

Improved estimates of a growth model and body composition of rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792) as function of feeding level, temperature and body size

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Abstract

The parameters in a growth model have been estimated from tank experiments with rainbow trout up to about 2000 g wet weight. Feeding experiments with commercial dry feed at temperatures from 5 to 20.1 °C and in days up to about one month during each experiment were performed. Faeces, excretions and respiration were estimated from daily samples. The body compositions of fish of different sizes and fed with different feeding levels were analysed. A growth model based upon energy flow and partitioning was set up. The growth rate and the proportions of the different terms in the budget of energy and nitrogen can be calculated for fish sizes up to about 2000 g wet weight and varying temperatures up to 20.1 °C. The growth model was used to predict the course of growth and total food consumption with varying temperatures and feeding regimes.

Keywords: growth, growth model, body composition, rainbow trout, feeding level, temperature, body size.

Introduction

From & Rasmussen (1984) presented a growth model for rainbow trout based upon energy flow and partitioning and the chemical composition of the fish. That work was carried out on rainbow trout of 3-400 g, because at that time the Danish freshwater trout-farm production was exclusively based on production of rainbow trout at 180-300 g. But since a production of large rainbow trout in salt water has started. Since the market for bigger fish was established, a minor production of big fish raised in freshwater now takes place, too. Therefore it became a natural demand to make new feeding experiments and recalculate new parameters to predict the growth of bigger fish, and to extend the relationships for the chemical composition originally determined for smaller fish, too.

Model

The basis for animal life and by this growth is food consumption of the specimen. Hence a growth model will be a description of the fates of the food consumed:

$$C = F + \bar{U} + R + \Delta B;$$

C is gross energy intake; F is faeces; U is excretions both from the kidney and across the gill epithelium; R is total metabolism, equal to the sum of standard metabolism, swimming metabolism and digestion and deposition, and ΔB is growth (i.e. energy gain).

Faeces derive from non-assimilated feed and consist of solid and soluble matters. In practice soluble faeces also include cell epithelium and digestive enzymes from the digestive tract.

Excretions are separated in endogenous (non-fed fish) and exogenous (fed fish) nitrogen excretions. In practice the first terms can be estimated in starving fish and the second term can be calculated as the difference between the amount of nitrogenous compounds from fed and starving fish.

Total metabolism equals the sum of standard metabolism (R_s), swimming metabolism ($R_a = \text{non-feeding} + \text{feeding activity}$), and digestion and deposition (R_d).

Following ingestion of a meal, the rate of metabolism expressed in units of heat production, increases. This increase is generally known as 'specific dynamic action'. Energy requirements for absorption, digestion, transportation, and deposition of food materials are distinct from those for specific dynamic action but experimentally difficult to separate. Where the distinction is not made the term 'apparent specific dynamic action' is appropriate.

Briefly, the model is based upon the equation:

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

where

dw/dt = weight change per unit time

w_t = weight of fish at time t

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').

In the anabolic term the quantity absorbed is a function of the quantity eaten. The catabolic term is comprised by two terms representing the catabolism of a starving fish, and the catabolism resulting from feeding and the subsequent processing of food.

The anabolic term

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 ($^{\circ}\text{C}$)
- m = exponent of anabolism
- f = feeding level, (can vary from 0 to 1)
- t = time (day).

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 $f = 1$.

There is general agreement about the assumption that the feeding rate increases with increasing temperature up to a maximum point beyond which it decreases.

If only temperatures below the temperature (i.e., where normal trout farming activities take place) for maximum feeding rate are considered, $h(T)$ can be described as:

$$h(T) = b_1 \cdot \exp(b_2 \cdot T) \tag{2'}$$

where b_1 and b_2 are constants.

Faeces. These consist of both solid and soluble faeces for $f > 0$.

Production of solid faecal matter can be described by the equation:

$$dB/dt_{\text{solid}} = b_1 \cdot f^{b_2} \cdot \exp(b_3 \cdot T) \cdot w_t^{b_4} \tag{3}$$

and soluble faeces as:

$$dB/dt_{\text{soluble}} = b_1 \cdot [\exp(b_2 \cdot f) - 1] \cdot \exp(b_3 \cdot T) \cdot w_t^{b_4} \tag{4}$$

where $b_1 - b_4$ are constants and faeces $\rightarrow 0$ for $f \rightarrow 0$.

As the nitrogen content only has been measured in solid faeces and not in suspended and dissolved faeces a total nitrogen content in the faeces has been determined as:

faeces = food - growth - urine - starvation =

$$b_1 \cdot [\exp(b_2 \cdot f) - 1] \cdot \exp(b_3 \cdot T) \cdot w_t^{b_4} \tag{3) + (4) for } f > 0$$

and where food, growth, and urine are the observed values and starvation is calculated from (5).

The catabolic term

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

$$dw/dt_{\text{starving}} = k(T)w_t^n \tag{5}$$

where

- $k(T)$ = coefficient of catabolism, temperature dependent
- n = exponent of catabolism

$k(T)$ can, in the same way as $h(T)$, be considered as a function of temperature. Starving catabolism consists of weight-loss from endogenous excretion, standard metabolism and a little non-feeding swimming activity.

$$k(T) = k_1 \cdot \exp(k_2 \cdot T) \quad (5')$$

where k_1 and k_2 are constants.

Excretion. Excretion (i.e., exogenous) can be described by the following for $f > 0$:

$$dU/dt = \mu_1 \cdot [\exp(\mu_2 \cdot f) - 1] \cdot \exp(\mu_3 \cdot T) \cdot w_t^{\mu_4} \quad (6)$$

where $\mu_1 - \mu_4$ are constants and $dU/dt \rightarrow 0$ for $f \rightarrow 0$.

