De Truttae Nutritione et Incremento

Feeding and Growth Parameters of the Rainbow Trout, *Oncorhynchus mykiss*

(Latin: Trutta Borenis, Español: Trucha arco iris, Francais: Truite arc-en-ciel)

An overview of Data from the Literature and the Internet

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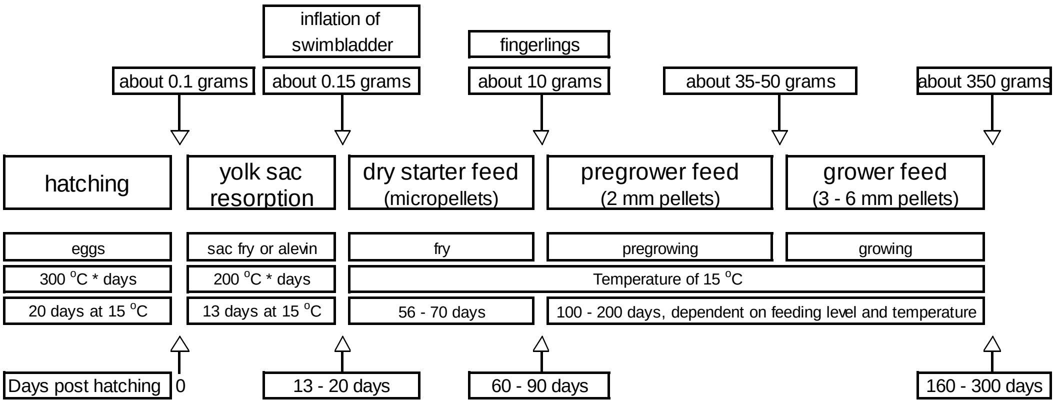
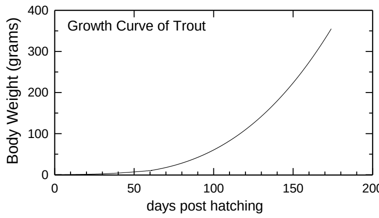
Summary

1. *Life cycle of the trout*

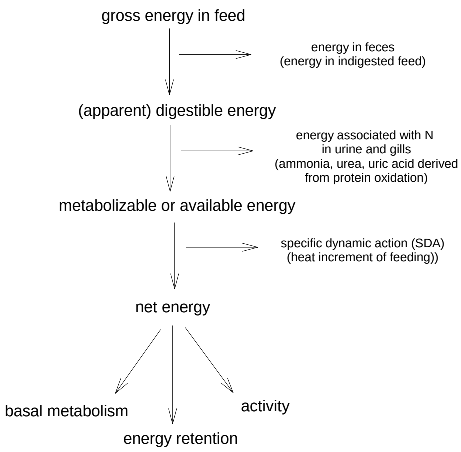


2. *Typical growth curve of trout* (at a temperature of 15 °C and fed a high performance feed containing 45% protein and 28% fat at a level of 12 gram per kg metabolic weight ($BW(kg)^{0.80}$)).



3. *Trout feeds can be analyzed with the Weende analysis* into the 5 major compounds, i.e. protein, fat, moisture, ash and fiber. The % protein and % fat are two major characteristics of trout feeds.

4. *The energy in a trout feed* can be described in terms of (1) gross energy, (2) digestible energy, (3) metabolizable energy and (4) net energy.



5. *The maintenance energy expenditure of a trout at* 15 °C can approximately be described by the formula:

$$\textbf{Energy Expenditure} = 50 * BW(kg)^{0.80} \textbf{ (kJ per day)} \qquad (1)$$

And the efficiency of deposition of energy above maintenance is about 65% (independent of the temperature).

6. *The effect of the temperature T (°C) on the energy expenditure* is exponential and the energy expenditure of a trout at a temperature of $T = T_2$ is:

$$\textbf{Energy Expenditure}_{\text{at } T2} = \textbf{Energy Expenditure}_{\text{at } T1} * e^{0.095(T2 - T1)} \qquad (2)$$

When the energy expenditure = 50 * $BW(kg)^{0.80}$ kJ per day at T_1 = 15 °C, then combining (1) and (2) gives:

$$\textbf{Energy Expenditure}_{\text{at } T = T} = 12.0254 * e^{0.095 * (T)} * BW(kg)^{0.80} \textbf{ (kJ per day)} \qquad (3)$$

7. *The body composition of a trout* can be described by allometric equations of the form: $y = a * BW(g)^b$:

Moisture (%) = 92.25 BW(g) $^{-0.0543}$
Fat (%) = 3.235 BW(g) $^{0.243}$
Protein (%) = 13.36 BW(g) $^{0.036}$
Ash (%) = 2.1978 BW(g) $^{-0.004}$
Energy (kJ/g) = 3.84 BW(g) $^{0.1510}$

Moisture (g) = 0.9225 BW(g) $^{0.9458}$
Fat (g) = 0.03235 BW(g) $^{1.243}$
Protein (g) = 0.1336 BW(g) $^{1.036}$
Ash (g) = 0.021978 BW(g) $^{0.996}$
Energy (kJ) = 3.84 BW(g) $^{1.1510}$

There is a negative linear correlation between the % body fat and % body water in trout:

% body fat = 66.72 – 0.81 * % body fat **(4)**

8. *The relationship between the body weight (grams) and the body length* (centimeters) of a trout can be described by the allometric equation:

Body Weight (grams) = 0.00424 * Body Length (centimeters)$^{3.3807}$. **(5)**

The condition factor of a trout is the weight of a trout per cubic length and is described by the allometric equation:

Condition factor = [100 * (body weight (grams))] / [(body length (centimeters))^{3}] **(6)**

9. *The feed intake in trout* can be described by allometric scaling formulae of the general form:y = a*BW(kg) ^{b} in two different ways:

(a) as percentage of body weight (grams per 100 grams of fish per day) or
(b) in grams per kg metabolic weight (per BW(kg) $^{0.80}$) per day

The feed intake expressed in % of body weight per day can be converted into the feed intake expressed in grams per kg metabolic weight (per BW(kg) $^{0.80}$) per day with the formula:

Feed Intake in grams per kg metabolic weight = c = 10 *(% feed intake) / (BW(kg) $^{-0.20}$) **(7)**

and the feed intake expressed in grams per kg metabolic weight (c, per BW(kg)$^{0.80}$) per day can be converted in the feed intake expressed as % of body weight per day with the formula:

% feed intake = (c/10) * BW(kg) $^{-0.20}$ **(8)**

where c is the feed intake per kg metabolic weight (per kg BW(kg)$^{0.80}$) per day.

The effect of the temperature T (^{o}C) on the feed intake is exponential and the feed intake of a trout at a temperature of T = T_2 is:

Feed intake at T_2 = Feed intake at T_1 * e$^{0.095(T2 - T1)}$ **(9)**

A typical *low feeding level* for trout at 15 ^{o}C is 9.25 grams of feed per kg metabolic weight (per BW(kg) $^{0.80}$) for all sizes of trout or (converting with formula 8) % feed intake = 0.925 * BW(kg) $^{-0.20}$ and including the effect of the temperature T in ^{o}C (with formula 9) results in the formula:

feed intake in grams per kg metabolic weight $_{\text{at temperature T}}$ = 2.345 * e $^{0.095 * (T)}$
or
% feed intake $_{\text{at temperature T}}$ = 0.2345 * BW(kg) $^{-0.20}$ * e $^{0.095 * (T)}$

and a typical *high feeding curve* for trout at 15 ^{o}C is 17.5 grams of feed per kg metabolic weight (per BW(kg) $^{0.80}$) for all sizes of trout or (converting with formula 8) % feed intake = 1.75 * BW(kg) $^{-0.20}$ and including the effect of the temperature T in ^{o}C (with formula 9) results in the formula:

feed intake in grams per kg metabolic weight $_{\text{at temperature T}}$ = 4.209 * e $^{0.095 * (T)}$
or
% feed intake $_{\text{at temperature T}}$ = 0.4209 * BW(kg) $^{-0.20}$ * e $^{0.095 * (T)}$

These feeding curves involve that the feed intake expressed in grams per kg metabolic weight *at a defined temperature* is independent of the body weights and is the same for all body weights and that also the ratio of metabolizable energy for production / metabolizable energy for maintenance (Mp/Mm) *at a defined temperature* is the same for all body weights.

10. *The criteria for a good trout feed* (or a good trout feed ingredient) can be summarized with the 4 P ‘s concept:

1.	**P**alatability	Attractive feed to assure a high feed intake.
2.	**P**erformance	A good feed conversion ratio FCR or feed efficiency ratio (FER).
3.	**P**ollution	High digestibility and faeces that are compact and thus easily to collect.
4.	**P**rice	The price should be right and the feed should be cost effective.

Contents

1. Life Cycle of the Rainbow Trout

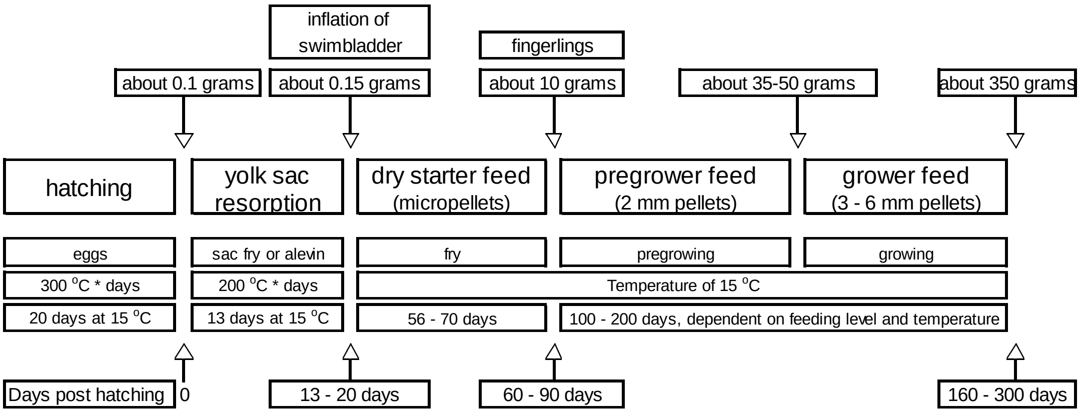


Figure 1
Life cycle of the trout

Trout eggs are relatively large in diameter (3 - 7 mm). Fertilized eggs of rainbow trout usually hatch in 300 °C days, this means that the hatching time is dependent on the temperature. For example, when the temperature is 15 °C, then the hatching time will be 300 / 15 = 20 days (15 * 20 = 300). Body weights of newly hatched are about 0.1 grams and the body weights is about 0.15 grams after resorption of the yolk sac.

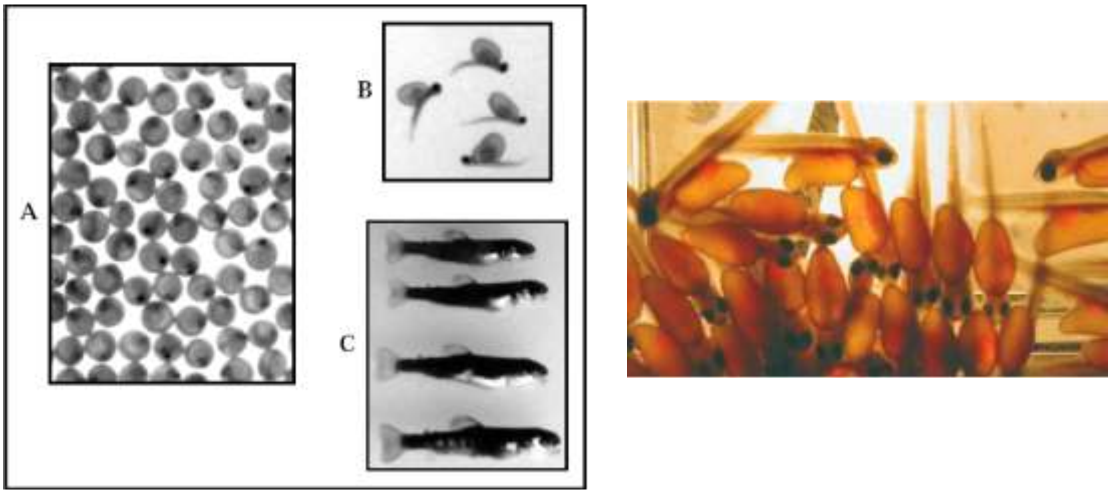


Figure 2
Eyed eggs (A); Sac fry or alevins (B); Small fingerlings (C) and sac fry or alevins 1 day after hatching (picture on the right).

The name alevin is derived from the Latin allevare and the French allever. This verb means to lift up or to rear. The name fry is derived from the Latin fricare and the French freier or frier, and this verb means to rub, or to spawn. The word to spawn is derived from the Latin expandere and means to spread out, and to spawn means to produce or to deposit eggs.

At the time of hatching, trout alevins have a large reserve of yolk remaining from the egg. As an example, rainbow trout alevin wet weight is approximately 70% yolk and 30% embryo. This yolk is denser than water causing the alevins to dwell on the bottom. As the alevins consume (or metabolize) the yolk to meet their energy needs, their wet weight actually increases. This occurs because tissues (muscle, organs etc.) have a higher moisture or water content than the yolk does. Research has shown that 1 gram of yolk is converted to between 2 – 3 grams of tissue. The alevin weight continues to increase until just before the completion of the yolk absorption. This stage has been termed "Maximum Alevin Wet Weight" (MAWW) (Figure 3) and occurs near the optimal time for ponding and the initiation of feeding. The graph below demonstrate the occurrence of this developmental; stage (at 10 ^{o}C). The swim bladder starts to develop and the larvae are now emerging to the surface and looking for feed.

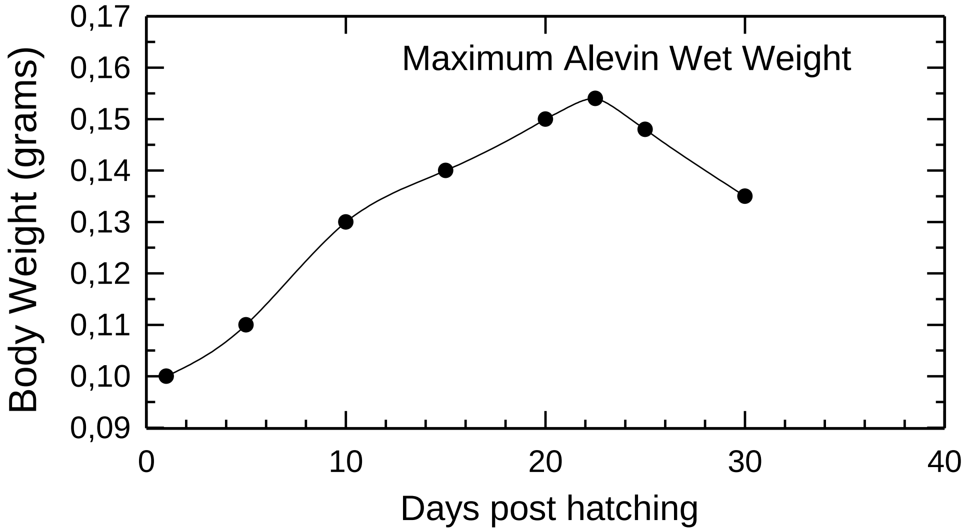


Figure 3
Maximum Alevin Wet Weight (MAWW)

The larvae can be fed (this is not necessary) for one day with artemia and then transferred to dry starter feed. It takes about 8 – 10 weeks for the larvae to reach a body weight of about 10 grams and the larvae are then called fingerlings because they have the size of a finger (8 – 11 cm).

The fingerlings are first fed with pre-grower diets (about 2 mm pellets) and then with grower diets after they have reached a body weight of about 35 – 50 grams. It will take up to about 200 days (depending on the water temperature and the feeding level) for the 10 grams fingerlings to reach a body weight of about 350 grams, the so-called table size trout.

The minimum temperature for growth is about 5 ^{o}C. At this temperature and below, the appetite is suppressed, the digestive system operates very slowly and trout require only a maintenance diet. The optimum temperature of the trout is about 8 – 18 ^{o}C.

Trout (male and female) are able to reproduce themselves when they are approximately 3 - 4 years old.

The production of rainbow trout has grown exponentially since the 1950s, especially in Europe and more recently in Chile. This is primarily due to increased inland production in countries such as France, Italy, Denmark, Germany and Spain to supply the domestic markets, and mariculture in cages in Norway and Chile for the export market. Chile is currently the largest producer. Other major producing countries include Norway, France, Italy, Spain, Denmark, USA, Germany, Iran and the UK.

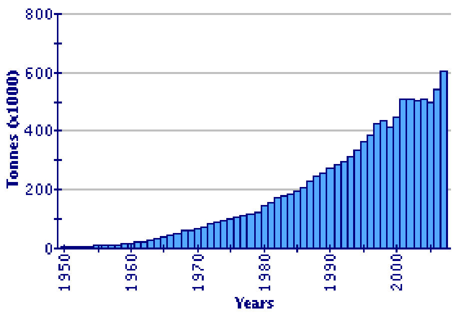


Figure 4
Global production of Oncorhynchus mykiss (Source FAO)

The trout is a carnivorous fish species and feeds predominantly on fish in its natural habitat. The length of the intestine is very short (about 0.7 times the body length) which is characteristic for carnivorous animal species.

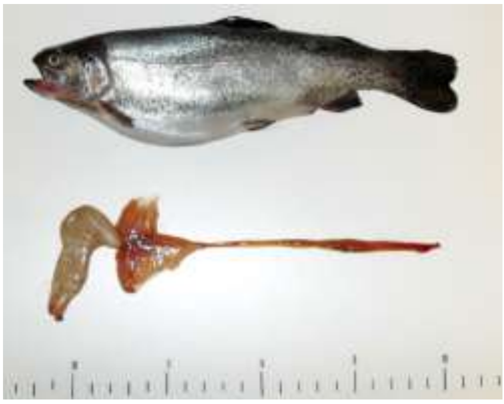


Figure 5
The intestine of the trout including the stomach and the pyloric caecum between the stomach and the intestines.

2. The Composition of Trout Feeds

Around the year 1860, the researchers Henneberg and Stohmann at the Agricultural Research Institute in Weende in Germany proposed to partition animal feeds into six major compounds, i.e. (1) moisture, (2) protein, (3) fat, (4) ash, (5) crude fibre and the so called (6) nitrogen free extract (NFE). The moisture, protein, ash and fibre were measured and the NFE was calculated as the difference between the total amount of the feed and these five measured compounds. This so-called Weende analysis is still being used for the analysis of (fish) feeds and foods.

Trout feeds are mostly characterized by their protein and fat levels and the ratio of protein / energy (mg protein / kJ energy). The protein in the feed is primarily needed for the build-up of (muscle) tissues and the fat is a major source of energy and for accretion of fat tissue. Protein drives the growth but there is a maximum amount of protein that can be deposited per day. Thus, it is important that sufficient protein (and protein with the right amino acid composition) is taken up to achieve this maximum protein deposition and growth. On the other hand, the intake of excess of protein that exceeds the maximum capacity to deposit the protein, and also excess of energy will result in the deposition of fat and result in fatty fish. Thus, the right ratio of energy to protein and the right amount of feed is important for optimal growth and trout composition.

The amount of carbohydrates in trout feeds are usually low, since trout are carnivorous and have a low capacity to digest carbohydrates. As a consequence, the energy in the diet has to be derived from fat and fat has a higher energy density than carbohydrates. For that reason, fish feeds are more concentrated and have thus also a higher protein level (up to about 40 – 45%) and energy density than feeds for terrestrial (omnivorous or herbivorous) farm animals.

In addition, trout is carnivorous and eats in its natural habitat other fish, thus the composition of the diet of the trout is thus more or less similar to the composition of the trout itself. A trout of 250 grams contains approximately 70% water, 12% fat, 16% protein and 2% ash (see paragraph 14). Trout feed contains about 5% moisture and when we reduce the % moisture of a trout (70%) to 5% moisture, then the composition of the trout would be 5% moisture, 51% protein, 38% fat and 6% ash, which is comparable with the composition of a high performing trout feed.

The digestible protein / digestible energy ratio is thus an important characteristic of a fish feed, and as a rule of thumb, this ratio in the trout feed (for growing trout) should be similar to the ratio of protein / energy of the fish itself. This way, a maximal retention of dietary protein, an expensive ingredient of trout feed, is achieved. When the trout grows larger, the protein / energy ratio of the trout becomes lower (the percentage fat of the trout increases whereas the percentage protein remains the same), and as a consequence, the ratio protein / energy in the diet should also decrease in order to maintain a maximum protein retention. This phenomenon is called phase feeding or the protein sparing effect of fat (see paragraph 15).

3. Energy in Trout Feeds

Fats, carbohydrates and proteins are the major sources of energy in trout feeds. The energy density of these three compounds is different and the amount of energy in a trout feed is related to the amount of fat, carbohydrates and proteins in the feed. The energy in a trout feed can be expressed as gross, digestible and metabolizable energy (Figure 6).

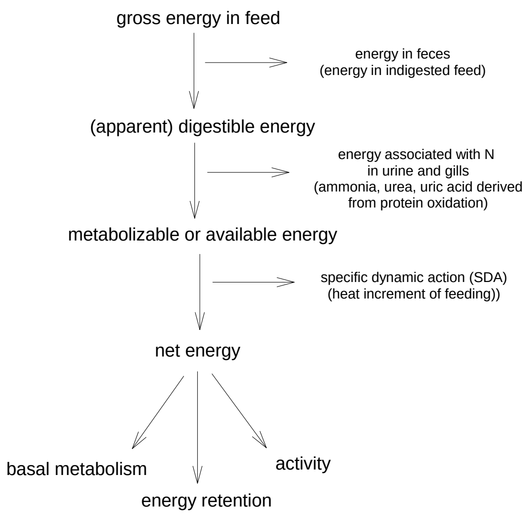


Figure 6
Gross, digestible, metabolizable, and net energy

Gross Energy

The gross energy is the energy or heat that is generated when the feed is completely oxidized. The law of Hess (1838) states that the heat produced in a chemical reaction is always the same regardless of whether it proceeds directly or via a number of intermediate steps (the law of constant heat summation). It means effectively that the heat of metabolizing a nutrient through a complex web of metabolic reactions in the body may be determined and duplicated by measuring the heat produced by burning the same nutrient in a bomb calorimeter. The gross energy can thus be determined by complete combustion of the feed in a so called bomb calorimeter and by measuring the amount of energy or heat that is released. This way, the amount of gross energy can be determined in a complete feed or in only fat, carbohydrates or proteins (Table 1).

Table 1

Energy values of various dietary compounds as used in fish nutrition.

	Gross Energy in 1 gram nutrient (kJ/gram)	Metabolizable Energy in 1 gram nutrient (kJ/gram)	Digestibility (%)	Digestible energy in feed (kJ/gram nutrient)	Metabolizable energy in feed (kJ/gram nutrient)
Crude Fat	39.60	39.60	90 (90-95)	35.64	35.64
Crude Protein	23.65	19.67	95 (85-95)	22.50	18.69
NFE or Carbohydrates	17.50	17,50	70 (40-90)	12.25	12,25
Fiber and Cellulose	17.50	17,50	0	0	0

The gross energy and metabolizable energy in 1 gram of fat or carbohydrate are the same. However, the metabolizable energy in 1 gram of protein is the gross energy minus the energy that is excreted into the urine in the form of ammonia (85%) and urea (15%) (see Appendix 3, footnote 6 (g)). The values for gross energy and for the metabolizable energy in 1 gram nutrient can be used for all fish species. However, the values for the digestibilities (and thus the values for the digestible and metabolizable energy in the feed) may vary and is dependent on the type of the diet and the fish species.

Fish metabolize and oxydize predominantly fat and proteins and the average energy equivalent of oxygen (Eeq O_2) for fat (13.72 kJ per gram oxygen) and for protein (13.79 per gram oxygen in ammoniatelic fish) (see Appendix 3) is about 13.75 kJ per gram oxygen. Thus, the energy expenditure or heat production of the fish in kJ can be calculated by multiplying the oxygen uptake (grams) of a fish by 13.75.

Digestible Energy

The digestible energy is the amount of gross energy in the feed that is digested and is taken up by the fish. The digestibility of fat, carbohydrates and proteins is different and is dependent on various factors. Some raw materials are better digested than others and also the feeding level plays a role; a higher feed intake results usually in a lower digestion of the feed. The average digestibilities are given in Table 1 and are generally used to calculate the digestible energy in a fish feed.

Metabolizable Energy

The metabolizable energy is the energy in the feed that the trout can actually utilize. Metabolizable energy is the digested energy that the body can use and is available to the body. The (gross) energy of the digested carbohydrates and fat are completely available for the body. The fish can completely oxidize the fat and carbohydrates to generate energy. The metabolizable energy of fat and carbohydrates would be equal to the gross energy when fat and carbohydrates would be completely digested. Proteins, on the other hand, contain nitrogen and the nitrogen that is released during the oxidation of proteins as ammonia can only be excreted by the fish in the form of ammonia and urea. About 85% of the released nitrogen is excreted as ammonia through the gills and about 15% as urea in the urine. Ammonia and urea contain substantial amounts of energy, i.e. ammonia has an energy density of 20.7 kilojoule (kJ) per gram and 1 gram urea an energy density of 10.8 kJ per gram. This means that the fish can not completely use the gross energy in the proteins. Protein contains 23.65 kJ gross energy per gram and the fish can only use 19.67 kJ per gram (see Appendix 3, footnote 6 (g) for the calculations and values) .

Net Energy

The processing of the nutrients after digestion (storage, de-amination, synthesis such as the synthesis of urea etc. (see Appendix 3)) requires energy and this energy is called the specific dynamic action (SDA) or the thermic effect of feed or food (TEF). The net energy is the metabolizable energy corrected for the energy of the SDA. Net energy is thus the energy that can eventually be used for the maintenance, activity and growth.

Calculation of the energy in a trout feed

The amount of energy in a trout feed can be easily calculated with the data in Table 1. The percentages of fat, protein, ash and fibre are usually declared on the label on the bag of the trout feed and the percentage of moisture is usually about 4 - 8%. The percentage of carbohydrates (also called the nitrogen free extract, or NFE) is calculated as (100 - % protein - % fat - % ash - % fibre -% moisture). Table 2 gives as example of a trout feed with 45% protein, 30% fat, 10% ash and 1% fibre. Thus the percentage of carbohydrates or NFE = (100 – 45% protein – 30% fat - 10% ash – 1% fibre – 4% moisture) = 10%.

Energy is usually expressed in joules (J) or kilojoules (kJ; 1 kJ = 1000 joules). Sometime, energy is also expressed in calories (cal) or kilocalories (kcal); 1 cal = 4.184 joule. In the metric system and in science only joules are used.

Table 2
Composition of a typical trout feed

Nutrient	% in diet	Gross Energy in 1 gram nutrient (kJ/gram)	Metabolizable Energy in 1 gram nutrient (kJ/gram)	Gross Energy in 1 gram feed (kJ/gram)	Digestibility (%)	Digestible Energy in 1 gram feed (kJ/gram)	Metabolizable Energy in 1 gram feed (kJ/gram)
Protein	45,0	23,65	19,67	10,64	95,00	10,11	8,40
Fat	28.0	39,60	39,60	11,09	90,00	9,98	9,98
Ash	9,0						
Moisture	5,0						
Fiber	1,0	17,50	0,00	0,18	0,00		
NFE	12,0	17,50	17,50	2,10	60,00	1,26	1,26
Total	100,0			24,01		21,35	19.64

NFE, nitrogen free extract, the carbohydrate faction. DP/DE (digestible protein/digestible energy) = (450*0.95) / 21.35 = 20.02 mg/kJ

4. Feed Sizes for Trout

The size of the feed is dependent on the body weight and body length of the trout. The feed sizes as recommended by the fish feed manufacturers Coppens International and Biomar are given in Table 3.

5. Energy Expenditure of Trout and the Effect of the Temperature

In non-growing trout on a maintenance diet, there is an energy balance, i.e. the intake of energy equals the energy expenditure or heat production. The maintenance energy expenditure or heat production of a trout is composed of the basal metabolic rate or routine metabolism (measured in the fasting situation) and the specific dynamic action (SDA) of the feed, The SDA is the energy that is used for the various metabolic processes involved the processing of the feed after digestion, such as for example deamination and synthesis of proteins and conversion of carbohydrates and proteins into fats etc. Eventually, all the energy that is digested is dissipated as heat (energy expenditure or heat production) when there is an energy balance. The maintenance energy expenditure of a trout at 15 ^{o}C is about 50 * BW(kg)$^{0.80}$ kJ per day and the fasting or routine metabolisme is about 35 * BW(kg)$^{0.80}$ kJ per day.

Table 3
Pellet size of trout feed

Coppens International (2010)			Biomar (2014)			
Body Weight (grams)	Trout Length (cm)	Pellet Size (mm)	Body Weight (grams)	Trout Length (cm)	Pellet Size (mm)	Type Feed
<0.2	< 0.2	0.3 - 0.5	0.2 - 0.4	3 - 4	0.5	starter
0.2 - 0.5	2 - 3	0.5 - 0.8	0.4 - 1.5	4 - 5	0.8	starter
0.5 - 2	3 - 5	0.8 - 1.2	1.5 - 5	5 - 8	1.1	starter
2 - 10	5 - 10	1.2 - 1.5	5 - 15	8 - 11	1.5	starter
10 - 35	10 - 15	2	15 - 50	11 - 16	2	pregrower
35 - 200	15 - 25	3	50 - 100	16 - 21	3	grower
200 - 500	25 - 34	4.5	100 - 450	21 - 33	4.5	grower
> 500	> 34	6	> 450	> 33	6	grower

Data from the website of www.Coppens.eu (accessed in 2010) and from www.biomar.com (accessed 2014)

In growing, weight-gaining trout, however, a part of the energy intake is retained and stored in the body (predominantly in the form of protein and fat and some glycogen) and the efficiency of energy storage is defined as the amount of energy stored, divided by the energy intake above maintenance. The average efficiency of energy storage above maintenance is about 65%, but is different for fat (about 75%) and protein (about 53%). The efficiency of energy storage is independent of the temperature.

The maintenance energy expenditure of a trout at a temperature of 15 ^{o}C can approximately be described by the allometric scaling formula (Gillooly et al., 2001, Glencross 2009) :

$$\textbf{Energy Expenditure} = 50 * \textbf{BW(kg)}^{0.80} \textbf{ kJ per day}$$

where 50 is the normalization constant and 0.80 is the scaling coefficient for fish. BW(kg)$^{0.80}$ is defined as the so-called metabolic weight.

The various metabolic processes in the body that generate the metabolic rate or the energy expenditure are a complex of biochemical reactions and the effect of the body temperature on all these biochemical reactions follows the same pattern as the effect of the temperature on a single (bio)chemical reaction. The effect of the temperature on the velocity of a chemical reaction is described by the formula of Arrhenius and is exponential. Thus the effect of the temperature on the energy expenditure of a trout should also be exponential (see Gillooly et al. (2001) and Clarke and Johnston (1999)).

