish. 7: 129-136.
- Jobling, M., 1981a: The influences of feeding on the metabolic rate of fishes: A short review. – J. Fish. Biol. 18: 385-400.
- Jobling, M., 1981b: Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish. – J. Fish. Biol. 19: 245-257.
- Jonnard, R., 1945: Determination of total nitrogen in proteins and their hydrolyzates. – Ind. Eng. Chem. Anal. Ed. 17: 246-249.
- 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. – J. Fish. Res. Bd. Canada 28(6): 809-814.
- Kerr, S.R., 1971c: A simulation model of lake trout growth. – J. Fish. Res. Bd. Canada 28(6): 815-819.
- Kinne, O., 1960: Growth, food intake, and food conversion in a euryplastic fish exposed to different temperatures and salinities. – Physiol. Zool. 33: 288-317.
- Kirk, P.L., 1947: The chemical determination of proteins. – Adv. Protein Chem. 3: 139-167.
- Kjosbakken, J., 1970: Nitrogenekstraktiver i sild, lodde og makrell. (Nitrogen extractives in herring, capelin and mackerel.) (In Norwegian with English summary). Univ. Trondheim.

- Koroleff, F.: Bestämning av ammoniak i vatten. (Determination of ammonia in water.) (In Swedish.) Havsforskningsinstitutet, Helsingfors, Finland.
- Krokhin, E.M., 1959: Determination of the daily food ration of young sockeye and three-spined stickleback by the respiration method. – Fish. Res. Bd. Canada Translation Series 209.
- Lieth, H., 1968: The measurement of calorific values of biological material and the determination of ecological efficiency. – In F.E. Eckardt (ed.): Functioning of Terrestrial Ecosystems at the Primary Production Level, pp. 233-242. Proc. of the Copenhagen Symp., UNESCO.
- Love, R.M., 1970: The chemical biology of fishes. – Academic Press.
- Love, R.M., 1980: The chemical biology of fishes. Vol. 2: Advances 1968-1977. Academic Press.
- Lukton, A. & H.S. Olcott, 1958: Content of free imidazole compounds in the muscle tissue of aquatic animals. – Food Research 23: 611-618.
- Maciolek, J.A., 1962: Limnological organic analyses by quantitative dichromate oxidation. – U.S. Dept. of the Interior Fish and Wildlife Service. Bureau of Sport Fisheries and Wildlife. Res. Rep. 60.
- Marr, D.H.A., 1966: Influence of temperature on the efficiency of growth of salmonid embryos. – Nature, November 25, 1966 5065(212): 957-959.
- Menzel, D.W., 1960: Utilization of food by a Bermuda reef fish *Epinephelus guttatus*. – J. Cons. Perm. int. Explor. Mer. 25: 216-222.
- Mezincescu, M.D. & F. Szabo, 1936: Method for determination of the non-protein of tissue. – J. Biol. Chem. 115: 131-138.
- Miller, P.J., 1973: Effects of photoperiod on growth in gobiid fish. – Proceeding of the Challenger Society IV(4): 197-198.
- Miura, T., N. Suzuki, M. Nagoshi & K. Yamamura, 1976: The rate of production and food consumption of the biwamasu, *Oncorhynchus rhodurus*, population in lake Biwa. – Res. Popul. Ecol. 17: 135-154.
- Morgulis, S., 1918: Studies on the nutrition of fish. Experiments on brook trout. – Journ. Biol. Chem. 36: 391-413.
- Nightingale, J.W., 1974: Bioenergetic responses of nitrogen metabolism and respiration to variable temperature and feeding interval in Donaldson strain rainbow trout. – Ph. D. Thesis, Univ. of Washington, Seattle.
- Niimi, A.J., 1972a: Total nitrogen, nonprotein nitrogen, and protein content in largemouth bass (*Micropterus salmoides*) with reference to quantitative protein estimates. – Can. J. Zool. 50: 1607-1610.
- Niimi, A.J., 1972b: Bioenergetics and growth of largemouth bass (*Micropterus salmoides*) with feeding in relation to body weight and temperature. – Ph. D. Thesis. University of Guelph.
- Niimi, A.J. & F.W.H. Beamish, 1974: Bioenergetics and growth of largemouth bass (*Micropterus salmoides*) in relation to body weight and temperature. – Can. J. Zool. 52: 447-456.
