

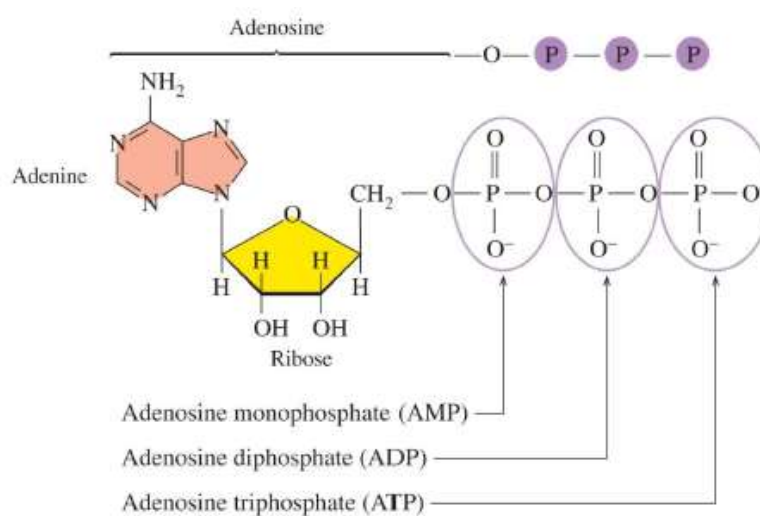
Some Aspects of Energy Metabolism in Homeothermic and in Poikilothermic Animals (particularly in Fish)

An Overview of Data from the Literature and the Internet

Composit et scripsit:

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The Netherlands, Anno Domini MMXV (2015)

Preface

In this article, some aspects of energy metabolism in homeothermic and poikilothermic animals (particularly in fish) are described with references to the literature and the internet. Much of this material, however, is also applicable to energy metabolism in humans.

This article is composed of two parts.

(1) The first part (pages 7 – 24):

The first part gives a concise description of the basics of some aspects of energy metabolism and gives the information that is needed for practical applications.

(2) The second part (pages 26 – 166):

The second part, the Appendices, gives a more comprehensive and detailed description of the material of the first part. In this second part also the derivations of the various formulae are described and also more detailed Tables with data are presented. In addition, a large number of Figures is given.

An overview of the various subjects in the first part and the second part (the Appendices) is presented in the list of contents on page 3 - 6.

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Some Aspects of Energy Metabolism in Homeothermic and Poikilothermic Animals

1. Introduction

In adult, non-growing humans and animals, there is an energy balance, i.e. the intake of energy equals the energy expenditure (or heat production). The energy expenditure or heat production of the body is composed of basal metabolic rate (BMR) (about 60% in humans), postprandial thermogenesis or Specific Dynamic Action (SDA) or Thermic Effect of Food or Feed (TEF) (about 8% in humans), and physical activity thermogenesis (AT) (about 32% in humans). Thus, all the energy intake is dissipated as heat (energy expenditure or heat production) when there is an energy balance. In growing, weight-gaining humans and animals, however, some 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 is about 65%, but is different for fat (about 75%) and protein (about 53%).

2. Feed Composition and Gross, Digestible, Metabolizable, and Net Energy

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.

The fats, proteins and carbohydrates (the NFE fraction) are the major source of energy in a feed or food. The energy densities of these three compounds are different and the amount of energy in a feed or food is related to the amount of fat, carbohydrates and proteins in the feed. The energy in a feed can be expressed as gross, digestible, and net metabolizable energy (Figure 1).

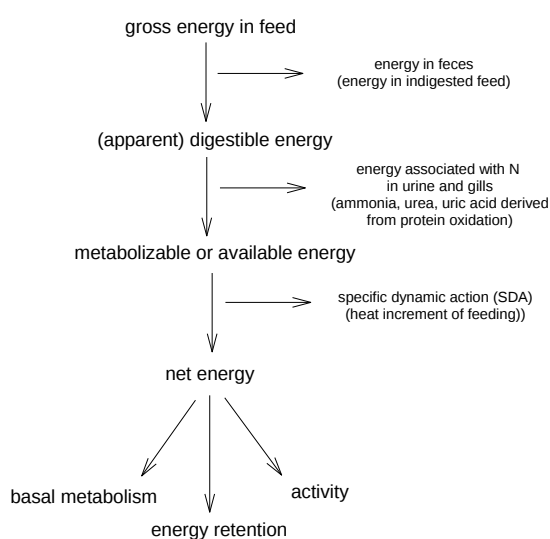


Figure 1
 Gross, digestible, metabolizable, and net energy in a feed

Gross Energy

Gross energy is the energy that is released when nutrients, i.e. carbohydrates, fats and proteins are completely oxidized, e.g. in a bombcalorimeter. The law of Germain Henri Hess (1838) states that the heat produced in a chemical reaction is always the same regardless of whether it proceeds directly or through 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 bombcalorimeter. The gross energy can thus be determined by complete combustion of a feed in a so called bombcalorimeter 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.

Digestible Energy

Digestible energy is the gross energy corrected for digestion (Figure 1) and is the amount of gross energy in the feed that is digested and is taken up by the animal. For example when the digestibility of the energy is 95%, then the gross energy has to be multiplied by 0.95 to obtain the digestible energy. 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 for human diets as reported by Atwater are given in Table 1 and the commonly used digestibilities for fish feeds in Table 3.

Metabolizable Energy

The metabolizable energy is the energy in the feed that the animal 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. However, the (gross) energy in digested protein is not completely available to the body. When proteins are oxidized in the body, the nitrogen in the protein has to be excreted as ureum (terrestrial animals: ureotelic or ureoteles), uric acid (birds, reptiles, insects: uricotelic or uricoteles) or ammonia (fish: ammoniotelic or ammonioteles). The body can excrete nitrogen only in the form of these compounds which contain a considerable amount of energy. Thus, the metabolizable or available energy of protein is the gross energy minus the energy in the excreted nitrogen products (ammonia, urea, uric acid, creatinine, creatine) (see Appendix 4 page 29 – 31 for the calculations and values and Appendices 5 and 6 for the energy densities of these nitrogen compounds). Thus, a part of the energy in the digested protein is excreted into the urine and the available (metabolizable) energy in the digested protein is thus less than the gross energy in the digested protein (Figure 1). Atwater and Rubner already recognized this phenomenon as far as in 1900 and these corrections are known as the Atwater coefficients (Table 1 and Appendix 1 page 26). Rubner (in Europe) made a correction for the energy excreted in ureum, uric acid or ammonia, and Atwater (in the USA) made in addition a correction for the digestibility of the fat, protein and carbohydrates in the diet. In fish and birds, it is difficult to measure the excretion of nitrogen in the urine, since fish excrete the urine in the water and birds excrete the uric acid together with the feces in the cloaca. Therefore, mostly the digestible energy is used in fish and bird nutrition.

Net Energy

The processing of the nutrients after digestion (storage, de-amination, synthesis, e.g. the synthesis of urea from ammonia etc. see Appendix 4, page 29 – 31 for the calculations)) requires energy and this energy is called the specific dynamic action (SDA) or the thermic effect of feed or food (TIF). 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 maintenance, activity and growth.

Table 1
Factors used in human nutrition (see Appendices 1 and 2 page 26 for more details)
Atwater factors for heat of combustion, coefficient of availability (digestibility) and available (metabolizable) energy for nutrients in a mixed human diet.

	Gross Energy (heat of combustion)		Energy generated in body		Digestibility (%)	Digestible Energy		Metabolizable Energy (Atwater general factors)		Metabolizable Energy (Atwater general factors) (rounded-off) (kcal/g)
	(kcal/g)	(kJ/g)	(kcal/g)	(kJ/g)		(kcal/g)	(kJ/g)	(kcal/g)	(kJ/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 (Ethanol)	7,07	29,58	7,07	29,58	98	6,93	28,99	6,93	28,99	7

Data from:

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).

The general Atwater factors for protein, fat, 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 rounded-off Atwater general factors are used by nutritionists and dieticians to calculate the energy densities of human diets. An example of the use of the Atwater factors is given in the example below and in Appendix 2 page 27. 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.

Example: calculation of the metabolizable energy in milk for human consumption by using the Atwater coefficients. 1 kcal = 4.184 kJ

	Energy Density Atwater values		Composition of milk g/100 g	Total Energy in Milk	
	kcal	kJ		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

Table 2
Factors used in animal nutrition (see Appendix 3 page 28 for more details).
Constants for carbohydrate, fat, and protein, when oxidized in the animal body according to Brouwer.

	O ₂ Consumption		CO ₂ Production		RQ (CO ₂ /O ₂)	Energy generated In body		Eeq O ₂		Eeq CO ₂		Atwater Digest. Coeff.	Metabolizable Energy (kJ/g)
	(g/g)	(L/g)	(g/g)	(L/g)		(kcal/g)	(kJ/g)	(kJ/g)	(kJ/L)	(kJ/g)	(kJ/L)		
Protein	1,366	0,957	1,52	0,774	0,809	4,40	18,41	13,48	19,24	12,11	23,79	92	16,94
Fat	2,875	2,013	2,81	1,431	0,711	9,50	39,75	13,83	19,75	14,15	27,78	95	37,76
Starch	1,184	0,829	1,629	0,829	1,00	4,20	17,57	14,84	21,20	10,79	21,20	97	17,05
Saccharose	1,122	0,786	1,543	0,786	1,00	3,96	16,57	14,77	21,08	10,74	21,08	97	16,07
Glucose	1,066	0,746	1,466	0,746	1,00	3,74	15,65	14,68	20,98	10,67	20,98	97	15,18

Data from:

Brouwer 1965, see McLean and Tobin (1987) page 303. 1 kcal = 4.184 kJ.

The values in this Table are only slightly different from the values of Atwater. 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. The weight of 1 liter O₂ is 1.428 grams and the weight of 1 liter CO₂ is 1.963 grams at 1 bar and a temperature of 0 °C (273.15 °K). (Appendix 8 page 38).

Eeq O₂ and Eeq CO₂ are the number of kJ that are generated when 1 gram of O₂ is consumed or 1 gram of CO₂ is produced.

Table 3
Factors used in fish nutrition (see Appendix 4 page 29 for more details).
 Energy values of various dietary compounds as used in fish nutrition (trout).

	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 metabolizable energy in 1 gram of fat or carbohydrate is similar to the gross energy in 1 gram of fat or carbohydrate. However, the metabolizable energy in 1 gram of protein is the gross energy (23.65 kJ) minus the energy that is excreted into the urine in the form of ammonia (85%) and urea (15%) (a total of 3.98 kJ, see Appendix 4, footnote 6 (g), page 31, thus 23.65 – 3.98 = 19.67 kJ). 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 O₂) for fat (13.72 kJ per gram oxygen) and for protein (13.79 per gram oxygen in ammoniatic fish) (see Appendix 4 page 29) 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.

Table 4
 Calculation of the energy density of a fish feed (trout feed).

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	10,11	8,40
Fat	28	39,6	39,60	11,088	90	9,98	9,98
Ash	9						
Moisture	5						
Fiber	1	17,5	0	0,175	0		
NFE	12	17,5	17,50	2,1	60	1,26	1,26
Total	100			24,01		21,35	19.64

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

3. Metabolic Rate as a Function of Body Weight

(see Appendices 9 on page 39, 13 and 14 on page 58 for more details)

The oxidation of nutrients such as carbohydrates, fats and proteins results in the generation of energy and this energy is used for maintenance, work and growth. All the energy that is not retained in the body in the form of growth is eventually released as heat. This energy expenditure or metabolic rate can be expressed in kJ per day or in wats (W, rate of heat production in joules per second). The basal or resting heat production is dependent on the body size with an allometric relationship (see Appendix 13 and 14) of the form (White and Seymour, 2005):

$$\text{Heat Production or Energy Expenditure (kJ/day)} = a * BW^b$$

where Heat Production or Energy Expenditure is the metabolic rate in kJ/day, a is the normalisation constant (unit per BW^b when BW = 1), BW is the body weight in kg and b is the scaling exponent or scaling coefficient. The total heat production (kJ per day) is plotted vs the body weights (kg) on double logarithmic graph paper (log – log or ln - ln) and a linear plot arises. The slope and the intercept of this linear plot can be calculated by linear regression.

The slope is b in the formula $a BW^b$. The intercept is $\log a$ and the anti – $\log$ (or anti $\ln$) of the value of $\log$ (or $\ln$) a is a of the formula $a BW^b$.

Kleiber reported as far back as 1932 that the metabolic rate of various animal species as a function of their body weight follows allometric scaling laws (see Appendix 13 and 14). He plotted the basal metabolic rate (BMR) of various animal species of different sizes vs their body weights on double logarithmic graph paper and observed a linear relationship. The graph below shows a data set of various animal species of different sizes (the so-called mouse – elephant graph) (the data in the Figure 2 are from Kleiber, 1975, *The Fire of Life*, page 203 and 207).