The effect of the temperature (T) on the energy expenditure of the trout is thus exponential and is described by the formula (Elliott 1976):

$$\textbf{Energy Expenditure at } T_2 = \textbf{Energy Expenditure at } T_1 * e^{0.095(T2-T1)}$$

Example:
The Energy Expenditure of a trout at 15 ^{o}C is 50 kJ per kg metabolic weight (per BW(kg) $^{0.80}$.

The Energy Expenditure of a trout at 10 ^{o}C is then:
Energy Expenditure $_{at\ T = 10}$ = energy expenditure $_{at\ T= 15}$ * $e^{0.095(T2 – T1)}$ or
Energy Expenditure at $_{T = 10}$ = 50 * BW(kg) $^{0.80}$ * $e^{0.095(10 – 15)}$ = 31 * BW(kg) $^{0.80}$ kJ

The (maintenance) energy expenditure of a trout at T_1 = 15 ^{o}C is 50 * BW(kg)$^{0.80}$ kJ per day and therefore:

$$\text{Energy Expenditure at } T_2 = 50 * BW(kg)^{0.80} * e^{0.095 * (T2-15)}$$

$$\text{Energy Expenditure at } T_2 = 50 * BW(kg)^{0.80} * (e^{0.095 * (T2)} / e^{0.095 * (15)})$$

$$\text{Energy Expenditure at } T_2 = 50 * BW(kg)^{0.80} * (e^{0.095 * (T2)} / e^{0.095 * (15)})$$

$$\text{Energy Expenditure at temperature } T_2 = T = (50 / e^{0.095 * 15}) * BW(kg)^{0.80} * e^{0.095 * (T)}$$

$$\mathbf{\text{Energy Expenditure}_{\text{at temperature } T = T} = 12.0254 * BW(kg)^{0.80} * e^{0.095 * (T)}}$$

Example:
The temperature is 15 ^{o}C, then: Energy Expenditure $_{at\ temperature\ T = 15}$ = 12.0254 * $e^{0.095 * 15}$ = 50 * BW(kg) $^{0.80}$ kJ
The temperature is 10 ^{o}C, then: Energy Expenditure $_{at\ temperature\ T = 15}$ = 12.0254 * $e^{0.095 * 10}$ = 31 * BW(kg) $^{0.80}$ kJ

Example:
The formula for the metabolic rate of a trout is:
Energy expenditure = a * BW(kg)$^{0.80}$
where the body weights are expressed in kg. We can also convert this formula into a formula where the body weights are expressed in grams. The formula is then:
Energy Expenditure = x * BW(g)$^{0.80}$
We can calculate the value of x as following:
Energy Expenditure = a * BW(kg)$^{0.80}$ = x * [BW(kg)*1000)(g)]$^{0.80}$

Solving for x gives:
x = [a * BW(kg)$^{0.80}$] / [BW(kg)*1000)(g)]$^{0.80}$ =
x = [a * BW(kg)$^{0.80}$] / BW(kg)$^{0.80}$ * 1000 $^{0.80}$ = a / 1000 $^{0.80}$

thus the formula becomes then:
Energy Expenditure = (a / 1000 $^{0.80}$) * BW(g)$^{0.80}$ where the body weights are now expressed in grams.

On the other hand, when the body weight is expressed in grams, and we want to express the body weights in the formula again in kg, then the formula becomes again:

Energy Expenditure = a * 1000 $^{0.80}$ * BW (kg)

Thus:

Conversion from kg into grams: Divide a (the normalization constant) by 1000$^{0.80}$ (0.80 is scaling factor or coefficient)
Conversion from grams into kg: Multiply a (the normalization constant) by 1000$^{0.80}$ (0.80 is scaling factor or coefficient)

Example:
We have a trout of 150 grams:
The energy expenditure is then 50 * BW(kg)$^{0.80}$ = 50 * 0.15 $^{0.80}$ = 10.96 kJ per day (weight in kilograms) or
The energy expenditure is then (50 / 1000$^{0.80}$) * BW(g) $^{0.80}$ = 0.199 * 150 $^{0.80}$ = 10.96 kJ per day (weight in grams)

6. Feed Intake and Feeding Levels

We can express the feed intake in:

(a) in percentage of body weight (most commonly used way) or
(b) in grams per kg metabolic weight (per $BW(kg)^{0.80}$).

We can convert the feed intake expressed as percentage of body weight into the feed intake expressed in grams per kg metabolic weight (per $BW(kg)^{0.80}$) and the other way around by means of formulae given below.

(a) Feed intake expressed per kg metabolic weight (per $BW(kg)^{0.80}$).

The energy expenditure of a trout is expressed in kJ per kg metabolic weight (per $BW(kg)^{0.80}$) and the maintenance metabolic rate or energy expenditure of a trout at 15 ^{o}C is described by the allometric scaling formula (see paragraph 5):

$$\text{Energy Expenditure} = 50 * BW(kg)^{0.80} \text{ kJ per day}$$

The maintenance energy expenditure of the trout at 15 ^{o}C is 50 kJ per kg metabolic weight (per $BW(kg)^{0.80}$) and the trout should thus have a metabolizable energy intake of 50 kJ per $BW(kg)^{0.80}$ or have a feed intake per $BW(kg)^{0.80}$ that supplies this 50 kJ per $BW(kg)^{0.80}$ for maintenance. Therefore, the (maintenance) feed intake should follow the same pattern as the (maintenance) energy expenditure and the (maintenance) feed intake (or energy intake) should thus also be expressed in grams per kg metabolic weight (per $BW(kg)^{0.80}$).

When the feed intake is c grams per kg metabolic weight (per $BW(kg)^{0.80}$), then he total feed intake is:

$$\text{Feed Intake (grams)} = c * BW(kg)^{0.80}.$$

where BW is the body weight of the trout in kg.

When more feed and thus more metabolizable energy per kg metabolic weight (per $BW(kg)^{0.80}$) is administered than required for maintenance (Mm), then the excess of the feed intake or the excess of metabolizable energy intake will be used for growth or production (Mp). The ratio of metabolizable energy for production / metabolizable energy for maintenance (Mp/Mm) is defined as:

$$\frac{\mathrm{Mp}}{\mathrm{Mm}} = \frac{(\text{feed intake} * \text{energy density feed}) * BW(kg)^{0.80} - (\text{maintenance feed intake} * \text{energy density feed}) * BW(kg)^{0.80}}{(\text{maintenance feed intake} * \text{energy density feed}) * BW(kg)^{0.80}} \text{ or}$$

$$\frac{(\text{feed intake} - \text{maintenance feed intake}) * (\text{energy density feed}) * BW(kg)^{0.80}}{(\text{maintenance feed intake}) * \text{energy density feed} * BW(kg)^{0.80}} \text{ or}$$

$$\frac{(\text{feed intake} - \text{maintenance feed intake})}{(\text{maintenance feed intake})}$$

where the feed intake represents the feed intake per kg metabolic weight (per $BW(kg)^{0.80}$, the maintenance feed intake represents the maintenance feed intake per kg metabolic weight (per $BW(kg)^{0.80}$) (a constant quantity at each temperature to support the maintenance energy expenditure), and the energy density of the feed is the metabolizable energy per gram feed (kJ/g).

The Mp/Mm is determined by the feed intake (or metabolizable energy intake) per kilogram metabolic weight (per $BW(kg)^{0.80}$) and changes when the feed intake per kilogram metabolic weight (per $BW(kg)^{0.80}$) changes (see Figure 18, page 52). Each defined level of feed intake c (or metabolizable energy intake) per kg metabolic weight (per $BW(kg)^{0.80}$) above maintenance is associated with a defined ratio of metabolizable energy for production / metabolizable energy for maintenance (Mp/Mm) (Figure 18, page 52)

Thus, when the *same* amount of feed per kg metabolic rate (per $BW(kg)^{0.80}$) is administered to *different* sizes trout, then also the ratio of Mp/Mm will be the *same* for all these different sizes trout. An increase or decrease of the feed intake per kg metabolic weight (per $BW(kg)^{0.80}$), however, will result in more or less metabolizable energy available for growth or production and thus also result in an increase or decrease of the ratio Mp/Mm (see Figure 18).

(b) Feed intake expressed as % of body weight.

It is, however, more common and practical to express the feed intake as % of body weight. The feed intake per kg metabolic weight (per $BW(kg)^{0.80}$) can be converted into the feed intake expressed as percentage of body weight and the other way around. When the feed intake per kg metabolic weight ($BW(kg)^{0.80}$ = c, then the total feed intake is:

$$\text{Total feed intake (grams)} = c * BW(kg)^{0.80} \text{ grams, and}$$

$$\text{Feed intake (grams) per kilogram trout} = (c * BW(kg)^{0.80}) / BW(kg) = c * BW(kg)^{(0.80-1)}$$

$$\text{Feed Intake (grams) per 100 gram trout} = (c * BW(kg)^{-0.20}) / 10$$

$$\textbf{\% feed intake per day (or feed intake per 100 gram of fish)} = \mathbf{(c/10) * BW(kg)^{-0.20}} \qquad \textbf{(1)}$$

where c (grams) is the feed intake per kg metabolic weight ($BW(kg)^{0.80}$) per day and the BW(kg) is expressed in kg and the scaling coefficient is - 0.20.

On the other hand, we can also calculate the feed intake per kg metabolic weight ($BW(kg)^{0.80}$) per day (c) when the % feed intake for a defined size trout is known. Thus:

$$\text{\% feed intake per day} = (c/10) * BW(kg)^{-0.20} \text{ or}$$

$$\textbf{Feed Intake per kg metabolic weight} = \mathbf{c = 10 * (\textbf{\% feed intake per day}) / (BW(kg)^{-0.20})} \qquad \textbf{(2)}$$

Thus we can express the feed intake in:

(a) in percentage of body weight (most commonly used way) or
(b) in grams per kg metabolic weight (per $BW(kg)^{0.80}$).

By means of the two formulas above (formula 1 and 2), we can convert the feed intake expressed as percentage of body weight into the feed intake expressed in grams per kg metabolic weight (per $BW(kg)^{0.80}$) and the other way around.

Conversion of the feed intake either expressed as % of body weight or in expressed in grams per kg metabolic weight (per $BW(kg)^{0.80}$).

when the feed intake per gram metabolic weight (per $BW(kg)^{0.80}$) is c, then:

$$\textbf{\% feed intake per day (or feed intake per 100 gram of fish)} = \mathbf{(c/10) * BW(kg)^{-0.20}} \qquad \textbf{(1)}$$

when the % feed intake is: (% feed intake per day), then

feed Intake per kg metabolic weight = c = 10 *(% feed intake per day) / (BW(kg) $^{-0.20}$) (2)

For the calculations of the *total* feed intake for a defined size trout, we have to know either the *feed intake per kg* metabolic weight or the *percentage feed intake* for each defined size trout (see example below).

Example:
For example, the feed intake expressed in grams per kg metabolic weight (c) is 12 grams per kg metabolic weight (per BW(kg)$^{0.80}$).

The total feed intake of a trout of 300 grams is: 12 * BW(kg)$^{0.80}$ = 12 * (0.3)$^{0.80}$ = **4.58** grams.

We can convert the feed intake expressed per kg metabolic weight (c) into the feed intake expressed as % of body weight with the formula (1):

% feed intake per day (or feed intake per 100 gram of fish) = (c/10) * BW(kg) $^{-0.20}$ = 1.2 * BW(kg) $^{-0.20}$
% feed intake of a trout of 300 grams = 1.2 * BW(kg) $^{-0.20}$ = 1.2 * (0.3) $^{-0.20}$ = 1.5267%

The total feed intake of a trout of 300 gram is: (1.5267/100) * 300 = **4.58** grams

Feed intake (a) as % of body weight or (b) per kg metabolic weight (per BW(kg)$^{0.80}$) can be described by allometric scaling formulae.

The feed intake expressed as % of body weight can be expressed as a function of the body weight by an allometric scaling formula (see formula 1). As a general form of this allometric scaling formula we could use the formula x * BW(kg) ^{p} where x is the normalization constant and p the scaling coefficient:

feed intake as percentage of body weight = x * BW(kg) ^{p}

When we use the formula (formula 2), to convert the feed intake expressed in % of body weight into the feed intake formula expressed in grams per kg metabolic weight (per BW(kg)$^{0.80}$) then:

feed Intake per kg metabolic weight = c = 10 *(% feed intake per day) / (BW(kg) $^{(-0.20)}$)

and replacing % feed intake per day for x * BW(kg) ^{p} gives:

feed Intake (g) per kg metabolic weight = c = 10 *(x * BW(kg) ^{p}) / (BW(kg) $^{(-0.20)}$) or

feed intake (g) per kg metabolic weight (per BW(kg)$^{0.80}$ = c = x * 10 *BW(kg) $^{(p+0.20)}$

where c is the feed intake per kg metabolic weight (per BW(kg) $^{0.80}$).

Thus, the feed intake per kg metabolic weight (per BW(kg)$^{0.80}$) can also be described as a function of the body weight by an allometric scaling formula. As a general form of this allometric scaling formula we could use the formula z * BW(kg) ^{w} where z is the normalization constant and w the scaling coefficient:

feed intake per kg metabolic weight (per BW(kg)$^{0.80}$) = z * BW(kg)^{w}

we can convert this formula into a formula that describes the feed intake as % of body weight with the conversion formula 1:

% feed intake per day (or feed intake per 100 gram of fish) = (c/10) * $BW(kg)^{-0.20}$

where c is the feed intake per kg metabolic weight (per $BW(kg)^{0.80}$) and replacing c by z * $BW(kg)^{w}$ gives:

% feed intake per day (or feed intake per 100 gram of fish) = (z*$BW(kg)^{w}$/10) * $BW(kg)^{-0.20}$ or

% feed intake per day (or feed intake per 100 gram of fish) = (z/10*$BW(kg)^{w-0.20}$)

Thus, both the feed intake expressed in % of body weight and the feed intake expressed in gram per kg metabolic weight (per $BW(kg)^{0.80}$) are functions of the body weights and can be described by allometric scaling formulae. Further, the allometric scaling formula describing the feed intake either expressed as % of body weight or in grams per kg metabolic weight (per $BW(kg)^{0.80}$) can be converted from one to another (see below).

<u>Conversions of the allometric scaling formulas describing the feed intake either expressed as % of body weight or in grams per kg metabolic weight (per $BW(kg)^{0.80}$) as a function of the body weight:</u>

When the feed intake in grams per kg metabolic weight (per $BW(kg)^{0.80}$) (as a function of the BW) is described by the general allometric formula:

feed intake per kg metabolic weight (per $BW(kg)^{0.80}$) = z * $BW(kg)^{w}$, *then (formula 1)***:**

% feed intake = z/10 $BW(kg)^{(w-0.20)}$ **(3)**

When the % feed intake (as a function of the BW) is described by the general allometric formula:

% feed intake = x $BW(kg)^{p}$, *then (formula 2):*

feed intake per kg metabolic weight (per $BW(kg)^{0.80}$) = x * 10 * $BW(kg)^{(p+0.20)}$ **(4)**

<u>Example 1:</u>
The formula for the feed intake expressed in % of body weight is described by the formula:
% feed intake = 1.2 * $BW(kg)^{-0.25}$.
The formula for the feed intake expressed in grams per kg metabolic weight is then (formula 4):
Feed intake per $BW(kg)^{0.80}$ = 1.2 * 10 * $BW(kg)^{(-0.25+0.20)}$ = 12 $BW(kg)^{-0.05}$
Feed intake per $BW(kg)^{0.80}$ of a fish of 200 grams per day = 12 * $(0.2)^{-0.05}$ = 13.0
And the total feed intake of a fish of 200 grams per day = 13 * $(0.2)^{0.80}$ = **3.58** grams per day.

<u>Example 2:</u>
The formula for the feed intake expressed in grams per kg metabolic weight is:
feed intake per $BW(kg)^{0.80}$ = 12 $BW(kg)^{-0.05}$
The formula for the feed intake expressed in % of body weight is then (formula 3):
Feed intake as % of body weight = 12/10 $BW(kg)^{(-0.05-0.20)}$ = 1.2 * $BW(kg)^{-0.25}$
The % feed intake of a fish of 200 grams = 1.2 * $(0.2)^{-0.25}$ = 1.79 % per day.
And the total feed intake of a fish of 200 grams per day = 200 * 1.79/100 = **3.58** grams per day.

When the scaling coefficient p of the formula that expresses the feed intake in % of the body weight is – 0.20 or % feed intake = x * BW(kg) $^{-0.20}$, then conversion of this formula into grams per kg metabolic weight (per BW(kg)$^{0.80}$), gives:

feed intake (g) per kg metabolic weight (per BW(kg) $^{0.80}$ = c = x * 10 *BW(kg) $^{(-0.20 + 0.20)}$ or

feed intake (g) per kg metabolic weight (per BW(kg) $^{0.80}$ = c = x * 10

and the feed intake per kg metabolic weight (per BW(kg)$^{0.80}$) is ***independent*** of the body weight and is the same for all the various body weights. As discussed earlier, a defined feed intake per kg metabolic weight (per BW(kg)$^{0.80}$) is associated with a defined ratio of metabolizable energy for production / metabolizable energy for maintenance (Mp/Mm) (see also Figure 18). Thus, when the scaling coefficient of the formula that describes the feed intake as % of body weight is - 0.20, then both the feed intake per kg metabolic weight (per BW(kg) $^{0.80}$) and the ratio of metabolizable energy for production / metabolizable energy for maintenance (Mp/Mm) are the same for all sizes of trout and is independent of the trout size (see also Figure 18). Some examples are given below.

Example 1:
We have for example the feeding curve: % feed intake = 1.2 * (BW(kg)) $^{-0.25}$. We can convert this formula into a formula that describes the feed intake per kg metabolic weight (per BW(kg)$^{0.80}$) with the conversion formula 2:
feed intake (g) per kg metabolic weight (per BW(kg) $^{0.80}$) = c = 10 * (% feed intake) / BW(kg) $^{-0.20}$
replace % feed intake by 1.2 * (BW(kg) $^{-0.25}$:
feed intake (g) per kg metabolic weight (per BW(kg) $^{0.80}$) = c = 10 * (1.2 * *BW(kg) $^{-0.25}$) / BW(kg) $^{-0.20}$ or
feed intake (g) per kg metabolic weight (per BW(kg) $^{0.80}$) = c = 10 * 1.2 * BW(kg) $^{-0.25}$ * BW(kg) $^{0.20}$ (formula 4) or
feed intake (g) per kg metabolic weight (per BW(kg) $^{0.80}$) = c = 12 *BW(kg) $^{(-0.25 + 1.20)}$ or
feed intake (g) per kg metabolic weight (per BW(kg) $^{0.80}$) = c = 12 * BW(kg) $^{(-0.05)}$

Example 2:
(1) We have for example a feeding curve that is be described by the allometric scaling formula:
% feed intake (gram per 100 gram trout) = 1.2 * BW(kg) $^{-0.25}$ (see example 1)
When we have a trout of 200 grams (0.20 kg), the percentage feed intake is then:
% feed intake (gram per 100 gram trout) = 1.2 * (0.20) $^{-0.25}$ = **1.79**%
The total feed intake of the trout of 200 grams is :
Total feed intake of the trout of 200 grams = percentage feed intake/100 * BW(grams)
Total feed intake of the trout of 200 grams = (1.79/100) * 200 grams = **3.58 grams**

(2) The feed intake expressed as % of body weight can be converted into the feed intake expressed in grams per kg metabolic weight (per BW(kg) $^{0.80}$) with the formula 2:
feed Intake per kg metabolic weight = c = 10 *(% feed intake per day) / (BW(kg) $^{-0.20}$) (formula 2)
replace % feed intake per day in the formula by 1.2 * BW(kg) $^{-0.25}$:
feed Intake per kg metabolic weight = c = 10 *(1.2 * (BW(kg) $^{-0.25}$) / (BW(kg) $^{-0.20}$) (formula 4) or
feed Intake per kg metabolic weight = c = 12 * (BW(kg) $^{-0.05}$.
When we have a trout of 200 grams (0.20 kg), the feed intake per kg metabolic weight (per BW(kg) $^{0.80}$) is then:
feed intake per gram metabolic weight (per BW(kg) $^{0.80}$) = 12 * (0.2) $^{-0.05}$ = **13.00**
The total feed intake of the trout of 200 grams (0.20 kg) is :
Total feed intake of the trout of 200 grams = c * BW(kg) $^{0.80}$
Total feed intake of the trout of 200 grams =13 * (0.20) $^{0.80}$ = **3.58 grams**

Example 3:
Suppose that the % feed intake for a trout of 200 grams is **1.79%** per day and the total feed intake of a trout of 200 grams is:
Total feed intake = 1.79/100) * 200 = **3.58** grams.

The feed intake expressed per kg metabolic weight (per BW(kg) $^{0.80}$) is calculated as following:
Formula 2 to convert the feed intake expressed as % of body weight into the feed intake per kg metabolic weight is: feed intake per kg metabolic weight = c = 10 *(% feed intake per day) / (BW(kg) $^{-0.20}$) (formula 2):
feed intake per kg metabolic weight = c = 10 *(1.79) / (0.20) $^{-0.20}$ = **12.97** grams per (BW(kg) $^{0.80}$)
Total feed intake = 12.97 * (0.20) $^{0.80}$ = **3.58** grams

Thus the feed intake of the trout of 200 grams is either **1.79**% of body weight or **12.97** grams per kg metabolic weight (per BW(kg) $^{0.80}$) and the total feed intake for the trout of 200 grams is **3.58** grams per day.

<u>Example 4:</u>
The feeding curves expressed either as % of body weight or as grams per kg metabolic weight (per $BW(kg)^{0.80}$) or as percentage of body weight are in example 2:
(1) % feed intake (gram per 100 gram trout) = $1.2 * BW(kg)^{-0.25}$
(2) feed Intake per kg metabolic weight = c = $12 * (BW(kg)^{-0.05}$.

(ad 1) The total feed intake is: (percentage feed intake /100) * BW(gram) = (percentage feed intake /100) * BW(kg)*1000 = $[(1.2 * BW(kg)^{-0.25} / 100] * BW(kg)*1000$ = **$12 * BW(kg)^{0.75}$** grams or
(ad 2) Total feed intake = $c * BW(kg)^{0.80} = [12 * BW(kg)^{-0.05}] * BW(kg)^{0.80}$ = **$12 * BW(kg)^{0.75}$ grams**

<u>Example 5:</u>
<u>(a) We have the feeding curve:</u>
% feed intake = $1.2 * BW(kg)^{-0.20}$ and the scaling coefficient is – 0.20

We can convert this formula into the feed intake per kg metabolic weight (per $BW(kg)^{0.80}$) with formula 2:
feed Intake per kg metabolic weight = c = 10 *(% feed intake per day) / ($BW(kg)^{-0.20}$)
replace % feed intake per day in the formula by $1.2 * BW(kg)^{-0.20}$:
feed Intake per kg metabolic weight = c = $10 *(1.2 * BW(kg)^{-0.20}) / (BW(kg)^{-0.20})$
feed Intake per kg metabolic weight = c = **12**
Thus, the feed intake per kg metabolic weight (per $BW(kg)^{0.80}$) is independent of the body weight and is the same for all body weights, as shown in the examples below:

(1)The feeding level for a trout of 200 grams is $1.2 * (0.2)^{-0.20}$ = 1.66 %.
The feeding level per kg metabolic weight can be calculated with formula 2:
Feed intake per kg metabolic weight = c = 10 *(% feed intake per day) / ($BW(kg)^{-0.20}$) or
Feed Intake per kg metabolic weight = $10 * 1.66 / (0.2)^{-0.20}$ = 12.03 (~ **12**)

(2)The feeding level for a trout of 400 grams is $1.2 * (0.4)^{-0.20}$ = 1.44 %
The feeding level per kg metabolic weight can be calculated with the formula (2):
Feed intake per kg metabolic weight = c = 10 *(% feed intake per day) / ($BW(kg)^{-0.20}$) or
Feed intake per kg metabolic weight = c = $10 * 1.44 / (0.4)^{-0.20}$ = 11.99 (~ **12**).

Thus, the feed intake per kg metabolic rate is the same for different sizes trout.

<u>(b) Now we have the feeding curve:</u>
% feed intake = $1.2 * BW(kg)^{-0.25}$ and the scaling coefficient of this formula is -0.25 and is different from - 0.20

We can convert this formula into the feed intake per kg metabolic weight (per $BW(kg)^{0.80}$) with formula 2:
feed Intake per kg metabolic weight = c = 10 *(% feed intake per day) / ($BW(kg)^{-0.20}$)
replace % feed intake per day in the formula by $1.2 * BW(kg)^{-0.25}$:
feed Intake per kg metabolic weight = c = $10 *(1.2 * BW(kg)^{-0.25}) / (BW(kg)^{-0.20})$
feed Intake per kg metabolic weight = c = $12 * BW(kg)^{-0.05}$
Thus, the feed intake per kg metabolic weight (per $BW(kg)^{0.80}$) is now dependent of the body weight and is different for all body weights, as shown in the examples below:

(1) The feeding level for a trout of 200 grams is $1.2 * (0.2)^{-0.25}$ = 1.79 %
The feeding level per kg metabolic weight can be calculated with the formula 2:
Feed Intake per kg metabolic weight = c = 10 *(% feed intake per day) / ($BW(kg)^{-0.20}$) or
Feed Intake per kg metabolic weight = c = $10 * 1.79 / 0.2^{-0.20}$ = **12.97**

(2) The feeding level for a trout of 400 grams is $1.2 * (0.4)^{-0.25}$ = 1.51 %
The feeding level per kg metabolic weight can be calculated with the formula:
Feed Intake per kg metabolic weight = c = 10 *(% feed intake per day) / ($BW(kg)^{-0.20}$) or
Feed Intake per kg metabolic weight = c = $10 * 1.51 / (0.4)^{-0.20}$ = **12.57**.

Thus, the feed intake per kg metabolic weight is now different for different sizes trout.

<u>Example 6:</u>
When we have a feeding curve: % feed intake = $1.2 * BW(kg)^{-0.20}$, then we can convert this feeding curve into a feeding curve expressed in grams per kg metabolic weight (per ($BW(kg)^{0.80}$ with the conversion formula 2:
feed Intake (g) per kg metabolic weight (per $BW(kg)^{0.80}$) = c = 10 * (% feed intake per day) / $(BW(kg)^{(-0.20)}$
feed intake (g) per kg metabolic weight (per $BW(kg)^{0.80}$) = c = $10 * 1.2 * (BW(kg)^{(-0.20)} / (BW(kg)^{(-0.20)}$ = 12
and this is true for all sizes of trout.

When we have a feeding curve: feed intake per kg metabolic weight (per $BW(kg)^{0.80}$) of c = 12 grams (which is a constant value for all body weights) then we can convert this feeding level into the feed intake as % of body weight with the conversion formula 1:
% feed intake per day (or feed intake per 100 gram of fish) = (c/10) * $BW(kg)^{(-0.20)}$
% feed intake per day (or feed intake per 100 gram of fish) = (12/10) * $BW(kg)^{(-0.20)}$ = 1.2 * $BW(kg)^{-0.20}$

Example 7: we have for example a feed with a metabolizable energy density of 19.64 kJ / gram (feed in Table 2) and a feed intake of 12 grams per kg metabolic weight (per $BW(kg)^{0.80}$) for all sizes of trout and the % feed intake is then 1.2 * $BW(kg)^{-0.20}$ (thus the scaling factor is – 0.20).
The maintenance energy expenditure of trout is about 50 * $BW(kg)^{0.80}$ at 15 °C (see paragraph 5).
The energy expenditure of a trout of 200 grams is: 50 * $(0.2)^{0.8}$ = 13.79 kJ per day. The intake of energy from the feed is 12 * 19.64 * $BW(kg)^{0.80}$ = 12 * 19.64 * $(0.2)^{0.80}$ = 65.03 kJ. The ratio Mp/Mm = (65.03 – 13.79) / 13.79 = **3.71**.
The energy expenditure of a trout of 400 grams is 50 * $(0.4)^{0.80}$ = 24.02 kJ and the intake of energy from the feed is 12 * 19.64 * $BW(kg)^{0.80}$ = 12 * 19.64 * $(0.4)^{0.80}$ = 113.23 kJ. The ratio of metabolizable energy for production / metabolizable energy for maintenance or Mp/Mm = (113.23 – 24.02) / 24.02 = **3.71** (see also Figure below).

Similarly, we can demonstrate that the the Mp/Mm varies with different body weights when the scaling exponent of the feeding curve is different from – 0.20 and the feed intake per kg metabolic weight (per $BW(kg)^{0.80}$) also varies for the different sizes of trout (see Figure below).

The feeding curves represent a linear plot when plotted on double logarithmic scales (characteristic of the allometric scaling formula). The Figures above show feeding curves where the feeding level is either expressed in % of body weight or as grams per kg metabolic weight (per $BW(kg)^{0.80}$). In addition the top panel of the Figure shows the ratio of metabolizable energy for production / metabolizable energy for maintenance (Mp/Mm). The ratio of metabolizable energy for production to the metabolizable energy for maintenance (Mp / Mm) is calculated for a trout diet with 19.64 kJ/gram metabolizable energy (See diet Table 2 or 6) at a temperature of 15 °C.