Oxygen consumption. Oxygen consumption for $f > 0$ can be described as:

$$dA/dt = a_1 \cdot [\exp(a_2 \cdot f) - 1] \cdot \exp(a_3 \cdot T) \cdot w_t^{a_4} \quad (7)$$

where $a_1 - a_4$ are constants and $dA/dt \rightarrow 0$ for $f \rightarrow 0$.

Oxygen consumption therefore consists of 'apparent specific dynamic action' and swimming-activity associated with feeding.

From & Rasmussen (1984) showed that the feed intake was increasing up to 20.1 °C, beyond which temperature it decreases. The growth equation can then be written down as follows for $T \leq 20.1$ °C:

$$dw/dt = (2) - (3) - (4) - (7) - 1.8 \cdot (6) - (5) \quad (8)$$

where (6) is measured as g ammonia-N and converted to g COD (i.e., $1.8 \cdot (6)$) and the other expression in g COD. For nitrogen the equation can be written down as:

$$dw/dt = (2) - ((3) + (4)) - (6) - (5) \quad (9).$$

The unit used in a growth equation

The only terms in which all the quantities in a growth model can be measured are energy and nitrogen. For energy an appropriate unit is kJ or kcal, but because respiration and soluble faeces in the present research are determined in oxygen equivalents (i.e., 'the COD-method') g oxygen is used. The coefficient used to convert COD (chemical oxygen demand) on dead material is generally accepted to be 3.42 kcal/g oxygen and 14.60 kJ/g oxygen. The inorganic material (NH₃-N) in the excretory product, cannot be measured in this unit, but g ammonia-N can be converted to g COD by multiplying with 1.8, From & Rasmussen (1984).

Material and methods

Sexually immature rainbow trout (approximately 300-2000 g) from the Danish Trout Culture Research Station were used in the experiments which took place in circular glass-fibre tanks.

Water from the river Brøns was filtered through a sand filter and led to a glass-fibre basin where aeration, and heating or cooling took place. From here the water was pumped up into the experimental tanks. The oxygen content in each tank was measured at least once a day by means of Winkler titration and was always $100\% \pm 10\%$ of air saturation. This was achieved by means of an oxygen regulating system connected to an electronical oxygen-meter, (Radiometer TOX 40).

Before the start of an experiment the fish were acclimated to the experimental temperature and fibre tank for two-three weeks, and fed *ad libitum* each day.

The room had a 12 h light - 12 h dark photoperiod during acclimation and the experimental periods.

Immediately before the start and after the end of an experiment the fish were starved, in order to weigh the fish with empty stomachs 5°C : 6 days; 10°C : 5 days; 15°C : 3 days; 18°C : 2 days, see From & Rasmussen (1984). Before weighing each trout was anaesthetized with chlorbutolum (0.04% solution), and blotted using a wet cloth. The fish were weighed one by one to the nearest grammes. The start mean weight was called $w(0)$ and the mean weight after n days for $w(n)$. $(w(0) + w(n))/2$ gives w_i in formulae (2)-(6).

During all the experiments there were within each tank at least 10 specimen.

The tank bottom was sloping towards the centre, tank diameter was 1.3 m, water depth at the periphery was 31 cm, and at the centre it was 55 cm, which gave a water volume of approximately 560 l.

The fish were fed by commercial dry feed, Brande 3800/50. Dry matter of the different batches was analysed and ranged from 90.51% to 92.80% with a mean of 91.93%. The energetical value ranged from 1.55 to 1.65 g COD/g dry weight with a mean of 1.60 g COD/g dry weight.

At maximum rations ($f = 1$), the fish were fed each hour in the light period. The feeding was stopped when 2-3 pellets were at the bottom. These pellets were picked up again. The total amount of pellets divided with the number of fish and days gives dR/dt , formula (2), from which h_1 and h_2 and m are calculated.

At $f = 0.5 - 0.8$, the fish were fed 2-3 times each day and at lower feeding levels they were fed once a day to ensure a more even distribution of the feed to all the fish. Based on the parameters of (2) and guesstimates of the increase of the mean weights from the parameters in From & Rasmussen (1984) guesstimates of the ration per fish per day were calculated. After the feeding the total amount of pellets divided with the number of fish and days gives dR/dt which with the calculated parameters of h_1 , h_2 and m the feeding level f can be calculated.

At $f = 0$ the fish were starved during a period and the decrease in mean weight gives dw/dt_{starving} , formula (6), from which k_1 , k_2 and n are calculated.

The solid faeces were collected in a container mounted beneath the centre. The container was emptied each day, and the faeces were deep-frozen. At the end of the experiment the energy and nitrogen contents of the solid faeces were determined from a subsample. The total amount of solid faeces divided with the number of fish and days gives dB/dt_{solid} , formula (3).

At the inlet and outlet of each tank, waterpumps were continuously collecting about two litres each day. One subsample was deep-frozen, and the sum of these

daily subsamples was after the experiment analysed for amount of suspended and dissolved faeces by COD. Another subsample had each day its amount of $\text{NH}_3\text{-N}$ determined photometrically. The amounts were determined as difference between outlet and inlet multiplied with the waterflow. The total amount of soluble faeces and excretion divided with the number of fish and days gives dB/dt_{soluble} , formula (4) and dU/dt , formula (6).

The content of dry matter, protein (nitrogen $\times 6.25$), lipid, ash, and energy was determined for fish from 300 g to 3.3 kg. The energy was determined by COD.

At the start and at the end of an experiment fish were taken for analysis for dry weight, nitrogen, and energy by means of COD.

The analyses (i.e., dry matter, COD, nitrogen and lipid) used in the present study were as described by From & Rasmussen (1984).

$w(0)$ and $w(n)$ were recalculated from wet weight to energy and nitrogen using the above mentioned analysis.

Results

Body composition

The present data have been pooled with the data given in From & Rasmussen (1984). The following relationships given in Tables 1-5 have in this way been found. The data are given with 95% confidence limits, number of observations N and multiple coefficient of correlation R^2 .