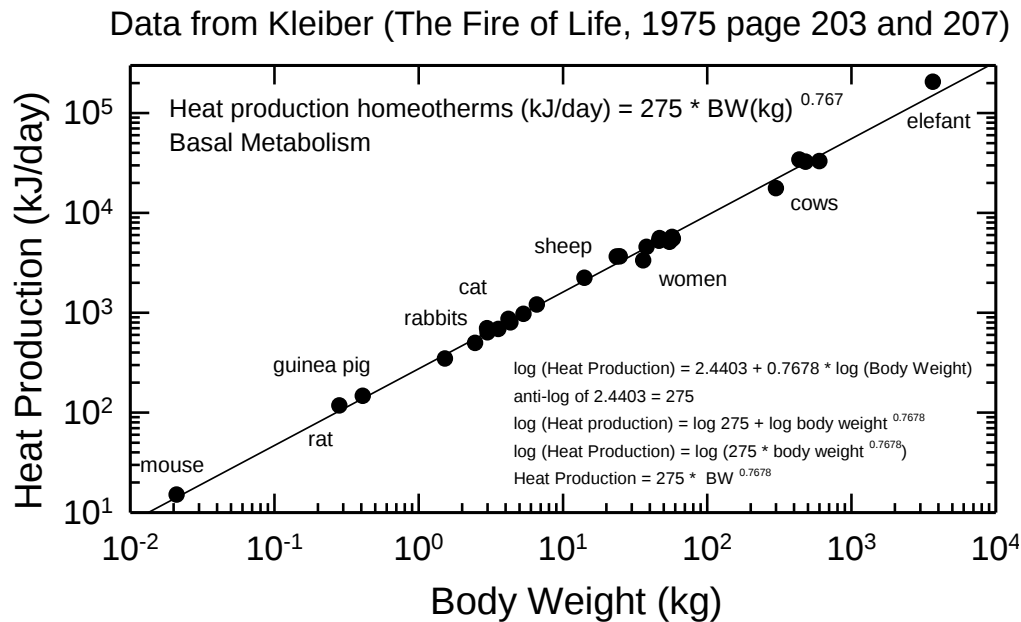


Figure 2
Heat Production as function of body weight in various species

Kleiber concluded (1975, *The Fire of Life*, page 214) that “for practical purposes, one may assume that the mean standard metabolic rate (kcal) of mammals is seventy times the three-fourth power of their body weight (in kg) per day”. Thus, the basal metabolic rate is:

$$\text{Basal Metabolic Rate (BMR) or Heat Production (kcal/day)} = 70 BW^{0.75}$$

or in kJ (1 kcal = 4.184 kJ):

$$\text{Basal Metabolic Rate (BMR) or Heat Production (kJ/day)} = 293 BW^{0.75} \text{ or about } 300 BW^{0.75}$$

One may assume that the basal metabolic rate in animals is about 75% of the total metabolic rate (total metabolic rate comprises basal metabolic rate (BMR) or routine metabolism in fish, Specific Dynamic Action (SDA, heat production as a result of food consumption) and physical activity thermogenesis (AT).

Also within a particular animal species, the metabolic rate as a function of the body weight can be described according to a scaling formula. The example below shows a graph of the heat production or metabolic rate of carp of various sizes as described by Huisman (1974, Dissertation, Wageningen University, The Netherlands, the dissertation can be downloaded from the digital library of Wageningen University).

Data from E.A. Huisman (Dissertation, 1974, page 58 and 59)

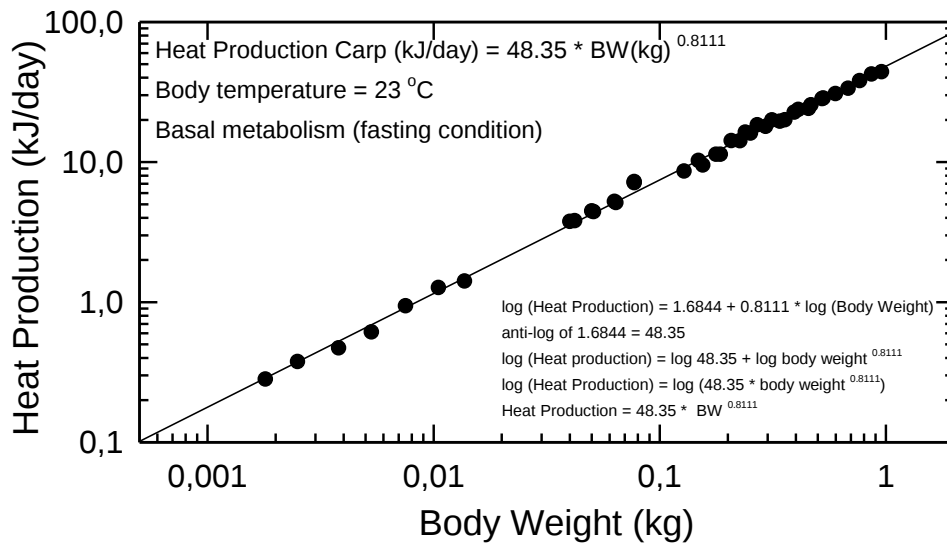


Figure 3

Heat production as function of body weight in carps

The weight or scaling exponent or coefficient for carp in the studies of Huisman (1974) was 0.811. Carke and Johnston (1999) reported that the average weight exponent for fish is 0.80 and a weight exponent of 0.80 is now mostly used for fish. More graphs describing the relationship between body weight and heat production or energy expenditure in various fish species are given in Appendix 25 – 29 on page 96.

The metabolic rates and scaling coefficients of various animal species are given in Appendix 9.

Example: The total fasting heat production of carp as measured by Huisman (1974) is $47.82 \cdot BW(kg)^{0.811}$ kJ per day. The total fasting heat production of a carp of 750 grams is then: $47.82 \cdot (0.750)^{0.811} = 37.87$ kJ per day.

Example: The maintenance metabolic rate of a trout is $48.3 \cdot BW(kg)^{0.80}$ kJ (Glencross, 2009) and the maintenance energy expenditure of a lean Zucker rat is $427 \cdot BW(kg)^{0.75}$ kJ (Pullar and Webster 1977), see Appendix 9. Thus, the energy expenditure of a trout of 250 grams is $43.2 \cdot 0.25^{0.80} = 14.3$ kJ and the energy expenditure of a rat of 250 grams is $427 \cdot 0.25^{0.75} = 151.0$ kJ, thus more than a tenfold of that of a trout!

4. The (exponential) Effect of Temperature on the Metabolic Rate in Fish

(see Appendix 15 on page 62 for more details)

The effect of the temperature on the metabolic rate or heat production (in kJ per day per kg $BW^{0.80}$) in fish is exponential. The general formula that describes the effect of the temperature (T) on the heat production is:

$$\text{Heat Production per kg } BW^{0.80} \text{ at } T_2 = \text{Heat Production per kg } BW^{0.80} \text{ at } T_1 \cdot e^{\alpha(T_2 - T_1)}$$

Studies of Winberg (1956) have indicated that in general the value for α is about 0.095 and a similar value for α has been reported by Elliott (1976) in the Brown Trout. However, the effect of the temperature on the metabolic rate may differ in different fish species and thus the values for α may also differ (see Appendix 15 (page 62) and 30 – 39 (page 101).

Example: Suppose that the Heat Production of a trout at a temperature of 15 °C is: $HP = 50 \text{ BW(kg)}^{0.80}$.
 Formula: Heat Production per kg BW^{0.80} at T_2 = Heat Production per kg BW(kg)^{0.80} at T_1 * $e^{\alpha(T_2 - T_1)}$.
 We can use the value of 0.095 for α for trout as calculated from the data reported by Elliott (1976).
 The Heat Production at a temperature of 10 °C = $e^{0.095(10-15)} 50 \text{ BW(kg)}^{0.80} = 0.62 * 50 \text{ BW(kg)}^{0.80} = 31 \text{ BW(kg)}^{0.80}$

We can also calculate how many degrees the temperature has to increase to double or triple the heat production (see Appendix 15). The increase in temperature to double the metabolic rate or heat production is:

$$T_2 - T_1 = \ln 2 / \alpha$$

Similarly, the required increase in body temperature to triple the metabolic rate or heat production is:

$$T_2 - T_1 = \ln 3 / \alpha$$

Example: We can use the value of 0.095 for α for trout as calculated from the data reported by Elliott (1976). Now we can calculate how many degrees the temperature has to be increased to double the metabolic rate of the trout, i.e. when the factor $e^{0.095(T_2 - T_1)} = 2$ or $(T_2 - T_1) - \ln 2 / 0.095 = 7.3$ centigrades. Thus, when we increase the temperature 7.3 degrees from e.g. 2 °C to 9.3 °C, the metabolic rate will double, and similarly, when we increase the temperature another 7.3 degrees from 9.3 °C to 16.6 °C, the metabolic rate will double again. Lowering the temperature by 7.3 degrees, on the other hand, will lower the metabolic rate into half.

5. Calculation of Energy Expenditure from the Consumption of O₂ and the Production of CO₂ and urinary Nitrogen (indirect Calorimetry)

(see Appendix 12 on page 50 for more details)

The oxydation of fat, carbohydrates and proteins results in the uptake of O₂, the production of CO₂ and the release of energy. The amount of O₂ consumed and the amount of CO₂ and energy released depends on the type of fuel (Appendix 1 (page 26), 3 (page 28), and 4 (page 29)). The ratio (CO₂/O₂, mol CO₂/mol O₂ or liters CO₂/liters O₂ (the volume of 1 mol CO₂ is the same as of 1 mol O₂, and is 22.414 liters at 0 °C and 1 bar, Appendix 8 on page 38) is called the respiration quotient (RQ) and is 1.00 for carbohydrates, 0.71 for fat, and about 0.82 for proteins (depending on the excretion products of the nitrogen, i.e. ammonia, urea or uric acid (Appendix 1 (page 26), 3 (page 28), and 4 (page 29))). Further, the amount of energy released when 1 liter of oxygen is used for the oxidation of carbohydrates, fat and proteins, the so called energy equivalents of O₂ (Eeq O₂) is 21.20, 19.75 and 19.24 kJ per liter oxygen, respectively (Appendix 3). In addition, the amount of energy released when 1 liter of CO₂ is produced, the so called energy equivalents of CO₂ (Eeq CO₂), is 21.20, 27.78 and 23.79, respectively (Appendix 3 on page 28). Thus, with these values, the amount of energy can be calculated from the amount of oxygen consumed and the amount of CO₂ produced and these values are used for the calculation of the energy expenditure from gaseous exchange.

The heat production (kcal or kJ) from the O₂ consumption (liters), CO₂ production (liters) and urinary N production (grams, a measure of the protein oxidation) is given by the following formula (Brouwer 1965, see McLean and Tobin 1987, page 303) (liters are at 0 °C and at 1 bar and then 1 liter O₂ = 1.428 gram and 1 liter CO₂ = 1.964 gram and 1 kcal = 4.184 kJ):

Formula of Brouwer:

$$\text{Total Energy Expenditure (kJ)} = 16.175 \text{ O}_2 \text{ (liters)} + 5.021 \text{ CO}_2 \text{ (liters)} - 5.987 \text{ N(g)}$$

or

$$\text{Energy Expenditure (kJ) / liter O}_2 = 16.175 + 5.021 \times (\text{liters CO}_2 / \text{liters O}_2) - 5.987 \text{ N(g) / liters O}_2$$

Example: A reference man of 70 kg consumes per day 500 liters of O₂, produces 425 liters of CO₂ and excretes 12 grams of nitrogen in the urine. The energy expenditure or heat production per day is then:
 Total energy expenditure = 16.175 * 500 + 5.021 * 425 + 5.987 * 12 = 10150 kJ per day.

When only carbohydrates and fats are oxidized, the formula becomes;

$$\text{Total Energy Expenditure} = 16.175 \text{ O}_2 \text{ (liters)} + 5.021 \text{ CO}_2 \text{ (liters)}$$

or

$$\text{Energy expenditure (kJ) / liter O}_2 = 16.175 + 5.021 \times (\text{liters CO}_2 / \text{liters O}_2)$$

where (liters CO₂ / liters O₂) is the respiration quotient (RQ).