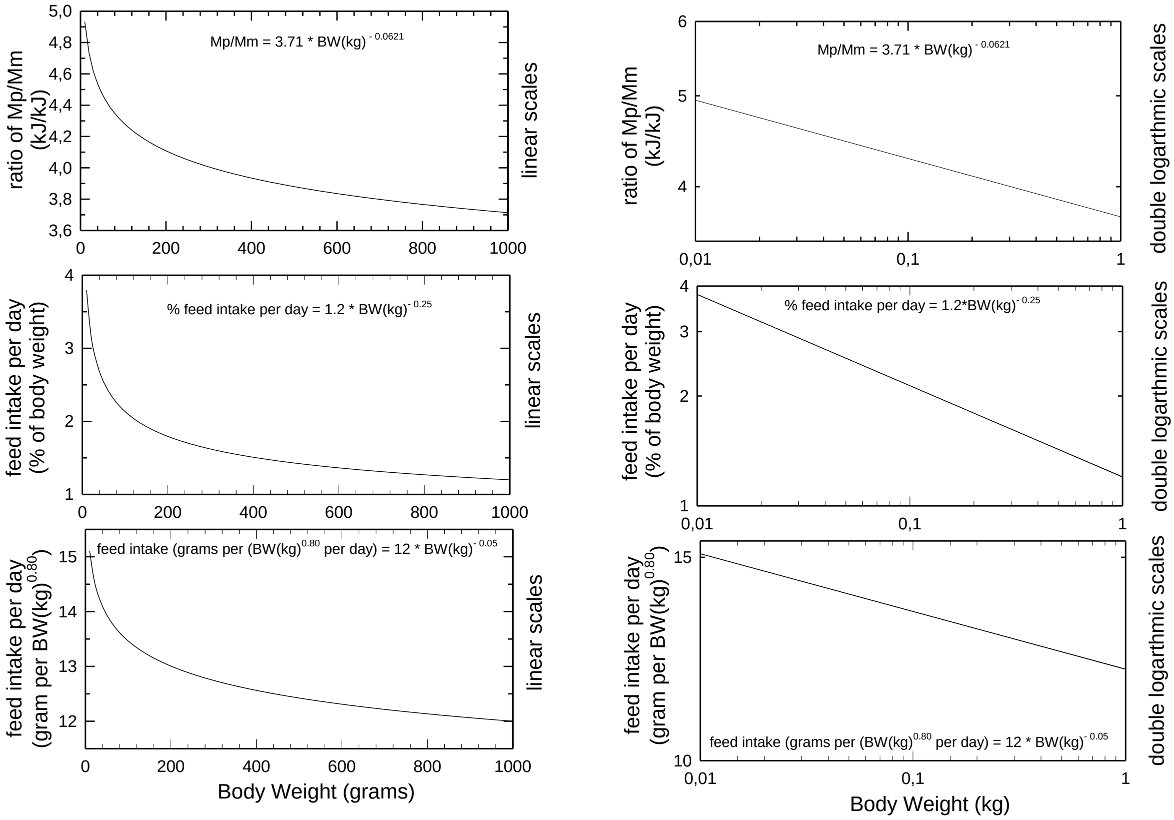


Figure
Feeding curve expressed as % of body weight with a scaling coefficient different from – 0.20

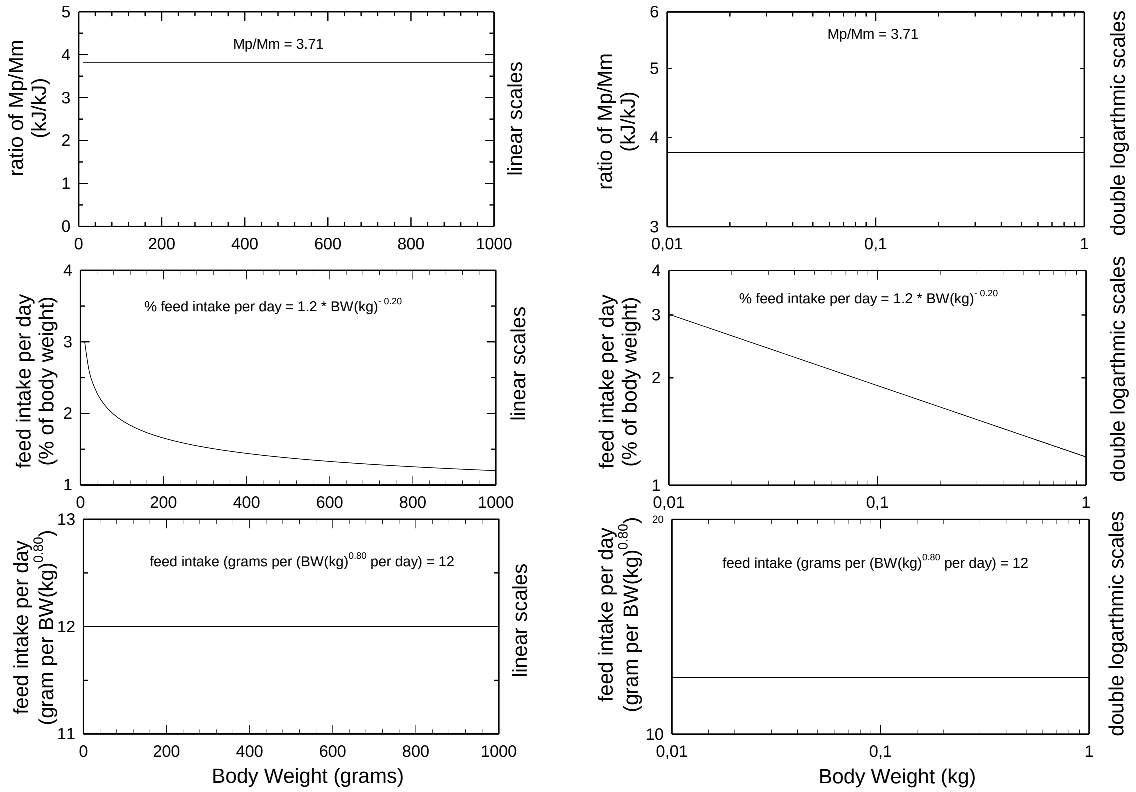


Figure
Feeding curve expressed as % of body weight with a scaling coefficient of – 0.20

Example 8:
The body weights in the formulas that describe the feeding curves are expressed in kilograms. It is also possible to convert the body weights in the formulas from kilograms into grams. The procedure is as following (see also paragraph 5, formula for the energy expenditure of a trout):
For example, the formula for a feeding curve (see above), expressed as % of body weight is:
% feed intake (gram feed per 100 gram trout) = a * $BW(kg)^{b}$
where the body weights are expressed in kilograms. We can convert this formula into a formula where the body weights are expressed in grams. The formula is then:
% feed intake (gram feed per 100 gram trout) = x * $BW(g)^{b}$
We can calculate the value of x as following:
% feed intake = a * $BW(kg)^{b}$ = x * $[BW(kg)*1000(g)]^{b}$

Solving for x gives:
x = [a * $BW(kg)^{b}$] / [BW(kg)*1000)(g)]b =
x = [a * $BW(kg)^{b}$] / $BW(kg)^{b}$ * 1000^{b} = a / 1000^{b}
thus the formula becomes then:
% feed intake = (a / 1000^{b}) * $BW(g)^{b}$ where the body weights are now expressed in grams.

<u>*Thus:*</u>
<u>*Conversion from kg into grams:*</u> Divide a (the normalization constant) by 1000^{b} (b is scaling factor or coefficient)
<u>*Conversion from grams into kg:*</u> Multiply a (the normalization constant) by 1000^{b} (b is scaling factor or coefficient)

7. The (exponential) Effect of the Temperature on the Feeding Level

The effect of temperature on the feeding level is of particular interest in trout since trout are poikilotherm and the metabolic rate of a trout is dependent on the water and body temperature. The energy required to support the metabolic rate or energy expenditure is supplied by the energy in the feed and therefore, the effect of the temperature on the energy or feed intake should follow the same pattern as the effect of the temperature on the metabolic rate or energy expenditure. The effect of the temperature on the heat production or metabolic rate of a trout is exponential and described by the formula (Elliott 1976, see page 933 and equation 12; for the temperature range of 7.1 – 19.5 ^oC):

$$\text{Energy Expenditure per kg BW}^{0.80} \text{ at } T_2 = \text{Energy Expenditure per kg BW}^{0.80} \text{ at } T_1 * e^{0.095(T2 - T1)}$$

The formula that describes the effect of temperature on the feed intake is thus analogous to the formula that describes the effect of the temperature on the metabolic rate and is:

$$\textbf{Feeding level in g per kg BW(kg)}^{0.80} \textbf{ at } T_2 = \textbf{feeding level in g per kg BW(kg)}^{0.80} \textbf{ at } T_1 * e^{0.095 * (T2-T1)}$$

and

$$\textbf{Feeding level in \% of body weight at } T_2 = \textbf{Feeding level in \% of body weight at } T_1 * e^{0.095 * (T2-T1)}$$

Example: We have a feeding level of 15 grams per kg metabolic weight (BW $^{0.80}$) for the trout at a temperature of 15 ^oC. We want to calculate the feeding level at a temperature of 10 ^oC.
Formula: Feeding level at $T=T_2$ = (feeding level at $T=T_1$) * e $^{0.95*(T2-T1)}$
Feeding level at (T=10 ^oC) = 15 * e $^{0.095*(10-15)}$ = 9.33 grams of feed per kg metabolic weight.
We can also calculate the feeding level at a temperature of 5 ^oC. There are two ways for these calculations.
1. The feeding level at 15 ^oC is 15 grams. Thus:
Feeding level at (T=5 ^oC) = 15 * e $^{0.095*(5-15)}$ = 5.80 grams of feed per kg metabolic weight.
2. The feeding level at 10 ^oC is 9.10 grams. Thus:
Feeding level at (T=5 ^oC) = 9.33 * e $^{0.095*(5-10)}$ = 5.80 grams of feed per kg metabolic weight.

As discussed in paragraph 6, each defined level of feed intake per kg metabolic weight (per BW(kg) $^{0.80}$) above the maintenance feed intake is associated with a defined ratio of metabolizable energy for production / metabolizable energy for maintenance (Mp/Mm). When the same amount of feed per kg metabolic rate is administered to different sizes trout, then also the ratio of Mp/Mm will be the same for all these different sizes trout (see also Figure 18). When the effect of the temperature on the feed intake expressed per kg metabolic weight (per BW(kg)$^{0.80}$) follows the same pattern as the effect of the temperature on the metabolic rate, then the ratio of Mp/Mm will not only be similar for the various body weights, but also be similar for the various temperatures (see example below). The feed intake per kg metabolic weight (per BW(kg) $^{0.80}$) will of course decrease or increase when the temperature will decrease or increase), but not the ratio of Mp/Mn.

Example: The feed intake of trout is for example 12 grams per kg metabolic weight (per (BW(kg) $^{0.80}$) for all sizes trout at a temperature of 15 ^oC, thus the total feed intake (grams per trout) = 12 * BW(kg) $^{0.80}$. The feed intake of a trout of 100 grams is: 12 * (0.1) $^{0.80}$ = 1.9 grams and the feed intake of a trout of 200 grams is: 12 * 0.2 $^{0.80}$ = 3.3 grams of feed. The metabolizable energy density of the feed is for example 19.64 kJ per gram (diet of Table 2). Thus the feed intake of 1.9 grams of feed represents the energy intake of 1.9 * 19.64 = 37.32 kJ and the feed intake of 3.3 grams of feed represents an energy intake of 3.3 * 19.64 = 64.81 kJ. The maintenance energy expenditure of a trout of 100 grams at 15 ^oC = 50 * BW(kg) $^{0.80}$ = 50 * (0.1) $^{0.80}$ = 7.92 kJ per day and the energy intake is 37.32 kJ and the ratio of Mp/Mn = (37.32 – 7.92) / 7.92 = **3.71**. The maintenance energy expenditure of a trout of 200 grams at 5 ^oC is: 50 * (0.2) $^{0.80}$ = 13.80 kJ per day and the energy intake is 64.81 kJ and the ratio of Mp/Mm = (64.81 – 13.80) / 13.80 = **3.70**

The effect of the temperature on the maintenance metabolic rate is:

$$\text{Metabolic rate at } T_2 = \text{metabolic rate at } T_1 * e^{0.095 * (T2-T1)}$$

And the metabolic rate at 10 ^oC is:

$$\text{Metabolic rate at } T_2 = 50 * e^{0.095 * (10-15)} = 31.09$$

Thus the maintenance metabolic rate of a trout of 100 grams at 10 ^{o}C is: 31.09 * (0.1) $^{0.80}$ = 4.92 kJ per day and the maintenance metabolic rate of a trout of 200 grams is: 31.09 * (0.2) $^{0.80}$ = 8.58 kJ per day.

The effect of the temperature on the feed intake is:

$$\text{Feeding level in g per kg BW(kg)}^{0.80} \text{ at } T_2 = \text{feeding level in g per kg BW(kg)}^{0.80} \text{ at } T_1 * e^{\,0.095 * (T2\text{-}T1)}$$

And the feed intake at a temperature of 10 ^{o}C is:

$$\text{Feeding level in g per kg BW(kg)}^{0.80} \text{ at } T_2 = 12 * e^{\,0.095 * (10\text{-}15)} = 7.46$$

Thus the feed intake of a trout of 100 grams at 10 ^{o}C is 7.46 * BW(kg) $^{0.80}$ = 7.46 * (0.1) $^{0.80}$ = 1.18 grams and this amount represents 1.18 * 19.64 = 23.17 kJ. The Mp/Mm = (23.17 – 4.92) / 4.92 = **3.71**.

The feed intake of a trout of 200 grams at 10 ^{o}C is 7.46 * BW(kg) $^{0.80}$ = 7.46 * (0.2) $^{0.80}$ = 2.06 grams and represents 2.06 * 19.64 = 40.46 kJ. The Mp/Mm = (40.46 – 8.58) / 8.58 = **3.71**.

8. Feeding Levels for Trout at the internet

Fish feed manufacturers usually give feeding tables for their feeds and the feeding tables are expressed as percentage of the body weights. As an example of a feeding table, we will take the recommended low and high feeding levels for trout as given by the feed manufacturer Biomar. The feeding table is given in Tables 4 and 5. We plotted the feeding levels vs the body weights of the trout at the various temperatures (Figures 7 and 8 , bottom panel (*note* that the body weights in the formulas are expressed in *kilograms!*). Linear plots arise when the data were plotted on a double logarithmic scale (Figure10 and 11, middle panels (note that the body weights in the formulae and in this graph are expressed in *kilograms!*). The slope and the intercept of these plots can be calculated with linear regression (Figures 7 and 8, middle panel) and allometric equations can be constructed (Figures 7 and 8, bottom panel) of the form:

$$\% \text{ feed intake} = a * \text{BW(kg)}^{b}$$

where a is the normalization constant and b is the scaling coefficient and the body weights BW(kg) are expressed in *kilograms*.

Table 4a

Feeding levels for trout as recommended by Biomar (low feeding levels)

Feeding levels expressed in % of body weight.

Feed sizes (mm)	Body Length (cm)	Type Feed	Body Weight (grams)		Feeding Level (% of body weight Temperature (^oC)									
			Range	Average	2	4	6	8	10	12	14	16	18	20
0,5	3 - 4	Inicio Plus	0,2 - 0,4	0,3	1,22	1,44	1,80	2,08	2,65	3,27	3,52	3,64	3,5	2,94
0,8	4 - 5	Inicio Plus	0,4 - 1,5	0,95	1,05	1,25	1,56	1,80	2,30	2,83	3,06	3,16	3,04	2,55
1,1	5 - 8	Inicio Plus	1,5 - 5	3,75	0,92	1,09	1,37	1,58	2,02	2,5	2,69	2,78	2,68	2,24
1,5	8 - 11	Inicio Plus	5 - 15	10	0,75	0,89	1,11	1,29	1,65	2,04	2,2	2,27	2,18	1,83
2	11 - 15	Inicio Plus	15 - 30	22,5	0,63	0,75	0,94	1,09	1,39	1,72	1,86	1,92	1,85	1,54
2	15 - 16	Inicio Plus	30 - 50	40	0,58	0,69	0,86	1,00	1,28	1,58	1,71	1,76	1,69	1,42
3	16 - 21	Efico Enviro 920	50 - 100	75	0,52	0,62	0,77	0,9	1,15	1,42	1,53	1,59	1,52	1,27
4,5	21 - 26	Efico Enviro 920	100 - 200	150	0,45	0,54	0,67	0,78	1.00	1,24	1,34	1,38	1,33	1,11
4,5	26 - 29	Efico Enviro 920	200 - 300	250	0,41	0,49	0,61	0,71	0,91	1,13	1,22	1,26	1,21	1,01
4,5	29 - 23	Efico Enviro 920	300 - 450	375	0,38	0,45	0,56	0,65	0,83	1,03	1,11	1,15	1,1	0,92
6	33 - 36	Efico Enviro 920	450 - 600	525	0,35	0,41	0,52	0,6	0,77	0,95	1,02	1,06	1,02	0,85
6	36 - 40	Efico Enviro 920	600 - 800	700	0,33	0,39	0,49	0,57	0,73	0,91	0,98	1,01	0,97	0,81
6	40 - 43	Efico Enviro 920	800 - 1000	900	0,31	0,37	0,46	0,53	0,68	0,84	0,91	0,94	0,9	0,76

The data were retrieved from the website of Biomar (www.biomar.com, accessed 2014)

Table 4b

Feeding levels for trout as recommended by Biomar (low feeding levels)

Feeding levels expressed in grams per kg metabolic weight (per BW(kg) $^{0.80}$.)

Feed sizes (mm)	Body Length (cm)	Type Feed	Body Weight (grams)		Feeding Level (gram per kg BW(kg) $^{0.80}$) Temperature (^{o}C)									
			Range	Average	2	4	6	8	10	12	14	16	18	20
0,5	3 - 4	Inicio Plus	0,2 - 0,4	0,3	2,41	2,84	3,55	4,11	5,23	6,46	6,95	7,19	6,91	5,80
0,8	4 - 5	Inicio Plus	0,4 - 1,5	0,95	2,61	3,11	3,88	4,48	5,72	7,04	7,61	7,86	7,56	6,34
1,1	5 - 8	Inicio Plus	1,5 - 5	3,75	3,01	3,57	4,48	5,17	6,61	8,18	8,80	9,10	8,77	7,33
1,5	8 - 11	Inicio Plus	5 - 15	10	2,99	3,54	4,42	5,14	6,57	8,12	8,76	9,04	8,68	7,29
2	11 - 15	Inicio Plus	15 - 30	22,5	2,95	3,51	4,40	5,10	6,51	8,05	8,71	8,99	8,66	7,21
2	15 - 16	Inicio Plus	30 - 50	40	3,05	3,62	4,52	5,25	6,72	8,30	8,98	9,25	8,88	7,46
3	16 - 21	Efico Enviro 920	50 - 100	75	3,10	3,69	4,59	5,36	6,85	8,46	9,11	9,47	9,05	7,57
4,5	21 - 26	Efico Enviro 920	100 - 200	150	3,08	3,69	4,58	5,34	6,84	8,48	9,17	9,44	9,10	7,60
4,5	26 - 29	Efico Enviro 920	200 - 300	250	3,11	3,71	4,62	5,38	6,90	8,56	9,25	9,55	9,17	7,65
4,5	29 - 23	Efico Enviro 920	300 - 450	375	3,12	3,70	4,60	5,34	6,82	8,47	9,12	9,45	9,04	7,56
6	33 - 36	Efico Enviro 920	450 - 600	525	3,08	3,60	4,57	5,27	6,77	8,35	8,97	9,32	8,97	7,47
6	36 - 40	Efico Enviro 920	600 - 800	700	3,07	3,63	4,56	5,31	6,80	8,47	9,13	9,40	9,03	7,54
6	40 - 43	Efico Enviro 920	800 - 1000	900	3,04	3,62	4,50	5,19	6,66	8,22	8,91	9,20	8,81	7,44

The feeding level expressed in % feed intake were converted into grams per kg metabolic weight (per BW(g)$^{0.80}$) with the formula:

Feed intake per kg metabolic weight (per BW(kg)$^{0.80}$) = 10 *(% feed intake per day) / (BW(kg) $^{-0.20}$) (see text).

For example, the feeding level of a trout with an average body weight of 40 grams is 1.76% at a temperature of 16 ^{o}C.
Feed intake per kg metabolic weight (per BW(kg)$^{0.80}$ = 10 * 1.76 / 0.04 $^{-0.20}$ = 9.25 grams per kg metabolic weight (per BW(kg) $^{0.80}$).

Table 5a

Feeding levels for trout as recommended by Biomar (high feeding levels)

Feeding levels expressed in % of body weight.

Feed sizes (mm)	Body Length (cm)	Type Feed	Body Weight (grams)		Feeding Level (% of body weight Temperature (°C)									
			Range	Average	2	4	6	8	10	12	14	16	18	20
0,5	3 - 4	Inicio Plus	0,2 - 0,4	0,3	1,49	1,73	2,15	2,85	4,15	5,78	6,92	7,67	7,28	4,01
0,8	4 - 5	Inicio Plus	0,4 - 1,5	0,95	1,26	1,47	1,82	2,42	3,54	4,95	5,95	6,61	6,27	3,41
1,1	5 - 8	Inicio Plus	1,5 - 5	3,75	1,08	1,26	1,56	2,08	3,06	4,29	5,17	5,76	5,46	2,94
1,5	8 - 11	Inicio Plus	5 - 15	10	0,86	1,00	1,24	1,66	2,45	3,44	4,16	4,64	4,39	2,35
2	11 - 15	Inicio Plus	15 - 30	22,5	0,71	0,83	1,03	1,38	2,03	2,86	3,46	3,87	3,66	1,95
2	15 - 16	Inicio Plus	30 - 50	40	0,64	0,75	0,93	1,25	1,84	2,60	3,15	3,52	3,33	1,77
3	16 - 21	Efico Enviro 920	50 - 100	75	0,57	0,67	0,83	1,11	1,64	2,32	2,81	3,14	2,97	1,58
4,5	21 - 26	Efico Enviro 920	100 - 200	150	0,49	0,58	0,72	0,96	1,41	2,00	2,42	2,71	2,56	1,36
4,5	26 - 29	Efico Enviro 920	200 - 300	250	0,45	0,52	0,65	0,87	1,28	1,81	2,20	2,46	2,32	1,23
4,5	29 - 23	Efico Enviro 920	300 - 450	375	0,40	0,47	0,59	0,79	1,16	1,64	1,99	2,23	2,11	1,11
6	33 - 36	Efico Enviro 920	450 - 600	525	0,37	0,44	0,54	0,72	1,07	1,51	1,84	2,06	1,94	1,03
6	36 - 40	Efico Enviro 920	600 - 800	700	0,36	0,42	0,52	0,69	1,03	1,45	1,76	1,97	1,86	0,98
6	40 - 43	Efico Enviro 920	800 - 1000	900	0,33	0,39	0,48	0,65	0,95	1,35	1,64	1,83	1,73	0,91

The data were retrieved from the website of Biomar (www.biomar.com, accessed 2014)

Table 5b

Feeding levels for trout as recommended by Biomar (high feeding levels)

Feeding levels expressed in grams per kg metabolic weight (per BW(kg) $^{0.80}$.)

Feed sizes (mm)	Body Length (cm)	Type Feed	Body Weight (grams) Range	Body Weight (grams) Average	Feeding Level (gram per kg BW(kg) $^{0.80}$) Temperature (^{o}C) 2	4	6	8	10	12	14	16	18	20
0,5	3 - 4	Inicio Plus	0,2 - 0,4	0,3	2,94	3,42	4,24	5,63	8,19	11,41	13,66	15,14	14,37	7,92
0,8	4 - 5	Inicio Plus	0,4 - 1,5	0,95	3,13	3,65	4,52	6,02	8,80	12,31	14,79	16,43	15,59	8,48
1,1	5 - 8	Inicio Plus	1,5 - 5	3,75	3,53	4,12	5,10	6,81	10,01	14,04	16,92	18,85	17,86	9,62
1,5	8 - 11	Inicio Plus	5 - 15	10	3,42	3,98	4,94	6,61	9,75	13,69	16,56	18,47	17,48	9,36
2	11 - 15	Inicio Plus	15 - 30	22,5	3,32	3,89	4,82	6,46	9,50	13,39	16,20	18,12	17,14	9,13
2	15 - 16	Inicio Plus	30 - 50	40	3,36	3,94	4,89	6,57	9,67	13,66	16,55	18,49	17,49	9,30
3	16 - 21	Efico Enviro 920	50 - 100	75	3,40	3,99	4,94	6,61	9,77	13,82	16,74	18,70	17,69	9,41
4,5	21 - 26	Efico Enviro 920	100 - 200	150	3,35	3,97	4,93	6,57	9,65	13,69	16,56	18,54	17,52	9,31
4,5	26 - 29	Efico Enviro 920	200 - 300	250	3,41	3,94	4,93	6,59	9,70	13,72	16,67	18,64	17,58	9,32
4,5	29 - 23	Efico Enviro 920	300 - 450	375	3,29	3,86	4,85	6,49	9,53	13,48	16,36	18,33	17,34	9,12
6	33 - 36	Efico Enviro 920	450 - 600	525	3,25	3,87	4,75	6,33	9,41	13,27	16,18	18,11	17,05	9,05
6	36 - 40	Efico Enviro 920	600 - 800	700	3,35	3,91	4,84	6,42	9,59	13,50	16,39	18,34	17,32	9,13
6	40 - 43	Efico Enviro 920	800 - 1000	900	3,23	3,82	4,70	6,36	9,30	13,22	16,06	17,92	16,94	8,91

The feeding level expressed in % feed intake were converted into grams per kg metabolic weight (per BW(g)$^{0.80}$) with the formula:

Feed intake per kg metabolic weight (per BW(kg)$^{0.80}$) = 10 *(% feed intake per day) / (BW(kg) $^{-0.20}$) (see text).

For example, the feeding level of a trout with an average body weight of 40 grams is 3.52% at a temperature of 16 ^{o}C.
Feed intake per kg metabolic weight (per BW(kg)$^{0.80}$ = 10 * 3.52 / 0.04 $^{-0.20}$ = 18.49 grams per kg metabolic weight.

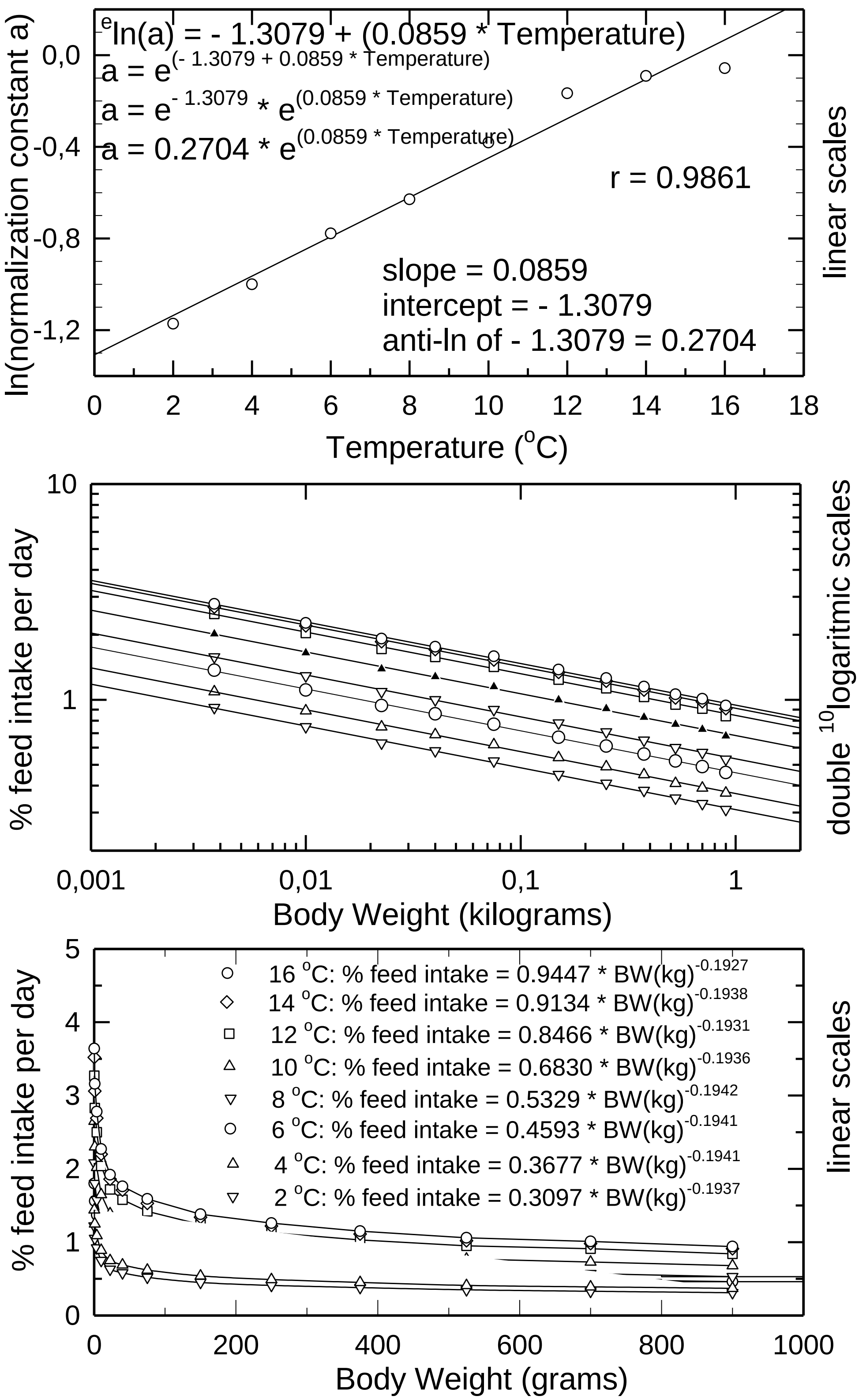


Figure 7
Feeding curves (data from table 4a, low feeding levels)

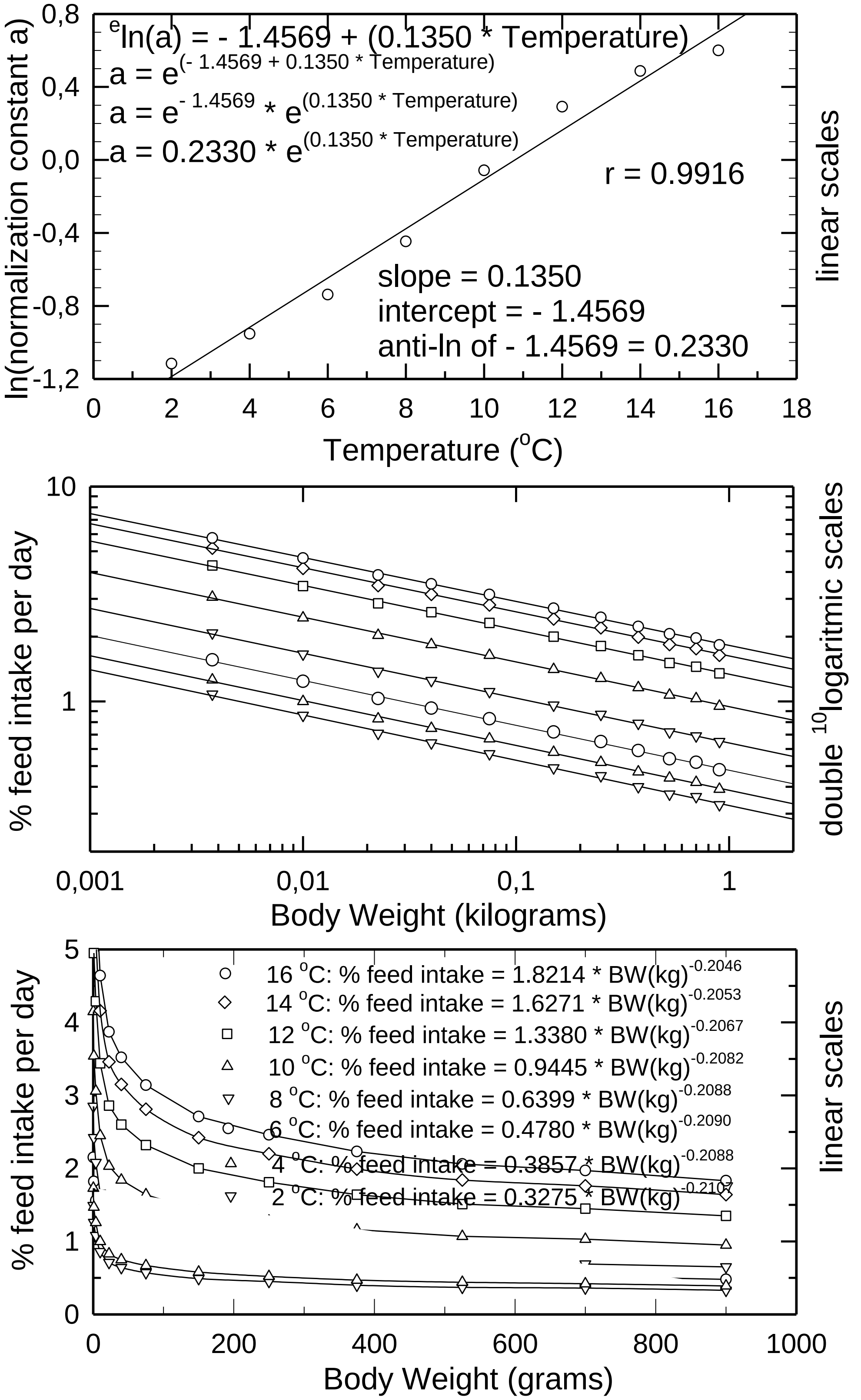


Figure 8
Feeding curves (data from Table 5a, high feeding levels)

For example, the (high) feeding levels (Table 5a) expressed in % of body weight were plotted vs the body weights in kilograms for a temperature of 16 ^oC (Figure 8, middle panel). The regression line describing this linear plot was calculated to be :

$$\log (\% \text{ feed intake}) = \text{intercept} + b * \log BW(kg)$$

$$\log (\% \text{ feed intake}) = 0.2604 - 0.2046 * \log BW(kg)$$

$$\text{anti-log of } 0.2604 = 1.8214$$

$$\log \% \text{ feed intake} = \log 1.8214 - 0.2046 * \log BW(kg)$$

$$\log \% \text{ feed intake} = \log 1.8214 + \log (BW(kg)^{-0.2046}$$

$$\log \% \text{ feed intake} = \log 1.8214 + \log BW(kg)^{-0.2046}$$

$$\log \% \text{ feed intake} = \log (1.8214 * BW(kg)^{-0.2046})$$

$$\% \text{ feed intake} = 1.8214 * BW(kg)^{-0.2046}$$

(for the properties of logarithms, see Appendix 10)

The calculated allometric equations for the various temperatures are:

$$16\ ^oC\text{: \% feed intake} = 1.8214 * BW(kg)^{-0.2046}$$
$$14\ ^oC\text{: \% feed intake} = 1.6271 * BW(kg)^{-0.2053}$$
$$12\ ^oC\text{: \% feed intake} = 1.3380 * BW(kg)^{-0.2067}$$
$$10\ ^oC\text{: \% feed intake} = 0.9445 * BW(kg)^{-0.2082}$$
$$8\ ^oC\text{: \% feed intake} = 0.6399 * BW(kg)^{-0.2088}$$
$$6\ ^oC\text{: \% feed intake} = 0.4780 * BW(kg)^{-0.2090}$$
$$4\ ^oC\text{: \% feed intake} = 0.3857 * BW(kg)^{-0.2088}$$
$$2\ ^oC\text{: \% feed intake} = 0.3275 * BW(kg)^{-0.2107}$$

The average scaling coefficient of these formulas is – 0.2078 and _note_ that the body weights in these formulae are here expressed in _kilograms_.