- Nose, T., 1967: On the metabolic fecal nitrogen in young rainbow trout. – Bull. Freshwater Fish. Fish. Res. Lab. 17: 97-106.
- Nottingham, P.M., 1952: The alkaline hydrolysis and hydrolytic products of fish protein. – Ph. D. Thesis, University of Aberdeen.
- Ostapenya, A.P., 1971: Biomass and how to express it. – In G.G. Winberg (ed.): Methods for Estimation of Production of Aquatic Animals, pp. 11-31. Academic Press.
- Page, W.F., 1895: Feeding and rearing fishes, particularly trout, under domestication. – Bulletin, U.S. Fish Commission, pp. 289-314.
- Paine, R.T., 1966: Endothermy in bomb calorimetry. – Limnol. Oceanogr. 11: 126-129.
- 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.
- Pandian, T.J., 1967: Intake, digestion, absorption and conversion of food in the fishes *Megalops cyprinoides* and *Ophiocephalus striatus*. – Marine Biol. 1: 16-32.
- Papst, M.H., G.B. Ayles & S. Uraivan, 1982: A model for estimating the growth of cultured rainbow trout (*Salmo gairdneri* Richardson). – 146th Technical Report from the Western Region, Winnipeg.

- Parker, R.R. & P.A. Larkin, 1959: A concept of growth in fishes. – J. Fish. Res. Bd. Canada 16(5): 721-745.
- Pearse, A.S., 1924: Amount of food eaten by four species of fresh-water fishes. – Ecology V(3): 254-258.
- Pearse, A.S. & H. Achtenberg, 1920: Habits of yellow perch in Wisconsin lakes. – Bulletin of the United States Bureau of Fisheries XXXVI: 295-366.
- Pentelov, 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., 1909: Die Ernährung der Fische. – Zeitschrift für allgemeine Physiologie, Jena XIX: 147-242.
- Pütter, A., 1920: Studien über physiologische Ähnlichkeit VI: Wachstumsähnlichkeiten. – Pflügers Arch. Gesamte Physiol. Menschen Tiere 179-180: 298-340.
- Rafail, S.Z., 1968: A statistical analysis of ration and growth relationship of plaice (*Pleuronectes platessa*). – J. Fish. Res. Bd. Canada 25(4): 717-732.
- Rasmussen, G., 1977: Fiskeribiologiske undersøgelser. (Fishery biological investigations). (In Danish). – In Rapport 34: Gudenåundersøgelsen. Dambrugsundersøgelsen, pp. 49-55.
- Rasmussen, G. & B. Therkildsen, 1979: Food, growth, and production of *Anguilla anguilla* L. in a small Danish stream. – Rapp. P.-v. Réun. Cons. int. Explor. Mer. 174: 32-40.
- Rebsdorf, Å. & B. Therkildsen, 1978: Bestemmelse af organisk stof i recipientvand og på faste prøver ved en modificeret COD-metode. (Determination of organic matter in recipient water and on solid samples by means of a modified COD-method). (In Danish). – Vand 1: 2-7.
- Ricker, W.E., 1979: Growth rates and models. – In W.S. Hoar, D.J. Randall & J.R. Brett (eds): Fish Physiology. Vol. VIII. Bioenergetics and Growth, pp. 678-743. Academic Press.
- Rottiers, D.V. & R.M. Tucker, 1982: Proximate composition and calorific content of eight lake Michigan fishes. – Technical Papers of the U.S. Fish and Wildlife Service 108.
- Ryland, J.S. & J.H. Nichols, 1967: Effect of temperature on the efficiency of growth of plaice larvae. – Nature 214: 529-530.
- Saunders, R.L., 1963: Respiration of the Atlantic cod. – J. Fish. Res. Bd. Canada 20(2): 373-386.
- Scheiner, D., 1976: Determination of ammonia and Kjeldahl nitrogen by indophenol method. – Water Research 10: 31-36.
- Shewan, J.M., 1951: The chemistry and metabolism of the nitrogenous extractives in fish. – In R.T. Williams (ed.): The Biochemistry of Fish. Biochemical Society Symposia 6, pp. 28-48. Cambridge.