Many fish species are carnivorous and use predominantly proteins and fats as fuel. The energy equivalents of O₂ (Eeq O₂) for fats and proteins (for ammoniotelic animals such as fish) are 13.72 and 13.79 kJ per gram oxygen, respectively (values of Elia and Livesey 1992, see Appendix 4) The average of these two values is 13.75 kJ per gram oxygen or 13.75 * 1.428 = 19.64 kJ per liter oxygen (1 liter O₂ weighs 1.4258 grams, Appendix 8) and a similar value of has been reported by Elliott (1975). Thus in fish, the heat production or energy expenditure (kJ) can be estimated by multiplying the grams of oxygen consumption by 13.75 or the liters of oxygen consumption by 19.64. Conversely, the consumption of O₂ (in grams) by fish can be calculated by dividing the energy expenditure by 13.75.

$$\text{Total Energy Expenditure in Fish (kJ)} = \text{grams oxygen uptake} * 13.75 \text{ (kJ)}$$

Example: Suppose that the total heat production of a fish is 50 kJ per day. The O₂ consumption is then 50/13.75 = 3.64 grams of O₂ per day.

6. Energy for Maintenance and Energy for Growth (Fat and Protein Deposition)

(see Appendix 17 on page 72 and Appendix 18 on page 73 for more details)

In a growing animal, energy is used for maintenance and for growth. The energy expenditure or heat production under fasting or maintenance conditions is given by the allometric formula $a \cdot BW^b$ as explained above. The energy intake above maintenance will be used for growth, i.e. fat and protein deposition. Expressed in a formula:

$$\text{Metabolizable Energy Intake} = ME_m + (1/k_d) * ER$$

where ME_m is the energy expenditure or heat production for maintenance ($a \cdot BW^b$), ER is the energy retained and k_d is the efficiency of energy deposition or fraction of the total energy used for growth that is retained in the body. Energy is predominantly deposited in the form of protein and fat and the energy for growth can be partitioned in energy for fat deposition and energy for protein deposition. The formula becomes then:

$$\text{Metabolizable Energy Intake} = ME_m + 1/k_p \text{ PD} + 1/k_f \text{ LD}$$

where PD and LD are the protein and lipid deposition (kJ/d), respectively, and k_p is the energetic efficiency of protein deposition and k_f the energetic efficiency of lipid deposition. Appendix 9 gives an overview of various reported values for ME_m and k_d and k_f and k_p in various animal species. There are considerable variations in reported values for k_p and k_f, but the k_p is typically smaller than k_f. For example, the NRC (1998) reports for pigs a k_p value of

0.53 and a k_f value of 0.75. Thus, for the deposition of 1 gram of protein (23.65 kJ gross energy) is needed $(1/0.53) * 23.65 = 45$ kJ of total energy and for the deposition of 1 grams of fat (39.6 kJ) is needed $(1/0.75) * 39.6 = 53$ kJ of total energy (the energy of the deposited 1 gram of fat plus the energy needed for this deposition). Or, for the deposition of 1 kJ as protein is needed $(1/0.53) * 1 = 1.89$ kJ and for the deposition of 1 kJ as fat $(1/0.75) * 1 = 1.33$ kJ, thus more energy is needed for the deposition of 1 kJ as protein than as fat. In animal nutrition, a average value of about 0.65 for k_d (efficiency of total energy deposition above maintenance) is mostly used for the efficiency of the deposition of the total energy in the body.

When an animal is fed more energy then is needed for maintenance, the excess of energy will be deposited in the form of protein and fat. Protein is essential for growth, since protein drives the growth. The amount of protein and fat that is deposited can be measured by carcass analysis. Figure 4 shows the amount of protein and fat that are deposited when increasing amounts of metabolizable energy are fed to a lean Zucker rat. More details and graphs are given in Appendix 17 (page 72), 18 (page 73), and 40 – 44 (page 114).

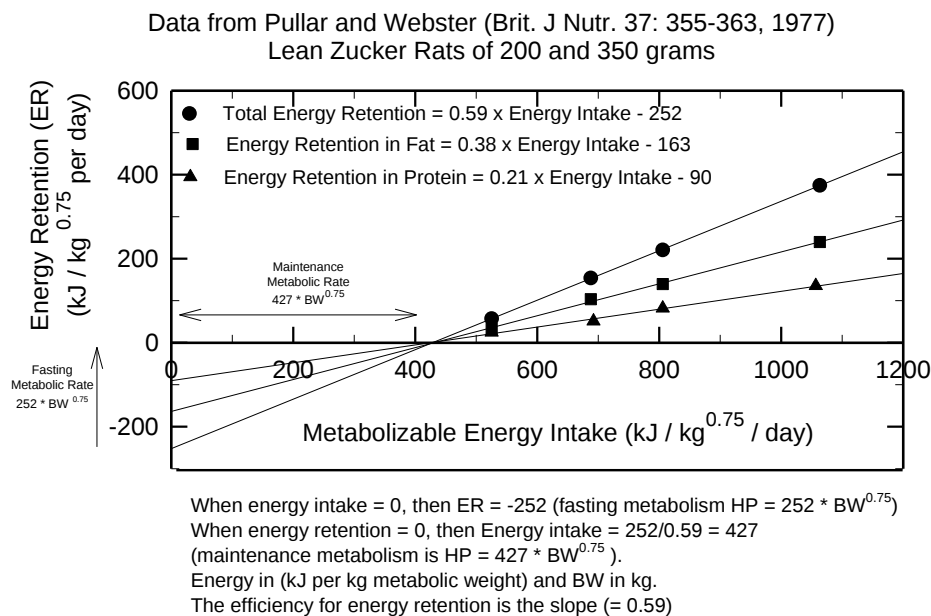


Figure 4
 Energy, fat and protein retention as a function of metabolizable energy intake

7. Feed Intake and Feeding Levels

(see Appendix 19 on page 74 for more details)

The feed intake can be expressed in grams per kg metabolic weight (BW(kg)^b). The feeding of grams of feed per kg BW^b involves that the amount of feed (and energy) parallels or follows the heat production or metabolic rate of different size fish.

The formula that gives the total amount of the feed intake per day is then:

$$\text{Feed Intake per day (grams)} = c * \text{BW(kg)}^b$$

where BW is expressed in kg and c is the feed intake (grams) per kg metabolic weight (BW(kg)^b) per day and b is the scaling coefficient or exponent. The scaling coefficient or

exponent b is in most terrestrial animals 0.75 and for most fish species 0.80 and the formula for fish is then:

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

Example: The feeding level for fish is 15 grams per kg BW(kg)^b per day and the scaling coefficient for fish is 0.80 and the weight of the fish is 250 grams. The feed intake of this fish with a body weight of 250 grams is then per day:

Formula: Feed Intake per day (grams) = c * BW(kg)^b

Feed intake per day = 15 * (0.250)^{0.80} = **4.95** grams

The feed intake per 100 gram fish is then 4.95 * (100 / 250) = 1.97 grams or a feeding level of 1.97% per day

We can also express the feed intake per day per 100 gram animal (% feed intake), then the formula becomes (see Appendix 19):

$$\% \text{ feed intake per day (feed intake per 100 gram of animal)} = (c/10) * \text{BW(kg)}^{(b-1)}$$

where c (grams) is the feed intake per kg metabolic weight (BW(kg)^b) per day and the BW is expressed in kg.

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 specific size fish is known (see Appendix 19 on page 74) Thus:

$$\text{feed intake per kg metabolic weight} = c = 10 * (\% \text{ feed intake per day}) / (\text{BW(kg)}^{(b-1)})$$

Example: The feed intake per kg metabolic weight (per BW(kg)^b) is 15 = c and the body weight of a fish is 250 grams and the scaling coefficient for fish is 0.80. The feed intake expressed in % of body weight is calculated as:

Formula: % feed intake per day (feed intake per 100 gram of animal or fish) = (c/10) * BW(kg)^(b-1)

% feed intake = (15/10) * (0.250)^(0.80-1) = 1.98 % (see also example above).

The total feed intake of a fish of 250 grams = 250 * (1.98 / 100) = **4.95** grams

Example: The feed intake as % feed intake for a fish is 1.97% per day and the scaling coefficient for fish is 0.80 and the body weight of the fish is 250 grams. The feed intake expressed per kg metabolic weight (BW(kg)^b) is calculated as:

Formula: feed intake per kg metabolic weight (per BW(kg)^b) = c = 10 * (% feed intake per day) / (BW(kg)^(b-1))

feed intake per kg metabolic weight = c = 10 * (1.98) / (0.25)^(0.8-1) = 15 grams per (BW(kg)^{0.80}).

The total feed intake of a fish of 250 grams = 15 * BW(kg)^{0.80} = 15 * (0.25)^{0.80} = **4.95** grams

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

(see Appendix 20 on page 79 for more details)

The effect of temperature on the feeding level is of particular interest in fish since fish are poikilotherm and the metabolic rate of a fish is dependent on the water and body temperature. Feeding 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 fish. Therefore, the effect of the temperature on the feed intake should be the same as the effect on the heat production or metabolic rate. The general 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:

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

Studies of Winberg (1956) have indicated that the value for α in the formula describing the effect of the temperature on the heat production (see above) and thus also on the feed intake is in general about 0.095 and a similar value for α has been reported by Elliott (1976) in the Brown Trout. However, the effect of the temperature on the metabolic rate may differ in different fish species and thus the values for α may also differ (see Appendix 15 (page 62) and Appendices 30 – 39 on page 101).

Example: We have a feeding level of 15 grams per kg metabolic weight ($BW^{0.80}$) for the trout at a temperature of 15 °C. We want to calculate the feeding level at a temperature of 10 °C.
 Formula: Feeding level at $T=T_2 = (\text{feeding level at } T=T_1) * e^{\alpha(T_2-T_1)}$
 We can use the value of 0.095 for α for trout as reported by Elliott (1976).
 Feeding level at ($T=10$ °C) = $15 * e^{0.095*(10-15)} = 9.33$ grams of feed per kg metabolic weight.
 We can also calculate the feeding level at a temperature of 5 °C. There are two ways for these calculations.
 1. The feeding level at 15 °C is 15 grams. Thus:
 Feeding level at ($T=5$ °C) = $15 * e^{0.095*(5-15)} = 5.80$ grams of feed per kg metabolic weight.
 2. The feeding level at 10 °C is 9.33 grams. Thus:
 Feeding level at ($T=5$ °C) = $9.33 * e^{0.095*(5-10)} = 5.80$ grams of feed per kg metabolic weight.

Examples of various feed intake levels and at different temperatures in trout are given in Appendix 19, 20, 90, 91.

9. Body Composition

(see Appendix 21 on page 81 for more details)

The major components of the body are water, protein fat and ash. The % of water in mammals is approximately 70 -75%, protein 16%, ash 2 - 4% and the % of fat 10 – 20%. The amounts of these individual components can be described as a function of body weight by the allometric scaling formula:

$$Y = \text{amount (grams)} = a * BW^b$$

where Y is the amount of water, protein, fat, or ash, a is the normalization constant and b is the scaling coefficient or exponent.

For example (Figure 5, top panel ,data from Appendices 68 and 69 on page 142), the total amount of body fat (grams) in trout is plotted vs the corresponding body weights (grams) on double logarithmic graph paper (log – log) and a linear plot arises. A regression line can be constructed:

$$^{10}\log \text{ fat (grams)} = - 1.4789 + 1.1776 * ^{10}\log BW(g)$$

$$\text{anti-log of } - 1.4789 = 0.0332$$

$$^{10}\log \text{ fat (grams)} = ^{10}\log 0.0332 + 1.1776 * ^{10}\log BW(g)$$

$$^{10}\log \text{ fat (grams)} = ^{10}\log 0.0332 + ^{10}\log BW(g)^{1.1776}$$

$$^{10}\log \text{ fat (grams)} = ^{10}\log (0.0332 * BW(g)^{1.1776})$$

$$\text{fat (grams)} = 0.0332 * BW(g)^{0.1776}$$

Thus, the slope of the regression line is 0.1776 and represents the scaling coefficient b and the anti-log of the intercept of the regression is 0.0332 and represents the normalization constant a of the formula $a * BW^b$.

Further, the percentage of fat in the trout is the absolute amount of fat in grams divided by the body weight in grams and multiplied by 100%:

$$\% \text{ fat} = 0.0332 * (\text{BW(g)}^{0.1776} / \text{BW(g)}) * 100\% = 3.32 * \text{BW(g)}^{(1.1776 - 1)} = 3.32 * \text{BW(g)}^{0.1776}$$

Similarly, the formulas for the amounts and the percentages of water, protein and ash can be calculated (Figure 5).