Thus, these allometric formulas or functions (of the general form $a*BW(kg)^b$) describe the % feed intake as a function of the body weights in kg. We can also convert these formula into allometric formulas that describe the feed intake per kg metabolic weight (per $BW(kg)^{0.80}$) as a function of the body weights. The formula to convert the feed intake expressed as % of body weight into the feed intake expressed as grams per metabolic weight (per $BW(kg)^{0.80}$) is:

$$\text{Feed Intake per kg metabolic weight} = c = 10 *(\% \text{ feed intake per day}) / (BW(kg)^{-0.20})$$

For example, at a temperature of 16 ^oC, the formula for the feed intake expressed as % of body weight is:

$\% \text{ feed intake} = 1.8214 * BW(kg)^{-0.2046}$

Substitution into the conversion formula gives:

$$\text{Feed Intake per kg metabolic weight} = c = 10 *(1.8214*BW(kg)^{-0.2046}) / (BW(kg)^{-0.20}) \text{ or}$$

$$\text{Feed Intake per kg metabolic weight} = c = 18.214*BW(kg)^{-0.0046}$$

Similarly, the feed intakes expressed in grams per kg metabolic weight can be calculated for the other temperatures:

16 ^oC: feed intake (grams per kg metabolic weight) = 18.214* BW(kg) $^{-0.0046}$
14 ^oC: feed intake (grams per kg metabolic weight) = 16.271 * BW(kg) $^{-0.0053}$
12 ^oC: feed intake (grams per kg metabolic weight) = 13.380 * BW(kg) $^{-0.0067}$
10 ^oC: feed intake (grams per kg metabolic weight) = 09.445 * BW(kg) $^{-0.0082}$
8 ^oC: feed intake (grams per kg metabolic weight) = 06.399 * BW(kg) $^{-0.0088}$
6 ^oC: feed intake (grams per kg metabolic weight) = 04.780 * BW(kg) $^{-0.0090}$
4 ^oC: feed intake (grams per kg metabolic weight)= 03.857 * BW(kg) $^{-0.0088}$
2 ^oC: feed intake (grams per kg metabolic weight)= 03.275 * BW(kg) $^{-0.0107}$

Note that the scaling coefficient is very small and approaches zero; the factor BW(kg) – b will thus approach a value of 1 and the feed intake per kg metabolic weight (per BW(kg)$^{0.80}$ will thus become independent of the body weight and be the same for the different body weights (see also Tables 4b and 5b).

Conversely, the feed intake per kg metabolic weight can be converted into the feed intake expressed as percentage of body weight with the formula 1:

% feed intake per day (or feed intake per 100 gram of fish) = (c/10) * BW(kg) $^{-0.20}$

For example, at a temperature of 16 ^oC, the formula for the feed intake in grams per kg metabolic weight is:

Feed intake per kilogram metabolic weight (per BW(kg)$^{0.80}$) = 18.214* BW(kg) $^{-0.0046}$

Substitution into the conversion formula gives:

% feed intake = [(18.214 * BW(kg) $^{-0.0046}$)/10] * (BW(kg) $^{-0.20}$) or

% feed intake = 1.8214*BW(kg) $^{-0.2046}$

We discussed in paragraph 7 that the effect of the temperature on the feeding level of a trout should be exponential, since the effect of the temperature on the metabolic rate or the energy expenditure of a trout is also exponential. The energy required to support the metabolic rate or energy expenditure is supplied by the energy in the feed and therefore, the effect of the temperature on the energy or feed intake should be the same as the effect of the temperature on the metabolic rate or energy expenditure. Therefore, we will consider the effect of the temperature on the feed intake and on the feeding curves and levels as exponential.

Therefore, we also plotted the various normalisation constants of the feeding curves for the various temperatures of the fish feed company Biomar on a semi-logarithmic scale. When we plot the ln values of the normalisation constant vs the temperature, also a linear plot arises (Figures 7 and 8). The data of the normalization constants in Figures 7 and 8, top panel (low and high feeding levels), were analyzed by linear regression and the effect of the temperature on the normalization constants as a function of the temperature can be described by the exponential function (e.g. the low feeding level):

$$a = 0.2704 * e^{(0.0859 * \text{temperature})}$$

Thus, “a” represents the normalization constants for the various feeding curves as a function of the temperature T. We can now replace the value of “a” in each of the allometric equations for each temperature with $0.2704 * e^{(0.0859 * \text{temperature})}$ and the general formula that describes the (low) feeding levels of Table 4a becomes then (the average scaling coefficient of the formulas in Figure 7 is – 0.1936) :

$$\textbf{\% feed intake at temperature T} = 0.2704 * e^{(0.0859 * \text{temperature})} \; \mathbf{* BW(kg)^{-0.1936}}$$

Similarly, the general formula that describes the (high) feeding levels of Table 5a becomes (the average scaling coefficient of the formulae in Figure 8 is – 0.2078):

$$\textbf{\% feed intake at temperature T} = 0.2330 * e^{(0.1350 * \text{temperature})} \; \mathbf{* BW(kg)^{-0.2078}}$$

and this formula also describes thus the % feed intake at any temperature and for any body weight as given by the feed manufacturer Biomar.

Example:
The normalisation constant as function of the temperature for the high feeding levels is described by the formula:
The normalisation constant a = $0.2330 * e^{(0.1350 * \text{temperature})}$
Thus the normalisation constant for a temperature of 10 ^{o}C is then:
Normalisation constant a at temperature T = 10 ^{o}C = $0.2330 * e^{(0.1350 * 10)} = 0.8988$ (compare with the value of 0.9445 in Figure 8).

Example:
The % feed intake as a function of the temperature for the high feeding levels is described by the formula:
% feed intake at temperature T =$0.2330 * e^{(0.1350 * \text{temperature})} * BW(kg)^{-0.2078}$
Thus the % feed intake at a temperature of 10 ^{o}C for a trout of 40 grams (0.040 kg) is then:
% feed intake = $0.2330 * e^{(0.1350 * 10)} * (0.040)^{-0.2078}$ = 1.71% (compare with the value of 1.84 in Table 5a)

Further, e.g. for the low feeding levels,

$$\text{\% feed intake at temperature } T_2 = 0.2704 * e^{(0.0859 * T2)} * BW(kg)^{-0.1936} \text{ and}$$

$$\text{\% feed intake at temperature } T_1 = 0.2704 * e^{(0.0859 * T1)} * BW(kg)^{-0.1936} \text{ or}$$

$$(\text{\% feed intake at temperature } T_2) / (\text{\% feed intake at temperature } T_1) =$$

$$(0.2704 * e^{(0.0859 * T2)} * BW(kg)^{-0.1936}) / 0.2704 * e^{(0.0859 * T1)} * BW(kg)^{-0.1936} =$$

$$e^{(0.0859 * T2 - T1)}$$

or for the low feeding levels:

$$\textbf{(\% feed intake at temperature } \mathbf{T_2}\textbf{) = (\% feed intake at temperature } \mathbf{T_1}\textbf{) * } \mathbf{e^{(0.0859 * T2 - T1)}}$$

Similarly, for the high feeding levels:

$$\textbf{(\% feed intake at temperature } \mathbf{T_2}\textbf{) = (\% feed intake at temperature } \mathbf{T_1}\textbf{) * } \mathbf{e^{(0.1350 * T2 - T1)}}$$

Example:
The (high) feeding level at a temperature of 15 ^{o}C is:

$$\text{\% feed intake at temperature T} = 15\ ^{o}\text{C} = 0.2330 * e^{(0.1350 * 15)} * BW(kg)^{-0.2078}$$
$$\text{\% feed intake at temperature T} = 15\ ^{o}\text{C} = 1.7652 * BW(kg)^{-0.2078}$$

The (high) feeding level at a temperature of 10 ^{o}C is:

% feed intake at temperature T = 10 ^oC = 0.2330 * e $^{(0.1350 * 10)}$ * BW(kg) $^{-0.2078}$
% feed intake at temperature T = 10 ^oC = 0.8988 * BW(kg) $^{-0.2078}$

When we know the feeding level at a temperature of 15 ^oC, we can also calculate the feeding level at a temperature of 10 ^oC with the formula:

(% feed intake at temperature T_2) = (% feed intake at temperature T_1) * e $^{(0.1350 * T2 - T1)}$ or

(% feed intake at T_2 = 10 ^oC) = (% feed intake at T_1 = 15 ^oC) * e $^{(0.1350 * 10 - 15)}$ or

(% feed intake at T_2 = 10 ^oC) = 1.7652 * BW(kg) $^{-0.2078}$ * e $^{(0.1350 * 10 - 15)}$ or

(% feed intake at T_2 = 10 ^oC) = 0.8988 * BW(kg) $^{-0.2078}$

The scaling coefficients of the feeding curves expressed as % of body weight were on average - 0.1936 for the low feeding levels and on average – 0.2078 for the low feeding levels. These scaling coefficients of the various feeding curves (expressed in % of body weight are very close to a value of - 0.20. As pointed out before (see paragraph 6), a scaling coefficient of - 0.20 for the formula that describes the feed intake expressed in % of body weight means that the feeding level expressed in grams per kg metabolic weight (per (BW(kg) $^{0.80}$) is then independent of the body weights and similar for the various sizes of trout. The data in Table 4b and 5b show indeed that for each temperature, the feed intake per kg metabolic weight is comparable for all the different body weights. This result also means that the ratio of metabolizable energy for production / metabolizable energy for maintenance (Mp/Mm) will be similar for all the different body weight at each temperature. However, the effect of the temperature on the feeding levels was different for the low and the high feeding levels and was e $^{(0.0859 * (T2 - T1))}$ for the low feeding level and e $^{(0.1350 * (T2- T1))}$ for the high feeding level. Note that we described in paragraph 7 that the effect of the temperature on the feeding level was **e** $^{\mathbf{0.095 * (T2 - T1)}}$

9. Procedure for the Construction of Feeding Curves for Trout:

We can construct two different types of feeding curves:

(a) where the ratio of Mp/Mm is the same for all different sizes of trout and independent of the body weights; the feed intake per kg metabolic weight (per BW(kg) $^{0.80}$) is then also the same for all the various sizes of trout and is also independent of the body weights. In this situation, the scaling coefficient of the feeding curve or formula describing the feed intake as percentage of body weight (% feed intake = x * BW(kg) ^{p}) has to be p = – 0.2 (see paragraph 6 page 17).

(b) where the ratio of Mp/Mm is different for all different sizes of trout and dependent on the body weights and thus relatively less energy is used for growth and relatively more for maintenance when the trout grows larger. The feed intake per kg metabolic weight (per BW(kg) $^{0.80}$) is then also different for all the various sizes of trout and is dependent on the body weights. In this situation, the scaling coefficient of the feeding curve or formula describing the feed intake as percentage of body weight (% feed intake = x * BW(kg) ^{p}) has to be different from – 0.20 (or p ≠ – 0.20) (see paragraph 6 page 17).

We will construct feeding curves for both types of feeding curves.

(a) *The feed intake per kg metabolic weight (per BW(kg)$^{0.80}$ and the ratio of Mp/Mm are the same for all different sizes of trout.*

We can construct feeding curves (see paragraph 6) of the general allometric form (feed intake expressed as % of body weight):

$$\% \text{ feed intake} = x * BW(kg)^{p}$$

or of the general allometric form (feed intake expressed as gram per kg metabolic weight):

$$\text{feed intake (in grams per kg metabolic weight)} = z * BW(kg)^{w}$$

Thus the feed intake can be expressed at two different ways:

(1) in % of body weight (grams per 100 gram of fish) per day: % feed intake = $x * BW(kg)^{p}$
(2) in grams per kg metabolic weight (per $BW(kg)^{0.80}$) per day: $c = z * BW(kg)^{w}$

Where c is the feed intake per kg metabolic weight (per $BW(kg)^{0.80}$).

The two ways of expressing the feed intake can be converted into each other by the two formulas (formulas 1 and 2 of paragraph 6):

$$\% \text{ feed intake per day (or feed intake per 100 gram of fish)} = (c/10) * BW(kg)^{-0.20}$$

and

$$\text{Feed Intake per kg metabolic weight} = c = 10 * (\% \text{ feed intake per day}) / (BW(kg)^{-0.20})$$

As indicated in paragraph 6 (page 17), the feed intake per kg metabolic weight and the ratio Mp/Mm is the same for all different sizes of trout when the scaling coefficient p = - 0.20 in the formula:

$$\% \text{ feed intake} = x * BW(kg)^{p} = x * BW(kg)^{-0.20}$$

Conversion into the feed intake per kg metabolic weight (per $BW(kg)^{0.80}$) with formula 2:

$$\text{Feed Intake per kg metabolic weight} = c = 10 * (\% \text{ feed intake per day}) / (BW(kg)^{-0.20})$$

And replacing % feed intake per day by $x * BW(kg)^{-0.20}$:

$$\text{Feed Intake per kg metabolic weight} = c = 10 * (x * BW(kg)^{-0.20}) / (BW(kg)^{-0.20}) = 10 * x$$

and the feed intake per kg metabolic weight (per $BW(kg)^{0.80}$) is a constant and independent of the body weights, or the feed intake per kg metabolic weight (per $BW(kg)^{0.80}$.) is the same for all different sizes of trout.

Thus we can construct a feeding curve of the general formula:

$$\% \text{ feed intake} = x * BW(kg)^{-0.20}$$

We could choose a value of x = 1.75 for the high feeding level and a value of 0.925 for the low feeding level at a temperature of 15 ^{o}C:

$$\% \text{ feed intake} = 1.75 * BW(kg)^{-0.20} \text{ (high feeding level) and}$$

$$\% \text{ feed intake} = 0.925 * BW(kg)^{-0.20} \text{ (low feeding level)}$$

and the feed intake per kg metabolic weight (per $BW(kg)^{0.80}$) is then:

feed intake per kg metabolic weight (per $BW(kg)^{0.80}$) = 10 * 1.75 = 17.5 (high feeding level)
feed intake per kg metabolic weight (per $BW(kg)^{0.80}$) = 10 * 0.925 = 9.25 (low feeding level)

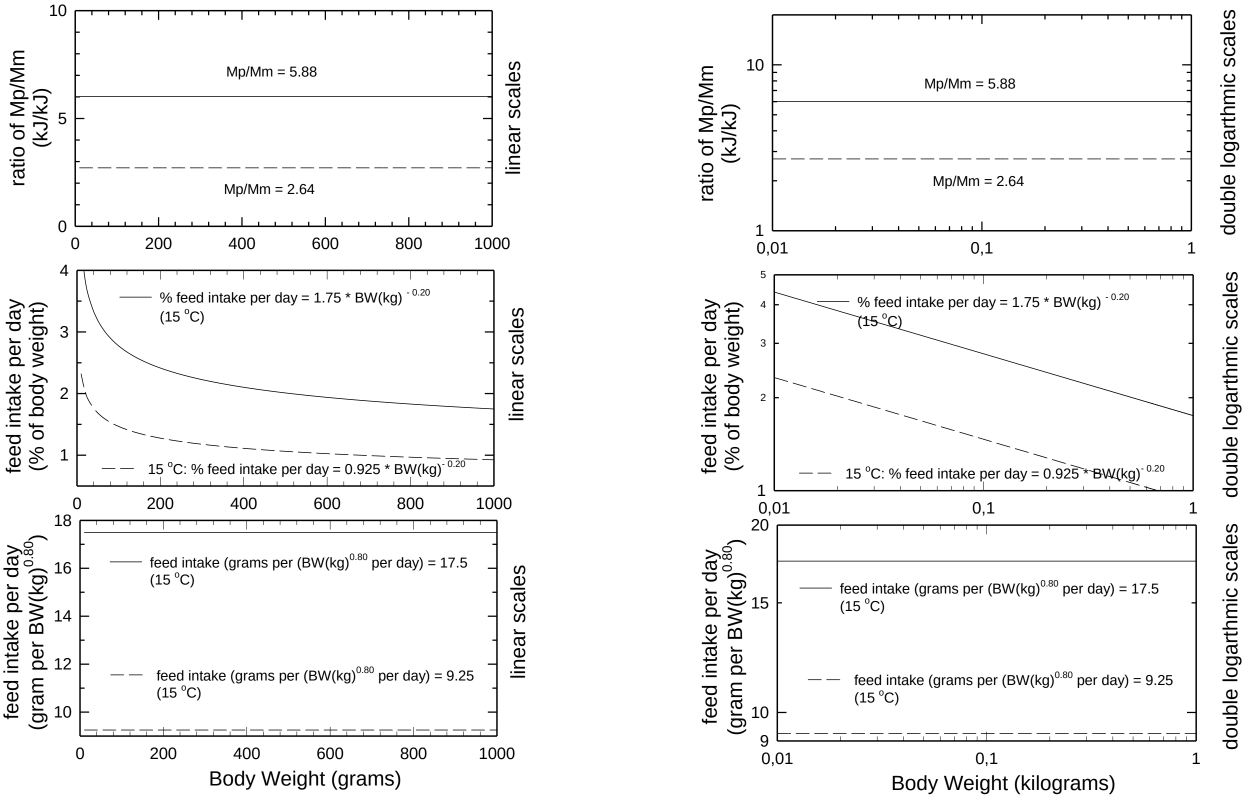


Figure 9

Standard feeding curves (high and low feeding levels) at 15 °C. The feed intake per kg metabolic weight (per $BW(kg)^{0.80}$) (bottom panel) and the ratio Mp /Mm (top panel) is the same for all the various body weights (compare with Figure 10 where the feed intake per $BW(kg)^{0.80}$ and the ratio Mp/Mm is different for the various body weights). The ratio of metabolizable energy for production to the metabolizable energy for maintenance (Mp / Mm) is calculated for a trout diet with 19.64 kJ/gram metabolizable energy (see diet Table 2 or 6) at a temperature of 15 °C.

Further, the effect of the temperature on the feeding level is (see paragraph 7)

$$\text{\% feed intake at } T_2 = \text{\% feed intake at } T_1 * e^{0.095 * (T2-T1)} \text{ or}$$

$$\text{\% feed intake at } T_2 = \text{\% feed intake at } T_{1=15} * e^{0.095 * (T2-15)} \text{ or}$$

$$\text{\% feed intake at } T_2 = \text{\% feed intake at } T_{1=15} * e^{0.095 * (T2)} * e^{0.095 * (-15)}$$

Replacing % feed intake (<u>*low*</u> feeding levels) at $T_{1=15}$ by 0.925 * $BW(kg)^{-0.20}$ gives:

$$\text{\% feed intake at } T_2 = 0.925 * BW(kg)^{-0.20} * e^{0.095 * (T2)} * e^{0.095 * (-15)} \text{ or}$$

$$\mathbf{\text{\% feed intake}_{\text{at temperature T}} = 0.2225 * BW(kg)^{-0.20} * e^{0.095 * (T)}} \textit{ (low feeding levels at T=T)}$$

Replacing % feed intake (<u>*high*</u> feeding levels) at $T_{1=15}$ by 1.75 * $BW(kg)^{-0.20}$ gives:

$$\% \text{ feed intake at } T_2 = 1.75 * BW(kg)^{-0.20} * e^{0.095 * (T2)} * e^{0.095 * (-15)} \text{ or}$$

$$\mathbf{\% \text{ feed intake}_{\text{at temperature } T} = 0.4209 * BW(kg)^{-0.20} * e^{0.095 * (T)}} \textit{ (high feeding levels at T=T)}$$

And similarly,

$$\mathbf{\text{feed intake per } BW(kg)^{0.80}_{\text{at temperature } T} = 2.225 * e^{0.095 * (T)}} \textit{ (low feeding levels at T=T)}$$

$$\mathbf{\text{feed intake per } BW(kg)^{0.80}_{\text{at temperature } T} = 4.209 * e^{0.095 * (T)}} \textit{ (high feeding levels at T=T)}$$

Note that the temperature has an effect on the feed intake, but not on the ratio of metabolizable energy for production / metabolizable energy for maintenance (Mp/Mm) (see paragraph 7, page 21 bottom).

(b) *The feed intake per kg metabolic weight (per $BW(kg)^{0.80}$ and the ratio of Mp/Mm are different for all different sizes of trout.*

We can construct feeding curves (see paragraph 6) of the general allometric form (feed intake expressed as % of body weight):

$$\% \text{ feed intake} = x * BW(kg)^{p}$$

or of the general allometric form (feed intake expressed as gram per kg metabolic weight):

$$\text{feed intake (in grams per kg metabolic weight)} = c = z * BW(kg)^{w}$$

Thus the feed intake can be expressed at two different ways:

(1) in % of body weight (grams per 100 gram of fish) per day: % feed intake = $x * BW(kg)^{p}$
(2) in grams per kg metabolic weight (per $BW(kg)^{0.80}$) per day: $c = z * BW(kg)^{w}$

Where c is the feed intake per kg metabolic weight (per $BW(kg)^{0.80}$).

The two ways of expressing the feed intake can be converted into each other by the two formulas (formulas 1 and 2 of paragraph 6) and where c is the feed intake per kg metabolic weight:

$$\% \text{ feed intake per day (or feed intake per 100 gram of fish)} = (c/10) * BW(kg)^{-0.20}$$

and

$$\text{Feed Intake per kg metabolic weight} = c = 10 * (\% \text{ feed intake per day}) / (BW(kg)^{-0.20})$$

As indicated in paragraph 6 (page 17), the feed intake per kg metabolic weight and the ratio Mp/Mm is the same for all different sizes of trout when the scaling coefficient p = - 0.20 in the formula:

$$\% \text{ feed intake} = x * BW(kg)^{p} = x * BW(kg)^{-0.20}$$

Then,

$$\text{Feed Intake per kg metabolic weight} = c = 10 * (\% \text{ feed intake per day}) / (BW(kg)^{-0.20})$$

And replacing % feed intake per day by $x * BW(kg)^{-0.20}$:

Feed Intake per kg metabolic weight = c = 10 * (x * BW(kg) $^{-0.20}$) / (BW(kg) $^{-0.20}$) = 10 * x

It is, however, possible that the growth potential of the trout decreases when the trout grows larger and that relatively less energy can be used for growth or production, We do, however, not have data that indicate that the growth potential and the ratio of metabolizable energy for production / metabolizable energy for maintenance (Mp/Mm) decreases when the trout grows larger and we do also not know what the maximum ratio of Mp/Mn is for the trout. When we assume that the growth potential decreases when the trout grows larger, then the ratio Mp/Mm (metabolizable energy for production / metabolizable energy for maintenance) will decrease when the tout grows larger. From this perspective, it may be desirable to construct feeding curves that involve a lower ratio of Mp /Mm and thus a lower feed intake per kg metabolic weight when the trout grows larger. As discussed in paragraph 6 (page 17), the feed intake per kg metabolic weight (per (BW(kg) $^{0.80}$) and the ratio Mp/Mm will be the same for all sizes of trout, when the scaling coefficient p of the formula that describes the feed intake as percentage of body weight (% feed intake = x * BW(kg) ^{p}) is p = - 0.20. In addition, when the effect of the temperature on the feed intake follows the same pattern as the effect of the temperature on the metabolic rate, then the ratio Mp/Mn will also be the same at various temperatures (see chapter 7).

Suppose that we want to construct a feeding curve that has a feeding level of 20 grams of feed per kg metabolic weight (per BW(kg)$^{0.80}$) for a trout of 10 grams (0.01 kg) and decreases gradually to a feed intake of 15 grams per kg metabolic weight for a trout of 1000 grams (1 kg) at a temperature of 15 ^{o}C. The ratio of Mp/Mm is then 6.83 for a trout of 1 gram and 4.89 for a trout of 1000 grams when we feed the diet of Table 2 or 6 (see calculations below).

Calculation of the ratio Mp/Mm:
We have for example a feed with a metabolizable energy density of 19.64 kJ / gram (feed in Table 2 or 6) and the feed intake is 20 grams per kg metabolic weight (per BW(kg)$^{0.80}$) for of trout 0.01 kg.
The maintenance energy expenditure of trout is about 50 * BW(kg)$^{0.80}$ at 15 ^{o}C (see paragraph 5).
The energy expenditure of a trout of 10 grams is: 50 * (0.01)$^{0.8}$ = 1.26 kJ per day. The intake of energy from the feed is 20 * 19.64 * BW(kg)$^{0.80}$ = 20 * 19.64 * (0.01)$^{0.80}$ = 9.87 kJ. The ratio Mp/Mm = (9.87 – 1.26) / 1.26 = **6.83**.
The feed intake is 15 grams per kg metabolic weight for a trout of 1 kg. The energy expenditure of a trout of 1000 grams is 50 * (1)$^{0.80}$ = 50 kJ and the intake of energy from the feed is 15 * 19.64 * BW(kg)$^{0.80}$ = 15 * 19.64 * (1)$^{0.80}$ = 300.75 kJ. The ratio of metabolizable energy for production / metabolizable energy for maintenance or Mp/Mm = (294.60 – 50) / 50 = **4.89**.

The formula that describes the feed intake (expressed in grams per kg metabolic weight or per BW(kg)$^{0.80}$) as a function of the body weight (kg) is given by the general allometric equation:

feed intake (gram per BW(kg)$^{0.80}$) = z * BW(kg) ^{w}

As seen with allometric functions, plotting the feed intake (expressed in grams per kg metabolic weight (BW(kg)$^{0.80}$) vs the body weights (in kilograms) results in a linear plot when the data are plotted on a double logarithmic scale. Thus the two values of 20 grams feed intake and 15 grams feed intake (per BW(kg)$^{0.80}$) for a trout of 10 and 1000 grams at a temperature of 15 ^{o}C, respectively, are two points of a linear plot on a double logarithmic scale. The two values are plotted on a double logarithmic scale vs the body weights and the intercept and the slope of the linear line through these two points are calculated by linear regression. We calculated (Figure 10, right bottom panel) that the formula for the feed intake per kg metabolic weight (per BW(kg)$^{0.80}$) was:

feed intake (grams per BW(kg)$^{0.80}$) = 15.00 * BW(kg) $^{-0.0625}$ (1)

and the feeding curve is given in the left bottom panel of Figure 10.