- Smith, K.L., Jr., 1973: Energy transformation by the sargassum fish, *Histrio histrio* (L.). – J. Exp. Mar. Biol. Ecol. 12: 219-227.
- Smith, R.R., G.L. Rumsey & M.L. Scott, 1978a: Net energy maintenance requirements of salmonids as measured by direct calorimetry: Effect of body size and environmental temperature. – The Journal of Nutrition 108(6): 1017-1024.
- Smith, R.R., G.L. Rumsey & M.L. Scott, 1978b: Heat increment associated with dietary protein, fat, carbohydrate and complete diets of salmonids: Comparative energetic efficiency. – The Journal of Nutrition 108(6): 1025-1032.
- Smith, S., 1946: Studies in the development of the rainbow trout (*Salmo irideus*). – J. Exp. Biol. 23: 357-378.
- Solomon, D.J. & A.E. Brafield, 1972: The energetics of feeding, metabolism and growth of perch (*Perca fluviatilis* L.). – J. Anim. Ecol. 41: 699-718.
- Sparre, P., 1976: A markovian decision process applied to optimization of production planning in fish farming. – Meddr. Danm. Fisk.- og Havunders. N.S. 7: 111-197.
- Sperber, O., J. From & P. Sparre, 1977: A method to estimate the growth rate of fishes, as a function of temperature and feeding level, applied to rainbow trout. – Meddr. Danm. Fisk.- og Havunders. N.S. 7: 275-317.
- Staples, D.J. & M. Nomura, 1976: Influence of body size and food ration on the energy budget of rainbow trout *Salmo gairdneri* Richardson. – J. Fish. Biol. 9: 29-43.
- Stauffer, G.D., 1973: A growth model for salmonids reared in hatchery environments. – Ph. D. Thesis, Univ. of Washington, Seattle.

- Subba Rao, G.N., 1948: Physico-chemical investigations on the muscle proteins of some commercial species of fish caught in North East Scottish waters. – Thesis, University of Aberdeen.
- Swift, D.R., 1963: Influence of oxygen concentration on growth of brown trout, *Salmo trutta* L. – Trans. Amer. Fish. Soc. 92(3): 300-301.
- Swift, D.R., 1964: The effect of temperature and oxygen on the growth rate of the windermere char (*Salvelinus alpinus willughbii*). – Comp. Biochem. Physiol. 12: 179-183.
- Tseitlin, V.B., 1980: Duration of gastric digestion in fishes. – Mar. Ecol. Prog. Ser. 2: 277-280.
- Tyler, A.V., 1970: Rates of gastric emptying in young cod. – J. Fish. Res. Bd. Canada 27: 1177-1189.
- Ursin, E., 1967: A mathematical model of some aspects of fish growth, respiration, and mortality. – J. Fish. Res. Bd. Canada 24(11): 2355-2453.
- Ursin, E., 1979: Principles of growth in fishes. – Symp. zool. Soc. Lond. 44: 63-87.
- Vinogradov, A.P., 1953: The elementary chemical composition of marine organisms. – Yale Univ. Press, New Haven, Conn., pp. 463-566.
- Warren, C.E. & G.E. Davis, 1967: Laboratory studies on the feeding, bioenergetics, and growth of fish. – In S.D. Gerking (ed.): The Biological Basis of Freshwater Fish Production, pp. 175-214. Blackwell Scientific Publications.
- Warren, C.E. & P. Doudoroff, 1971: Bioenergetics and growth. – In Biology and Water Pollution Control, pp. 135-167. Saunders.
- Weatherley, A.H., 1972: Growth and ecology of fish populations. – Academic Press.
- Winberg, G.G., 1960: Rate of metabolism and food requirements of fishes. – Fish. Res. Bd. Canada. Translation Series 194.
- Windell, J.T., 1967: Rates of digestion in fishes. – In S.D. Gerking (ed.): The Biological Basis of Freshwater Fish Production, pp. 151-173. Blackwell Scientific Publications.
- Windell, J.T., 1978: Digestion and daily ration of fishes. – In S.D. Gerking (ed.): Ecology of Freshwater Fish Production, pp. 159-183. Blackwell Scientific Publications.
- Wingfield, C.A., 1940: The effect of certain environmental factors on the growth of brown trout (*Salmo trutta* L.). – Jour. Exp. Biol. 17: 435-448.