The proportion of protein in the body is rather constant (about 16%) and the same is true for the ash content (about 4% in mammals and about 2.5% in fish). However, the fat and water content can vary considerably and is dependent on various factors such as e.g. the feeding level and the composition of the diets. Further, the % fat and the % water are negatively correlated with each other (Figure 6, data from Figure 5), a high % fat is associated with a low % water, whereas the % protein and % ash does not change (sometimes only slightly). When the correlation between % water and % fat is known, then the proportion of fat in the body can be derived from the % water in the body. The % water of the body can be easily measured by drying in an oven. Figure 5 shows an example of the body composition of trout. The compositional data are from various articles from the literature (see Appendices 68 and 69 on page 142). See also Appendix 45 – 83 (page 119) for the composition of other fish species and pigs.

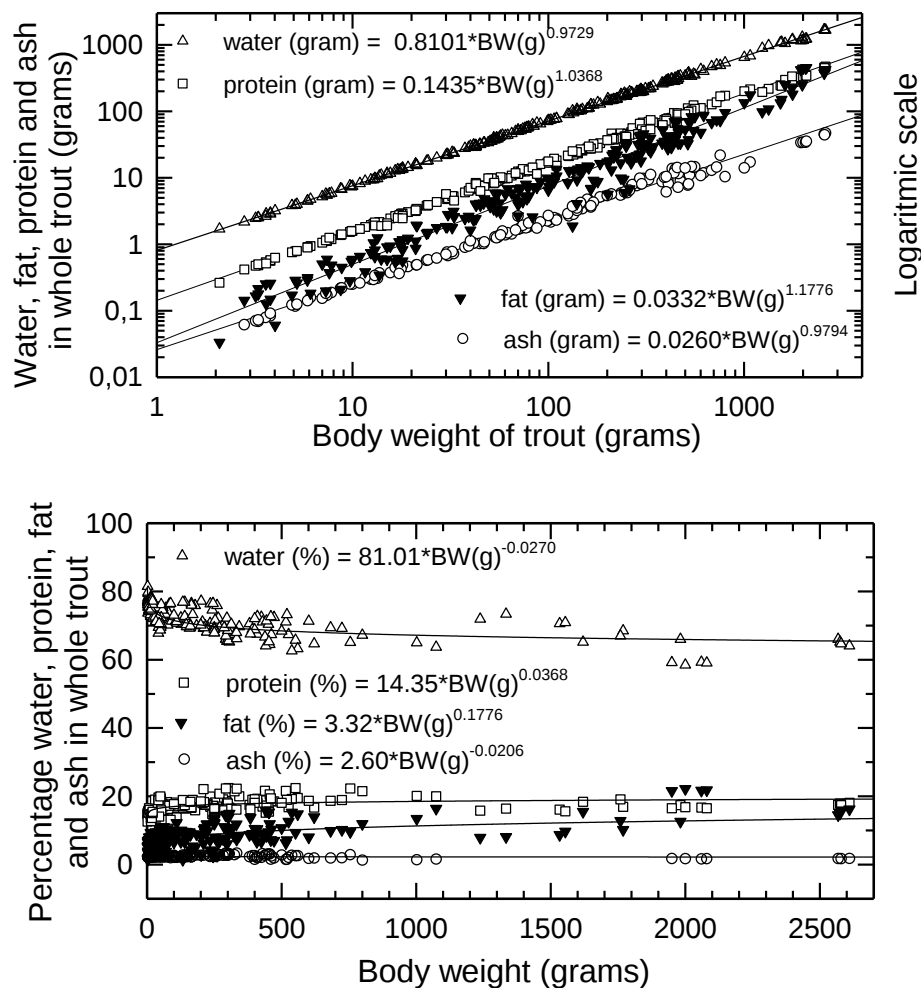


Figure 5
 Body composition of trout

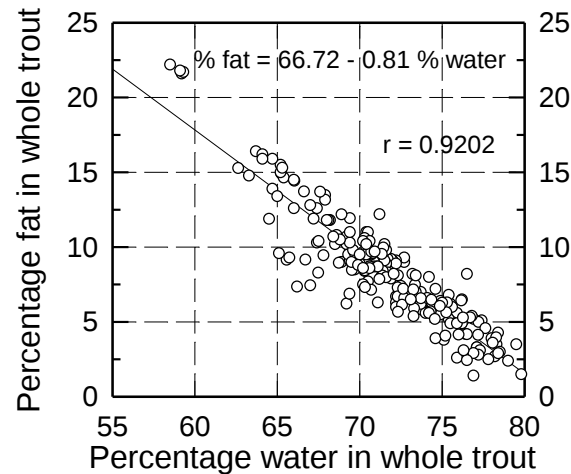


Figure 6
 Correlation between the % water and % fat in trout

10. Calculation of the Growth and the Energy Budget of an Animal

We will calculate the energy budget of a trout as an example. However, the energy budget of other fish species and other animals can be calculated in a similar way.

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

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

Where $a \cdot \text{BW}^{0.80}$ 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 $\text{BW}(\text{kg})^{0.80}$). The feed intake expressed in % of body weight is:

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

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

The composition of a typical high performance trout diet is given in the Table 5.

Table 5
 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	39,60	11,088	90	9,98	9,98	20,56
Ash	9							
Moisture	5							
Fiber	1	17,5	0	0,175	0			
NFE	12	17,5	17,50	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 fraction. DP/DE (digestible protein/digestible energy) = $(450 \cdot 0.95) / 21.35 = 20.02$ mg/kJ

The maintenance heat production of a trout of 0.10 kg at 15 °C 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 Appendix 74):

$$\begin{aligned}\text{Fat (g)} &= 0.03235 \text{ BW(g)}^{1.243} = 0.03235 * (100)^{1.243} = 9.91 \text{ grams of fat} \\ \text{Protein (g)} &= 0.1336 \text{ BW(g)}^{1.036} = 0.1336 * (100)^{1.036} = 15.77 \text{ grams of protein}\end{aligned}$$

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). 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 4 page 29 - 31 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 O₂ in fish is 13.75 kJ / gram O₂, i.e. the consumption of 1 gram of O₂ by the trout generates 13.75 kJ energy, see footnote of Table 3 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 $23.01 \text{ (gross energy deposited)} / (2.06 \text{ (feed intake)}) \times 21.35 \text{ (digestible energy in 1 gram of feed)} = 52\%$.

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

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

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.

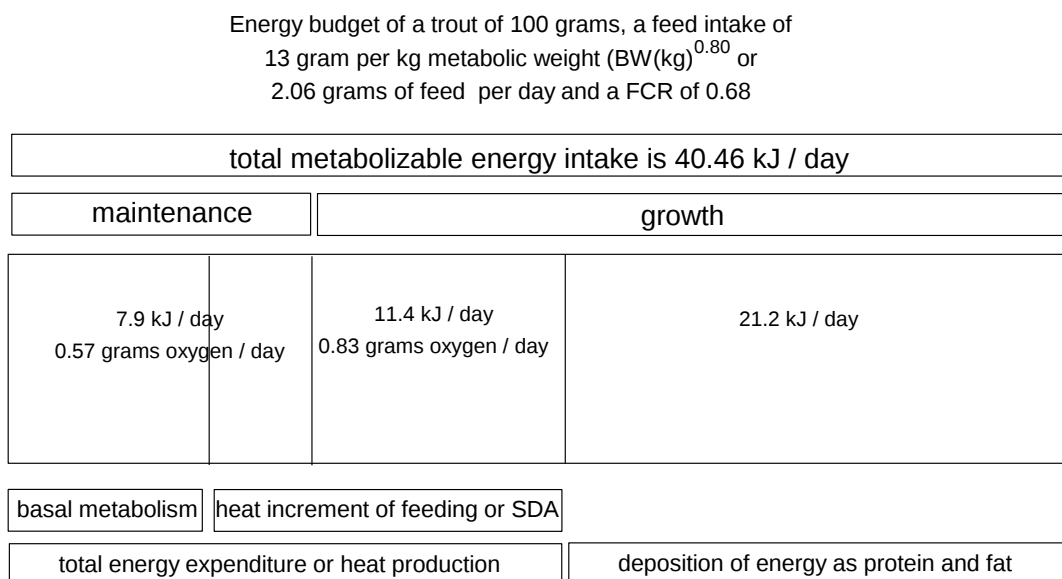


Figure 7
Energy budget of a trout

11. Growth Curves in Fish Biology

(see Appendix 22 on page 85 for more details)

Two major types of growth curves are used in fish biology, 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 is used to describe the growth of fish larvae, up to about 10 grams, and the power growth curve to describe the growth of larger size fish.

The exponential growth curve is described by the formula:

$$BW_1 = BW_0 e^{\alpha t}$$

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

$$\ln(BW_1) = \ln(BW_0 * e^{\alpha t}) = \ln BW_0 + \alpha t \ln e = \ln BW_0 + \alpha t$$

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. The slope α and the intercept of this linear plot ($\ln BW_0$) can be calculated by linear regression and the anti- $\ln$ of the value of the intercept ($\ln BW_0$) is BW_0 .

The slope α can also be calculated 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 , then we can calculate the body weights at each time point with the formula for any value of BW_0 .

An example of the exponential growth curve is given in Figure 8.

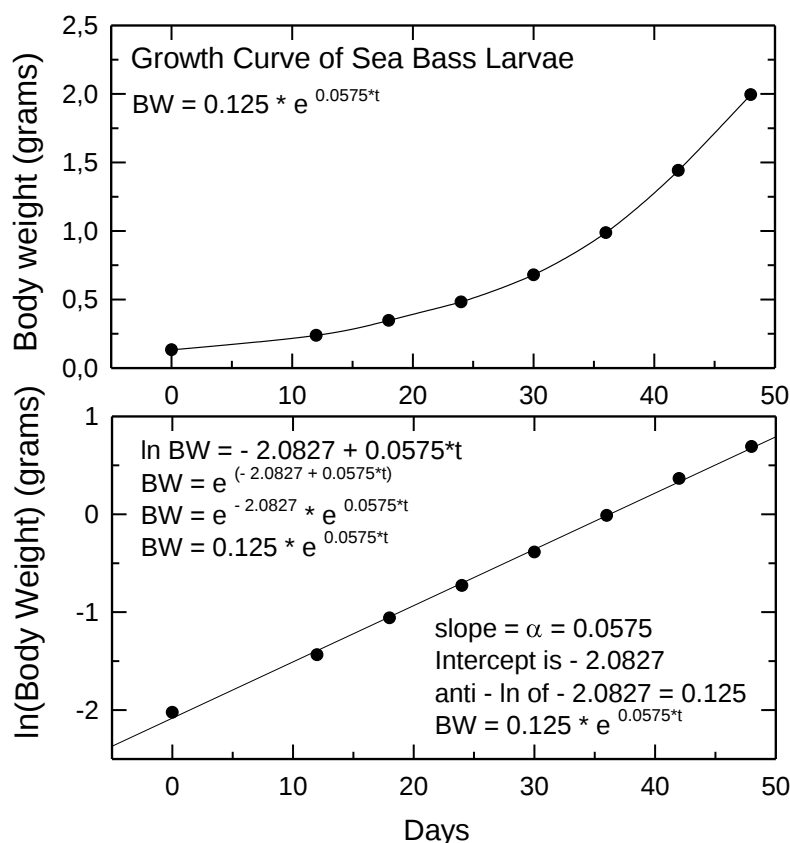


Figure 8
 Exponential growth curve of Sea Bass larvae

Example: The growth of sea bass larvae is for example described by the exponential function:
 $BW_1 = BW_0 * e^{\alpha t} = 0.125 * e^{0.0575 * t}$ where BW_0 is the BW at $t = 0$ and is in this example 0.125 grams
 The body weight at $t = 10$ days is:
 $BW_1 = 0.125 * e^{0.0575 * 10} = 0.222$ grams.
 The body weight after another 10 days is:
Method 1:
 $BW_1 = BW_0 * e^{\alpha t} = 0.222 * e^{0.0575 * 10} = 0.395$ grams
Method 2:
 $BW_1 = BW_0 * e^{\alpha t} = 0.125 * e^{0.0575 * 20} = 0.395$ 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:

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

The power growth curve is described by the formula:

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

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 $BW^{1/3}_{\text{day}=0}$ is the body weight raised to the power 1/3 when $t = 0$. The slope c multiplied by 100 is called the Daily Growth Coefficient (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 $BW^{1/3}_{\text{day}=0}$ can be calculated with linear regression. Sometimes, also a power different from 1/3 can be used to fit a power growth curve. The correct power can be found by trial and error.

The formula can also be written as:

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

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

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

An example of the power growth curve is given in Figure 9.