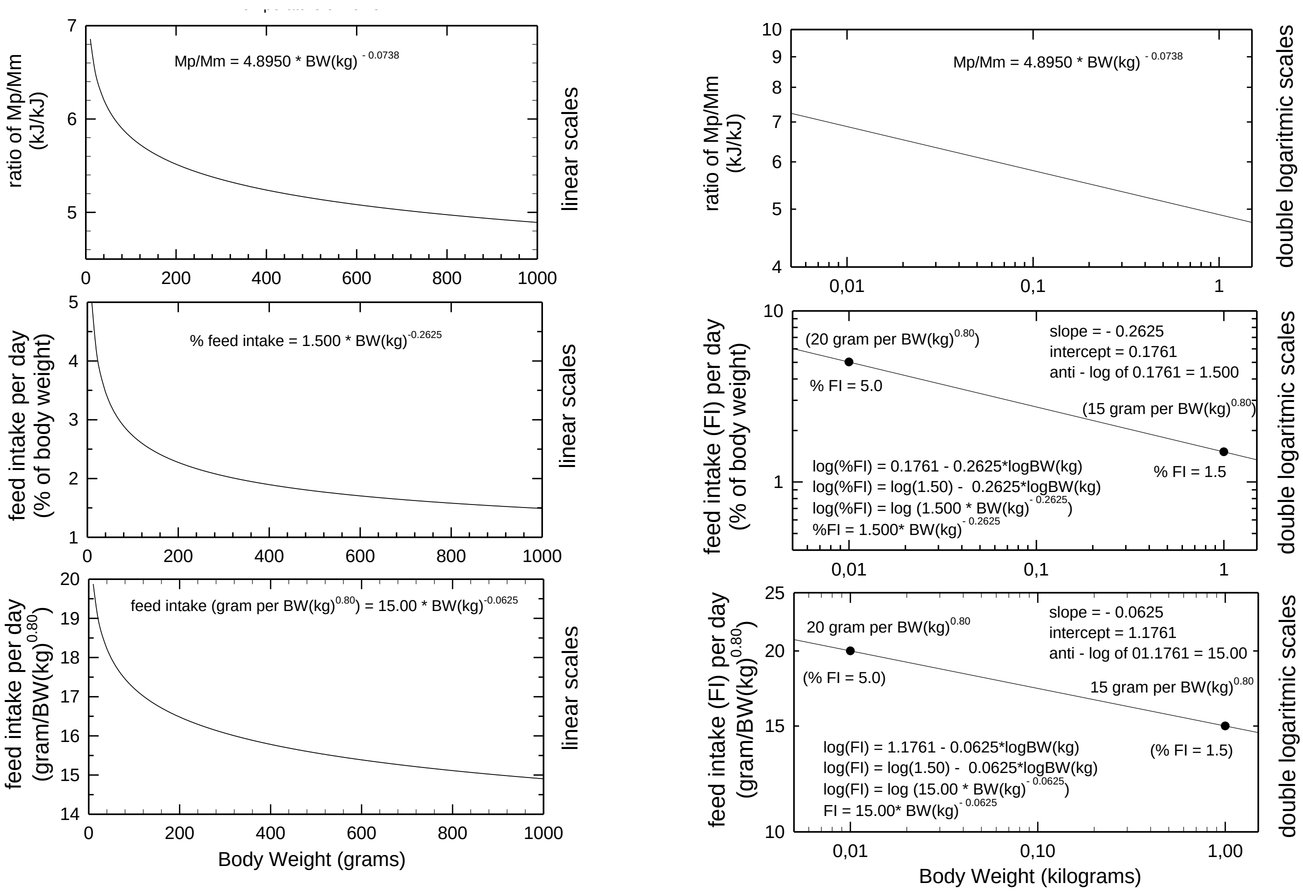


Figure 10

Feed intake decreases from 20 gram of feed per kg metabolic weight for a trout of 10 grams (5.0238 % feed intake) to 15 gram of feed per kg metabolic weight (1.5 % feed intake) for a trout of 1000 grams (at a temperature of 15 ^{o}C) The ratio of metabolizable energy for production to the metabolizable energy for maintenance (Mp / Mm) is calculated for a trout diet with 19.64 kJ/gram metabolizable energy (See diet Table 2 or 6) at a temperature of 15 ^{o}C. Compare with Figure 9, where the feed intake per kg metabolic weight (per BW(kg) $^{0.80}$ and the ratio Mp / Mm is the same for all the various body weights.

The feed intake expressed in % of body weight can now be converted into the feed intake per kg metaboiic weight (per BW(kg) $^{0.80}$) with the formula (formula 1 of paragraph 6, page 15):

$$\text{\% feed intake per day (feed intake per 100 gram of trout)} = (c/10) * BW(kg)^{-0.20}$$

where c is feed intake per kg metabolic weight (BW $^{0.80}$) and body weight in kg. Replacing of c = feed intake (grams per BW(kg)$^{0.80}$) by 15 * BW(kg) $^{-0.0625}$ in the formula gives:

$$\text{\% feed intake per day} = (15 * BW(kg)^{-0.0625}/10) * BW(kg)^{-0.20} \quad \text{or}$$

$$\textbf{\% feed intake per day} = \mathbf{1.5 * BW(kg)^{-0.2625}} \qquad \textbf{(2)}$$

And the feeding curve is given in the left middle panel of Figure 10.

We can easily convert a feeding curve expressed in grams per kg metabolic weight (per BW(kg)$^{0.80}$) into a feeding curve expressed in % of body weight and the other way around with the formulas (see formula 1 and 2 of paragraph 6, page 15).

% feed intake per day (feed intake per 100 gram of trout) = (c/10) * $BW(kg)^{-0.20}$

where c is feed intake per kg metabolic weight ($BW^{0.80}$) and

Feed Intake per kg metabolic weight = c = 10 *(% feed intake per day) / ($BW(kg)^{-0.20}$)

See Examples below.

Example:
The feed intake per kg metabolic weight is for example described by the allometric formula (see Figure 10):
(1)Feed intake (gram per $BW(kg)^{0.80}$) = c = 15 * $BW(kg)^{-0.0625}$
We can convert the feed intake expressed in % of body weight into a feed intake expressed in grams per kg metabolic weight (per $BW(kg)^{0.80}$) with the formula:
(2) % feed intake per day (feed intake per 100 gram of trout) = (c/10) * $BW(kg)^{-0.20}$
Substituting (1) into (2):
% feed intake per day (feed intake per 100 gram of trout) = (15 * $BW(kg)^{-0.0625}$/10) * $BW(kg)^{-0.20}$ or
% feed intake per day (feed intake per 100 gram of trout) = (1.5 * $BW(kg)^{-0.2625}$ (see Figure 10)

Similarly:
The % feed intake is for example described by the allometric formula (see Figure 10):
(1) % feed intake = 1.5 * $BW(kg)^{-0.0625}$
We can convert the feed intake expressed in grams per kg metabolic weight (per $BW(kg)^{0.80}$) into a feed intake expressed in % of body weight with the formula:
(2) feed intake per kg metabolic weight = c = 10 *(% feed intake per day) / ($BW(kg)^{-0.20}$)
Substituting (1) into (2):
feed intake per kg metabolic weight = c = (10 * 1.5 * $BW(kg)^{-0.2625}$) / ($BW(kg)^{-0.20}$ or
feed intake per kg metabolic weight = c = 15 * $BW(kg)^{-0.0625}$ (see Figure 10)

Further, we can also include the effect of the temperature on the feeding level with the formula (see paragraph 7):

Feed intake (grams per $BW(kg)^{0.80}$ at T_2 = Feed intake (grams per $BW(kg)^{0.80}$) at T_1 * $e^{0.095 * (T2-T1)}$

where T is the temperature in ^oC and $T_1 = 15\ ^oC$.

feed intake (grams per $BW(kg)^{0.80}$) at T_2 = 15.0 * $BW(kg)^{-0.0625}$ * $e^{0.095 * (T2-T1)}$

feed intake (grams per $BW(kg)^{0.80}$) at T_2 = 15.0 * $BW(kg)^{-0.0625}$ * $e^{0.095 * (T2)}$/ $e^{0.095 * (T1)}$

feed intake (grams per $BW(kg)^{0.80}$) at T_2 = 15.0 * $BW(kg)^{-0.0625}$ * $e^{0.095 * (T2)}$ * $e^{0.095 * (-15)}$

feed intake (grams per $BW(kg)^{0.80}$) $_{\text{at temperature T = T}}$ = 3.608 * $BW(kg)^{(-0.0625)}$ * $e^{0.095 * (T)}$ **(3)**

and conversion into feed intake expressed in % of body weight with formula 1 of paragraph 6, page 15

% feed intake $_{\text{at temperature T = T}}$ = 0.3608 * $BW(kg)^{(-0.2625)}$ * $e^{0.095 * (T)}$ **(4)**

Thus, these formulae 3 and 4 describes the feed intake for various sizes trout at various temperatures where the feed intake expressed in grams per kg metabolic weight ($BW(kg)^{0.80}$) decreases from about 20 to about 15 grams for a trout of 10 grams and 1000 grams, respectively. This way, various types of feeding formulas can be developed. Figure 10 shows that the ratio Mp/Mm (metabolizable energy for production / metabolizable energy for maintenance) now decreases when the trout grows larger (in contrast to Figure 9, where this ratio is independent of the body weights and remains the same for all the different sizes of trout).

Thus, various types of feeding curves can be constructed, depending on the requirements. For example, a feeding curve can be constructed for a particular feed where the ratio of the Mp/Mm has to decrease from a value of 5 for a trout of 10 grams to a value of 3 for a trout of 350 grams.

10. Growth Curves for Trout

(for more details, see the article: *Some aspects of energy metabolism in homeothermic animals and poikilothermic fish*)

Two major types of growth curves can be used for trout, the exponential growth curve and the power growth curve, also called the Daily Growth Coefficient (DGC) growth curve (Iwama, 1981, Kaufman, 1981). The exponential growth curve can be used to describe the growth of trout larvae, up to about 10 grams, and the power growth curve to describe the growth of larger size trout.

<u>The exponential growth curve is described by the formula:</u>

$$\mathbf{BW_1 = BW_o\ e^{\alpha t}}$$

which is an exponential function where t is the time in days and BW_0 is the body weight when t=0. The logarithmic and linear form is:

$$\ln (BW_1) = \ln (BW_o * e^{\alpha t}) = \ln BW_o + \alpha t \ln e = \ln BW_o + \alpha t$$

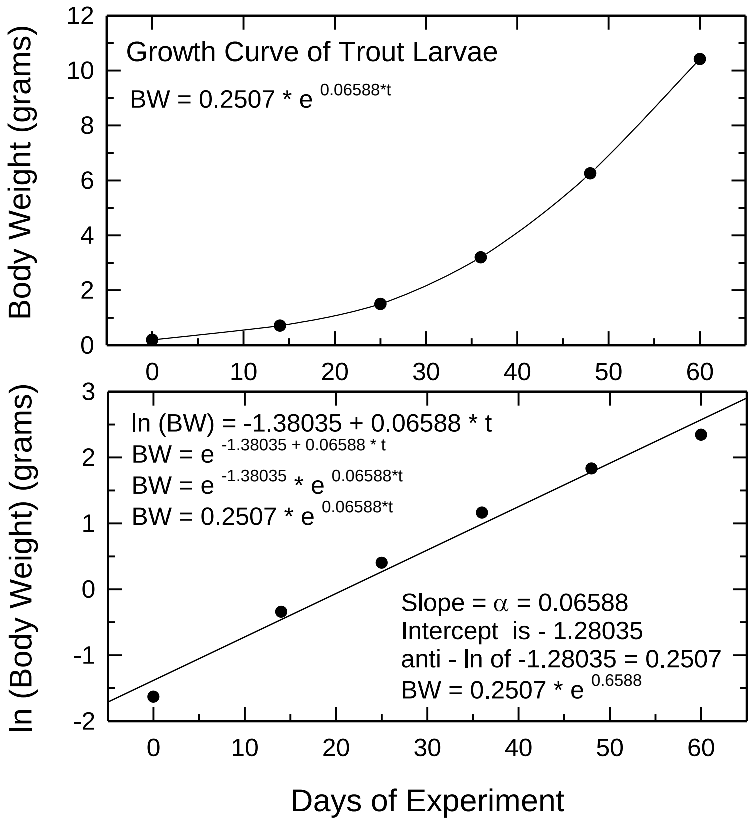


Figure 11

Exponential growth curve of trout larvae. Data were collected by the author.

A growth curve fits an exponential growth curve when a linear plot arises when the ln values of the body weights are plotted vs the time. An example of the exponential growth curve is given in Figure 11. The ln values of the body weights are plotted vs the time (days). The slope α and the intercept (ln BW_0) of this linear plot can be calculated by linear regression and the slope α is the exponent of the function and the anti-ln of the intercept (ln BW_0) is BW_0 at t=0.

The slope α can also be estimated by taking two points of the graph and using the formula (shortened method):

$\alpha = \ln BW_{t=t2} - \ln BW_{t=t1}$

When we have calculated the value of α and BW_0 (the anti-ln of the intercept), then we can calculate the body weights at each time point with the formula: $BW_1 = BW_o\, e^{\alpha t}$ for any value of BW_0.

***Example**:* The growth of trout larvae is for example described by the exponential function:
$BW_1 = BW_0 * e^{\alpha t} = 0.2507 * e^{0.06588*t}$ where BW_o is the BW at t = 0 and is in this example 0.2507 grams
The body weight at t = 10 days is:
$BW_1 = 0.2507 * e^{0.06588*10} = 0.4845$ grams.
The body weight after another 10 days is:
Method 1:
$BW_1 = BW_o * e^{\alpha t} = 0.4845 * e^{0.06588*10} = 0.936$ grams
Method 2:
$BW_1 = BW_o * e^{\alpha t} = 0.2507 * e^{0.06588*20} = 0.936$ grams.

Further, we can calculate the time that is needed to double the body weights:

$$t = t_2 - t_1 = \frac{\ln 2}{\alpha}$$

Similarly, the time needed to triple the body weights is:

$$t = t_2 - t_1 = \frac{\ln 3}{\alpha}$$

Example: When α = 0.06588, then the time to double the body weights is: ln 2 / 0.06588 = 10.5 days.
Note that the time to double (or triple) the body weights is independent of the initial body weight.

Note that the time to double (or triple) the body weights is independent of the initial body weight.

In addition, we can calculate the % of growth per unit of time

$$\textbf{\% growth per time unit of } t_1\text{-}t_0 = 100\% * (e^{\alpha(t1-t0)} - 1)$$

And the % growth per day is

$$\textbf{\% growth per day} = 100\% * (e^{\alpha} - 1)$$

Note that the % growth per day is independent of the (initial) body weight.

Example: Suppose that we calculated from the experimental data that α = 0.05 we want to calculate the % growth per day, thus t_1-t_0 = 1 day. % growth per day = 100% * (e^{α} – 1) % growth per day = 100% * ($e^{(0.05 *1)}$ – 1) = 5.157 % per day

This result means that the body weights will increase every day with 5.16%, independently of the (initial) body weights. A similar phenomenon is seen with an amount of money on the bank with a so called compound interest rate per year; every year the amount of money will increase with the percentage of the interest rate, independent of the (initial) amount of money on the bank.

The percentage growth per day is usually called the specific growth rate (SGR). In financial terms it is called the interest rate per year. Mostly, the value of α is used as the SGR, but this is not really correct, although the differences between the value of α and the SGR as calculated above is not much different (5.0 vs 5.12% in the example above).
Similarly, we can calculate the % growth per 2 days, 3 days etc.

<u>The power growth curve is described by the formula:</u>

$$\mathbf{BW^{1/3}{}_{day=1} = BW^{1/3}{}_{day=0} + c\ t}$$

which is a linear function where $BW^{1/3}$ is the body weight raised to the power 1/3, t is time (days), c is the slope of the graph, and $BW^{1/3}{}_{day=0}$ is the body weight raised to the power 1/3 when t=0. The slope c multiplied by 100 is called the Daily Growth Coëfficient (DGC, *Iwama 1981*). A growth curve fits a power growth curve when a linear graph arises when the values of the body weights raised to the power 1/3 are plotted vs the time. The slope c of this linear plot and the intercept $BW^{1/3}{}_{day=0}$ can be calculated with linear regression. Also a power coefficient different from 1/3 has sometimes to be used to fit a power growth curve. The correct power coefficient can be found by trial and error. A correct power coefficient means that the body weights raised to the power coefficient and plotted vs the time results in a linear curve.

The formula can also be written as:

$$BW_{day=1} = (BW^{1/3}{}_{day=0} + c\ t)^3$$

and, since the daily growth coefficient is defined as: (DGC) is c * 100:

$$BW_{day=1} = (BW^{1/3}{}_{day=0} + (DGC/100)\ t)^3$$

When we know the DGC, we can calculate with this formula the body weights $BW_{day=1}$ at various time points for any value of $BW_{day=0}$.

<u>How to calculate the the DGC:</u>

<u>Method 1.</u>
When a set of growth data are given (various time points with various body weights), then all the (body weights)^d are plotted versus the time. Then, by means of a linear regression analysis, the intercept (intercept is BW^d when time = 0) and the slope (x 100 = DGC) can be calculated. The value for d has to be determined by trial and error. A correct value for d has been found when the graph of the values of the (body weights)^d vs the time is a linear graph. For trout of about 20 – 500 grams a value for d of 0.333 appears to be suitable.

<u>Method 2.</u>
When only the body weights at two time points are known and one is confident that these two time points are the points of a linear curve describing the BW^d vs time, then the slope can be calculated as follows:

$$BW^{d}_{day=1} = BW^{d}_{day=o} + c*days$$

$$c = (BW^{d}_{day=1} - BW^{d}_{day=o}) / days$$

This c is per definition the slope of the graph (c). The DGC is then c*100. The DGC is expressed as % (weight gain)^{d} per day.

$$\text{Daily Growth Coefficient} = DGC = 100\% * (BW^{d}_{day=1} - BW^{d}_{day=o}) / days$$

Figure 12 shows a power growth curve of trout. The best fit value of d (the exponent of the body weight) was 1/3 = 0.33. This value was found by trial and error, i.e. a linear graph is generated when the body weights raised to this power are plotted vs the time (see bottom panel of Figure 12).

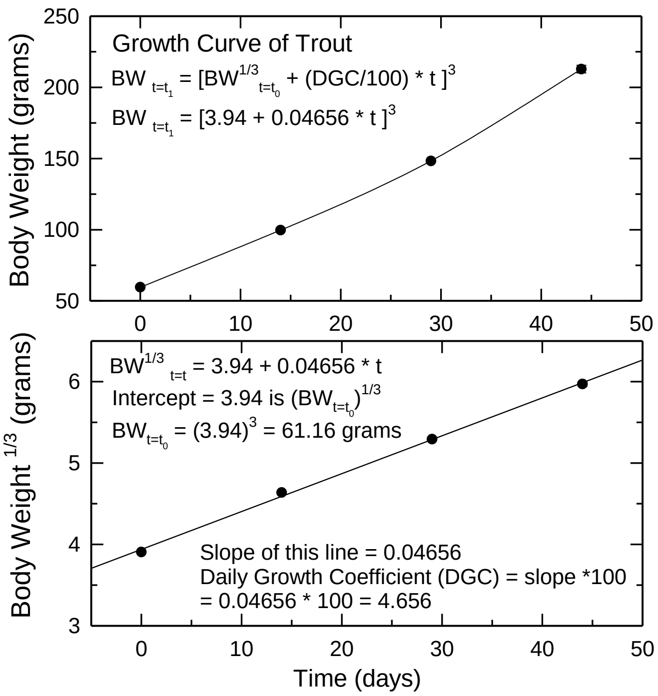


Figure 12
Power growth curve of trout. Data were collected by the author.

The calculated DGC can be used to predict body weights after a defined number of days as:

Final Body Weight = [(Initial Body Weight) $^{1/3}$ + (DGC/100) * days on diet)] ^{3}

Further, when the final body weight is known, the number of days, and the DGC, then the initial body weight can be calculated:

Initial Body Weight = [(Final Body Weight) $^{1/3}$ – (DGC/100) * (days on diet)]^{3}

Similarly, when the initial body weight is known and the DGC, then it can be calculated after how many days a defined body weight has been reached:

Days on Diet = 100 * [(Final Body Weight) $^{1/3}$ – (Initial Body Weight) $^{1/3}$)] / (DGC)

Example: The body weight at day 90 is 11.7 grams and the body weight at day 200 is 129.9 grams and d = 1/3, thus number of days is 110 days, then the DGC is:

$$DGC = 100\% * (BW^{1/3}_{day=1} - BW^{1/3}_{day=o}) / days$$
$$DGC = 100 \times [(129.9)^{1/3} - (11.7)^{1/3}] / 110 = 2.54 \% \text{ (weight gain)}^{1/3} \text{ per day}$$

Example: The initial body weight is 50 grams and d = 1/3 and the DGC is 2.54. Then the body weight after 20 days can be calculated as

$$\text{Final Body Weight} = [(\text{Initial Body Weight})^{1/3} + (DGC/100) * \text{days on diet})]^{3}$$
$$\text{Final Body Weight} = [(50)^{1/3} + (2.54 / 100)*20]^{3} = 73.4 \text{ grams.}$$

Example: The final body weight is 73.4 grams after 20 days and the DGC is 2.54. Then the initial body weight is:

$$\text{Initial Body Weight} = [(\text{Final Body Weight})^{1/3}] – [(DGC/100) * (\text{days on diet})]^{3}$$
$$\text{Initial Body Weight} = [(73.4)^{1/3} – (2.54/100) * (20)]^{3} = 49.8 \text{ grams}$$

***Example*:** The initial body weight is 50 grams and d = 1/3 and the DGC is 2.54. How long does it take to double the body weight?

$$\text{Days on Diet} = 100 * [(\text{Final Body Weight})^{1/3} – (\text{Initial Body Weight})^{1/3})] / (DGC)$$
$$\text{Days on Diet} = 100 * [(100)^{1/3} – (50)^{1/3})] / (2.54) = 37.7 \text{ days}$$

Note that the time to double the body weight is dependent on the initial body weight (see example below). The time to double the body weight for an exponential growth curve is independent of the initial body weight.

Example: The initial body weight is 100 grams and d = 1/3 and the DGC is 2.54. How long does it take to double the body weight?

$$\text{Days on Diet} = 100 * [(\text{Final Body Weight})^{d} – (\text{Initial Body Weight})^{d})] / (DGC)$$
$$\text{Days on Diet} = 100 * [(200)^{1/3} – (100)^{1/3})] / (2.54) = 47.5 \text{ days}$$

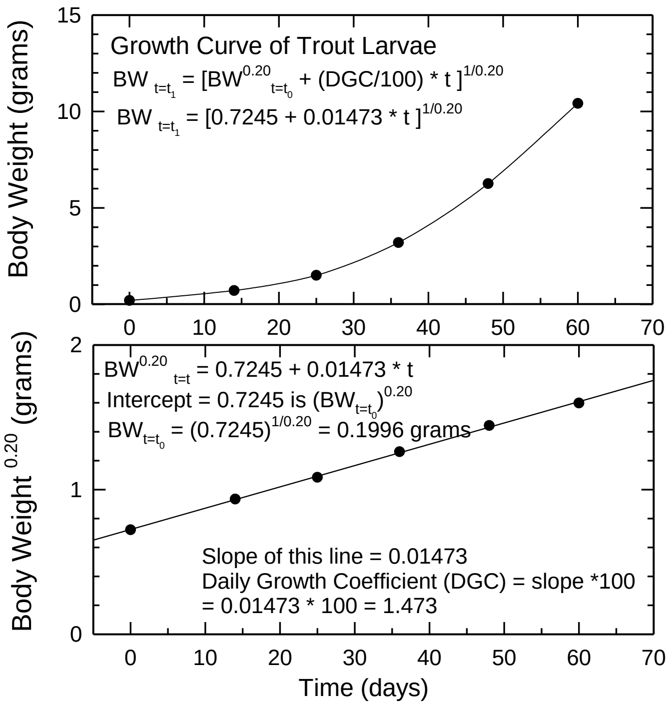


Figure 13
Power growth curve of trout larvae. Data were collected by the author

The exponential growth curve is mostly used to describe the growth of trout larvae up to about 10 grams whereas the power growth curve is used for larger size trout. However, the power growth curve can also be used to describe the growth rate of trout larvae, but a power coefficient smaller than 1/3 = 0.333 has to be used. The correct power coefficient has to be found by trial and error and we found that a power curve with a power coefficient of

0.20 can also describe the growth rate of trout larvae instead of an exponential growth curve. Dumas et al. (2007b) described that various power coefficients may be used dependent on the size of the trout and the growth stanza. Figure 13 shows that the growth curve of trout larvae can also be described by a power growth curve instead of an exponential growth curve.

11. The Relationship between Body Weight and Body Length: the Condition Factor

The relationship between the body weight and length in fish (and also in humans and probably also in other animal species) can be described by the allometric function (Froese 2006, Nash 2006):

$$\text{Body weight} = a^*(\text{length})^b$$

where the body weight is expressed in grams and the length in centimeters, b is the scaling exponent or coefficient and a is the normalization constant (body weight per length^b). The formula can be rearranged and becomes then:

$$a = (\text{body weight}) / (\text{length})^b.$$

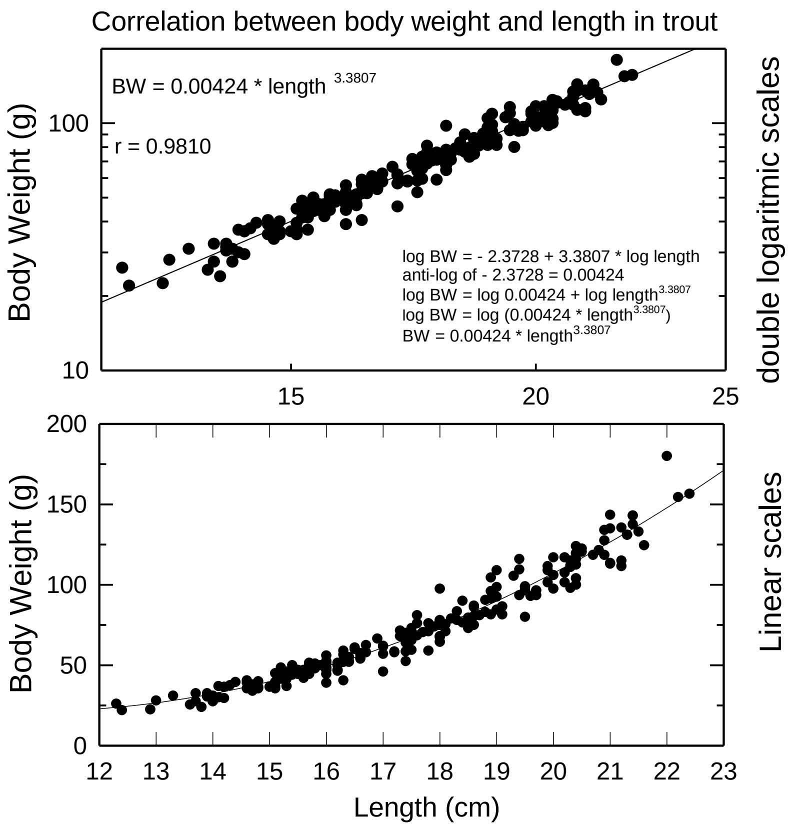


Figure 14
Correlation between body length and body weight in trout

When the body weights of fish are plotted vs the length, the scaling exponent b is about 3 and the normalization constant “a” multiplied by 100 is defined as the condition factor of a fish (Nash et al. 2006).

$$\text{Condition factor} = 100 * (\text{body weight (g)}) / (\text{length (cm)})^3$$

Thus the condition factor is the weight of a fish per cubic length. The higher the weight of the fish of a specific length, the higher the condition factor will be.

Figure 14 shows the relationship between the body weights and the body lengths in trout. Data were collected by the author. The body weights in grams are plotted vs the body lengths in centimeters on double logarithmic graph paper (e.g. log – log paper). The slope of this line is b in the formula $a*BW^b$. The intercept of the line is log a and the anti-log of log a is a in the formula $a*BW^b$.

Example: We can calculate from the graph above that describes the correlation between the body weight and body length in trout, that the body weight of a trout with a length of 15 centimeter is:
Body weight = $0.00424 * 15^{3.3807}$ = 40.8 grams.
The condition factor of this trout of 40 8 grams and 15 cm long = 100 * (40.8)/ (15^3) = 1.21

12. Body Composition of the Trout

The major components of the trout are water, protein, fat and ash. The proportion of protein in the body is rather constant (about 15 - 20%) and the same is true for the ash content (about 2%). However, the fat and water content can vary strongly and is dependent on various factors such as e.g. the feeding level and the composition of the diets. The percentage of ash and protein in the body is rather constant and a high percentage of body fat will thus result in a low percentage of water. As a consequence, the percentage of water is negatively correlated with the percentage of fat, i.e. a high % fat is associated with a low % water. When the correlation between water content and fat content is known, then the proportion of fat in the body can be derived from the water content in the body. The water content of the body of experimental animals can be easily measured by drying in an oven.

The amount of protein, fat, water and ash in the body can be described by the allometric scaling equation:

$$\text{amount (\%)} = a*BW(g)^b$$

where a is the normalization constant, BW is the body weight in grams and b is the scaling coefficient. Dumas et al. (2007) have described the body composition of trout of various body weights based on a large number of carcass analysis data from the literature. The formulae for the percentages of protein, fat, ash and water are:

Moisture (%) = $92.25\ BW(g)^{-0.0543}$
Fat (%) = $3.235\ BW(g)^{0.243}$
Protein (%) = $13.36\ BW(g)^{0.036}$
Ash (%) = $2.1978\ BW(g)^{-0.004}$
Energy (kJ/g) = $3.84\ BW(g)^{0.1510}$

mg protein per kJ in trout = $34.78\ BW(g)^{-0.1150}$

Moisture (g) = $0.8198\ BW(g)^{0.9787}$
Protein (g) = $0.1266\ BW(g)^{1.0545}$
Fat (g) = $0.027\ BW(g)^{1.1647}$
Ash (g) = $0.0239\ BW(g)^{1.0482}$

Energy (kJ) = 3.929 BW $^{1.0975}$

Example: A trout has a body weight of 250 grams. The composition of the trout is then: Moisture (%) = 92.25 * 250 $^{-0.0543}$ = 68.4% Fat (%) = 3.235 * 250 $^{0.243}$ = 12.4% Protein (%) = 13.36 * 250 $^{0.036}$ = 16.3% Ash (%) = 2.1978 * 250 $^{-0.004}$ = 2.1% Energy (kJ/g) = 3.84 * 250 $^{0.1510}$ = 8.8 kJ/gram trout mg protein per kJ in trout = 34.78 * 250 $^{-0.1150}$ = 18.43 mg / kJ energy

Figure 16 shows the body composition of the trout (Dumas et al. 2007) and Figure 15 shows the correlation between the % of body water and the % of body fat in the trout (these data are from 23 studies from the literature that describe the body composition of trout of various body weights (*see article: Some aspects of energy metabolism in homeothermic animals and poikilothermic fish*).

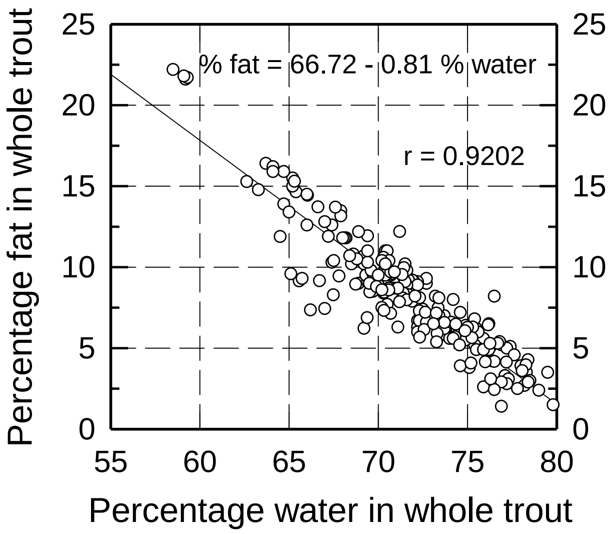


Figure 15
Correlation between body water and body fat. Data were collected by author from various studies in the literature.