If for example we have a fish with a body weight of 10 g wet weight and we want to calculate the course of growth with feeding level $f = 0.5$ and at a certain temperature we need the start mean weight $w(0)$ in g COD. The most convenient method

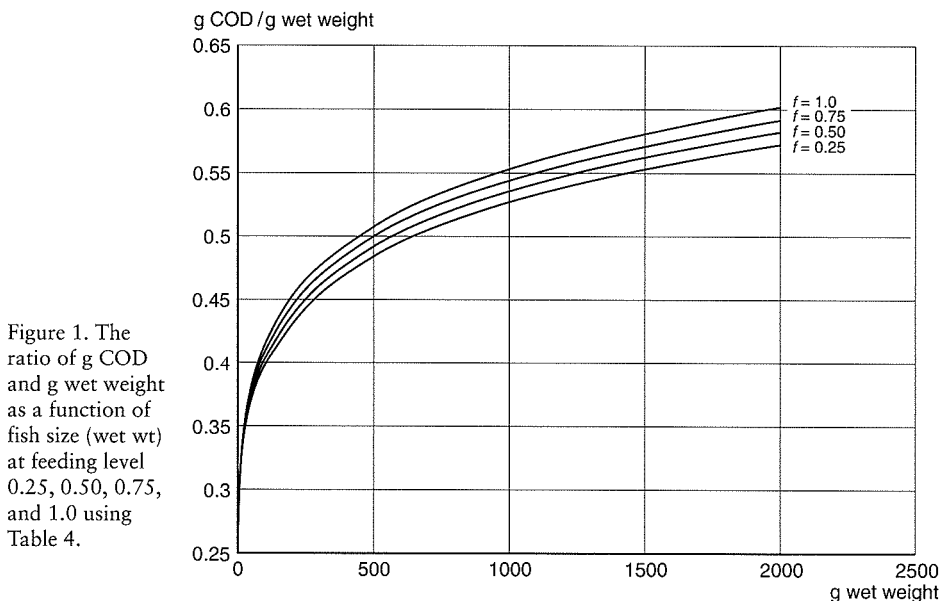


Table 1. $Y = a + bx$, where $x = \% \text{ water}$.

Y	a	b	Number	R ²
mg protein/g wet weight	327.99 (± 15.64)	-2.27 (± 0.22)	285	0.60
mg lipid/g wet weight	714.43 (± 16.34)	-8.76 (± 0.23)	285	0.95
mg ash/g wet weight	-23.37 (± 5.32)	0.65 (± 0.07)	286	0.51
kcal/g wet weight	7.9843 (± 0.1687)	-0.0875 (± 0.0024)	286	0.95
g COD/g wet weight	2.0710 (± 0.0720)	-0.0225 (± 0.0010)	369	0.86

Table 2. $Y = a + bx$, where $x = \text{kcal/g dry weight}$.

Y	a	b	Number	R ²
mg protein/g dry weight	1177.09 (± 48.31)	-98.13 (± 8.01)	285	0.68
mg lipid/g dry weight	-613.05 (± 68.68)	151.98 (± 11.38)	285	0.72
mg ash/g dry weight	331.04 (± 18.47)	-41.24 (± 3.06)	286	0.72

Table 3. $Y = ax^b$, where $x = \text{g wet weight}$.

Y	a	b	Number	R ²
% protein/g wet weight	13.27 $\begin{pmatrix} +0.24 \\ -0.22 \end{pmatrix}$	0.0408 (± 0.0030)	285	0.72
% lipid/g wet weight	1.7462 $\begin{pmatrix} +0.1835 \\ -0.1601 \end{pmatrix}$	0.2823 (± 0.0171)	285	0.79
% ash/g wet weight	3.3781 $\begin{pmatrix} +0.1949 \\ -0.1831 \end{pmatrix}$	-0.0730 (± 0.0097)	286	0.44
% dry matter	17.36 $\begin{pmatrix} +0.45 \\ -0.39 \end{pmatrix}$	0.0901 (± 0.0042)	286	0.87

Table 4. $Y = a(1 + bf)x^c$, where $x = \text{g wet weight}$ and $f = \text{feeding level}$.

Y	a	b	c	Number	R ²
kcal/g wet weight	0.8182 (± 0.0402)	0.0723 (± 0.0390)	0.1264 (± 0.0090)	317	0.80
g COD/g wet weight	0.2193 (± 0.0108)	0.0701 (± 0.0390)	0.1238 (± 0.0090)	317	0.79

Table 5. $Y = a + bx$, where $x = \text{weight of fish in kcal determined by bombing}$.

Y	a	b	Number	R ²
Weight of fish in g COD	0.1514 (± 0.3266)	0.2630 (± 0.0009)	404	1.00

will be to make analysis for each sample as has been used throughout this study. As a substitute we can either determine the water content from a homogenized sample dried at 45°C and use Table 1. Or we can use Table 3 which gives 21.36% dry matter and then Table 1 which gives 0.3017 g COD/g wet weight or $w(0) = 3.017$ g COD. Alternatively Table 4 gives 0.3019 g COD/g wet weight or $w(0) = 3.019$ g COD. Thus energy, protein (nitrogen), lipid and ash can be calculated very accurately by using the formulae.

The relationship g COD/g wet weight as a function of fish body weight (g wet weight) using Table 4 is shown in Figure 1 for four different feeding levels.

It has been stated, especially in older literature, that as a 'rule of thumb' the energy content of fish is about 1 kcal/g wet weight which is about 0.2924 g COD/g wet weight. For domesticated rainbow trout in the present study this is only true for fish with a body weight of about 3 g wet weight ($f = 1$) and 5 g wet weight ($f = 0$). The bias might be serious when simulating with large and smaller fish. For example a 100 g wet weight rainbow trout fed $f = 1$ has an energy content about 0.415 g COD/g wet weight.