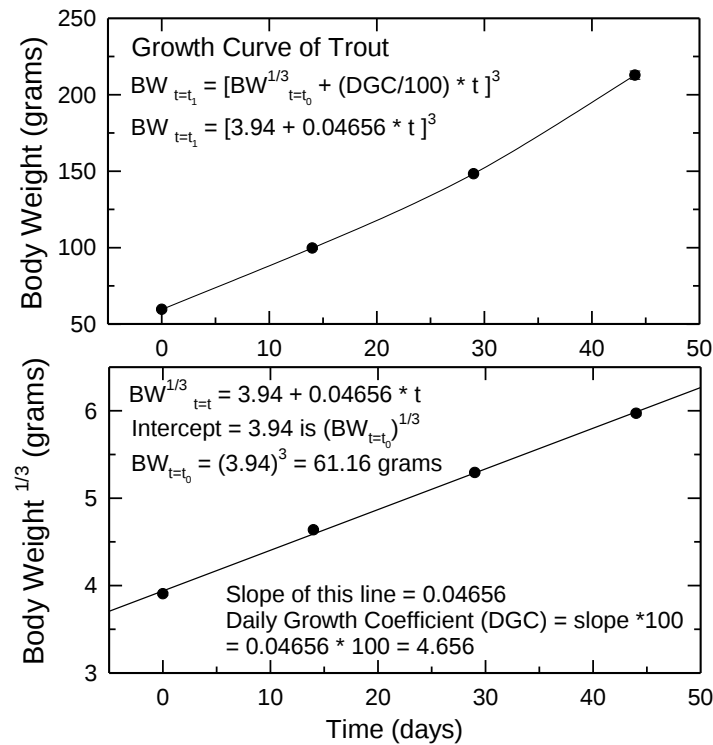


Figure 9
Power growth curve of trout

Example: we have calculated that the DGC is 4.656 and the body weight at $t = 0 = 61$ grams. The body weight after 15 days is:
 $BW_{day=15} = (BW_{day=0}^{1/3} + (DGC/100) t)^3 = (61^{1/3} + (4.656/100) 15)^3 = 99.6$ grams

Examples of growth curves are given in Appendix 84 - 89

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

(see Appendix 23 on page 93 for more details)

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):

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

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:

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

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.

The graphs below show 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 centimeter on double logarithmic graph paper (e.g. log – log paper). The slope of this line is b in the formula $a \cdot BW^b$. The intercept of the line is log a and the anti-log of log a is a in the formula $a \cdot BW^b$.

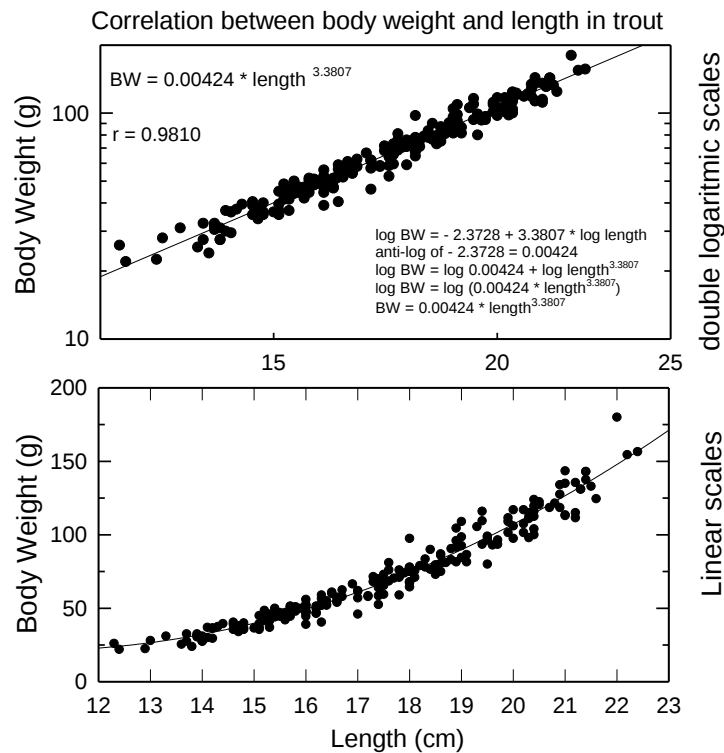


Figure 10
 Correlation between body weight and length in trout

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 = $0.00424 \cdot 15^{3.3807} = 40.8$ grams.
 The condition factor of this trout of 40.8 grams and 15 cm long = $100 \cdot (40.8) / (15^3) = 1.21$

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)
	(kcal/g)	(kJ/g)	(kcal/g)	(kJ/g)		(kcal/g)	(kJ/g)	(kcal/g)	(kJ/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 7: 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 $(0.16) \times 7.9 \text{ kcal} = 1.264 \text{ (1.25) kcal (5.29 kJ)}$ energy per gram absorbed or digested protein is lost in the urine. Thus the available energy per gram absorbed or digested protein is then $5.65 - 1.25 = 4.40 \text{ kcal (18.41 kJ)}$. The digestibility of protein is 92 %, thus, the digested and available energy (metabolizable energy) per gram consumed dietary protein is then $0.92 \times 4.4 = 4.0 \text{ kcal (16.73 kJ)}$

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 2 (Table)

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

	Metabolizable Energy Density (Atwater values)		Composition of milk (g/100 g)	Total Metabolizable Energy in Milk	
	(kcal/g)	(kJ/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 3 (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 (CO ₂ /O ₂)	Eeq O ₂				Eeq CO ₂				Atwater Digest. Coeff.	Metabolizable Energy	
		(kcal/g)	(kJ/g)	(g/g)	(L/g)	(g/g)	(L/g)		(kcal/g)	(kJ/g)	(kcal/L)	(kJ/L)	(kcal/g)	(kJ/g)	(kcal/L)	(kJ/L)		(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 CO₂ / mol O₂ or liters CO₂ / liters O₂), 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 O₂ = 18.41 / 1.366 = 13.477 kJ per gram O₂. Further, 1 ml O₂ = 1.428 gram O₂ (1 gram O₂ = 0.700 ml O₂) and 1 ml CO₂ = 1.962 mg CO₂ (1 grams CO₂ = 0.510 ml CO₂) at 1 bar and 273.15 °Kelvin (0 °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 considerably different from 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 4 (Table)

The values for energy generated in the body, Respiratory Quotient (RQ) and the Energy Equivalents EeqO₂ and EeqCO₂ for carbohydrate, fat, protein and alcohol according to data from Elia and Livesey (1992).

	MW	Energy Generated in the Body ¹		H ₂ O generated		O ₂ consumed			CO ₂ generated			RQ (CO ₂ /O ₂)	EeqO ₂ ⁴		EeqCO ₂ ⁴		Atwater Digest. Coeff. (%)	Metabol Energy (kJ/g)
		(kJ/mol)	(kJ/g)	(mol/mol)	(g/g)	(mol/mol)	(g/g)	(L/g)	(mol/mol)	(g/g)	(L/g)		(kJ/g)	(kJ/L)	(kJ/g)	(kJ/L)		
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 (dioleypalmitate) 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 ₆ H 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 ₂ H ₆ O)	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
<u>Kleibers standard protein</u>																		
<u>Data from Elia and Livesey⁵</u>																		
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
<u>Kleibers standard protein</u>																		
<u>Calculated⁶</u>																		
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 carbohydrates, 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 urea, ammonia, uric acid, creatine, creatinine, and allantoin. The protein in this Table refers to the Kleiber's standard protein (C₁₀₀ H₁₅₉ N₂₆ O₃₂ 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: C₁₀₀ H₁₅₉ N₂₆ O₃₂ S_{0.7} + 124.8 O₂ = 100 CO₂ + 78.8 H₂O + 13 N₂ + 0.7 H₂SO₄ + 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):

$C_{100}H_{159}N_{26}O_{32}S_{0.7} + 104 O_2 (= 22.414 \times 104 = 2331.06 \text{ liters}) = 86.6 CO_2 (= 22.414 \times 86.6 = 1941.05 \text{ liters}) + 50.6 H_2O + 11.7 N_2H_4CO \text{ (urea)} + 1.3 NH_4OH \text{ (ammonia)} + 0.43 N_3C_4H_7O \text{ (creatinine)} + 0.7 H_2SO_4$

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 $0^\circ C$ ($273.15^\circ K$).
 $1 \text{ mg } O_2 = 0.700 \text{ ml } O_2$ and $1 \text{ ml } O_2 = 1.428 \text{ mg } O_2$. Further $1 \text{ mg } CO_2 = 0.509 \text{ ml } CO_2$ and $1 \text{ ml } CO_2 = 1.963 \text{ mg } CO_2$

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 $13 \times 647 = 8411$ kJ of energy, which is excreted in the urine. The gross energy of protein is $23.65 \times 2260 = 53448$ 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): $C_{100}H_{159}N_{26}O_{32}S_{0.7} + 105.3 O_2 = 87 CO_2 + 52.8 H_2O + 13 N_2H_4CO \text{ (urea)} + 0.7 H_2SO_4$

The complete combustion of Kleiber's protein is

(1) $C_{100}H_{159}N_{26}O_{32}S_{0.7} + 124.8 O_2 = 100 CO_2 + 78.8 H_2O + 13 N_2 + 0.7 H_2SO_4 + 53448 \text{ kJ}$ and (complete combustion of protein)

(2) $13 N_2H_4CO \text{ (urea)} + 19.5 O_2 = 13 CO_2 + 26 H_2O + 13 N_2 + 13 \times 647 \text{ kJ} (= 8411 \text{ kJ})$ (complete combustion of urea)

Subtract (2) from (1): (compare McLean and Tobin 1987, page 33, and Blaxter 1989, page 12, law of Hess, law of constant heat summation).

$C_{100}H_{159}N_{26}O_{32}S_{0.7} + 105.3 O_2 = 87 CO_2 + 52.8 H_2O + 13 N_2H_4CO \text{ (urea)} + 0.7 H_2SO_4 + 45037 \text{ kJ}$ or $45037 / 2260 = 19.93$.

We can also assume that protein in general contains 16% nitrogen (The Kleiber's protein contains 16.1% 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 $0.34 \times 10.77 = 3.66$ 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 $6.5 \times 1921 = 12487$ kJ of energy, which is excreted in the urine. The gross energy of protein is $23.65 \times 2260 = 53448$ 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): $C_{100}H_{159}N_{26}O_{32}S_{0.7} + 95.5 O_2 = 67.5 CO_2 + 65 H_2O + 6.5 C_5H_4O_3N_4 \text{ (uric acid)} + 0.7 H_2SO_4$

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 $0.48 \times 11.40 = 5.47$ 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 $26 \times 353 = 9178$ kJ of energy, which is excreted in the urine. The gross energy of protein is $23.65 \times 2260 = 53448$ 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 $0.195 \times 20.73 = 4.04$ 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 $8.667 \times 2337 = 20255$ kJ of energy, which is excreted in the urine. The gross energy of protein is $23.65 \times 2260 = 53448$ 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 $0.43 \times 20.66 = 8.88$ 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 $8.667 \times 2324 = 20142$ kJ of energy, which is excreted in the urine. The gross energy of protein is $23.65 \times 2260 = 53448$ 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 $0.44 \times 20.18 = 8.88$ 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 $((0.16 \times 0.90 / 0.466) \times 10.77) + ((0.16 \times 0.05) / 0.371) \times 20.66 + ((0.16 \times 0.05 / 0.822) \times 20.73) = 3.975$ 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 $((0.16 \times 0.85 / 0.822) \times 20.73) + ((0.16 \times 0.15 / 0.466) \times 10.77) = 3.98$ 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 5 (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 ₅ H ₄ N ₄ O ₃	168,112		1921	11,4				11,4	1, 2,3
Creatinine	C ₄ H ₇ N ₃ O	113,12		2337	20,7				20,7	1, 2
Creatine	C ₄ H ₉ N ₃ O ₂	131.135		2324	17.7				17.7	1, 2
Benzoic acid (standard)	C ₇ H ₆ O 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 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 (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 °C (273.15 °K) 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 6 (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 ₅ H ₄ N ₄ O ₃	Creatinine C ₄ H ₇ N ₃ O	Creatine C ₄ H ₉ N ₃ O ₂
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 5 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, urea 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.

(a) **Urea.** Ammonia (NH₃) 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) and Blaxter (1989), page 76). 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 contains 16% 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 $(2 \times 28.014) / 60.056 = 46.6\%$ nitrogen (MW of N = 28.014 and MW urea = 60.056), thus the oxidation of 1 gram 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 $(0.3455 / 60.056) \times 340 = 1.956$ kJ metabolizable energy per gram protein.