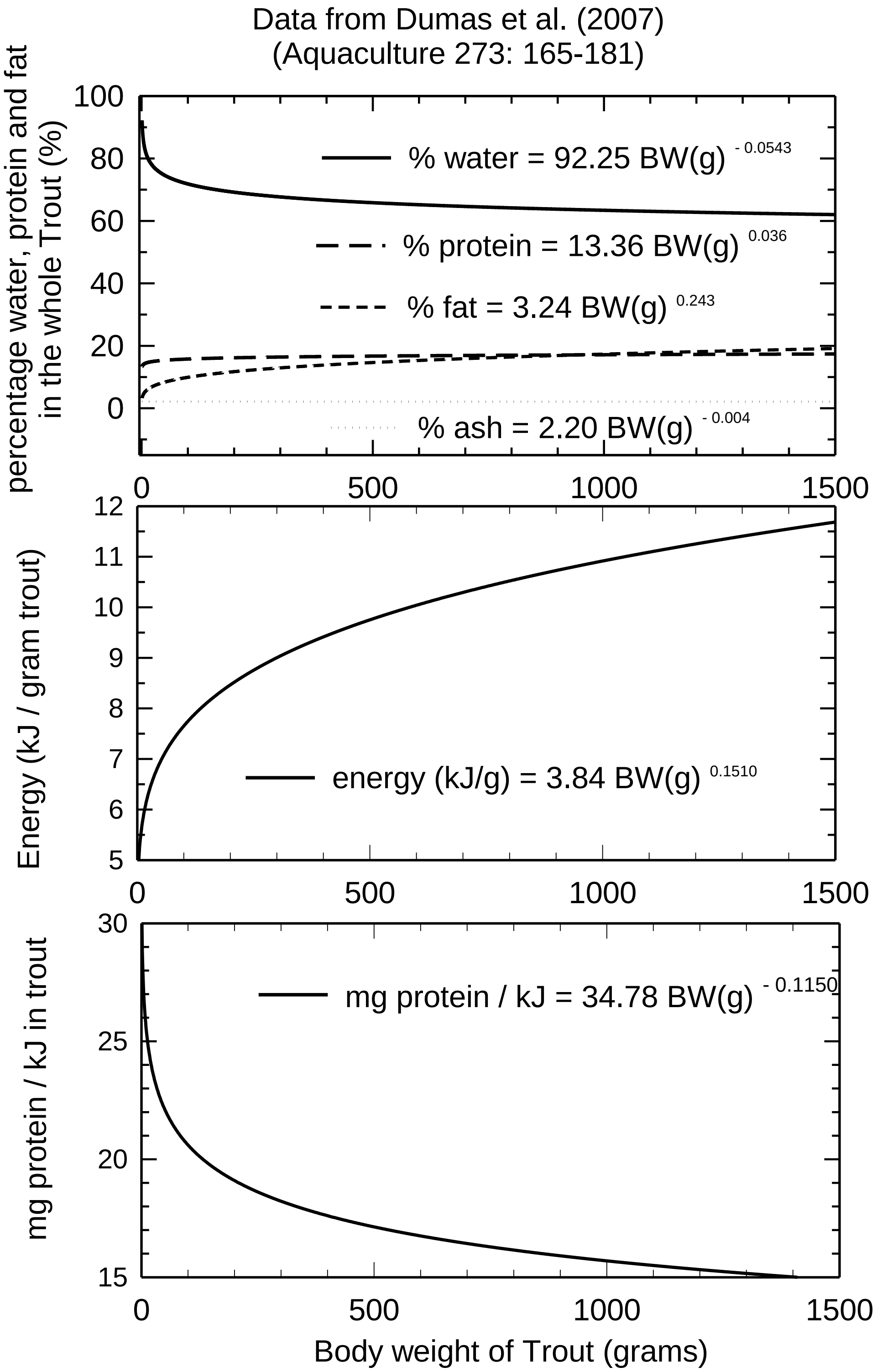


Figure 16

Body composition of trout. From: A. Dumas, C.F.M. de Lange, J. France and D.P. Bureau (2007) Quantitative description of body composition and rates of nutrient deposition in rainbow trout (*Oncorhynchus mykiss*). Aquaculture 273: 165 – 181.

13 Energy Budget of the Trout

The maintenance energy expenditure or heat production or metabolic rate of a trout at a temperature of 15 ^oC can be approximately described by the allometric scaling formula (Huisman 1974 and Glencross 2009):

$$\text{Maintenance Energy Expenditure} = 50 * BW(kg)^{0.80} \text{ kJ per day}$$

Trout are poikilotherm which means that the body temperature and the energy expenditure is dependent on the water temperature. The effect of the temperature on the energy expenditure or heat production is exponential (Elliott 1976) and can be described by the formula:

$$\text{Heat Production per kg } BW^{0.80} \text{ at } T_2 = \text{Heat Production per kg } BW^{0.80} \text{ at } T_1 * e^{0.095(T2 - T1)}$$

Example: the body weight of a trout is 250 grams and the maintenance energy expenditure of this trout is at a water temperature of 15 ^oC is:
Maintenance Energy Expenditure = 50 * 0.250 $^{0.80}$ = 16.5 kJ per day
The energy expenditure at a water temperature of 10 ^oC is:
Energy expenditure at 10 ^oC = 16.5 * e $^{0.095*(10-15)}$ = 10.3 kJ per day.

The energy budget of a growing trout is given by the formula:

$$\text{Energy Intake} = a*BW^{0.80} + (1/k) * \text{energy deposited.}$$

Where $a*BW^{0.80}$ is the maintenance heat production and k represents the efficiency of energy deposition above maintenance which is about 0.65 (65%).

Suppose we have a trout of 100 grams and the trout is fed at a level of 13 gram per kg metabolic weight (per $BW(kg)^{0.80}$). The feed intake expressed in % of body weight is:

$$\text{\% feed intake per day (feed intake per 100 gram of trout)} = (c/10) * BW(kg)^{-0.20}$$

$$\text{\% feed intake per day (feed intake per 100 gram of trout)} = (13/10) * (0.1)^{-0.20} = 2.06\%$$

The composition of a typical high performance trout diet is given in Table 6.

Table 6
Composition of a high performance trout diet

Nutrient	% in diet	Gross Energy in 1 gram nutrient (kJ/g)	Metabolizable Energy in 1 gram nutrient (kJ/g)	Gross Energy in 1 gram feed (kJ/g)	Digestibility (%)	Digestible Energy in 1 gram feed	Metabolizable Energy in 1 gram feed	Metabolizable Energy in 2,06 gram feed
Protein	45	23,65	19,67	10,64	95	10,11	8,40	17.30
Fat	28	39,6	39,6	11,09	90	9,98	9,98	20,56
Ash	9							
Moisture	5							
Fiber	1	17,5	0	0,175	0			
NFE	12	17,5	17,5	2,1	60	1,26	1,26	2,60
Total	100			24,01		21,35	19.64	40.46

NFE, nitrogen free extract, the carbohydrate faction. . DP/DE (digestible protein/digestible energy) = (450*0.95) / 21.35 = 20.02 mg/kJ

The maintenance heat production of a trout of 0.10 kg at 15 ^oC is about : 50 * BW $^{0.80}$ = 50 * $(0.10)^{0.80}$ = 7.92 kJ per day (metabolizable energy). About 75% of this amount is needed for basal metabolism and about 25% for heat increment of feeding (Specific Dynamic Action (SDA).

The metabolizable energy intake is 2.06 * 19.64 = 40.46 kJ and the metabolizable energy intake above maintenance and thus the energy available for growth is 40.46 – 7.92 = 32.54 kJ metabolizable energy.

The amount of protein and fat in a trout is described by the formula of Dumas (2007) (see page 48):

Fat (g) = 0.03235 BW(g) $^{1.243}$ = 0.03235 * (100) $^{1.243}$ = 9.91 grams of fat
Protein (g) = 0.1336 BW(g) $^{1.036}$ = 0.1336 * (100) $^{1.036}$ = 15.77 grams of protein

These formulae for the composition of the trout are derived from the carcass analyses of a large number of trout. However, the body composition may be affected by various factors such as feeding level etc. and the body composition as reported by Dumas et al. (2007) represents average values.

The metabolizable energy density of 1 gram of fat in the body is 39.6 kJ per gram (see Table 1 page 10). The metabolizable energy density of 1 gram of protein in the body is 19.67 kJ per gram (the energy of combustion of 1 gram of protein is 23.65 kJ per gram, but when protein is combusted in the body the nitrogen has to be excreted in the form of energy rich ammonia (85%) and urea (15%), thus only 19.67 kJ per gram protein is left as metabolizable energy or as energy available to the body, see Appendix 3 footnote 6 (g)).

The *metabolizable* energy density of a trout of 100 grams is thus: (9.91 * 39.6) + (15.77 * 19.67) = 702.6 kJ or 7.026 kJ per gram trout.

We have now available for growth above maintenance 32.54 kJ metabolizable energy and the efficiency of the deposition of energy for growth is on average about 65% (see for example Lupatsch 2003b), thus an amount of 0.65 * 32.54 = 21.15 kJ will be deposited which is equivalent to (21.15 / 7.026) = 3.01 grams of growth of the trout after 1 day. Thus, the feed conversion ratio (FCR) is then 2.06 / 3.01 = 0.68.

The total energy expenditure is the energy for maintenance and the energy costs for deposition, thus 7.92 + (0.35 * 32.54) = 19.31 kJ, which is equivalent to the consumption of 19.31 / 13.75 = 1.40 grams of oxygen (the energy equivalent of oxygen or Eeq O_2 in fish is 13.75 kJ / gram O_2, i.e. the consumption of 1 gram of O_2 by the trout generates 13.75 kJ energy, see footnote of Table 1 page 10), thus the oxygen consumption per g feed is 1.40 / 2.06 = 0.68 grams or 680 grams oxygen per kg feed.

Further, the ratio of energy used for growth and maintenance is 32.54 $_{\text{(energy used for growth)}}$ / 7.92 $_{\text{(energy used for maintenance)}}$ = 4.11.

The *gross* energy in 2.06 grams of feed is 2.06 * 24.01 = 49.46 kJ. The gross energy content of a trout of 100 grams is (9.91 $_{\text{(fat content of trout of 100 grams)}}$ * 39.6 $_{\text{(gross energy of 1 gram fat)}}$ + (15.77 $_{\text{(protein content of trout of 100 grams)}}$ * 23.65 $_{\text{(gross energy of 1 gram of protein)}}$ = 765.4 kJ / 100 grams trout or 7.65 kJ per gram of trout. The growth is 3.01 grams, thus an increase of 3.01 * 7.65 = 23.02 kJ gross energy.

The overall *gross energy* retention is thus 23.01 $_{\text{(gross energy deposited)}}$ / (2.06 $_{\text{(feed intake)}}$ * 24.01 $_{\text{(gross energy in 1 gram of feed)}}$) = 47% and the protein retention is (0.158 $_{\text{(grams protein per gram trout)}}$ * 3.01 $_{\text{(grams of growth)}}$) / (2.06 $_{\text{(grams of feed intake)}}$ * 0.45 $_{\text{(protein level in feed)}}$) = 51%

The overall *digestible energy* retention is 23.01 (gross energy deposited) / (2.06 (feed intake) * 21.35 (digestible energy in 1 gram of feed) = 52%.

The mg digestible protein / kJ digestible energy in the diet = [1000 (grams to mg)) * (0.45 (protein level in feed) * 0.95 (digestibility of protein)] / [21.35 (digestible energy in 1 gram of feed)] = **20.02** mg kJ (mg digestible protein per kJ digestible energy).

and this ratio in the trout itself is [(1000 (conversion of grams to mg) * 15.77 (gram protein per 100 gram trout))] / [(9.91 (gram fat in 100 gram trout) * 39.6(energy in 1 gram of fat)) + (15.77 (gram protein in 100 gram trout) * 23.65 (energy in 1 grams of protein))] = **20.10** mg kJ (mg protein per kJ energy in the trout).

Thus the retention of total digestible energy and the retention of the digestible protein in the diet are more or less similar when the ratio mg digestible protein / kJ digestible energy in the feed and the trout itself are also similar. When this ratio in the diet is lower than that in the trout, then the retention of protein will be higher than the retention of the energy. Phase feeding is based on the principle that the ratio protein / fat in the trout decreases when it grows larger, and this ratio in the diet should therefore also be lowered in order to obtain a high protein retention. This phenomenon is also called the protein sparing effect of fat.

The energy budget of the trout is visually presented in the figure below.

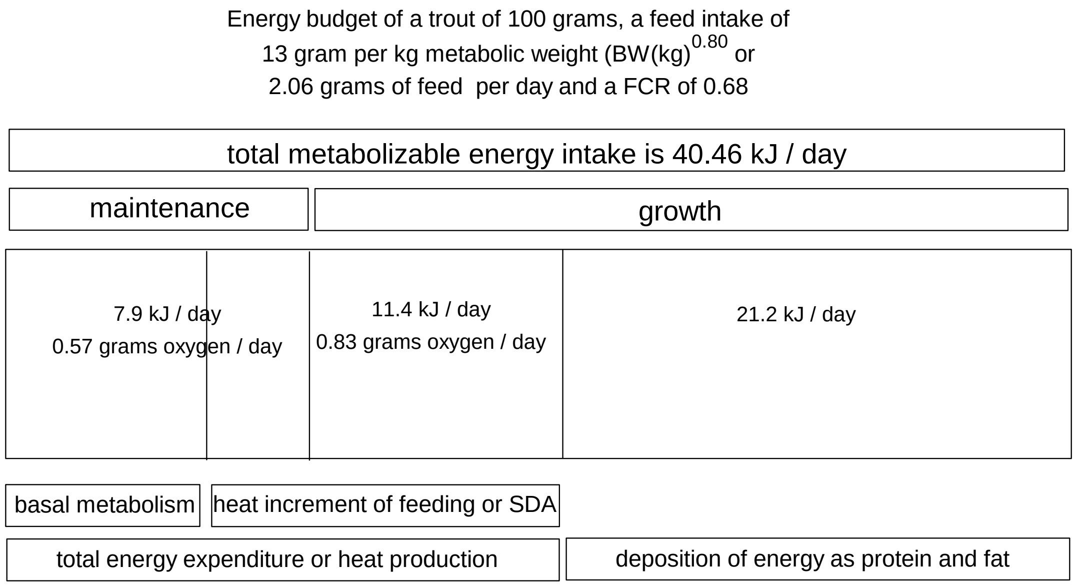


Figure 17
Energy budget of a trout

14 Determinants of the Feed Conversion Ratio (FCR)

The FCR is a commonly used characteristic for the growth performance of a trout feed and indicates the kilograms of feed that is needed to raise 1 kg of wet fish. However, the FCR is determined by two major factors, i.e. the feeding level and the size of the trout. Thus, when comparing two different type of feeds, the same feeding level and the same size trout should be used.

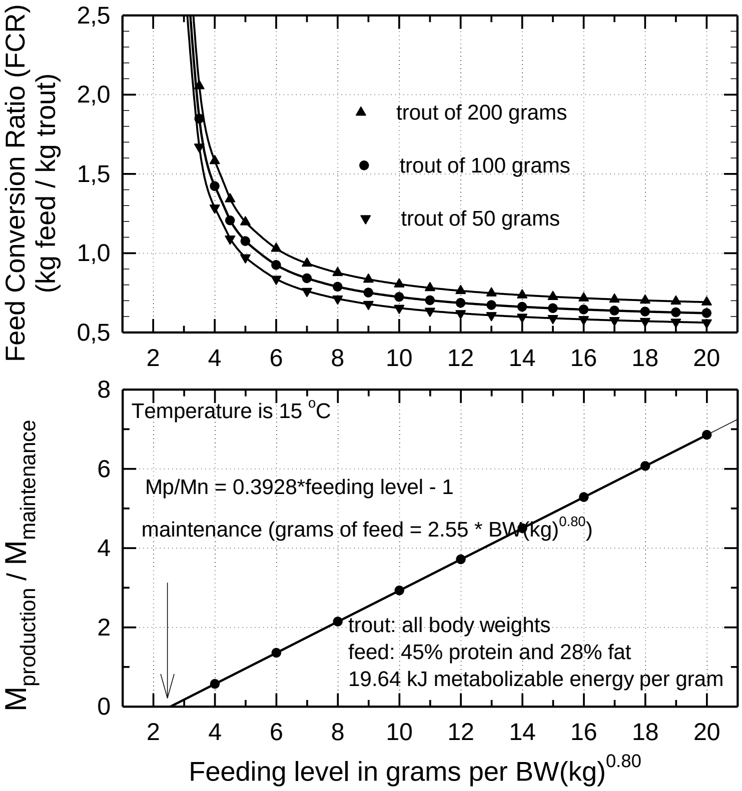


Figure 18

FCR and the Mp/Mn as a function of the body weight in trout

Feeding level

The feeding level can be expressed in grams per kg metabolic weight (per $BW(kg)^{0.80}$. The feeding of grams of feed per kg metabolic weight (per $BW(kg)^{0.80}$) involves that the amount of feed (and energy) parallels or follows the heat production or metabolic rate of different size trout. When the same feeding level expressed in grams per kg metabolic weight is used for different sizes of trout, then the proportion of the energy in the feed that is used for maintenance and the proportion that is used for growth will also remain the same, irrespectively of the weight of the trout. We can prove this phenomenon with an example. Suppose we have the 45/28 feed of Table 6. The metabolizable energy of this feed is 19.64 kJ per gram. The maintenance energy expenditure of a trout is $50*BW(kg)^{0.80}$ kJ per day at a temperature of 15 ^{o}C. If we have a trout of 100 grams and a feed intake of 13 grams per kg metabolic weight, then the maintenance energy expenditure is $50 * 0.1^{80}$ = 7.92 kJ per day, the feed intake is $13*BW(kg)^{0.80} = 13*0.1^{0.80}$ = 2.06 grams and the metabolizable energy intake is 2.06 * 19.64 = 40.46 kJ. Thus 40.64 – 7.92 = 32.72 kJ is left for growth and the ratio Mp/Mm (metabolizable energy for production / metabolizable energy for maintenance) = 32.72 / 7.92 = **4.13**. Now we have a trout of 200 grams. The maintenance energy expenditure is $50*0.2^{0.80}$ = 13.80 kJ per day. The feed intake is $13*0.2^{0.80}$ = 3.59 grams of feed or 3.59 * 19.64 = 70.51 kJ metabolizable energy. Thus 70.51 – 13.80 = 56.71 is left for growth and the ratio Mp/Mm (metabolizable energy for production / metabolizable energy for maintenance) = 56.71 / 13.80 = **4.11**.

Figure 18 shows the ratios of Mp/Mm as a function of the feeding level in grams per kg metabolic weight when a 45/28 (protein/fat) feed is fed (see Table 6 for the composition of this feed). The (metabolizable) energy expenditure of a trout at maintenance and at 15 ^{o}C is 50 $*BW(kg)^{0.80}$. The metabolizable energy density of the trout feed in Table 6 is 19.64 kJ per gram. Thus, 50/19.64 = 2.55 gram of feed per kg metabolic weight (per $BW(kg)^{0.80}$) is needed for maintenance and a feeding level of 2.55 gram per kg metabolic weight (per BW(kg) $^{0.80}$) reflects the maintenance level of a trout. Figure 18 shows the relation between the feeding level and the FCR, a higher feeding level results in a lower FCR. Further, the FCR is dependent on the body size of the trout (Figure 19).

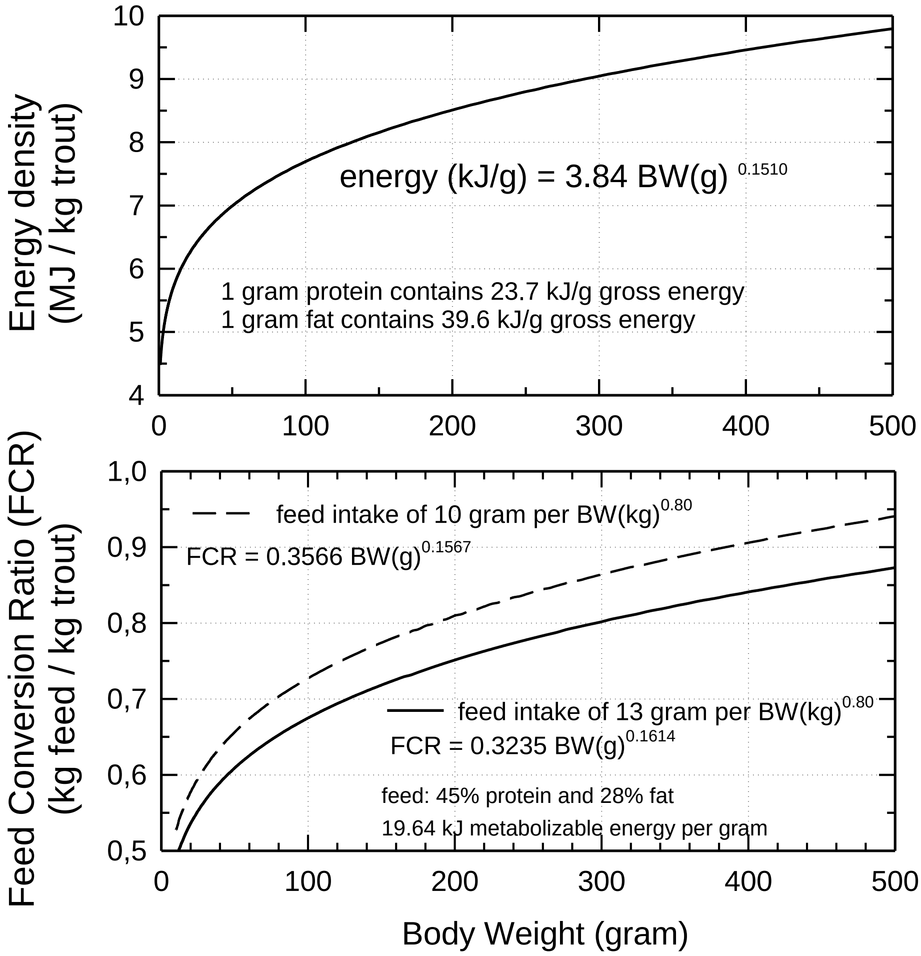


Figure 19
Energy density and FCR of a trout as a function of the body weight. The composition of the diet is given in Table 2 and 6.

Body size

The feed conversion ratio (FCR) is dependent on the size of the trout. The body composition of the trout changes and the energy density increases when the trout grows larger (Figure 15). Thus, more protein, fat and energy is needed to accrue 1 grams of body weight and as a consequence, the FCR will become higher (Figure 19). The FCR values in Figure 19 were calculated as indicated in paragraph 13 (energy budget of the trout).

15 Phase Feeding and the Protein sparing Effect of Fat in Trout

When the trout grows larger, the trout will become fatter and the ratio of protein to energy in the trout will decrease. Therefore relatively less protein and relatively more energy (fat) is needed for the accretion of 1 gram of body tissue (Figure 16 and 20).

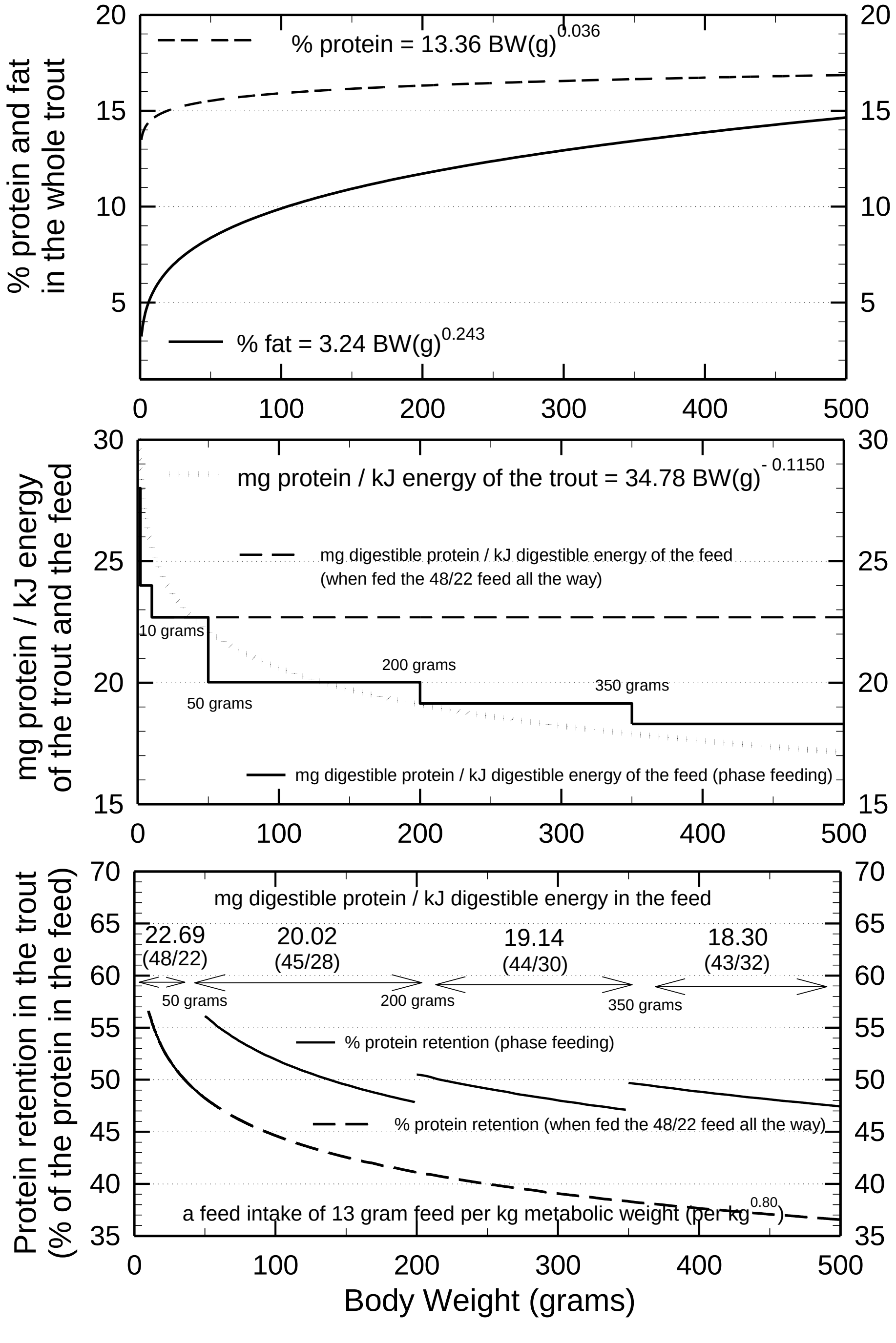


Figure 20
Protein retention in trout fed diets with varying protein/energy ratios.

This means that the ratio of protein to energy in the feed should also be lower in order to match the protein to energy ratio in the trout and to maintain a high protein retention. Protein is an expensive ingredient of trout feed and therefore, the protein retention in the trout should be as high as possible. In addition, a low protein retention results in a high level of excretion of nitrogen in the environment. We calculated the energy budget of the trout (as indicated above in the section about the energy budget in the trout and by using a computer spread sheet), starting with a trout of 10 grams up to a trout with a body weight of about 500 grams.

Table 7

Various growth parameters during phase feeding

	feeds phase feeding				feed no phase feeding
Protein / fat ratio	48 / 22	45 / 28	44 / 30	43 / 32	48 / 22
DP/DE	22.69	20.02	19.14	18.30	22.69
Gross Energy (kJ/gram)	22.69	24.01	24.56	25.12	22.69
Digestible Energy (kJ/gram)	20.10	21.35	21.84	22.33	20.10
Metabolizable Energy (kJ/gram)	18.28	19.64	20.17	20.70	18.28
Body weight range (grams)	10 - 50	50 - 200	200 - 350	350 - 500	10 - 500
Feeding level (g/BW(kg)$^{0.80}$	13	13	13	13	13
Feeding level (% of BW per day)	3.3 - 2.4	2.4 - 1.8	1.8 - 1.6	1.6 - 1.5	3.3 - 1.6
Dietary protein retention (%)	57 - 48	56 - 48	50 - 47	50 - 47	57 - 37
Dietary gross energy retention (%)	47	48	48	48	47
Ratio M_p / M_m	3.8	4.2	4.3	4.4	3.8
FCR (per day)	0.53 - 0.66	0.61 - 0.75	0.73 - 0.80	0.77 - 0.82	0.53 - 0.95

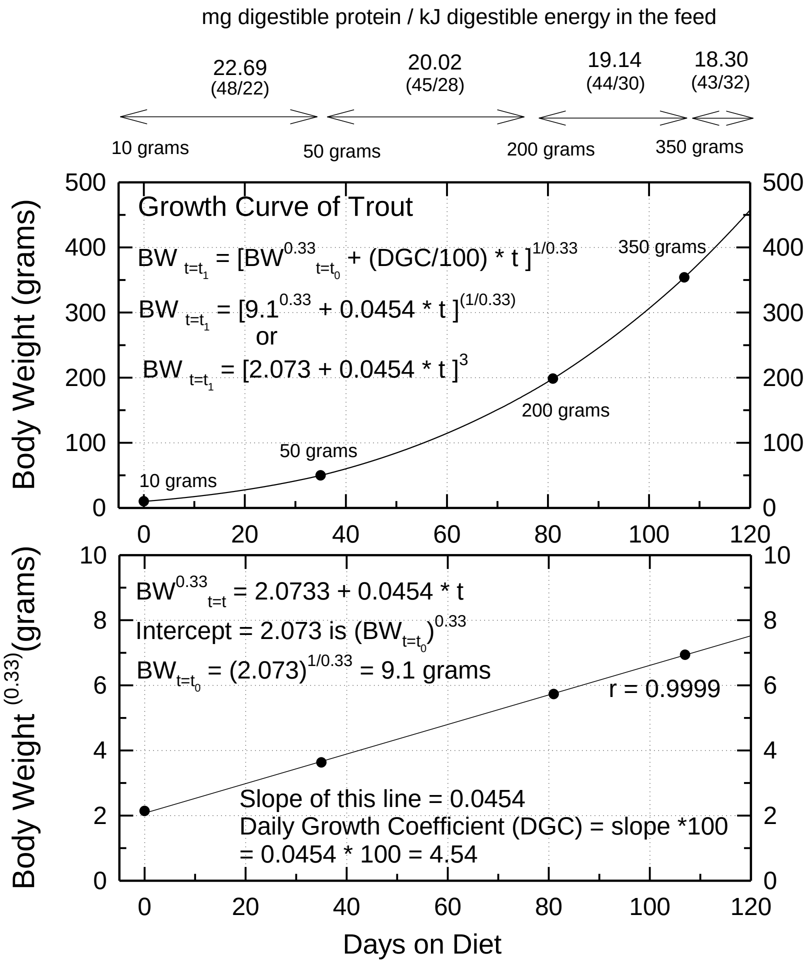


Figure 21
Growth curve a trout fed diets with varying protein/energy ratios.