Model

The data from the present experiments, and data given in From & Rasmussen (1984) for more than one fish in an aquarium have been pooled to calculate new parameters in the growth equation. The determinations of the parameters are given in Table 6-10, where the units are g COD and g nitrogen, and $T \leq 20.1^\circ\text{C}$. The data are given with 95% confidence limits, number of observations N (i.e., experiments) and multiple coefficient of correlation R^2 .

Table 6. Parameters of the anabolic term, $h(T)$. Weight of food and fish in g COD and in g nitrogen and $f = 1.00$.

Parameter	Estimate according to (2): $dR/dt = fh_1 \cdot \exp(b_2 \cdot T) w^m, f = 1, T \leq 20.1^\circ\text{C}$	
	COD N = 60 $R^2 = 0.97$	Nitrogen N = 58 $R^2 = 0.98$
b_1	0.0822 $\begin{pmatrix} +0.0156 \\ -0.0152 \end{pmatrix}$	0.0309 $\begin{pmatrix} +0.0021 \\ -0.0020 \end{pmatrix}$
b_2	0.0762 (± 0.0109)	0.0759 (± 0.0092)
m	0.6738 (± 0.0356)	0.7276 (± 0.0316)

Table 7. Parameters of the anabolic term, assimilation, weight of food and fish in g COD and in g nitrogen and $f > 0$.

Parameter	Estimate		
	Settable faeces according to (3): $b_1 \cdot f^{b_2} \cdot \exp(b_3 \cdot T) \cdot w^{b_4}$	Suspended + dissolved faeces according to (4): $b_1 [\exp(b_2 \cdot f) - 1] \cdot \exp(b_3 \cdot T) \cdot w^{b_4}$	Total faeces according to (3) + (4): $b_1 [\exp(b_2 \cdot f) - 1] \cdot \exp(b_3 \cdot T) \cdot w^{b_4}$
	g COD/individual/day w in g COD	g COD/individual/day w in g COD	g nitrogen/individual/day w in g nitrogen
	N = 171 $R^2 = 0.95$	N = 185 $R^2 = 0.59$	N = 148 $R^2 = 0.91$
b_1	0.00969 $\begin{pmatrix} +0.00220 \\ -0.00155 \end{pmatrix}$	0.0132 $\begin{pmatrix} +0.0055 \\ -0.0051 \end{pmatrix}$	0.00160 $\begin{pmatrix} +0.00009 \\ -0.00009 \end{pmatrix}$
b_2	1.3783 (± 0.1026)	1.2228 (± 0.3444)	2.2874 (± 0.2649)
b_3	0.0522 (± 0.0103)	0.0779 (± 0.0235)	0.0710 (± 0.0148)
b_4	0.7426 (± 0.0346)	0.4850 (± 0.0810)	0.6857 (± 0.0495)

Table 8. Parameters of catabolism, $k(T)$. Weight of fish in g COD and in g nitrogen and $f = 0$.

Estimate according to (5): $dw/dt = k_1 \cdot \exp(k_2 \cdot T)w^n$				
Parameter	COD		Nitrogen	
	N = 48	R ² = 0.88	N = 47	R ² = 0.80
k_1	0.00607	$\begin{pmatrix} +0.00326 \\ -0.00291 \end{pmatrix}$	0.00128	$\begin{pmatrix} +0.00020 \\ -0.00018 \end{pmatrix}$
k_2	0.0888	(± 0.0313)	0.1025	(± 0.0365)
n	0.8260	(± 0.0928)	0.7431	(± 0.1202)

Table 9. Parameters of catabolism, excretion. Weight of fish and urine in g COD and in g nitrogen and $f > 0$.

Estimate according to (6): $\mu_1 \cdot [\exp(\mu_2 \cdot f) - 1] \cdot \exp(\mu_3 \cdot T) \cdot w^{b_4}$				
Parameter	g COD/individual/day		g nitrogen/individual/day	
	N = 215	R ² = 0.87	N = 213	R ² = 0.88
μ_1	$1.7611 \cdot 10^{-4}$	$\begin{pmatrix} +0.6180 \cdot 10^{-4} \\ -0.3590 \cdot 10^{-4} \end{pmatrix}$	$6.3045 \cdot 10^{-4}$	$\begin{pmatrix} +0.3042 \cdot 10^{-4} \\ -0.3013 \cdot 10^{-4} \end{pmatrix}$
μ_2	2.3690	(± 0.2462)	2.4587	(± 0.2354)
μ_3	0.1025	(± 0.0172)	0.1004	(± 0.0164)
μ_4	0.7066	(± 0.0560)	0.7799	(± 0.0578)

Table 10. Parameters of catabolism, respiration. Weight of fish and food in g COD and $f > 0$.

Estimate according to (7): $a_1 \cdot [\exp(a_2 \cdot f) - 1] \cdot \exp(a_3 \cdot T) \cdot w^{a_4}$		
Parameter	g COD/individual/day	
	N = 120	R ² = 0.94
a_1	$7.4295 \cdot 10^{-3}$	$\begin{pmatrix} +0.8255 \cdot 10^{-3} \\ -0.5508 \cdot 10^{-3} \end{pmatrix}$
a_2	1.0208	(± 0.1412)
a_3	0.0659	(± 0.0075)
a_4	0.7010	(± 0.0447)