- Wood, A.H., 1932: The effect of temperature on the growth and respiration of fish embryos (*Salmo fario*). – J. Exp. Biol. 9: 271-276.

Appendix

In the Appendix the observations for the growth experiments are given (pp. 136-139). dR/dt , faeces, $\text{NH}_3\text{-N}$, and oxygen are given per fish per day. Ser/aqu means series and aquarium number.

11.02	15.00	68	15	0.37	0.50	28.26	0.484	1.75	3	25.1	0.590	7.94	34.6	22.75	3	30.2	0.737	10.54	41.5	23.32	0.95	35.6	300.4	5.987	143.0
11.03	15.00	30	15	0.74	1.10	61.62	1.055	3.83	3	25.3	0.595	8.00	34.9	22.75	3	37.5	0.875	13.75	50.8	23.97	1.81	79.6	781.8	14.879	238.1
11.04	15.00	88	15	0.19	0.25	13.91	0.238	0.86	3	53.2	0.593	7.98	34.8	22.75	3	26.4	0.609	8.34	31.7	21.23	0.38	13.6	200.4	4.548	208.9
11.05	15.00	41	15	0.20	0.44	24.78	0.424	1.54	2	53.4	1.357	17.98	71.3	23.13	2	56.5	1.361	16.58	66.6	21.43	0.59	21.8	347.6	4.548	208.9
11.06	15.00	26	15	0.38	0.89	49.85	0.853	3.09	2	53.2	1.402	18.57	73.7	23.13	2	64.7	1.643	23.71	87.9	24.29	1.28	44.8	538.7	8.692	271.8
11.07	15.00	20	15	0.59	1.44	80.74	1.382	5.01	2	54.1	1.374	18.20	72.2	23.13	2	71.9	1.817	31.62	106.9	25.03	2.46	89.5	525.9	15.969	341.0
11.08	15.00	14	15	0.80	1.98	111.19	1.903	6.90	2	168.5	1.364	18.07	71.7	23.13	2	183.5	4.854	72.71	298.0	27.91	0.56	17.6	2174.9	49.667	989.3
11.10	15.00	13	8	0.81	4.01	224.68	3.845	13.95	1	168.5	4.575	70.50	317.4	28.35	2	172.8	4.607	66.53	273.7	27.40	4.69	155.4	434.6	41.880	651.0
11.11	15.00	17	15	0.46	2.17	121.45	2.079	7.54	1	155.9	3.929	75.90	367.7	28.21	2	161.3	4.388	62.00	252.2	26.15	8.84	302.3	882.9	48.951	498.7
11.12	15.00	24	15	0.23	3.63	203.37	3.481	12.63	1	114.8	3.131	43.73	265.7	28.21	2	149.6	3.844	60.87	274.6	28.46	8.84	302.3	882.9	48.951	498.7
11.13	15.00	15	15	0.23	3.63	203.37	3.481	12.63	1	114.8	3.131	43.73	265.7	28.21	2	149.6	3.844	60.87	274.6	28.46	8.84	302.3	882.9	48.951	498.7
11.14	15.00	14	15	0.65	4.44	170.95	3.21	5.92	1	117.0	3.190	44.55	172.4	25.65	2	130.3	3.507	51.46	210.9	27.53	3.16	99.2	409.6	22.617	510.7
11.15	15.00	14	15	0.65	4.44	170.95	3.21	5.92	1	117.0	3.190	44.55	172.4	25.65	2	130.3	3.507	51.46	210.9	27.53	3.16	99.2	409.6	22.617	510.7
11.16	15.00	20	15	0.20	0.82	45.98	0.787	2.85	1	111.7	3.047	42.56	170.0	25.65	2	119.9	3.104	44.41	175.1	25.99	1.24	44.5	117.0	9.360	358.7
12.01	10.00	36	14	0.50	0.55	30.99	0.528	1.91	3	36.5	0.840	12.34	49.9	24.05	3	42.1	1.072	14.63	55.6	24.24	0.69	32.7	28.9	6.091	167.8