(b) **Uric acid:** 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 $7 \times 85 = 595$ kJ of metabolizable energy. The oxidation of 1 mol of Kleiber's protein to uric acid results in the formation of 6.5 mol uric acid, thus the costs are $6.5 \times 595 = 3867$ 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 contains 16% 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 $(4 \times 14.007) / 168.112 = 33.3\%$ nitrogen, thus the oxidation of 1 gram 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 $(0.4835 / 168.112) \times 595 = 1.71$ 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 calculations 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 protein fat, carbohydrate and complete diets in salmonids: Comparative energetic efficiency. Journal of Nutrition, 108: 1025-1032 (see page 1026). They describe that the theoretical costs for the synthesis of 1 mol urea is 88.4 kcal (= $88.4 \times 4.184 = 369.8$ kJ) and of 1 mol uric acid is 132.6 kcal (= $132.6 \times 4.184 = 554.7$ kJ)

Cho, C.Y., Slinger, S.J. and Bayley, H.S. (1982) Bioenergetics of salmonids 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 $0.466 \times 13 = 6.058$ kJ / gram urea, and $6.065 \times 60.065 = 364$ kJ per mol urea. Further, they describe that the energy costs for uric acid are 10 kJ / gram N, thus $0.333 \times 10 = 3.33$ kJ / gram uric acid, and $3.33 \times 168.112 = 560$ kJ per mol uric acid.

Cho, C.Y. & Kaushlik, S.J. (1990) Nutritional energetics in fish: energy and protein utilization 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 that 4 ATP mols are needed for the formation of 1 mol urea. Thus $4 \times 92.47 = 369$ 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 compounds. 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 7 (Table)

Formation of ATP during the oxidation of various nutrients

	MW	Energy Generated In body		Oxygen Consumption mol O ₂ /mol substrate	Yield of ATP		Energy Costs of ATP kJ/mol ATP	Oxygen Costs of ATP		Yield of ATP per oxygen consumption		Reference
		kJ/mol	kJ/g		mol ATP/mol substrate	mol ATP/g substrate		mol O ₂ /mol ATP	Liter O ₂ /mol ATP	mol ATP/mol O ₂	mol ATP/liter O ₂	
Glucose (C ₆ H 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 ₆ H 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 ₆ H 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 ₁₀₂ O 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 ₆ H 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 ₆ H 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 ₆ H 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 ₆ H ₁₄ N ₂ O 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 ₆ H 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 ₆ H ₁₄ N ₂ O 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 ₃ H ₇ NO ₂ S)	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 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

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, volume 132, page 315-3202.

E. Ferrannini (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, pages 76 and 77.

1 mol is 22.414 liter at 0 °C and 1 bar and 1 kcal = 4.184 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). Data in the Table above indicate that the costs (kJ per mol ATP) is about 80 kJ / mol ATP. Thus the efficiency of the formation of 1 mol ATP is thus about $30.5 / 80 = 38\%$.

A reference human of 70 kg consumes per day an amount of 500 liters O₂ and produces 425 liters of CO₂ and 12 grams of N in the urine. This 12 grams of nitrogen represents the oxidation of $6.25 \times 12 = 12$ grams of proteins. Further, according to the formula of Brouwer, the energy expenditure is then (see below):

Total Energy Expenditure = 16.175 VO₂ + 5.021 VCO₂ – 5.987 N

Total Energy expenditure = $16.175 \times 500 + 5.021 \times 425 - 5.987 \times 12 = 10150$ kJ per day.

MW of ATP = 475.19 and formula of ATP is: C₁₀H₁₆O₁₁N₅P₃, see Voet and Voet, page 17

(1) The energy expenditure of a reference man of 70 kg is 10150 kJ per day and this 10150 kJ energy produces $(10150 \text{ (kJ energy expenditure per day)} / 80 \text{ (average cost of 1 mol ATP)}) \times 475.19 \text{ (MW of ATP)} / 1000 \text{ (conversion of grams into kg)} = 60.29$ kg ATP is produced per day in a human of 70 kg.

(2). Ferrannini (1988) described a turnover rate or production of 1.3 mmol / min kg or in humans or $(1.3 \text{ mmol ATP per minute}) \times 475.19 \text{ (MW of ATP)} \times 60 \text{ (minutes per hour)} \times 24 \text{ (hours per day)} \times 70 \text{ (body weight of human)} / 1,000,000 \text{ (conversion of mg to kg)} = 62.3$ kg ATP is produced per day in a human of 70 kg.

(3). Voet and Voet (1995, Biochemistry, Second Edition, John Wiley and Sons, page 433) described that the amount of ATP produced and consumed per hour is ~1.5 kg (~3 mol) or $1.5 \text{ (kg ATP per hour produced)} \times 24 \text{ (hours per day)} = 36$ kg ATP produced per day for an average person.

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 $1.2 \text{ mmol} \times 70 \text{ (body weight of a human)} \times 475.19 \text{ (MW of ATP)} = 39916$ mg ATP = 40 grams ATP in a human of 70 grams.

The life span or the residence time of ATP in the body is then $1.3 \text{ (production of mmol ATP per min per kg body weight)} / 1.2 \text{ (mmol of ATP per kg in body)} = 0.9$ minute!

Appendix 8 (Table)

Calculations on the conversion of ml O₂ and CO₂ into grams O₂ and CO₂.

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 O₂ is expressed in liters or ml. These are liters at 0 °C and 1 bar. The volume of 1 mol of gas at 0 °C (or 273.15 ° K) and 1 bar is 22.414 liters and the volume of 1 mol of gas at 25 °C (298 °K) 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 °K (0 °C) is known (22.414 liters) then the volume at 25 °C can be calculated. $PV = RT$; $1 \times 22.414 = R \times 273.15$; or $22.414 / 275 = R$ (constant), thus $22.414 / 273.15 = \text{volume} / 298$, thus volume is 24.45 liter. The Gasconstant $R = 8.314 \text{ joule / degree / mol}$.

Thus, the volume of 1 mol of O₂ or CO₂ is thus 22.413 liters bij 0 °C. 1 liter gas of each compound also contains the same number of molecules (Number of Avogadro, 6.16×10^{23} particles per mol). The MW of O₂ is 32. and MW of CO₂ is 44. Thus 1 mol O₂ is 32 grams and the volume is 22.414 liters. Thus 1 mgram O₂ is $22.414 / 32 = 0.700 \text{ ml}$

And 1 ml O₂ = $32 / 22.414 = 1.428 \text{ mg}$.

Similar calculations can be done for CO₂.

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 °C (273.15 °K).

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 9 (Table)

Overview of metabolic rates and efficiency of energy storage in various species: data from the literature

		Fasting	Fasting	Maintenance	Efficiency	Efficiency	Efficiency		
		protein loss	energy expenditure	energy expenditure	of energy	of protein	of fat		
			or heat production	or heat production	deposition	deposition	deposition		
Species	Temperature				above	above	above	Body Weight	Reference
	(°C)	a*BW(kg) ^b	a*BW(kg) ^b	a*BW(kg) ^b	maintenance	maintenance	maintenance	(grams)	
		(g/day/kg BW ^b)	(kJ/day/kg BW ^b)	(kJ/day/kg BW ^b)	(k energy)	(k protein)	(k lipid)		
Homeotherms (animals and humans)			275 BW ^{0.767}					20 g - 3,6 tons	Kleiber (1975) 1
Humans			300 BW ^{0.75} (estimated)	432 BW ^{0.75}				72 kg	van Es et al. (1984)
Human Infants, low birth weight						0,42	0,85	1- 38 days old	Roberts and Young (1988)
Human Infants, low birth weight						0,51	0,85	2200	Towers et al. (1997)
Cats				435 BW ^{0.75}				adult cats	Kendall et al. (1983)
Dogs				550 BW ^{0.75}				10 - 55 kg	Kienzle and Rainbird (1991)
Cows				400-600 BW ^{0.75}				90 - 550 kg	van Es (1980)
Pigs				443 BW ^{0.75}		0,53	0,75	20 - 120 kg	NRC (USA) (1998)
Pigs				422 BW ^{0.75}	0,58			15 - 50 kg	Nieto et al. (2002)
Pigs				418 BW ^{0.75}	0,67			20 – 30 kg	Verstegen et al. 1973
Rats (Lean Zucker)			252 BW ^{0.75}	427 BW ^{0.75}	0,59	0,44	0,74	200 and 350	Pullar and Webster (1977) 1
Rats (Obese Zucker)			149 BW ^{0.75}	237 BW ^{0.75}	0,63	0,44	0,74	200 and 350	Pullar and Webster (1977) 1

		Fasting	Fasting	Maintenance	Efficiency	Efficiency	Efficiency		
		protein loss	energy expenditure	energy expenditure	of energy	of protein	of fat		
			or heat production	or heat production	deposition	deposition	deposition		
Species	Temperature				above	above	above	Body Weight	Reference
	(°C)	a*BW(kg) ^b	a*BW(kg) ^b	a*BW(kg) ^b	maintenance	maintenance	maintenance	(grams)	
		(g/day/kg BW ^b)	(kJ/day/kg BW ^b)	(kJ/day/kg BW ^b)	(k energy)	(k protein)	(k lipid)		
Chickens	23			469 BW ^{0,75}	0,57	0,58	0,55	21 - 49 days old	Sakomura et al. (2005)
Turkeys			449 BW 0,75	641 BW ^{0,75}		0,65	1,00	0,5 - 14 kg	Rivera-Torres et al. (2010)
Atlantic Salmon (<i>Salmo salar</i>)	8,5			19,6 ^{0,80}		0,52	0,80	456, initial	Azevedo et al. (2005)
Brown Trout (<i>Salmo Trutta L.</i>)	19,5		28,4 BW ^{0,6863}					10 - 250	Elliott (1976) 1
Brown Trout (<i>Salmo Trutta L.</i>)	15,0		23,2 BW ^{0,7677}					10 - 250	Elliott (1976) 1
Brown Trout (<i>Salmo Trutta L.</i>)	12,8		17,57 BW ^{0,7360}					10 - 250	Elliott (1976) 1
Brown Trout (<i>Salmo Trutta L.</i>)	9,5		12,88 BW ^{0,7399}					10 - 250	Elliott (1976) 1
Brown Trout (<i>Salmo Trutta L.</i>)	5,6		7,62 BW ^{0,7134}					10 - 250	Elliott (1976) 1
Brown Trout (<i>Salmo Trutta L.</i>)	5,6 - 19,5		4,91 * e ^{0,0959*T} * BW ^{0,729}					10 - 250	Elliot (1976) 1
Trout (<i>Oncorhynchus mykiss</i>)	15		30,8 BW ^{0,76}					1 - 57	Smith et al. (1975) 1
Trout (<i>Oncorhynchus mykiss</i>)	15		33,8 BW ^{0,80}	48,1 BW ^{0,80}				65 - 100	Huisman (1976)
Trout (<i>Oncorhynchus mykiss</i>)	15		33,3 BW ^{0,80}	42,7 BW ^{0,80}	0,78			65 - 100	Huisman (1976) 1
Trout (<i>Oncorhynchus mykiss</i>)	18		32,1 - 43,2 BW ^{0,824}	47,9 - 60,3 BW ^{0,824}				about 150	Kaushik and Gomes (1988) 1
Trout (<i>Oncorhynchus mykiss</i>)	15		36,6 BW ^{0,824}					not given	Cho and Bureau (1998)

		Fasting	Fasting	Maintenance	Efficiency	Efficiency	Efficiency		
		protein loss	energy expenditure	energy expenditure	of energy	of protein	of fat		
			or heat production	or heat production	deposition	deposition	deposition		
Species	Temperature				above	above	above	Body Weight	Reference
	(°C)	a*BW(kg) ^b	a*BW(kg) ^b	a*BW(kg) ^b	maintenance	maintenance	maintenance	(grams)	
		(g/day/kg BW ^b)	(kJ/day/kg BW ^b)	(kJ/day/kg BW ^b)	(k energy)	(k protein)	(k lipid)		
Trout (<i>Oncorhynchus mykiss</i>)	6, 9, 12, 15				0,61			13,3, initial	Azevedo et al. (1998)
Trout (<i>Oncorhynchus mykiss</i>)	15		23,75 BW ^{0,80}	34,96 BW ^{0,80}	0,68	0,54	0,90	14 - 383	Rodehutsord and Pfeffer (1999) 1
Trout (<i>Oncorhynchus mykiss</i>)	8,5			19,6 BW ^{0,80}		0,43	0,81	268, initial	Azevedo et al. (2005)
Trout (<i>Oncorhynchus mykiss</i> Walbaum)	8,5			19,2 BW ^{0,824}	0,63	0,63	0,72	150 - 600	Bureau et al. (2006)
Trout (<i>Oncorhynchus mykiss</i>)	15,6		33,1 BW ^{0,80}	48,3 BW ^{0,80}	0,69			about 55 - 160	Glencross (2009)
Trout (<i>Oncorhynchus mykiss</i>)	15,6		27,7 BW ^{0,80}	44,3 BW ^{0,80}	0,62			about 55 - 160	Glencross (2009)
Carp (<i>Cyprinus Carpio L.</i>)	23		48,4 BW ^{0,811}					2 - 950	Huisman (1974) 1
Carp (<i>Cyprinus Carpio L.</i>)	23		46,3 BW ^{0,80}	66,0 BW ^{0,80}				about 35 - 90	Huisman (1976)
Carp (<i>Cyprinus Carpio L.</i>)	23		50,7 BW ^{0,80}	58,9 BW ^{0,80}	0,86			about 35 - 90	Huisman (1976) 1
Grass Carp (<i>Ctenopharyngodon Idella, Val.</i>)	27		38,3 BW ^{0,80}					about 50 - 125	Huisman and Valentijn (1981)
Grass Carp (<i>Ctenopharyngodon Idella, Val.</i>)	27		37,8 BW ^{0,80}	51,0 BW ^{0,80}	0,74			about 50 - 125	Huisman and Valentijn (1981) 1
Carp (<i>Cyprinus carpio L.</i>)	25		25 BW ^{0,816}					0,86 - 2,14	Cui and Liu (1990)
Carp (<i>Cyprinus carpio L.</i>)	23			42,0 BW ^{0,75}	0,60-0,80	0,53	0,75		Schwarz and Kirchgessner (1984, 1995)
Carp (<i>Cyprinus carpio L.</i>)				51,0 BW ^{0,80}					Meyer-Burgdorff et al. (1989a)
Gold fish (<i>Carassius auratus</i>)	22		33,3 BW ^{0,85}					6,2	Van Waversfeld et al. (1989)