Table 8
Feeds used for phase feeding

digestible protein to digestible energy ratio of 22,69 and protein/fat ratio of 48/22

Nutrient	% in diet	Gross Energy in 1 gram nutrient (kJ/g)	Metabolizable Energy in 1 gram nutrient (kJ/g)	Gross Energy in 1 gram feed (kJ/g)	Digestibility (%)	Digestible Energy in 1 gram feed	Metabolizable Energy in 1 gram feed
Protein	48	23,65	19,67	11,35	95,00	10,78	8,97
Fat	22	39,60	39,60	8,71	90,00	7,84	7,84
Ash	10						
Moisture	5						
Fiber	1	17,50	0,00	0,18	0,00		
NFE	14	17,50	17,50	2,45	60,00	1,47	1,47
Total	100			22,69		20,10	18,28

digestible protein to digestible energy ratio of 20,02 and protein/fat ratio of 45/28

Nutrient	% in diet	Gross Energy in 1 gram nutrient (kJ/g)	Metabolizable Energy in 1 gram nutrient (kJ/g)	Gross Energy in 1 gram feed (kJ/g)	Digestibility (%)	Digestible Energy in 1 gram feed	Metabolizable Energy in 1 gram feed
Protein	45	23,65	19,67	10,64	95,00	10,11	8,41
Fat	28	39,60	39,60	11,09	90,00	9,98	9,98
Ash	9						
Moisture	5						
Fiber	1	17,50	0,00	0,18	0,00		
NFE	12	17,50	17,50	2,10	60,00	1,26	1,26
Total	100			24,01		21,35	19,65

digestible protein to digestible energy ratio of 19,14 and protein /at ratio of 44/30

Nutrient	% in diet	Gross Energy in 1 gram nutrient (kJ/g)	Metabolizable Energy in 1 gram nutrient (kJ/g)	Gross Energy in 1 gram feed (kJ/g)	Digestibility (%)	Digestible Energy in 1 gram feed	Metabolizable Energy in 1 gram feed
Protein	44	23,65	19,67	10,41	95,00	9,89	8,22
Fat	30	39,60	39,60	11,88	90,00	10,69	10,69
Ash	8						
Moisture	5						
Fiber	1	17,50	0,00	0,18	0,00		
NFE	12	17,50	17,50	2,10	60,00	1,26	1,26
Total	100			24,56		21,84	20,17

digestible protein to digestible energy ratio of 18,30 and protein/fat ratio of 43/32

Nutrient	% in diet	Gross Energy in 1 gram nutrient (kJ/g)	Metabolizable Energy in 1 gram nutrient (kJ/g)	Gross Energy in 1 gram feed (kJ/g)	Digestibility (%)	Digestible Energy in 1 gram feed	Metabolizable Energy in 1 gram feed
Protein	43	23,65	19,67	10,17	95,00	9,66	8,04
Fat	32	39,60	39,60	12,67	90,00	11,40	11,40
Ash	7						
Moisture	5						
Fiber	1	17,50	0,00	0,18	0,00		
NFE	12	17,50	17,50	2,10	60,00	1,26	1,26
Total	100			25,12		22,33	20,70

We used a feeding level of 13 grams of feed per kg metabolic weight (per $BW(kg)^{0.80}$) and four different trout diets with different protein to energy ratios. The composition of the four diets is shown in Table 8. The retention of the dietary protein is shown in Figure 20. Figure 20 indicates that phase feeding, i.e. lowering the mg of digestible protein to digestible energy in the feed when the trout grows larger, results in a higher protein retention than when only one type of diet is fed all the way. This phenomenon is called the protein sparing effect of fat. Figure 20 also indicates that the mg of digestible protein to digestible energy in the feed should be similar to the mg of protein to energy in the trout itself. This way, a protein retention of about 50% can be achieved. The various calculated growth parameters are given in Table 7 and the calculated (power) growth curve of the trout fed sequentially the four feeds is given in Figure 21.

16 Factors that affect the Performance of a Trout Feed: the 4 P's concept.

Protein drives the growth and the maximum growth of a trout is determined by the maximum capacity to deposit protein. Thus, it is important that sufficient protein (and protein with the right amino acid composition) can be taken up to achieve this maximum protein deposition and growth. On the other hand, the intake of excess of protein that exceeds the maximum capacity to deposit the protein, and also excess of energy will result in the deposition of fat and result in fatty fish. Thus, the right ratio of energy to protein and the right amount of feed is important for optimal growth.

A factor that determines the uptake of a feed is the *palatability* of the feed. A feed that is not attractive to the trout will result in a low feed intake and thus in a low protein intake. A high feed intake results also in less energy for maintenance during the whole life span of the trout.

Further, the *performance* of a feed or the feed conversion ratio (FCR) is important. Factors that affect the performance are for example the digestibility of the protein, fat and carbohydrates in the diet and the amino composition of the protein.

An important issue in aquaculture is also the *pollution*. The feeds should have a high digestibility and generate little feces and the waste generated be not loose but more compact in order to be able to collect easily the feces.

A final issue is the *price* of a trout feed. The price should be right and the feeds should be cost effective.

Thus, the criteria for a good trout feed (or a good trout feed ingredient) can be summarized with the 4 P's concept:

5.	**Palatability**	Attractive feed to assure a high feed intake.
6.	**Performance**	The FCR ratio should be as low as possible.
7.	**Pollution**	High digestibility and feces that are compact and thus easily to collect.
8.	**Price**	The price should be right and the feed should be cost effective.

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DTU Food Tables on the Internet (Danish Technical University): http://www.foodcomp.dk/v7/fcdb_default.asp

FAO website: Food Composition Tables for International Use (1955): http://www.fao.org/docrep/x5557e/x5557e00.htm#Contents

Appendix 1 (Table)

Atwater factors for heat of combustion, coefficient of availability and available energy for nutrients in a mixed diet
These data are used by nutritionists and dietitians to estimate the metabolizable energy of human diets

	Gross Energy		Energy Production in human body		Digestibility	Digested Gross Energy		Digestible and Metabolizable Energy (in human body)		Digestible and Metabolizable Energy (Atwater general factors) (rounded-off)
	(kcal/g)	(kJ/g)	(kcal/g)	(kJ/g)	(%)	(kcal/g)	(kJ/g)	(kcal/g)	(kJ/g)	(kcal/g)
Crude Protein	5,65	23,64	4,40	18,41	92	5,20	21,75	4,05	16,94	4
Crude Fat	9,40	39,33	9,40	39,33	95	8,93	37,36	8,93	37,36	9
Carbohydrate	4,15	17,36	4,15	17,36	97	4,03	16,84	4,03	16,84	4
Glucose (dextrose)	3,75	15,69	3,75	15,69	97	3,64	15,22	3,64	15,22	3.6
Alcohol	7,07	29,58	7,07	29,58	98	6,93	28,99	6,93	28,99	7

Data from:

(1) A.L. Merrill and B.K. Watt (1973) Energy values of foods, basis and derivation. Agricultural Research Service, United States Department of Agriculture, Agricultural Handbook No 74 (can be downloaded from the Internet.
(2) L.A. Maynard (1944) The Atwater system of calculating the caloric values of diets. Journal of Nutrition Vol : 443-452.
(3) A.C Bucholz and D.A. Schoeller (2004) Is a calorie a calorie? American Journal of Clinical Nutrition 79: S899 – S906.

The general Atwater factors for protein, fat and carbohydrate and alcohol are 4, 9, 4, and 7 kcal per gram (or 16.72, 37.62, 16.72, and 29.29 kJ, 1 kcal = 4.184 kJ). The gross energy is the energy of combustion as measured in a bomb calorimeter. The digestible energy corrects for the digestibility of the protein, fat and carbohydrates in the diet. The metabolizable energy is the energy that can be used (available energy) by the body for the various metabolic processes and is corrected for digestibility and energy lost in the urine. The metabolizable energy of fat and carbohydrates is similar to the digestible gross energy, but the metabolizable energy of protein is lower than the digestible gross energy of protein since a correction has to be made for the energy lost in the urine in the form of urea, ammonia, uric acid, creatine, creatinine, and allantoin. Atwater reported that 7.9 kcal or 33.02 kJ energy is lost in the urine per gram urinary nitrogen. Protein contains about 16% nitrogen, thus (0.16) * 7.9 kcal = 1.264 (1.25) kcal (5.29 kJ) energy per gram absorbed or digested protein is lost in the urine. Thus the available energy per gram absorbed or digested protein is then 5.65 – 1.25 – 4.40 kcal (18.41 kJ). The digestibility of protein is 92 %, thus, the digested and available energy (metabolizable energy) per gram consumed dietary protein is then 0.92 * 4.4 = 4.0 kcal (16.73 kJ)

The rounded-off Atwater general factors are used by nutritionists and dietitians to calculate the energy densities of diets (see example below).

Note that the values in this table are average values. There are various types of proteins and fats and carbohydrates each with different digestibilities, heat of combustion values etc. For example plant proteins have a lower digestibility than animal proteins.

Appendix 1a (Table)

Example of the use of the Atwater factors for the calculation of the metabollizable energy of a diet.

	Metabolizable Energy Density (Atwater values)		Composition of milk	Total Metabolizable Energy in Milk	
	(kcal/g)	(kJ/g)	(g/100 g)	(kcal/100 g)	(kJ/100 g)
Protein	4	16,74	5	20	83,68
Fat	9	37,66	1,5	13,5	56,48
Carbohydrates	4	16,74	5	20	83,68
Total				54	224

1 kcal = 4.184 kJ.

Appendix 2 (Table)

Constants for carbohydrate, fat, and protein, when oxidized in the animal body according to Brouwer. These data are used in animal nutrition.

	% Carbon	Energy Production In animal body		O_2 Consumption		CO_2 Production		RQ	Eeq O_2				Eeq CO_2				Atwater Digest.	Metabolizable Energy	
		(kcal/g)	(kJ/g)	(grams)	(liters)	(grams)	(liters)	(CO_2/O_2)	(kcal/g)	(kJ/g)	(kcal/L)	(kJ/L)	(kcal/g)	(kJ/g)	(kcal/L)	(kJ/L)	Coeffic.	(kcal/g)	(kJ/g)
Protein	52,00	4,40	18,41	1,366	0,957	1,520	0,774	0,809	3,22	13,48	4,60	19,24	2,89	12,11	5,68	23,79	92,0	4,05	16,94
Fat	76,70	9,50	39,75	2,875	2,013	2,810	1,431	0,711	3,30	13,83	4,72	19,75	3,38	14,15	6,64	27,78	95,0	9,03	37,76
Starch	44,45	4,20	17,57	1,184	0,829	1,629	0,829	1,000	3,55	14,84	5,07	21,20	2,58	10,79	5,07	21,20	97,0	4,07	17,05
Saccharose	42,11	3,96	16,57	1,122	0,786	1,543	0,786	1,000	3,53	14,77	5,04	21,08	2,57	10,74	5,04	21,08	97,0	3,84	16,07
Glucose	40,00	3,74	15,65	1,066	0,746	1,466	0,746	1,000	3,51	14,68	5,01	20,98	2,55	10,67	5,01	20,98	97,0	3,63	15,18

Data from:

E. Brouwer (1965) Report of subcommittee on constants and factors. In: Energy metabolism, Proceedings of the 3rd symposium, ed. K.L Blaxter, London: Academic Press, (Reproduced in: J.A. McLean and G. Tobin (1987), animal and human calorimetry, Cambridge University Press,1987 page 303).

The values in this Table are only slightly different from the values of Atwater (Table 1). The values in this table are not really constants, but averages, since there are various types of proteins, fats and carbohydrates with different heats of combustion, digestibilities etc. 1 kcal = 4.184 kJ.

The combustion energy of protein in the body is 4.40 kcal /g (18.41 kJ / g), this value is identical to the value reported by Atwater, the values for fat and starch and sucrose are only slightly different from those of Atwater. The composition of protein is: N: 16%; C: 52%; energy of combustion or gross energy (in bomb calorimeter): 5.7 kcal/g or 23.84 kJ/g (1 kcal = 4.184 kJ). RQ, respiratory coefficient (mol CO_2 / mol O_2 or liters CO_2 / liters O_2), Eeq, energy equivalent. The energy equivalents were calculated from the data of Brouwer. For example, 1 gram protein releases 18.41 kJ of energy and consumes 1.366 grams of oxygen: then Eeq O_2 = 18.41 / 1.366 = 13.477 kJ per gram O_2. Further, 1 ml O_2 = 1.428 gram O_2 (1 gram O_2 = 0.700 ml O_2) and 1 ml CO_2 = 1.962 mg CO_2 (1 grams CO_2 = 0.510 ml CO_2) at 1 bar and 273.15 ^{o}Kelvin (0 ^{o}Celsius) (Brouwer 1965, see McLean and Tobin 1987, page 302).

We used in this table the digestibility values as given by Atwater. However, the digestibilities in animals may be considerabley different fom those in humans.

The average N content of proteins is about 16%, but depends on the source of protein and the amino composition (see: Mariotti et al. 2008)

Appendix 3 (Table)

The values for energy generated in the body, Respiratory Quotient (RQ) and the Energy Equivalents EeqO_2 and EeqCO_2 for carbohydrate, fat, protein and alcohol according to data from Elia and Livesey (1992).

	MW	Energy Generated in the Body[1]		H_2O generated		O_2 consumed			C0_2 generated			RQ	EeqO_2[4]		EeqCO_2[4]		Atwater Digest.Coeffic	. Metabol Energy
		(kJ/mol)	(kJ/g)	(mol/mol)	(g/g)	(mol/mol)	(g/g)	(L/g)	(mol/mol)	(g/g)	(L/g)	(CO_2/O_2)	(kJ/g)	(kJ/L)	(kJ/g)	(kJ/L)	(%)	(kJ/g)
Protein (combustion)[2]	2260,0	53448	23,65	79,50	0,63	125,2	1,77	1,24	100,0	1,95	0,99	0,799	13,35	19,06	12,14	23,85	92	21,76
Protein (in body)[3]	2260,0	45376	20,08	50,60	0,40	104,0	1,47	1,03	86,6	1,69	0,86	0,833	13,64	19,47	11,91	23,38	92	18,47
Fat (dioleylpalmitate)[3]	859,4	34022	39,59	51,00	1,07	77,5	2,89	2,02	55,0	2,82	1,43	0,710	13,72	19,59	14,06	27,61	95	37,61
Carbohydrate (glucan)[3]	162,1	2840	17,52	5,00	0,56	6,0	1,18	0,83	6,0	1,63	0,83	1,000	14,79	21,12	10,76	21,12	97	16,99
Sacharose ($C_{12}H_{22}O_{11}$)	342,3	5641	16,48	11,00	0,58	12,0	1,12	0,79	12,0	1,54	0,79	1,000	14,69	20,98	10,68	20,98	97	15,99
Glucose ($C_6H_{12}O_6$)	180,2	2803	15,56	6,00	0,60	6,0	1,07	0,75	6,0	1,47	0,75	1,000	14,60	20,85	10,62	20,85	97	15,09
Alcohol (C_2H_6O)	46,1	1367	29,67	3,00	1,17	3,0	2,08	1,46	2,0	1,91	0,97	0,667	14,24	20,34	15,53	30,50	97	28,78
Kleibers standard protein Data from Elia and Livesey[5]																		
Protein to mixture[3]	2260,0	45376	20,08	50,60	0,40	104,0	1,47	1,03	86,6	1,69	0,86	0,833	13,64	19,47	11,91	23,38	92	18,47
Protein to urea	2260,0	45950	20,33	52,80	0,42	105,3	1,49	1,04	87,0	1,69	0,86	0,826	13,64	19,47	12,00	23,57	92	18,71
Protein to uric acid	2260,0	41880	18,53	65,00	0,52	95,5	1,35	0,95	67,5	1,31	0,67	0,707	13,71	19,57	14,10	27,69	92	17,05
Protein to ammonia	2260,0	46450	20,55	13,80	0,11	105,3	1,49	1,04	100,0	1,95	0,99	0,950	13,79	19,69	10,55	20,73	92	18,91
Protein to creatinine	2260,0	33960	15,03	48,47	0,39	79,3	1,12	0,79	65,3	1,27	0,65	0,824	13,38	19,11	11,81	23,20	92	13,82
Protein to allantoin	2260,0	43254	19,14	59,30	0,47	98,8	1,40	0,98	74,0	1,44	0,73	0,749	13,68	19,54	13,28	26,09	92	17,61
Kleibers standard protein Calculated[6]																		
Protein to mixture[3]	2260,0	44415	19,68	50,60	0,40	104,0	1,47	1,03	86,6	1,69	0,86	0,833	13,35	19,06	11,65	22,89	92	18,08
Protein to urea	2260,0	45037	19,93	52,80	0,42	105,3	1,49	1,04	87,0	1,69	0,86	0,826	13,37	19,09	11,76	23,10	92	18,33
Protein to uric acid	2260,0	40962	18,12	65,00	0,52	95,5	1,35	0,95	67,5	1,31	0,67	0,707	13,40	19,14	13,79	27,08	92	16,67
Protein to ammonia	2260,0	44270	19,59	13,80	0,11	105,3	1,49	1,04	100,0	1,95	0,99	0,950	13,14	18,76	10,06	19,76	92	18,02
Protein to creatinine	2260,0	33193	14,69	48,47	0,39	79,3	1,12	0,79	65,3	1,27	0,65	0,824	13,08	18,68	11,54	22,67	92	13,51
Protein to allantoin	2260,0			59,30		98,8			74,0									

Data are from:

M. Elia and G. Livesey (1992) Energy expenditure and fuel selection in biological systems: the theory and practice of calculations based on indirect calorimetry and tracer methods, World Review of Nutrition and Dietetics, volume 70, page 68-131 (see pages 71 and 78 for the equations of the oxidations of the carbohydrtaes, fats and proteins).

1.The energy generated is the energy generated in the body. For the protein, a correction is made for the energy excreted in the urine in the form of form of urea, ammonia, uric acid, creatine, creatinine, and allantoin. The protein in this Table refers to the Kleiber's standard protein ($C_{100}H_{159}N_{26}O_{32}S_{0.7}$ (MW = 2260, contains 16.1% N). The energy generated from the carbohydrates and the fat and alcohol in the body is identical to the energy generated in a bomb calorimeter.

2. Complete combustion of the Kleiber's protein in a bomb calorimeter. The heat of complete combustion of protein in the bomb calorimeter is 23.65 kJ/g (gross energy). The equation of the complete combustion is: $C_{100}H_{159}N_{26}O_{32}S_{0.7} + 124.8\ O_2 = 100\ CO_2 + 78.8\ H_2O + 13\ N_2 = 0.7\ H_2SO_4 + 53448$ kJ.

3. The Kleibers standard protein is metabolized to urea, creatinine and ammonia in the nitrogen mass ratio of 90:5:5 (See Elia and Livesey 1992, page 71):

$C_{100}H_{159}N_{26}O_{32}S_{0.7}$ + 104 O_2 (= 22.414 x 104 = 2331.06 liters) = 86.6 CO_2 (= 22.414 x 86.6 = 1941.05 liters) + 50.6 H_2O + 11.7 N_2H_4CO (urea) + 1.3 NH_4OH (ammonia) + 0.43 $N_3C_4H_7O$ (creatinine) + 0.7 H_2SO_4
For the heat of combustion released from the oxidation of fat and carbohydrates, see Elia and Livesey 1992, page 71 and for the oxidation of saccharose and glucose and alcohol (ethanol): K. Blaxter 1989, page 296.(*K. Blaxter (1989)* Energy metabolism in animals and man, Cambridge University press).

4. Eeq, energy equivalent. All values for the volumes of O_2 and CO_2 are at 1 bar and a temperature of 0 ^oC (273.15 ^oK).
1 mg O_2 = 0.700 ml O_2 and 1 ml O_2 = 1.428 mg O_2. Further 1 mg CO_2 = 0.509 ml CO_2 and 1 ml CO_2 ° 1,963 mg CO_2

Data on energy equivalents of oxygen consumption for protein, fat and carbohydrates have also been given in earlier literature , see: J.M. Elliot and W. Davison (1975) Energy equivalents of oxygen consumption in animal energetics. Oecologia (Berlin) Volume 19, pages 195-201.

5. Data are from Elia and Livesey 1992 (page 71 and 78).

6.These data are calculated as following: The N in the protein can be excreted in the form of ammonia, urea, creatinine, creatin, or allantoin. These compounds contain a considerable amount of energy (See Appendix Table 4 and 5).

(a). *Excretion of the nitrogen in the form of urea*: the energy density of urea (in solution) is 647 kJ per mol (647 / 60.056 = 10.77 kJ per gram). The oxidation of 1 mol of Kleiber's protein results in the formation of 13 mol urea (Elia and Livesey 1992, page 78). This amount of urea contains thus 13 x 647 = 8411 kJ of energy, which is excreted in the urine. The gross energy of protein is 23.65 x 2260 = 53448 kJ. Thus 53448 – 8411 = 45037 kJ is left. Thus, the available energy of the protein is then 45037 / 2260 = 19.93 kJ per gram protein.
Oxidation of Kleiber's protein (Kleiber's protein contains 16.1% protein): $C_{100}H_{159}N_{26}O_{32}S_{0.7}$ + 105.3 O_2 = 87 CO_2 + 52.8 H_2O + 13 N_2H_4CO (urea) + 0.7 H_2SO_4

The complete combustion of Kleiber's protein is
(1) $C_{100}\,H_{159}\,N_{26}\,O_{32}\,S_{0.7}$ + 124.8 O_2 = 100 CO_2 + 78.8 H_2O + 13 N_2 + 0.7 H_2SO_4 + 53448 kJ and (complete combustion of protein)
(2) 13 N_2H_4CO (urea) +19.5 O_2 = 13 CO_2 + 26 H_2O + 13 N_2 + 13 * 647 kJ (= 8411 kJ) (complete combustion of urea)
Substract (2) from (1): (compare McLean and Tobin 1987, page 33, and Blaxter 1989, page 12, law of Hess, law of constant heat summation).
$C_{100}\,H_{159}\,N_{26}\,O_{32}\,S_{0.7}$ + 105.3 O_2 = 87 CO_2 + 52.8 H_2O + 13 N_2H_4CO (urea) + 0.7 H_2SO_4 + 45037 kJ or 45037 / 2260 = 19.93.

We can also assume that protein in general contains 16% nitrogen (The Kleiber's protein contains16.1% protein). Thus the oxidation of 1 gram of protein results in the generation of 0.16 gram nitrogen. Urea contains 46.6% nitrogen, thus the oxidation of 1 gram of protein results in the formation of 0.16 / 0.46 = 0.34 grams of urea. The energy density of 1 gram of urea is 10.77 kJ, thus the energy of 0.34 grams of urea is 0.34 x 10.77 = 3.66 kJ and the available energy in 1 gram protein is then 23.65 – 3.66 = 19.99 kJ.

(b) *Excretion of the nitrogen in the form of uric acid*: the energy density of uric acid is 1921 kJ per mol (1921 / 168.112 = 11.42 kJ per gram). The oxidation of 1 mol of Kleiber's protein results in the formation of 6.5 mol uric acid (Elia and Livesey 1992, page 78). This amount of uric acid contains thus 6.5 x 1921 = 12487 kJ of energy, which is excreted in the urine. The gross energy of protein is 23.65 x 2260 = 53448 kJ. Thus 53448 – 12487 = 40961 kJ is left. Thus, the available energy of the protein is then 40961 / 2260 = 18.12 kJ per gram protein.
Oxidation of Kleiber's protein (Kleiber's protein contains 16.1% protein: $C_{100}H_{159}N_{26}O_{32}S_{0.7}$ + 95.5 O_2 = 67.5 CO_2 + 65 H_2O + 6.5 $C_5H_4O_3N_4$ (uric acid) + 0.7 H_2SO_4

We can also assume that protein in general contains 16% nitrogen. Thus the oxidation of 1 gram of protein results in the generation of 0.16 gram nitrogen. Uric contains 33.3% nitrogen, thus the oxidation of 1 gram of protein results in the formation of 0.16 / 0.33 = 0.48 grams of urea. The energy density of 1 gram of uric is 11.40 kJ, thus the energy of 0.48 grams of uric acid is 0.48 x 11.40 = 5.47 kJ and the available energy in 1 gram protein is then 23.65 – 5.47 = 18.18 kJ.

(c) *Excretion of the nitrogen in the form of ammonia*: the energy density of ammonia (in solution) is 353 kJ per mol (353 / 17.031 = 20.73 kJ per gram). The oxidation of 1 mol of Kleiber's protein results in the formation of 26 mol ammonia (Elia and Livesey 1992, page 78). This amount of ammonia contains thus 26 x 353 = 9178 kJ of energy, which is excreted in the urine. The gross energy of protein is 23.65 x 2260 = 53448 kJ. Thus 53448 – 9178 = 44270 kJ is left. Thus, the available energy of the protein is then 44270 / 2260 = 19.59 kJ per gram protein.
Oxidation of Kleiber's protein (Kleiber's protein contains 16.1% protein): $C_{100}H_{159}N_{26}O_{32}S_{0.7}$ + 105.3 O_2 = 100 CO_2 + 13.8 H_2O + 26 NH_4OH (ammonia) + 0.7 H_2SO_4

We can also assume that protein in general contains 16% nitrogen. Thus the oxidation of 1 gram of protein results in the generation of 0.16 gram nitrogen. ammonia contains 82.2% nitrogen, thus the oxidation of 1 gram of protein results in the formation of 0.16 / 0.822 = 0.195 grams of ammonia. The energy density of 1 gram of ammonia is 20.73 kJ, thus the energy of 0.13 grams of ammonia is 0.195 x 20.73 = 4.04 kJ and the available energy in 1 gram protein is then 23.65 – 4.04 = 19.61 kJ.

(d) *Excretion of the nitrogen in the form of creatinine*: the energy density of creatinine is 2337 kJ per mol (2337 / 113.120 = 20.66 kJ per gram). The oxidation of 1 mol of Kleiber's protein results in the formation of 8.667 mol creatinine (Elia and Livesey 1992, page 78). This amount of creatinine contains thus 8.667 x 2337 = 20255 kJ of energy, which is excreted in the urine. The gross energy of protein is 23.65 x 2260 = 53448 kJ. Thus 53448 – 20255 = 33193 kJ is left. Thus, the available energy of the protein is then 33193 / 2260 = 14.69 kJ per gram protein.
Oxidation of Kleiber's protein (Kleiber's protein contains 16.1% protein): $C_{100}H_{159}N_{26}O_{32}S_{0.7}$ + 79.3 O_2 = 65.332 CO_2 + 48.466 H_2O + 8.667 $N_3C_4H_7O$ (creatinine) + 0.7 H_2SO_4

We can also assume that protein in general contains 16% nitrogen. Thus the oxidation of 1 gram of protein results in the generation of 0.16 gram nitrogen. creatinine contains 37.147% nitrogen, thus the oxidation of 1 gram of protein results in the formation of 0.16 / 0.371 = 0.43 grams of creatinine. The energy density of 1 gram of creatinine is 20.66 kJ, thus the energy of 0.43 grams of creatinine is 0.43 x 20.66 = 8.88 kJ and the available energy in 1 gram protein is then 23.65 – 8.88 = 14.77 kJ.

(e) *Excretion of the nitrogen in the form of creatine*: the energy density of creatine is 2324 kJ per mol (2324 / 115.136 = 20.18 kJ per gram). The oxidation of 1 mol of Kleiber's protein results in the formation of 8.667 mol creatine (Elia and Livesey 1992, own calculation). This amount of creatine contains thus 8.667 x 2324 = 20142 kJ of energy, which is excreted in the urine. The gross energy of protein is 23.65 x 2260 = 53448 kJ. Thus 53448 – 20142 = 33306 kJ is left. Thus, the available energy of the protein is then 33306 / 2260 = 14.74 kJ per gram protein.
Oxidation of Kleiber's protein (Kleiber's protein contains 16.1% protein): $C_{100}H_{159}N_{26}O_{32}S_{0.7}$ + 79.288 O_2 = 65.332 CO_2 + 39.779 H_2O + 8.667 $N_3C_4H_9O_2$ (creatine) + 0.7 H_2SO_4

We can also assume that protein in general contains 16% nitrogen. Thus the oxidation of 1 gram of protein results in the generation of 0.16 gram nitrogen. Creatine contains 36.497% nitrogen, thus the oxidation of 1 gram of protein results in the formation of 0.16 / 0.365 = 0.44 grams of creatine. The energy density of 1 gram of creatine is 20.18 kJ, thus the energy of 0.44 grams of creatine is 0.44 x 20.18 = 8.88 kJ and the available energy in 1 gram protein is then 23.65 – 8.88 = 14.77 kJ.

(f) *Excretion of nitrogen in the form of a mixture of urea (90%), creatinine (5%) and ammonia (5%).* We can assume that protein in general contains 16% nitrogen. Thus the oxidation of 1 gram of protein results in the generation of 0.16 gram nitrogen. Urea contains 46.6% N and 10.77 kJ per gram urea, creatinine contains 37.1%N and 20.66 kJ per gram creatinine and ammonia contains 82.2% N and 20.73 kJ per gram ammonia. Thus the loss of energy is ((0.16 x 0.90 / 0.466) x 10.77) + ((0.16 x 0.05) / 0.371) x 20.66) + ((0.16 x 0.05 / 0.822) x 20.73) = 3.975 kJ per gram protein. Thus the available energy of 1 gram of protein is 23.65 – 3.975 = 19.68 kJ per gram protein.

(g) *Excretion of nitrogen in the form of a mixture of ammonia (85%) and urea (15%) as in fish.* We can assume that protein in general contains 16% nitrogen. Thus the oxidation of 1 gram of protein results in the generation of 0.16 gram nitrogen. Ammonia contains 82.2% N and 20.73 kJ per gram ammonia and urea contains 46.6% N and 10.77 kJ per gram urea, Thus the loss of energy is ((0.16 x 0.85 / 0.822) x 20.73) + ((0.16 x 0.15 / 0.466) x 10.77) = 3.98 kJ per gram protein. Thus the available energy of 1 gram of protein is 23.65 – 3.98 = 19.67 kJ per gram protein in fish.