With these parameter values the growth equation (formula 10) in units of g COD for $T \leq 20.1$ °C is:

$$\begin{aligned}
 dw/dt = & f \cdot 0.0822 \cdot \exp(0.0762 \cdot T)w^{0.6738} - 0.00969 \cdot f^{1.3783} \cdot \exp(0.0522 \cdot T)w^{0.7426} \\
 & - 0.0132 [\exp(1.2228 \cdot f) - 1] \exp(0.0779 \cdot T)w^{0.4850} \\
 & - 7.4295 \cdot 10^{-3} [\exp(1.0208 \cdot f) - 1] \exp(0.0659 \cdot T)w^{0.7010} \\
 & - 1.7611 \cdot 10^{-4} [\exp(2.3690 \cdot f) - 1] \exp(0.1025 \cdot T) \cdot w^{0.7066} \\
 & - 0.00607 \cdot \exp(0.0888 \cdot T)w^{0.8260}
 \end{aligned}$$

and the growth equation (formula 11) for units of g N for $T \leq 20.1^\circ\text{C}$ is:

$$\begin{aligned} dw/dt = & f \cdot 0.0309 \cdot \exp(0.0759 \cdot T) w^{0.7276} \\ & - 0.00160 [\exp(2.2874 \cdot f) - 1] \exp(0.0710 \cdot T) w^{0.6857} \\ & - 6.3045 \cdot 10^{-4} [\exp(2.4587 \cdot f) - 1] \exp(0.1004 \cdot T) w^{0.7799} \\ & - 0.00128 \cdot \exp(0.1025 \cdot T) w^{0.7431} \end{aligned}$$

From the growth equation different relationships have been calculated and shown in Figs 2-13.

In Figs 2-3 the growth of a fish with a start weight of 5 g wet weight is shown at four different feeding levels ($f = 0.25, 0.5, 0.75$ and 1.0) and two different tem-

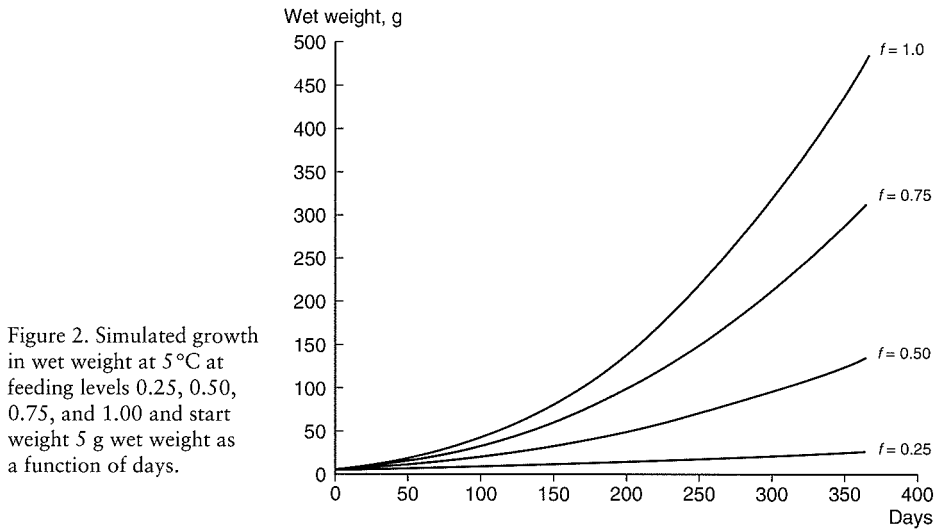


Figure 2. Simulated growth in wet weight at 5°C at feeding levels 0.25, 0.50, 0.75, and 1.00 and start weight 5 g wet weight as a function of days.

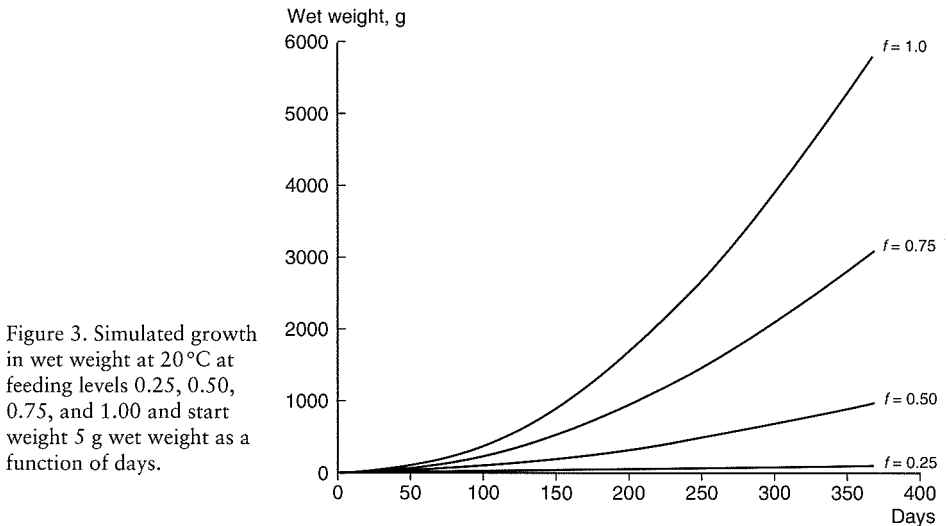


Figure 3. Simulated growth in wet weight at 20°C at feeding levels 0.25, 0.50, 0.75, and 1.00 and start weight 5 g wet weight as a function of days.

Figure 4. The size of the different terms in the energy budget as a function of feeding level f for a fish of 100 g wet weight at 5°C.

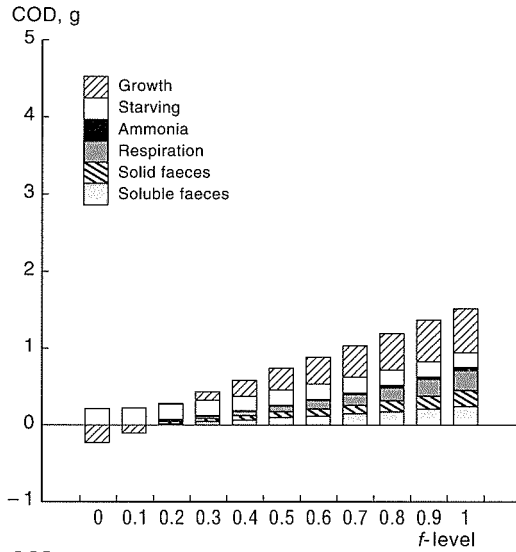
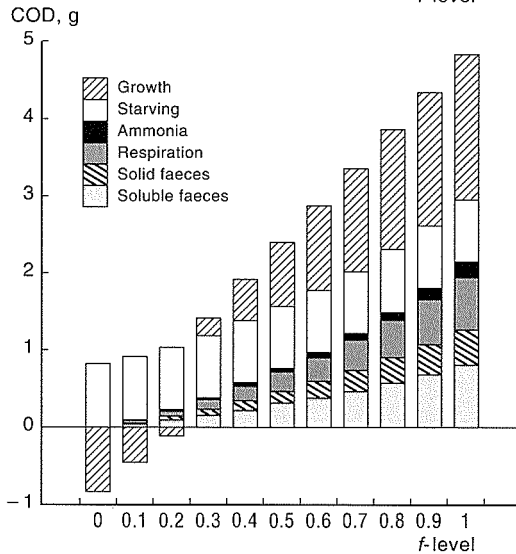