		Fasting	Fasting	Maintenance	Efficiency	Efficiency	Efficiency		
		protein loss	energy expenditure	energy expenditure	of energy	of protein	of fat		
			or heat production	or heat production	deposition	deposition	deposition		
Species	Temperature				above	above	above	Body Weight	Reference
	(°C)	a*BW(kg) ^b	a*BW(kg) ^b	a*BW(kg) ^b	maintenance	maintenance	maintenance	(grams)	
		(g/day/kg BW ^b)	(kJ/day/kg BW ^b)	(kJ/day/kg BW ^b)	(k energy)	(k protein)	(k lipid)		
Gold fish (<i>Carassius auratus</i>)	20		16,8 BW ^{0,85}					8,9	Van Waversfeld et al. (1989)
Gold fish (<i>Carassius auratus</i>)	25		41,3 BW ^{0,906}					0,86 - 2,14	Cui and Liu (1990)
Tilapia (<i>Rendalli bouenger</i>)	23		26,9 BW ^{0,80}					40 - 60	Caulton (1978) 1
Tilapia (<i>Oreochromis mossambicus</i>)	25		68,7 BW ^{0,928}					0,86 - 2,14	Cui and Liu (1990)
Tilapia (<i>Oreochromis niloticus</i>)	22	0,19 BW ^{0,70}	25,88 BW ^{0,80}	43,13 BW ^{0,80}	0,60			not given	Lupatsch (2008)
Tilapia (<i>Oreochromis niloticus</i>)	24	0,21 BW ^{0,70}	28,81 BW ^{0,80}	48,02 BW ^{0,80}	0,60			not given	Lupatsch (2008)
Tilapia (<i>Oreochromis niloticus</i>)	26	0,29 BW ^{0,70}	33,25 BW ^{0,80}	53,63 BW ^{0,80}	0,62			not given	Lupatsch (2008)
Tilapia (<i>Oreochromis niloticus</i>)	29	0,36 BW ^{0,70}	41,60 BW ^{0,80}	66,03 BW ^{0,80}	0,63			not given	Lupatsch (2008)
Tilapia (<i>Oreochromis niloticus</i>)	22 - 29	0,0221*e ^(0,09676*T) * BW ^{0,70}	5,65*e ^(0,06856*T) * BW ^{0,80}	11,05*e ^(0,0613*T) * BW ^{0,80}				not given	Lupatsch (2008) 1
Red Tilapia	20,9		26,77 BW ^{0,80}					15 - and 80	Hepner et al. (1983) 1
Red Tilapia	24,3		38,66 BW ^{0,80}					18 and 58	Hepner et al. (1983) 1
Tilapia (<i>Oreochromis niloticus</i>)	26	0,27 BW ^{0,70}	25,2 BW ^{0,80}	57 BW ^{0,80}	0,67			about 7 - 26	Meyer-Burgdorff et al. (1989)
Tilapia (<i>Oreochromis mossambica</i>)	25		39,18 BW ^{0,7183}					5 - 80	Job (1969) 1
Gilthead seabream (<i>Sparus aurata L.</i>)	23		29,87 BW ^{0,80}	45,95 BW ^{0,80}	0,65	0,53	0,76	30 - 160	Lupatsch et al. (2003)
Gilthead seabream (<i>Sparus aurata L.</i>)	23	0,33 BW ^{0,70}	33,65 BW ^{0,80}	61,74 BW ^{0,80}	0,54	0,34		about 17 - 110	Lupatsch et al. (1998)
European seabass (<i>Dicentrarchus labrax</i>)	23		30,29 BW ^{0,80}	44,54 BW ^{0,80}	0,68	0,53	0,90	15 - 140	Lupatsch et al. (2003)
European seabass (<i>Dicentrarchus labrax</i>)	23	0,39 BW ^{0,70}	33,70 BW ^{0,80}	43,6 BW ^{0,80}	0,68	0,52		about 10 - 170	Lupatsch et al.(2001)
White grouper (<i>Epinephelus aeneus</i>)	23		22,91 BW ^{0,80}	33,20 BW ^{0,80}	0,69	0,56	0,90	10 - 350	Lupatsch et al. (2003)

		Fasting	Fasting	Maintenance	Efficiency	Efficiency	Efficiency		
		protein loss	energy expenditure	energy expenditure	of energy	of protein	of fat		
			or heat production	or heat production	deposition	deposition	deposition		
Species	Temperature				above	above	above	Body Weight	Reference
	(°C)	a*BW(kg) ^b	a*BW(kg) ^b	a*BW(kg) ^b	maintenance	maintenance	maintenance	(grams)	
		(g/day/kg BW ^b)	(kJ/day/kg BW ^b)	(kJ/day/kg BW ^b)	(k energy)	(k protein)	(k lipid)		
White grouper (<i>Epinephelus aeneus</i>)	22	0,12 BW ^{0,70}	20,5 BW ^{0,80}	32,53 BW ^{0,80}	0,64			about 12 - 50	Lupatsch and Kissil (2005)
White grouper (<i>Epinephelus aeneus</i>)	24	0,19 BW ^{0,70}	26,0 BW ^{0,80}	40,70 BW ^{0,80}	0,65			about 90 - 170	Lupatsch and Kissil (2005)
White grouper (<i>Epinephelus aeneus</i>)	27	0,30 BW ^{0,70}	34,2 BW ^{0,80}	50,29 BW ^{0,80}	0,68			about 20 - 50	Lupatsch and Kissil (2005)
White grouper (<i>Epinephelus aeneus</i>)	22 - 27	0,00233*e ^(0,18081*T) *BW ^{0,70}	2,22*e ^(0,10149*T) *BW ^{0,80}	4,99*e ^(0,0860*T) *BW ^{0,80}				about 12 - 170	Lupatsch and Kissil (2005) 1
African Catfish (<i>Clarias gariepinus</i>)	30		39,26 BW ^{0,80}	47,20 BW ^{0,80}	0,83			about 1 - 300	Machiels and Henken (1986) 1
African Catfish (<i>Clarias gariepinus</i>)	25		22,04 BW ^{0,80}	27,58 BW ^{0,80}	0,80			about 1 - 222	Machiels and Henken (1986) 1
African Catfish (<i>Clarias gariepinus</i>)	20		19,91 BW ^{0,80}	23,48 BW ^{0,80}	0,85			about 1 - 100	Machiels and Henken (1986) 1
Atlantic Menhaden (<i>Brevoortia tyrannus</i>)	10		18,33 BW ^{0,7822}					6 - 78	Hettler (1976) 1
Atlantic Menhaden (<i>Brevoortia tyrannus</i>)	15		32,64 BW ^{0,7973}					6 - 79	Hettler (1976) 1
Atlantic Menhaden (<i>Brevoortia tyrannus</i>)	20		35,03 BW ^{0,7235}					5 - 74	Hettler (1976) 1
Atlantic Menhaden (<i>Brevoortia tyrannus</i>)	25		60,45 BW ^{0,8162}					7 - 81	Hettler (1976) 1
Atlantic Menhaden (<i>Brevoortia tyrannus</i>)	10 - 25		9,35 *e ^{0,0730*T} * BW ^{0,7798}					6 - 81	Hettler (1976) 1
Barramundi, Asean seabass	21		15,24 BW ^{0,82}	22,08 BW ^{0,82}	0,69			20 and 80, initial	Lupatsch (2003)
Barramundi, Asean seabass	27		30,45 BW ^{0,82}	44,78 BW ^{0,82}	0,68			20 and 80, initial	Lupatsch (2003)
Sturgeon (<i>Acipenser transmontanus</i>)	18		30,78 BW ^{0,66}					1940	Ruer et al. (1987) 1
Sturgeon (<i>Acipenser transmontanus</i>)	15		26,71 - 29,13 BW ^{0,80}					950	Burggren and Randall (1978) 1
Grey Mullet	27	0,35 BW ^{0,70}	43,5 BW ^{0,80}	76,3 BW ^{0,80}	0,57			300, initial	Lupatsch (2007)

1. Data recalculated.

Appendix 10 (Text)

Oxidation equations of various compounds. Values are expressed in mols.

Carbohydrates:

Glucose, MW = 180.16 (Elia and Livesey 1992 (page 76 and 104)

$C_6H_{12}O_6 + 6 O_2 (= 22.414 \times 6 = 134.48 \text{ liters}) = 6 CO_2 (134.48 \text{ liters}) + 6 H_2O (= 6 \times 18.015 \text{ (MW water)}) = 108.09 \text{ grams}) + 2803 \text{ kJ / mol} (= 15.56 \text{ kJ per gram}) + 36.7 \text{ mol ATP} (76.4 \text{ kJ / mol ATP}). RQ = 6/6 = 1.00$

Thus the oxidation of 1 gram of glucose requires $(134.48 / 180.16) = 0.746$ liters of O_2 and produces 0.746 liters of CO_2 and $(108.09 / 180.16) = 0.600$ grams water.

Carbohydrate (glucan), MW = 162.1 (Elia and Livesey 1992 (page 71 and 104)

$[C_6H_{10}O_5]_n + 6 O_2 (= 22.414 \times 6 = 134.48 \text{ liters}) = 6 CO_2 (= 22.414 \times 6 = 134.48 \text{ liters}) + 5 H_2O (5 \times 18.015 = 90.075 \text{ grams}) + 2840 \text{ kJ / mol} (= 17.52 \text{ kJ per gram}) + 36.7 \text{ mol ATP} (77.4 \text{ kJ / mol ATP}). RQ = 6/6 = 1.00$

Thus, the oxidation of 1 grams of glucan requires $(134.48 / 162.1) = 0.830$ liters of O_2 and produces 0.830 liters of CO_2 and $(90.075 / 162.1) = 0.556$ gram water.

Alcohol, MW = 46.1 (Elia and Livesey 1992 (page 71)

$C_2H_5OH + 3 O_2 (= 22.414 \times 3 = 67.24 \text{ liters}) = 2 CO_2 (= 22.414 \times 2 = 44.83 \text{ liters}) + 3 H_2O (= 3 \times 18.015 = 54.05 \text{ grams}) + 1367 \text{ kJ / mol} (= 29.65 \text{ kJ per gram}). RQ = 2/3 = 0.667$

Thus, the oxidation of 1 grams of alcohol requires $(67.24 / 46.1) = 1.46$ liters of O_2 and produces $(44.83 / 46.1) = 0.97$ liters of CO_2 and $(54.05 / 46.1) = 1.17$ grams of water.

Fats:

Palmitic acid, MW = 256.429 (Jéquier et al. 1987 (page 200)

$C_{16}H_{32}O_2 + 23 O_2 (= 22.414 \times 23 = 515.52 \text{ liters}) = 16 CO_2 (= 22.414 \times 16 = 525.52 \text{ liters}) + 16 H_2O (= 16 \times 18.015 \text{ (MW water)}) = 288.24 \text{ grams of water}) + 10033 \text{ kJ} + 129 \text{ ATP} (77.78 \text{ kJ / mol ATP}). RQ = 16/23 = 0.696.$

Thus, the oxidation of 1 grams of palmitate requires $515.52 / 256.429 = 2.01$ liters O_2 and produces $525.52 / 256.429 = 2.05$ liters CO_2 and $288.24 / 256.429 = 1.12$ grams of water.