12.02	10.00	61	14	0.65	0.76	42.77	0.728	2.64	3	38.7	0.913	13.65	49.8	24.40	3	34.0	0.858	11.91	44.4	23.49	0.42	59.2	33.4	3.658	126.4
12.04	10.00	80	14	0.16	0.14	7.89	0.134	0.49	4	27.7	0.673	8.45	32.4	22.19	4	27.9	0.780	8.66	32.5	22.67	0.19	8.3	113.3	7.188	263.9
12.05	10.00	36	14	0.18	0.56	14.42	0.246	0.89	3	66.9	1.416	18.74	73.4	22.22	3	58.3	1.510	19.96	77.9	23.86	0.33	12.9	62.3	2.592	183.5
12.06	10.00	21	14	0.35	0.58	32.63	0.356	2.02	3	66.9	1.416	18.74	73.4	22.22	3	58.3	1.510	19.96	77.9	23.86	0.33	12.9	62.3	2.592	183.5
12.07	10.00	15	14	0.52	0.93	52.57	0.895	3.25	3	74.3	1.926	26.81	102.9	25.63	3	71.8	1.927	25.56	91.9	23.86	0.73	27.4	7.7	4.741	271.8
12.08	10.00	9	14	0.74	1.41	79.51	1.354	4.91	2	79.5	2.009	31.22	121.9	26.40	2	82.8	2.423	31.21	115.7	24.33	1.46	62.9	113.5	8.023	323.4
12.09	10.00	150	14	0.27	0.16	7.44	0.127	0.46	10	11.6	0.270	4.02	15.2	23.73	10	12.4	0.286	4.00	15.1	22.20	0.17	8.2	31.0	1.920	55.3
12.10	10.00	84	14	0.38	0.23	14.54	0.248	0.90	10	18.7	0.468	6.70	25.0	24.33	10	20.5	0.493	7.39	26.9	23.39	0.42	18.3	97.6	3.778	127.2
12.11	10.00	184	14	0.35	0.13	7.38	0.126	0.46	10	7.9	0.180	2.61	10.0	23.28	10	8.8	0.196	2.97	10.9	21.95	0.21	9.0	10.5	2.022	50.8
12.12	10.00	416	14	0.30	0.91	51.45	0.876	3.18	2	164.9	4.546	72.02	270.0	28.09	2	174.1	4.798	72.53	266.0	26.89	1.45	61.9	1.9	11.361	470.4
12.13	10.00	11	14	0.70	1.90	107.00	1.822	6.61	2	33.3	0.076	1.11	3.2	22.73	20	3.8	0.076	1.25	4.5	21.03	0.10	4.6	1.9	1.039	22.4
12.14	10.00	16	14	0.50	1.44	80.92	1.378	5.00	2	134.3	3.541	49.68	199.1	25.97	2	150.9	3.996	58.40	235.0	25.97	3.23	142.5	54.5	23.927	695.1
12.15	10.00	47	32	0.46	0.36	20.41	0.341	1.18	11	14.3	1.394	62.40	239.4	27.59	2	160.7	4.456	63.95	239.9	25.97	2.15	92.5	175.0	7.848	351.3
13.01	5.00	25	32	0.30	0.19	10.92	0.183	0.63	3	44.1	1.082	15.40	58.0	24.37	5	54.1	1.394	18.97	73.8	24.44	0.62	28.7	378.1	3.411	122.0
13.02	5.00	45	32	0.46	0.36	20.41	0.341	1.18	11	43.1	1.082	15.40	58.0	24.37	5	54.1	1.394	18.97	73.8	24.44	0.62	28.7	378.1	3.411	122.0
13.03	5.00	30	32	0.58	0.34	19.49	0.326	1.13	6	24.0	0.684	8.45	31.0	21.75	5	38.1	1.109	11.34	43.2	22.42	0.70	32.6	89.6	3.661	95.6
13.04	5.00	29	32	0.22	0.12	6.97	0.141	0.40	6	28.7	0.702	8.68	31.8	21.75	4	31.0	0.739	8.68	31.6	21.13	0.18	8.9	93.4	1.216	51.9
13.05	5.00	27	32	0.16	0.15	8.46	0.141	0.40	6	60.7	1.579	19.76	73.9	23.02	3	63.4	1.644	17.20	64.4	21.12	0.24	11.4	89.1	1.080	87.6