Figure 5. The size of the different terms in the energy budget as a function of feeding level f for a fish of 100 g wet weight at 20°C.



peratures (5 and 20°C). From & Rasmussen (1984) showed that maximum growth takes place at 20.1°C and from Fig. 3 it is seen that a fish of 5 g at optimum conditions (i.e., no negative feed-back from insufficient content of oxygen and detrimental increase of metabolites) after one year will attain a size of about 6 kg provided the equation can be expanded to this size. But it must be stressed that the parameters in the model have only been estimated for fish up to about 2 kg wet weight.

In Figs 4-5 the size of the different terms at different feeding levels are shown for a fish of 100 g wet weight at two different temperatures (5 and 20°C). The sum of the terms equals food consumption. At feeding level $f = 0$ the terms of starving and growth of course equal zero.

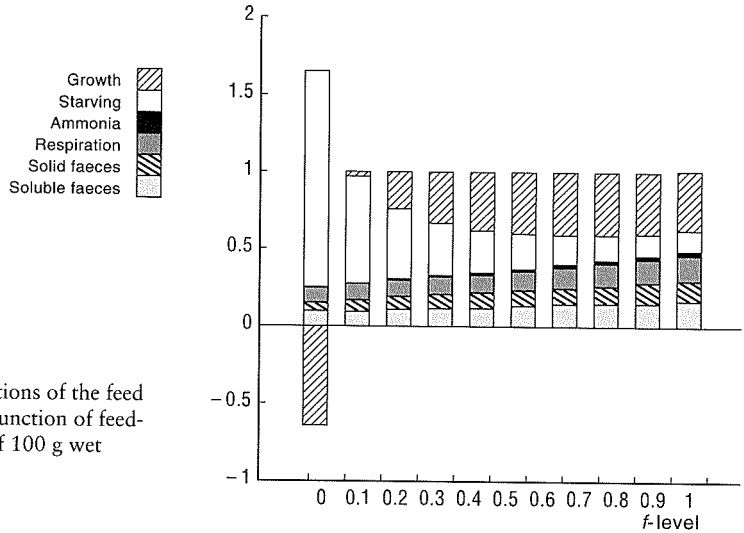


Figure 6. The proportions of the feed on energy basis as a function of feeding level f for a fish of 100 g wet weight at 5°C.

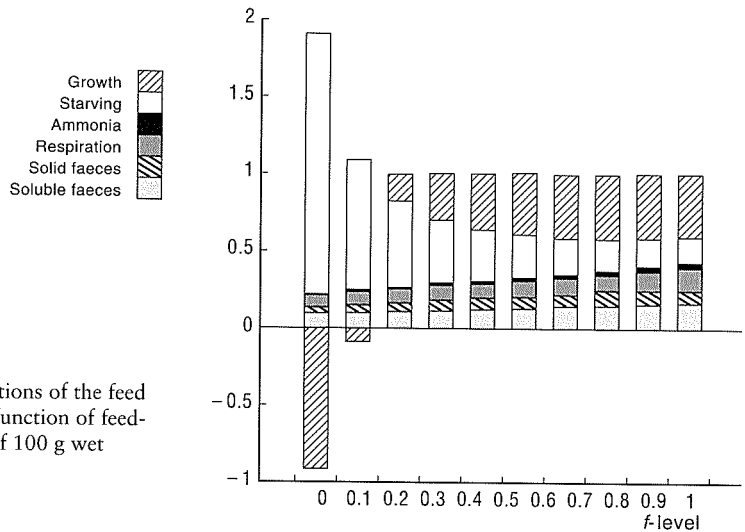


Figure 7. The proportions of the feed on energy basis as a function of feeding level f for a fish of 100 g wet weight at 20°C.

In Figs 6-7 is shown how much the different terms constitute of the feed on energy basis. It can e.g. be seen that f -maintenance (i.e., the feeding level where growth rate is zero) increases with increasing temperature. The feed conversion dw/dR depends very much on the feeding level. From low feeding level and negative growth the feed conversion increases to a maximum of about 40-50% at feeding levels from 0.5-0.7. These feeding levels therefore represent the most economically advantage of the feeding strategy, but not the highest growth rate dw/dt , see Figs 2-5. At higher feeding levels up to 1 the feed conversion decreases a little but the growth rate is very fast, see Figs 2-5.

In Figs 8-9 the same relationships are shown for nitrogen but the variations of the feed conversions are much more pronounced. At low temperature (5 °C) dw/dR reach a maximum of about 62% at $f = 0.4$ and decreases to about 28% at $f = 1.0$. At $f = 0.1$ about 33% of the feed is used for growth in very much contrast to what was found at an energy basis. At 20 °C at $f = 0.1$ $dw/dR = 8\%$, at $f = 0.4$ $dw/dR = 52\%$ and at $f = 1.0$ $dw/dR = 17\%$. It can therefore be concluded that at low f -levels the fish is a better nitrogen utilizer than energy utilizer, and that it is opposite at high f -levels.