Appendix 4 (Table)

The energy densities of various compounds

Compound	Formula	MW	Weight per liter (g)	Heat of Combustion (kJ/mol)	Heat of Combustion (kJ/g)	Heat of Combustion (kJ/liter)	Heat of Solution (kJ/mol)	Heat of Combustion (kJ/mol)	(kJ/gram)	Reference
Carbon	C	12,011								
Hydrogen	H	1,008								
Oxygen	O	15,999								
Nitrogen	N	14,007								
Sulfur	S	32,064								
Oxygen	O_2	31,998	1,4276							
Carbondioxyde	CO_2	44,009	1,9635							
Nitrogen	N_2	28,014	1,2498							
Hydrogen	H_2	2,016	0,0899	286	141,9	12,76			141.9	4
Methane	CH_4	16,043	0,7158	891	55,5	39,75			55,5	2,3,4
Ammonia	NH_3	17,031	0,7598	382	22,4	17,04	-29	353	20,7	1
Urea	$CO(NH_2)_2$	60,056		632	10,5		15	647	10,8	1, 2,3
Uric acid	$C_5H_4N_4O_3$	168,112		1921	11,4				11,4	1, 2,3
Creatinine	$C_4H_7N_3O$	113,12		2337	20,7				20,7	1, 2
Creatine	$C_4H_9N_3O_2$	131.135		2324	17.7				17.7	1, 2
Benzoic acid (standard)	$C_7H_6O_2$	122.123		3226.9	26.4				26.4	3

Data are from:

1. *M. Elia and G. Livesey (1992)* Energy expenditure and fuel selection in biological sysems: the theory and practice of calculations based on indirect calorimetry and tracer methods, World Review of Nutrition and Dietetics, volume 70, page 68-131 (page 84)
2. *K. Blaxter (1989)* Energy metabolism in animals and man, Cambridge University press, page 296-297.
3. Handbook of Chemistry and Physics 1995-1996 (page 5-76)
4,. E. Brouwer (1965) Report of subcommittee on constants and factors. In: Energy metabolism, Proceedings of the 3rd symposium, ed. K.L Blaxter, London: Academic Press, (Reproduced in: J.A. McLean and G. Tobin (1987), Animal and human calorimetry, Cambridge University Press,1987 page 302-303).

The heat of solution can be negative (heat is released when dissolved) or positive (heat is needed for solution).

The volume of 1 mol compound in gaseous form is 22.414 liters at 0 ^oC (273.15 ^oK) at 1 bar. For example, 1 mol oxygen weighs 31.998 grams and has a volume of 22.414 liters, thus the weight of 1 liter of oxygen is thus 31.998 / 22.414 = 1.4276 gams.

Appendix 5 (Table)

Calculations of the losses of energy during the oxidation of protein

End product of the nitrogen in protein after oxidation Formula	Ammonia NH_3	Urea $CO(NH_2)_2$	Uric Acid $C_5H_4N_4O_3$	Creatinine $C_4H_7N_3O$	Creatine $C_4H_9N_3O2$
Molecular Weight	17,031	60,065	168,112	113,120	115,136
Gram N per mol ammonia, urea, or uric acid etc.	14,0	28,0	56,0	42,0	42,0
Weight % N	82,2	46,6	33,3	37,1	36,5
Mol N per mol ammonia, urea, uric acid etc. (MW of N = 14,007)	1,00	2,00	4,00	3,00	3,00
kJ/mol ammonia, urea or uric acid etc. (See table with energy densities)	353	647	1921	2337	2324
kJ/gram ammonia, urea or uric acid etc.	20,7	10,77	11,4	20,7	20,2
kJ/mol N in ammonia, urea or uric acid etc.	353	324	480	779	775
kJ/gram N in ammonia, urea or uric acid etc. (Atwater reported in humans a value of 33.1 kJ per gram N)	25,2	23,1	34,3	55,6	55,3
grams N generated per gram protein catabolized (Kleiber's protein contains 15.5% N)	0,1611	0,1611	0,1611	0,1611	0,1611
kJ in ammonia, urea, or uric acid etc. generated / gram protein catabolized, calculated	4,06	3,72	5,52	8,96	8,91
Gram ammonia, urea, uric acid etc. generated / gram protein catabolized	0,196	0,345	0,483	0,434	0,441
mmol ammonia, urea, uric acid etc. generated /gram protein catabolized	11,50	5,75	2,88	3,83	3,83
kJ per mol ammonia, urea or uric acid (costs of synthesis), calculated	0	340	595		
kJ per gram ammonia, urea or uric acid (costs of synthesis)	0	5,7	3,5		
kJ per mol N in ammonia, urea or uric acid (cost of synthesis)	0	170	149		
kJ per g N in ammonia, uea or uric acid (costs of synthesis)	0	12,1	10,6		
kJ per gram protein catabolized (costs of synthesis)	0	1,96	1,71		
Gross Energy of protein (kJ per gram protein)	23,65	23,65	23,65	23.65	23.65
Energy lost in ammonia, urea, uric acid etc. (kJ /per gram protein)	4,06	3,72	5,52	8,96	8,91
Energy of protein after correction for loss in ammonia, urea,uric acid etc. (kJ per gram protein)	19,59	19,93	18,13	14,69	14,71
Digestion loss (8%, Atwater) (kJ per gram protein)	1,57	1,59	1,45	1,18	1,18
Available Energy (kJ from 1 gram protein intake)	18,02	18,33	16,68	13,52	13,53

Calculations of the energy costs of the production of urea and uric acid.

Urea. Ammonia (NH_3) is formed during the breakdown of proteins and amino acids. In mammals, the generated ammonia is subsequently converted into the water soluble urea. Four high energy phosphate bonds (ATP) (4 mol ATP per mol urea) are needed for this formation (see D. Voet and J.G. Voet (1995), Biochemistry, Second Edition, John Wiley and Sons, (page 732), the urea cycle and A.L. Lehninger (1970), Biochemistry, Worth Publishers Inc. New York (page 451). The costs of metabolizable energy for the formation of 1 mol ATP depend on the type of nutrient that is oxidized (see Appendix 7). For example, when fat (tripalmitin) is oxidized in the animal body, the cost for the formation of 1 mol ATP is 77.8 kJ of metabolizable energy. However, when proteins are oxidized, then the costs for the formation of 1 mol ATP is 86.9 kJ of metabolizable energy and this amount of required energy is also dependent on the amino acid composition. When lysine is oxidized, the costs for the formation of 1 mol ATP is 88.2 kJ, whereas these costs are 119.7 kJ / mol ATP when cysteine is oxidized. A.K. Martin and K.L. Blaxter (1965, The energy cost of urea synthesis in sheep, In: Proceedings of the 3th Symposium on Energy Metabolism, Blaxter K.L. Editor Academic Press London, Page 84-91), assumed that the average costs for the formation of 1 mol ATP were 92.5 kJ (22.1 kcal) of metabolizable energy per mol ATP. We will use in our calculations an average value of about 85 kJ / mol ATP. Thus, the costs for the formation of 1 mol urea are then 4 x 85 = 340 kJ of metabolizable energy. The oxidation of 1 mol Kleiber's protein results in the formation of 13 mol urea, thus the costs are 13 x 340 = 4420 kJ per mol Kleiber's protein (MW = 2260). Thus the costs for the formation of urea derived from 1 grams of Kleiber's protein are thus 4420 / 2260 = 1.95 kJ per gram protein. The actual costs are probably considerably higher, since recycling of urea (15 – 30%, see M. Walser and L.J.

Bodenlos 1959 Urea metabolism in man, Journal of Clinical Investigation 38:1617-1959) may take place (urea converted into ammonia in the gut and subsequently again converted into urea in the liver).

We can also assume that protein in general contains16% Nitrogen (Kleiber's protein contains 16.1%N), thus the oxidation of 1 gram of protein results in 0.161 grams of nitrogen. Urea contains (2 x 28.014) / 60.056) = 46.6% nitrogen (MW of N = 28.014 and MW urea = 60.056) , thus the oxidation of 1 grams of protein results in the formation of 0.161 / 0.466 = 0.3455 grams of urea (MW = 60.056). The formation of 1 mol urea requires 340 kJ of metabolizable energy, thus the costs for the formation of the urea generated from the oxidation of 1 gram of protein are then (0.3455 /60.056) x 340 = 1.956 kJ metabolizable energy per gram protein.

<u>Uric acid:</u> In birds and reptiles and insects, the ammonia is converted in the water insoluble uric acid. Seven high energy phosphate bonds (ATP) (7 mol ATP per mol uric acid) (see D. Voet and J.G. Voet (1995), Biochemistry, Second Edition, John Wiley and Sons, page 798) (and not six, as previously thought, see A.L. Lehninger (1970), Biochemistry, Worth Publishers Inc. New York, page 569) are required for the formation of uric acid. Ammonia is first converted into the purine inosine monophosphate, IMP (see D. Voet and J.G. Voet (1995), page 798, and A.L. Lehninger (1970), page 569) and subsequently converted into uric acid (D. Voet and J.G. Voet, page 817). If we again assume that the formation of 1 mol ATP requires an average of 85 kJ of metabolizable energy, then the costs for the formation of 1 mol uric acid are 7 x 85 = 595 kJ of metabolizable energy. The oxidation of 1 mol of Kleiber'protein to uric acid results in the formation of 6.5 mol uric acid, thus the costs are 6.5 x 595 = 3867 kJ per mol Kleiber's protein (MW = 2260). Thus the costs for the formation of uric acid from 1 gram of Kleiber's protein are 3867 / 2260 = 1.71 kJ.

We can also assume that protein in general contains16% Nitrogen (Kleiber's protein contains 16.1%N), thus the oxidation of 1 gram of protein results in 0.161 grams of nitrogen. Uric acid contains (4 x 14.007) / 168.112 = 33.3% nitrogen, thus the oxidation of 1 grams of protein results in the formation of 0.161 / 0.333 = 0.4835 grams of uric acid (MW = 168.112). The formation of 1 mol uric acid requires 595 kJ of metabolizable energy, thus the costs for the formation of the uric acid generated from the oxidation of 1 gram of protein are then (0.4835 / 168.112) x 595 = 1.71 kJ metabolizable energy per gram protein

The results of the calculations by various other authors are given in the Table below. The differences between the results of our calculations and those of other authors may be related to the different values that are used for the average amount of required metabolizable energy for the formation of 1 mol ATP and to the use of 6 high energy phosphate bonds in the calculatons of Cho et al.(1982) and Smith et al. (1978) (instead of 7, as reported later by Voet and Voet (1995) page 732) required for the formation of uric acid.

Energy (kJ) required for the formation of 1 mol		
Urea (MW=60,0560)	Uric acid (MW=168,112)	Reference
340	595	Our calculations
369		Martin and Blaxter 1965
370	555	Smith et al. 1978
364	560	Cho et al. 1982

Smith, R.R., Rumsey, G.L. and Scott, M.L. (1978) Heat increment associated with dietary potein fat, carbohydrate and compete diets in salmonids: Comparative energetic efficiency. Journal of Nutrition, 108: 1025-1032 (see page 1026). The describe that the theoretical costs for the synthesis of 1 mol urea is 88.4 kcal (= 88.4. X 4.184 = 369.8 kJ) and of 1 mol uric acid is 132.6 kcal (= 132.6 X 4.184 = 554.7 kJ)

Cho, C.Y., Slinger, S.J. and Bayley, H.S. (1982) Bioenergetics of salmoids fishes: energy intake, expenditure and production. Comparative Biochemistry and Physiology vol 73B, No1., pp 25-41. (see page 37). They describe that the energy costs for urea are 13 kJ/gN (urea contains 46,6% N, thus 0.466 x 13 = 6.058 kJ / gram urea, and 6.065 x 60.065 = 364 kJ per mol urea. Further , they describe tht the enegy costs for uric acid are 10 kJ /gram N, thus 0.333 x 10 = 3.33 kJ / gram uric acid, and 3.33 x 168.112 = 560 kJ per mol uric acid.

Cho, C.Y. & Kaushlik, S.J. (1990) Nutritional energetics in fish: energy and protein utiklization in rainbow trout (salmo gairdneri). In: Bourne, G.H. (ed): Aspects of food protection and energy values. World Rev. Nutr. Diet., Karger, Basel vol 61, pp 132-172 (see page 153)

Martin, A.K. and Blaxter, K.L. (1965, The energy cost of urea synthesis in sheep, In: Proceedings of the 3th Symposium on Energy Metabolism, Blaxter K.L. Editor, Academic Press London, Page 84-91) see page 83. They report that 22.1 kcal (= 92.47 kJ) from the combustion of absorbed food is needed for the formation of 1 mol ATP and hat 4 ATP mols are needed for the formation of 1 mol urea. Thus 4 x 92.47 = 369 kJ.

Note that the energy costs for the formation of ATP is dependent on the nutrient oxidized (see Footnote a).

The metabolizable energy of protein is lower than the gross energy of the protein, since energy is lost in the urine in the form of ammonia, urea, uric acid, and other N-containing compouds. Further, there is ATP needed for the formation of the urea, uric acid etc. (see Appendix 6, 4 mol ATP per mol urea and 7 mol ATP per mol uric acid) and the *net* yield of ATP due to the oxidation of proteins will thus be lower (or the energy needed per mol ATP higher, see Appendix 7 and Blaxter 1989, page 270 and page 76 and 77) than the yield of ATP due to the oxidation of fats and carbohydrates. A part of the ATP generated is used for formation of urea, uric acid , etc. The relative low yield of ATP of proteins is thus largely attributed to the ATP that is needed for the synthesis of e.g. urea (4 mol ATP per mol urea) and uric acid (7 mol ATP per mol uric acid) (see Blaxter 1989, page 76 and page 270 at the bottom).

Appendix 6 (Table)

Formation of ATP during the oxidation of various nutrients

		Energy Generated In body		Oxygen Consumption	Yield of ATP		Energy Costs of ATP	Oxygen Costs of ATP		Yield of of ATP per oxygen consumption		
	MW	kJ/mol	kJ/g	mol O_2/mol substrate	mol ATP/mol substrate	mol ATP/g substrate	kJ/mol ATP	mol O_2/mol ATP	Liter O_2/mol ATP	mol ATP/mol O_2	mol ATP/liter O_2	Reference
Glucose ($C_6H_{12}O_6$)	180,16	2803	15,56	6,0	36,7	0,204	76,4	0,163	3,66	6,12	0,27	Elia 1992, pg 104
Glycogen ($C_6H_{10}O_5$)n	162,14	2840	17,52	6,0	37,7	0,233	75,3	0,159	3,57	6,28	0,28	Elia 1992, pg 104
Carbohydrate (glucan) ($C_6H_{10}O_5$)n	162,14	2840	17,52	6,0	36,7	0,226	77,4	0,163	3,66	6,12	0,27	Elia 1992, pg 104
Dioleoylpalmitate ($C_{55}H_{10}2O_6$)	859,42	34022	39,59	77,5	429,4	0,500	79,2	0,180	4,05	5,54	0,25	Elia 1992, pg 104
Protein (Kleiber's protein)	2259,97	45376	20,08	104,0	522,2	0,231	86,9	0,199	4,46	5,02	0,22	Elia 1992, pg 104
Glucose ($C_6H_{12}O_6$)	180,16	2789	15,48	6,0	36,0	0,200	77,5	0,167	3,74	6,00	0,27	Schulz 1975, pg 205
Glycogen ($C_6H_{10}O_5$)n	162,14	2849	17,57	6,0	37,2	0,229	76,6	0,161	3,62	6,20	0,28	Schulz 1975, pg 205
Trioleate ($C_{57}H_{104}O_6$)	885,45	35197	39,75	80,0	452,3	0,511	77,8	0,177	3,96	5,65	0,25	Schulz 1975, pg 205
Soy protein							92,9			4,96	0,22	Schulz 1975, pg 205
Glucose ($C_6H_{12}O_6$)	180,16	2829	15,70	6,0	38	0,211	74,4	0,158	3,54	6,33	0,28	Van Milgen 2002, pg 3199
Tripalmitin ($C_{51}H_{98}O_6$)	807,34	31809	39,40	72,5	409	0,507	77,8	0,177	3,97	5,64	0,25	Van Milgen 2002, pg 3199
Lysine ($C_6H_{14}N_2O_2$)	146,19	3041	20,80	7,0	37	0,253	82,2	0,189	4,24	5,29	0,24	Van Milgen 2002, pg 3199
Other amino acids (see Milgen))												Van Milgen 2002, pg 3199
Glucose ($C_6H_{12}O_6$)	180,16	2816	15,63	6,0	36	0,200	78,2	0,167	3,74	6,00	0,27	Ferannini 1988, pg 289
Palmitate ($C_{16}H_{30}O_2$)	254,14	10033	39,48	23,0	131	0,515	76,6	0,176	3,94	5,70	0,25	Ferannini 1988, pg 289
Amino Acids		1987		5,1	23		86,4	0,222	4,97	4,51	0,20	Ferannini 1988, pg 289
Glucose	180,16	2803	15,56	6,0	35,5	0,197	79,0	0,169	3,79	5,92	0,26	Blaxter 1989, pg 70
Lysine ($C_6H_{14}N_2O_2$)	146,19	3037	20,77	7,0	36,0	0,246	84,4	0,194	4,36	5,14	0,23	Blaxter 1989, pg 77
Cysteine ($C_3H_7NO_2S$)	121,16	1938	16,00	4,5	12,5	0,103	155,0	0,360	8,07	2,78	0,12	Blaxter 1989, pg 77
Other Amino acids (see Blaxter)												Blaxter 1989, pg 77
Other Compounds (see Blaxter)												Blaxter 1989, pg 76

Data are from:
M. Elia and G. Livesey (1992) Energy expenditure and fuel selection in biological sysems: the theory and practice of calculations based on indirect calorimetry and tracer methods, World Review of Nutrition and Dietetics, volume 70, page 68-131
A.R. Schulz (1975) Computer based method for calculation of the available energy in protein, Journal of Nutrition, volume 105, page 200-207.
J. Van Milgen (2002) Modeling biochemical aspects of energy metabolism in mammals , Journal of Nutrition, volume132, page 315-3202.
E. Ferranini (1988) The theoretical bases of indirect calorimetry: A review, Metabolism, volume 37, pages 287-301.
K. Blaxter (1989) Energy metabolism in animals and man, Cambridge University press.

1 mol is 22.414 liter at 0 ^{o}C and 1 bar and 1 kcal = 4184 kJ. The free energy density of 1 mol ATP = 30.5 kJ (see D. Voet and J.G. Voet (1995), Biochemistry, Second Edition, John Wiley and Sons, page 340). Thus the efficiency of the formation of 1 mol ATP generated from the oxidation of glucose is thus 30.5 / 76.4 = 40% and the efficiency of the formation of ATP generated rom the oxidation of protein is 30.5 / 86.9 = 35%. The metabolizable energy in the protein and amino acids is the (digested) gross energy (energy of combustion in a calorimeter) corrected for the energy in the ureum (in dissolved form) that is formed during the breakdown in the body and excreted in the urine.

A reference human of 70 kg consumes per day an amount of 500 liters O_2 and produes 425 liters of CO_2 and 12 grams of N in the urine. This 12 grams of nitrogen represents the oxidation of 6.25 x 12 = 12 grams of proteins. Further, according to the formula of Brouwer, the energy expenditure is then (see below):

Total Energy Expenditure = 16.175 VO_2 + 5.021 VCO_2 – 5.987 N

Total Energy expenditure = 16.175 x 500 + 5.021 x 425 – 5.987 x 12 = **10293 kJ** per day.

Data in the Table indicate that the costs (kJ per mol ATP) is about 80 kJ / mol ATP. The energy density of ATP is 30.5 kJ per mol, thus the yield is about 30.5 / 80 = 38%. Thus, when the energy expenditure of a reference man of 70 kg is 10293 kJ per day, then the amount of energy converted into ATP is (0.38 x 10293) = 3911 kJ per day. This amount results in the formation of 3911 / 30.5 = 128 mol ATP per day in a man of 70 kg. This amount is then [128 / (24 x 60 x 70)] x 100 = 1.270 mmol per kg body weight per minute. Ferrannini (1988) describes a turnover rate of 1.3 mmol / min kg in humans, thus this amount is the amount that is produced per minute. The total amount of ATP in the body is 1.2 mmol per kg body weight (Ferrannini 1988) and the total amount in a 70 kg man is 1.2 mmol x 70 = 84 mmol ATP. MW of ATP = 475.19 (ATP, formula is: $C_{10}H_{16}O_{11}N_5P_3$, see Voet and Voet, page 17), thus, the amount of 84 mmol ATP is 84 x 475.19 = 3992 mg = 4 grams. The life span or the residence time of ATP in the body is then 1.3 / 1.2 = 0.9 minute!

Appendix 7 (Table)

Calculations on the conversion of ml O_2 and CO_2 into grams O_2 and CO_2.

In the article of *M. Elia and G. Livesey (1992,* Energy expenditure and fuel selection in biological systems: the theory and practice of calculations based on indirect calorimetry and tracer methods, World Review of Nutrition and Dietetics, volume 70, page 68-131), the O_2 is expressed in liters or ml. These are liters at 0 ^oC and 1 bar. The volume of 1 mol of gas at 0 ^oC (or 273.15 ^{o} K) and 1 bar is 22.414 liters and the volume of 1 mol of gas at 25 ^oC (298 ^oK) and 1 bar is 24.5 liters. This can be calculated with the formula of Boyle – Gay Lussac PV=RT, where P is pressure, V is volume, T is temperature in degrees Kelvin and R is the gasconstant. Thus, when the volume of 1 mol at 1 bar and Temperature 273.15 ^oK (0 ^oC) is known (22.414 liters) then the volume at 25 ^oC can be calculated. PV = RT; 1 x 22.414 = R x 273.15; or 22.414 / 275 = R (constant), thus 22.414 / 273.15 = volume / 298, thus volume is 24.45 liter. The Gasconstant R = 8.314 joule / degree / mol.

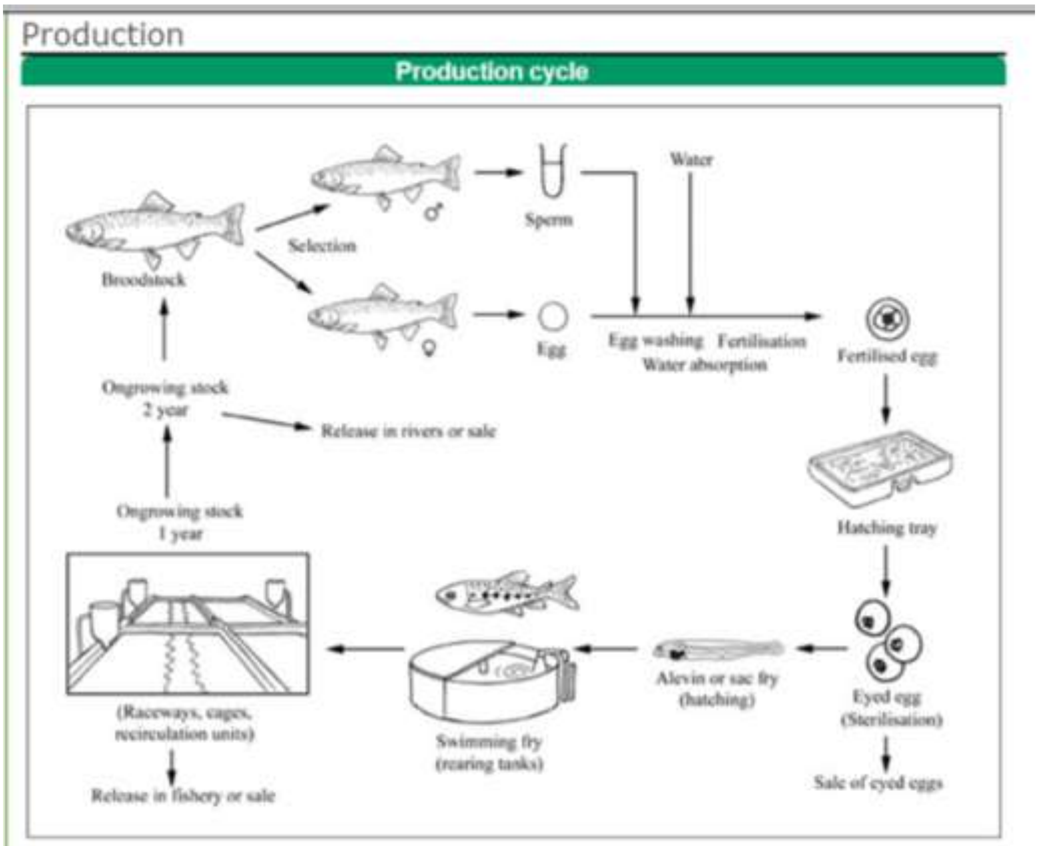
Thus, the volume of 1 mol of O_2 or CO_2 is thus 22.413 liters bij 0 ^oC. 1 liter gas of each compound also contains the same number of molecules (Number of Avogadro, 6.16 x 10^{23} particles per mol). The MW of O_2 is 32. and MW of CO_2 is 44. Thus 1 mol O_2 is 32 grams and the volume is 22.414 liters. Thus 1 mgram O_2 is 22.414 / 32 = 0.700 ml
And 1 ml O_2 = 32 / 22.414 = 1.428 mg.
Similar calculations can be done for CO_2.

1 mg O_2	= 0.700 ml O_2
1 ml O_2	= 1.428 mg O_2
1 mg CO_2	= 0.509 ml CO_2
1 ml CO_2	= 1.963 mg CO_2

All values are at 1 bar and temperature of 0 ^oC (273.15 ^oK).
See also J.A. McLean and G. Tobin (1987), Animal and human calorimetry. Cambridge University Press, page 40, they also use an oxygen density of 1.429 g/L. See also Brouwer in McLean and Tobin (1987) page 303.

Appendix 8

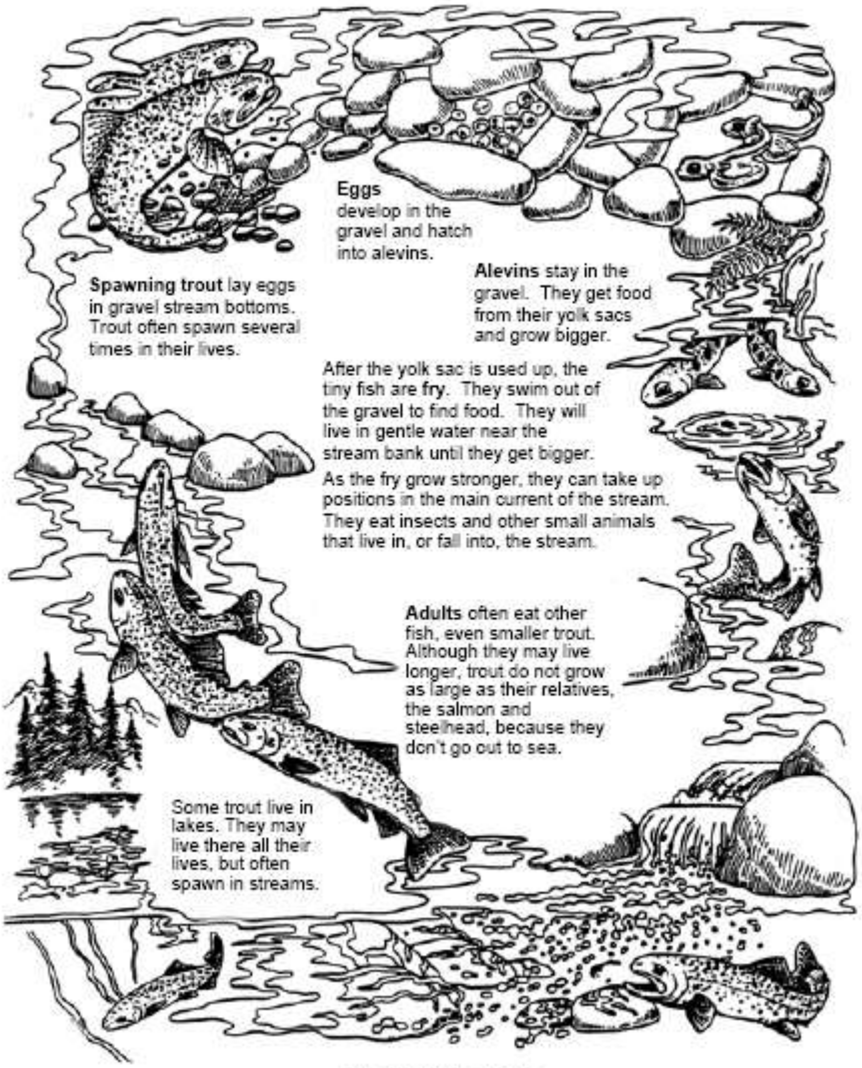
Production cycle of trout according to the FAO



Production cycle of Oncorhynchus mykiss

From the FAO website: http://www.fao.org/fishery/culturedspecies/Oncorhynchus_mykiss/en

Appendix 11



TROUT LIFE CYCLE

Appendix 10

<u>Properties of logarithms:</u>

$\ln(a) + \ln(b) = \ln(ab)$

$\ln(a) – \ln(b) = \ln(a/b)$

$a \ln(b) = \ln(b)^a$

$\ln(a)$ means ${}^{e}\ln(a)$.

g ^ $({}^{g}\log a) = a$

<u>proof:</u> *${}^{g}\log a = {}^{g}\log a$, and thus, per definition: g ^ $({}^{g}\log a) = a)$*

${}^{a}\log b = ({}^{g}\log b) / ({}^{g}\log a)$ or

$({}^{a}\log b) * ({}^{g}\log a) = ({}^{g}\log b)$

<u>proof:</u>

${}^{a}\log b = ({}^{g}\log b) / ({}^{g}\log a)$

${}^{a}\log b) * ({}^{g}\log a) = ({}^{g}\log b)$

$({}^{g}\log a$ ^ $({}^{a}\log b) = ({}^{g}\log b)$

a ^ $({}^{a}\log b) = b$

or

${}^{a}\log b = {}^{a}\log b$ (see above)

${}^{a}\log b = 1/ ({}^{b}\log a)$

<u>proof:</u>

${}^{a}\log b = {}^{b}\log b / {}^{b}\log a = 1/ ({}^{b}\log a)$

when ${}^{e}\ln(a) = b$, then this means $e^b = a$,

thus the anti - ln of b is a and is e^b

e = 2.71828 (and with many more decimals !!) and can be calculated on a calculator as the anti - ln of 1.

Note

$10^1 = 10$

$10^0 = 1$

$1^a = 1$

$\frac{1}{\infty} = 0$

$\frac{0}{1} = 0$

$\frac{1}{0}$ does not exist

0^a does not exist, and log(0) does also not exist.

The logaritmes of 0 and negative numbers do not exist.

Anti - ln of 1 = e = 2.71828 (^{e}ln e = 1)

Further:

$10^5 * 10^3 = 10^{(5+3)} = 10^8$

$10^5 / 10^3 = 10^{(5-3)} = 10^2$

a/b = c/d then: a*d = b*c (cross-wise multiplication)

$\sqrt[2]{10} = 10^{(1/2)}$ root is the inverse of the power

10 / 2 = 10 * (1/2)

$^2\log 50 = a$, then $2^a = 50$

$^a\log a = 1$ ($a^1 = a$)

$^a\log 1 = 0$ ($a^o = 1$)

The number e = 2.71:

The derivative of y = $^a\log x = (1/x)\ ^a\log 2.71$

Thus, when a = 2.7, then the derivative of y = $^{2.71}\log 2.71$ 1/x) = 1/x

Thus , the derivative can be simplified by taking a = 2.71 (^{e}log = ln, or the natural logaritme)