13.06	5.00	20	32	0.52	0.60	34.47	0.576	2.00	5	78.5	2.044	29.14	103.3	24.26	5	93.2	2.409	32.50	122.7	24.39	1.02	46.7	281.6	6.313	200.6
13.07	5.00	46	32	0.31	0.10	5.60	0.094	0.32	10	12.4	0.295	4.01	15.2	22.60	6	14.9	0.344	4.80	17.9	22.34	0.15	7.8	27.2	1.194	38.7
13.08	5.00	63	32	0.45	0.15	8.69	0.145	0.50	10	12.7	0.301	4.09	15.5	22.60	6	16.4	0.369	4.91	18.5	20.83	0.26	14.1	31.8	1.368	45.3
13.09	5.00	60	32	0.28	0.13	7.20	0.120	0.42	10	20.7	0.510	7.52	27.1	23.81	6	23.5	0.557	7.63	27.7	22.50	0.18	8.3	39.8	1.206	53.0
13.11	5.00	61	32	0.13	0.03	1.72	0.029	0.10	12	8.9	0.205	3.06	11.3	23.32	10	8.9	0.204	2.67	10.0	21.37	0.05	1.8	43.1	0.300	27.0
13.12	5.00	15	32	0.57	1.13	64.43	1.077	3.74	2	172.8	4.663	68.31	238.0	26.71	2	199.8	5.380	84.28	314.8	27.32	3.39	114.5	237.7	12.349	350.5
13.14	5.00	190	32	0.40	0.06	3.20	0.054	0.19	20	3.7	0.078	1.15	4.4	21.21	10	4.6	0.095	1.48	5.4	21.54	0.17	6.1	7.6	0.440	13.7
13.15	5.00	10	32	0.54	0.99	56.31	0.942	3.26	3	157.7	4.198	65.16	247.1	26.83	3	174.7	4.633	67.14	254.5	25.62	0.79	34.6	157.4	8.096	238.9
13.16	5.00	12	32	0.27	0.60	56.42	0.944	3.27	3	139.2	3.665	52.90	193.1	25.09	3	165.9	4.356	57.18	215.1	24.10	2.10	92.9	185.5	4.095	288.9
14.02	19.80	27	10	0.27	0.60	34.03	0.580	2.10	3	39.7	0.508	12.61	43.4	22.31	3	43.1	1.081	13.63	50.5	23.54	0.94	34.8	138.1	7.951	198.6
14.03	19.80	16	10	0.67	1.56	87.90	1.497	3.43	3	39.6	1.058	13.77	46.7	22.93	3	49.9	1.141	17.28	60.6	22.72	6.06	190.4	532.0	9.722	388.6
14.04	19.80	19	10	0.43	1.56	87.90	1.497	3.43	3	35.4	0.887	10.57	38.7	21.79	3	41.7	1.043	14.53	51.4	24.01	1.68	59.4	—	9.889	230.2
14.05	19.80	19	10	0.43	1.45	81.48	1.388	5.03	3	66.5	1.743	19.12	69.3	21.62	3	76.8	2.034	25.22	89.9	23.11	4.09	132.2	—	11.951	385.8
14.06	19.80	10	10	0.48	2.01	113.48	1.933	7.01	3	97.9	2.548	29.48	108.1	22.23	3	110.1	2.698	39.93	147.9	24.50	3.73	128.7	2427.2	14.231	532.3
14.07	19.80	32	10	0.59	0.74	41.87	0.713	2.59	5	15.3	0.376	4.48	16.4	21.46	5	17.9	0.411	5.12	18.7	21.24	0.82	34.2	344.2	4.389	133.4
14.08	19.80	45	10	0.37	0.44	24.51	0.417	1.51	5	15.3	0.376	4.56	17.0	22.50	5	32.8	0.794	11.19	40.4	23.53	2.54	119.1	501.2	5.325	245.5
14.09	19.80	20	10	0.69	1.16	65.53	1.116	4.05	5	23.5	0.572	6.54	25.6	22.08	5	18.4	0.417	6.89	24.7	24.53	1.57	70.9	443.6	2.159	179.9
14.10	19.80	27	10	0.63	0.73	40.85	0.696	2.52	5	13.8	0.327	4.67	17.0	23.11	5	18.4	0.282								