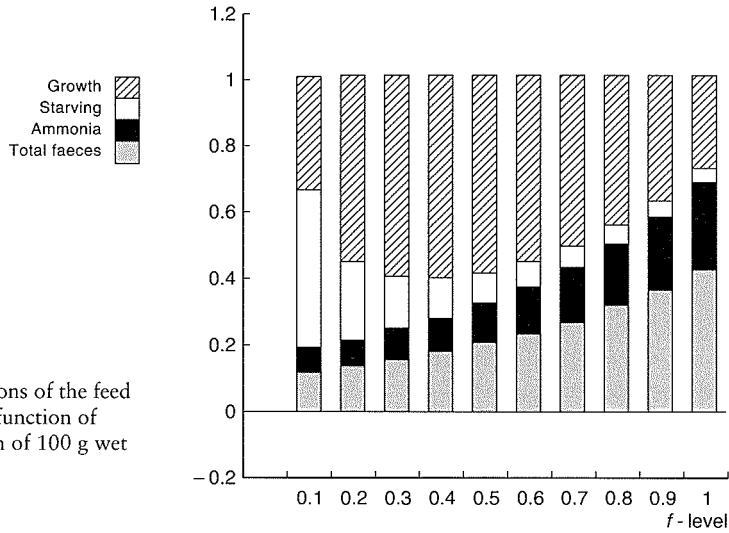


Figure 8. The proportions of the feed on nitrogen basis as a function of feeding level f for a fish of 100 g wet weight at 5 °C.

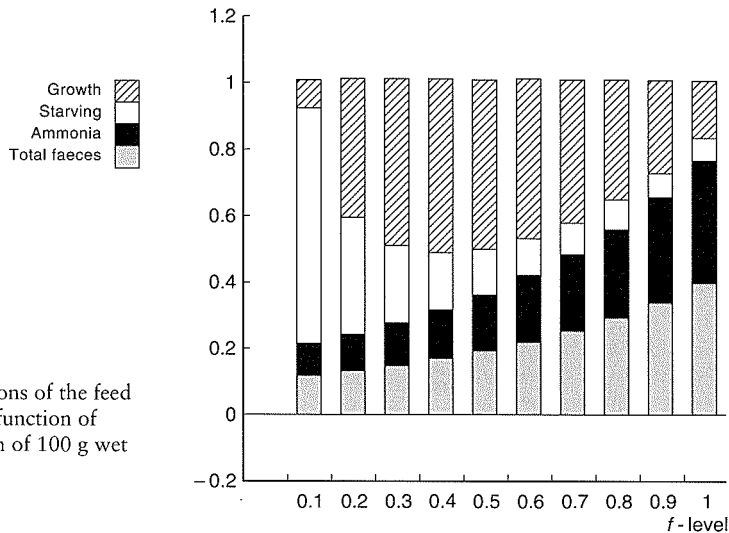


Figure 9. The proportions of the feed on nitrogen basis as a function of feeding level f for a fish of 100 g wet weight at 20 °C.

One very important conclusion is that when rainbow trout are fed with commercial pellets at high feeding level (e.g. $f = 1$) the growth rate is at the maximum at highest temperature (e.g. 20°C) on an energy basis but on nitrogen it is much more complicated. At low temperature (e.g. 5°C) the highest growth rate dw/dt takes place at $f = 0.75$ compared to $f = 1.0$ (28% for $f = 1$ compared with $0.75 \cdot 48\% = 36\%$). At high temperature (e.g. 20°C) we find that the fish have the highest growth rate dw/dt at $f = 0.75$ compared with $f = 1.0$ (17% compared with $0.75 \cdot 40\% = 30\%$).

In Figs 10-11 the feed conversion is shown at different feeding levels and temperatures as a function of fish size. It is seen that the feed conversion efficiency is decreasing with increasing fish size.

Figure 10. Feed conversion efficiency dw/dR on energy basis as a function of fish size at 5°C for feeding levels 0.25, 0.50, 0.75, and 1.0.

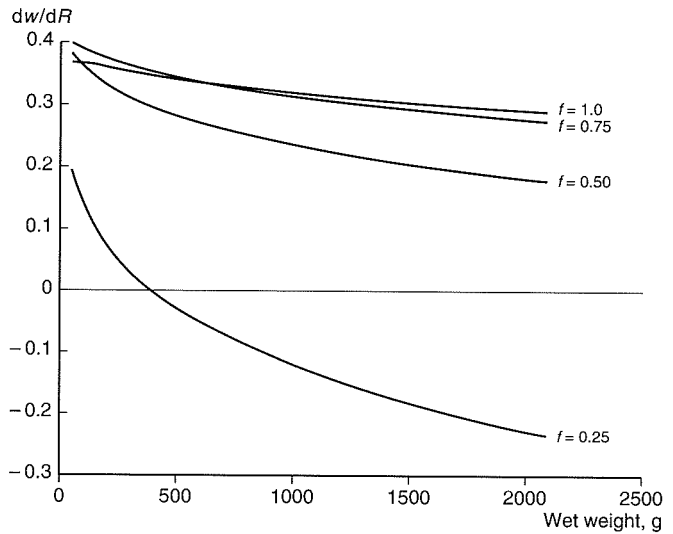
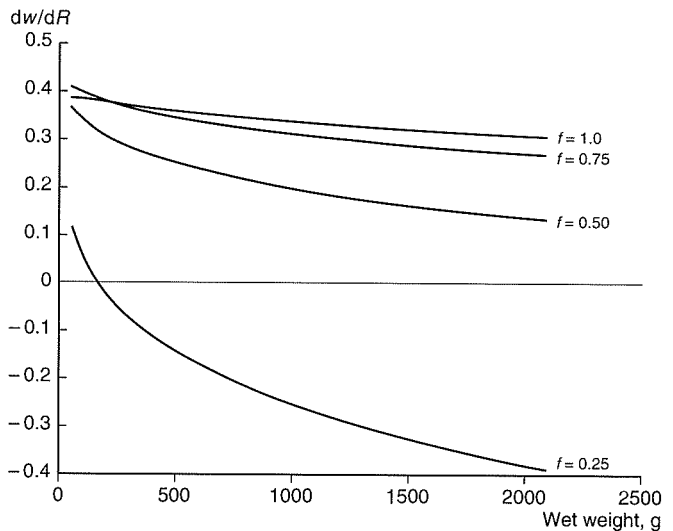


Figure 11. Feed conversion efficiency dw/dR on energy basis as a function of fish size at 20°C for feeding levels 0.25, 0.50, 0.75, and 1.0.



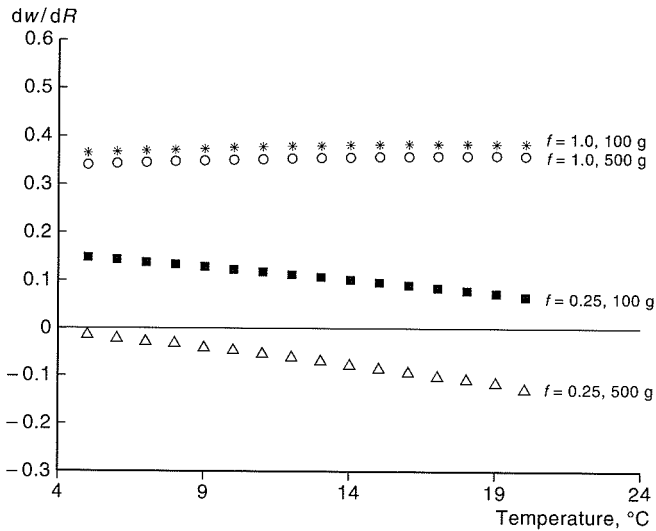


Figure 12. Feed conversion efficiency dw/dR on energy basis as a function of temperature at feeding levels 0.25, 0.50, 0.75, and 1.0 for fish of 100 g and 500 g wet weight.

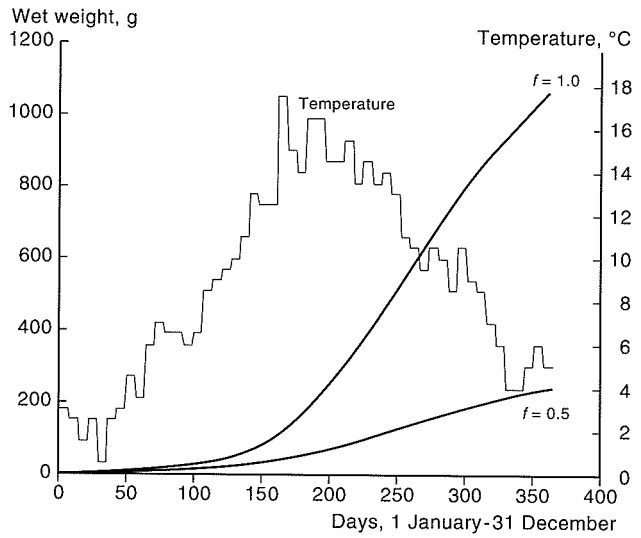


Figure 13. Growth of a rainbow trout in the period 1 January to 31 December at temperatures at the Danish Trout Culture Research Station for feeding levels 0.5 and 1.0.

Fig. 12 shows the feed conversion efficiency for a fish of 100 and 500 g wet weight at two different feeding levels ($f = 0.25$ and 1.0) as a function of temperature. It is seen that at high feeding level with increasing temperature and increasing fish size the feed conversion efficiency is nearly independent of temperature but as shown earlier the smaller fish is a little more efficient. At low feeding level the feed conversion decreases as function of temperature but more pronounced due to fish size than due to temperature.

In Fig. 13 is shown the temperature of the water at the Danish Trout Culture Research Station during a year. If the conditions are optimal with enough of feed, space, and oxygen it is seen that it is possible for a rainbow trout in one year to grow from 2.5 to 1200 g wet weight at the prevailing temperatures.

Discussion

If the feed in a growth equation is divided in growth, faeces, excretion, respiration, and starvation this equation will for COD consist of 23 and for nitrogen of 14 parameters. Amount of food and growth is relatively more simple to measure and probably determined with less uncertainties than the parameters in (2) - (7) due to collection and analysis uncertainties of the samples necessary for estimating the parameters. If we not are interested in the sizes of the different terms: faeces, respiration, excretion, and starvation we can write: $dw/dt = dR/dt - \text{remainder term}$, or remainder term = $dR/dt - dw/dt = (3) + (4) + (5) + (6) + (7)$. If we maintain that this gives the actually observed values, the following can be calculated:

$$\frac{\text{Remainder term} - [(3) + (4) + (5) + (6) + (7)]}{\text{Remainder term}} \quad (10)$$

Theoretically (10) should give zero.

A one-sample analysis of (10) gives the following:

Number of observations	208
Mean	-0.0228
Median	0.0254
Variance	0.0858

95% confidence interval for mean gives -0.0629 to 0.0172 and the mean is not significantly different from 0, $t = -1.1231$ and $p = 0.2627$.

So, it can be concluded that the sum of the calculated values (3) to (7) only are about 2% higher than the observed values for $dR/dt - dw/dt$, for which reason the growth equation will calculate a smaller weight increment as a function of time for a given feeding level and temperature than the observed values.

We can also say that the 'remainder term' is the answer book to the question whether the formulae (3) - (7) represent the true partitionings. The answer is confirmed by the analysis. Therefore it can be concluded that the parameters in the growth equation are determined with sufficiently accuracy to describe the growth of rainbow trout.

References

- From, J. & G. Rasmussen, 1984: A growth model, gastric evacuation, and body composition in rainbow trout, *Salmo gairdneri* Richardson, 1836. - Dana 3: 61-139.