Dioleoylpalmitate, MW = 859.42 (Elia and Livesey 1992 (page 71 and 104)

$C_{55}H_{102}O_6 + 77.5 O_2 (= 22.414 \times 77.5 = 1737.09 \text{ liters}) = 55 CO_2 (= 22.414 \times 55 = 1232.77 \text{ liters}) + 51 H_2O (= 51 \times 18.015 \text{ (MW water)}) = 918.77 \text{ grams of water}) + 34022 \text{ kJ / mol} (= 39.59 \text{ kJ per gram}) + 429.4 \text{ mol ATP} (79.2 \text{ kJ / mol ATP}). RQ = 55/77.5 = 0.710$

Thus, the oxidation of 1 gram of dioleoylpalmitate requires $1737.09 / 859.42 = 2.02$ liters O_2 and produces $1232.77 / 859.42 = 1.434$ liters of CO_2 and $(918.77 / 859.42) = 1.07$ grams of water.

Tripalmitate, MW = 807.34 (Van Milgen 2002)

$C_{51}H_{98}O_6 + 72.5 O_2 (= 22.414 \times 72.5 = 1625.02 \text{ liters}) = 51 CO_2 (= 22.414 \times 51 = 1143.11 \text{ liters}) + 49 H_2O (49 \times 18.015 = 882.74 \text{ grams}) + 31809 \text{ kJ / mol} (= 39.40 \text{ kJ per gram}) + 409 \text{ mol ATP} (77.8 \text{ kJ / mol ATP}). RQ = 51/72.5 = 0.703$

Thus, the oxidation of 1 gram of tripalmitate requires $1625.02 / 807.34 = 2.013$ liters O_2 and produces $1143.11 / 807.34 = 1.416$ liters CO_2 and $882.74 / 807.34 = 1.09$ grams of water.

Trioleate, MW = 885.45 (Schulz, 1975)

$C_{57}H_{104}O_6 + 80 O_2 (= 22.414 \times 80 = 1793.12 \text{ liters}) = 57 CO_2 (= 22.414 \times 57 = 1277.60 \text{ liters}) + 52 H_2O (52 \times 18.015 = 936.78 \text{ grams}) + 35197 \text{ kJ / mol} (= 39.75 \text{ kJ per gram}) + 452.3 \text{ mol ATP} (77.8 \text{ kJ / mol ATP}). RQ = 57/80 = 0.713$

Thus, the oxidation of 1 gram of trioleate requires $1793.12 / 885.45 = 2.025$ liters O_2 and produces $1277.60 / 885.45 = 1.443$ liters CO_2 and $936.78 / 885.45 = 1.06$ grams of water.

Proteins

The heat of complete combustion of 1 gram of Kleiber's standard protein in the bomb calorimeter is 23.65 kJ/g (gross energy). MW is 2260

The equation of the complete combustion is: $C_{100}H_{159}N_{26}O_{32}S_{0.7} + 124.8 O_2 = 100 CO_2 + 78.8 H_2O + 13 N_2 + 0.7 H_2SO_4 + 53448 \text{ kJ} (23.65 \text{ kJ per gram protein})$

Kleiber's standard protein (MW = 2260) to a mixture of urea, ammonia and creatinine (95:5:5) (Elia and Livesey 1992 (page 71 and 104))

$C_{100}H_{159}N_{26}O_{32}S_{0.7} + 104 O_2 (= 22.414 \times 104 = 2331.06 \text{ liters}) = 86.6 CO_2 (= 22.414 \times 86.6 = 1941.05 \text{ liters}) + 50.6 H_2O (= 50.6 \times 18.015 \text{ (MW water)} = 911.56 \text{ grams}) + 11.7 N_2H_4CO \text{ (urea)} + 1.3 NH_4OH \text{ (ammonia)} + 0.43 N_3C_4H_7O \text{ (creatinine)} + 0.7 H_2SO_4 + 45376 \text{ kJ / mol} (= 17.52 \text{ kJ per gram}) + 522.2 \text{ mol ATP} (= 86.9 \text{ kJ / mol ATP}). RQ = 86.6/104 = 0.833$

Thus the oxidation of 1 gram of protein requires $2331.06 / 2260 = 1.031$ liters O_2 and produces $1941.05 / 2260 = 0.859$ liters CO_2 and $(911.56 / 2260) = 0.403$ grams water.

Kleiber's standard protein (MW = 2260) to urea (Elia and Livesey 1992 (page 78))

$C_{100}H_{159}N_{26}O_{32}S_{0.7} + 105.3 O_2 (= 22.414 \times 105.3 = 2360.19 \text{ liters}) = 87 CO_2 (22.414 \times 87 = 195.00 \text{ liters}) + 52.8 H_2O (52.8 \times 18.015 = 951.19 \text{ grams}) + 13 N_2H_4CO \text{ (urea)} + 0.7 H_2SO_4 + 45950 \text{ kJ / mol} (= 20.33 \text{ kJ per gram}) RQ = 87/105.3 = 0.826$

Kleiber's standard protein (MW = 2260) to ammonia (Elia and Livesey 1992 (page 78))

$C_{100}H_{159}N_{26}O_{32}S_{0.7} + 105.3 O_2 = 100 CO_2 + 13.8 H_2O + 26 NH_4OH \text{ (ammonia)} + 0.7 H_2SO_4 + 46450 \text{ kJ / mol} (= 20.55 \text{ kJ per gram}). RQ = 100/105.3 = 0.950$

Kleiber's standard protein (MW = 2260) to uric acid (Elia and Livesey 1992 (page 78))

$C_{100}H_{159}N_{26}O_{32}S_{0.7} + 95.5 O_2 = 67.5 CO_2 + 65 H_2O + 6.5 C_5H_4O_3N_4 \text{ (uric acid)} + 0.7 H_2SO_4 + 41880 \text{ kJ / mol} (= 18.53 \text{ kJ per gram}). RQ = 67.5/95.5 = 0.707$

Kleiber's standard protein (MW = 2260) to creatinine (Elia and Livesey 1992 (page 78))

$C_{100}H_{159}N_{26}O_{32}S_{0.7} + 79.3 O_2 = 65.332 CO_2 + 48.466 H_2O + 8.667 N_3C_4H_7O \text{ (creatinine)} + 0.7 H_2SO_4 + 33960 \text{ kJ / mol} (= 15.03 \text{ kJ per gram}). RQ = 65.332/79.3 = 0.824$

Kleiber's standard protein (MW = 2260) to creatine (own calculation)

$C_{100}H_{159}N_{26}O_{32}S_{0.7} + 79.288 O_2 = 65.332 CO_2 + 39.779 H_2O + 8.667 N_3C_4H_9O_2 \text{ (creatine)} + 0.7 H_2SO_4 + 33380 \text{ kJ / mol} (= 14.74 \text{ kJ per gram}). RQ = 65.332/79.288 = 0.824$
See footnote 6e of Table 3.

Kleiber's standard protein (MW = 2260) to allantoin (Elia and Livesey 1992 (page 78))

$C_{100}H_{159}N_{26}O_{32}S_{0.7} + 98.8 O_2 = 74 CO_2 + 59.3 H_2O + 6.5 C_4H_6O_3N_4 \text{ (allantoin)} + 0.7 H_2SO_4 + 43254 \text{ kJ / mol} (= 19.13 \text{ kJ per gram}). RQ = 74/98.8 = 0.749$

Lysine (MW = 146.19) to urea (own calculations and Blaxter 1989, page 77)

$C_6H_{14}N_2O_2 + 7 O_2 = 5 CO_2 + 5 H_2O + 1 CON_2H_4$ (urea) + 3037 kJ / mol + 36 mol ATP (= 84.4 kJ / mol ATP). RQ = 5/7 = 0.7143

Cysteine (MW = 121.16) to urea (own calculations and Blaxter 1989, page 77)

$C_3H_7NO_2S + 4.5 O_2 = 2.5 CO_2 + 1.5 H_2O + 0.5 CON_2H_4$ (urea) + 1 H_2SO_4 + 1938 kJ / mol + 12.5 mol ATP (= 155.0 kJ / mol ATP). RQ = 2.5/4.5 = 0.5556

Alanine (MW = 89.09) to urea (see Blaxter 1989 page 12 and 77)

$C_3H_7NO_2 + 3 O_2$ (22.414 * 3 = 67.24 liters) = 2.5 CO_2 (22.414 * 2.5 = 56.04 liters) + 2.5 H_2O + 0.5 CON_2H_4 (urea, 0.5 * 28 = 14 grams N) + 1296 kJ + 15.5 ATP (= 1296 / 15.5 = 83.6 kJ / mol ATP)

or:

The complete combustion of alanine is:

(1) $C_3H_7NO_2 + 3.75 O_2 = 3 CO_2 + 3.5 H_2O + 0.5 N_2 + 1620$ kJ

(2) $0.5 CON_2H_4$ (urea) + $0.75 O_2 = 0.5 CO_2 + H_2O + 0.5 N_2 + 0.5 * 647$ kJ (complete combustion of urea)

Subtract (2) from (1): (compare McLean and Tobin 1987, page 33, and Blaxter 1989, page 12, law of Hess, law of constant heat summation).

$C_3H_7NO_2 + 3 O_2$ (22.414 * 3 = 67.24 liters) = 2.5 CO_2 (22.414 * 2.5 = 56.04 liters) + 2.5 H_2O + 0.5 CON_2H_4 (urea, 0.5 * 28 = 14 grams N) + 1296 kJ.

As indicated by Blaxter (Blaxter 1989, page 16) the energy loss or release of the reaction can also be calculated with the formula of Brouwer (Appendix 12). Blaxter (1989) calculated the factors for the Brouwer formula, when only glucose, palmitic acid and alanine are metabolized. The factors for the Brouwer formula are then (Blaxter 1989, page 13):

Heat production = 16.34 * O_2 (liters) + 4.5 * CO_2 (liters) – 3.292 N (grams) or

Heat production = 16.34 * 67.24 (liters O_2) + 4.5 * 56.03 (liters CO_2) – 3.292 * 14 (grams N) = 1304 kJ (is comparable to 1296 kJ above).

Appendix 11 (Text)

Synthesis of fat and glycogen from glucose. Values are expressed in mols.

After a meal, nutrients are temporarily stored to ensure a supply between meals. Glucose can be converted into fat, e.g. into palmitic acid and tripalmitate or glycogen. We will give an example of these conversions and calculate the losses of energy and ATP when glucose is temporarily stored as glycogen or tripalmitate.

We will use the following energy and ATP values for the various compounds (see Blaxter 1989 page 70 and 76):

1 mol palmitate generates 10039 kJ energy or 129 mol ATP ($10039 / 129 = 77.8$ kJ per mol ATP).

1 mol glycerol generates 1653 kJ energy or 21 mol ATP ($1653 / 21 = 78.0$ kJ/mol ATP).

1 mol glucose generates 2803 kJ energy or 35.5 mol ATP ($2803 / 35.5 = 79.0$ kJ per mol ATP).

1 mol tripalmitate generates ~31772 kJ energy or 407 mol ATP ($31772 / 407 = 78.0$ kJ per mol).

Calculation of the energy of 1 mol tripalmitate:

3 mol palmitic acid generates $3 * 3 * 10039 = 30117$ kJ energy

1 mol glycerol generates 1655 kJ energy

Total energy = $1655 + 30117 = 31772$ kJ

Glucose is converted into palmitic acid.

The biochemical pathway is (see page 80, Blaxter 1989):

$4.5 \text{ glucose} + 4 \text{ O}_2$ ($22.414 * 4 = 89.66$ liters) + $5 \text{ (ADP+Pi)} \rightarrow 1 \text{ palmitic acid} + 11 \text{ CO}_2$ ($22.414 * 11 = 246.55$ liters) + 5 ATP . The respiration quotient = $246.55 / 89.66 = 2.75$

MW $\text{O}_2 = 32$; MW $\text{CO}_2 = 44$; 1 gram $\text{O}_2 = 0.700$ liter O_2 ; 1 gram $\text{CO}_2 = 0.509$ liters CO_2 ; 1 mol = 22.414 liters.

In terms of energy

When we take only into account the starting (glucose) and end (palmitate) product:

4.5 mol glucose generates $4.5 * 2803 = 12614$ kJ and 1 mol palmitate generates 10039 kJ, thus the loss is ($12614 - 10039$) = 2575 kJ or the loss is $2575 / 12614 = 20.4\%$

As indicated by Blaxter (Blaxter 1989, page 16) the energy loss or release of the reaction can also be calculated with the formula of Brouwer (Appendix 12). Blaxter calculated the factors for the Brouwer formula, when only glucose, palmitic acid and alanine are metabolized. The factors for the Brouwer formula are then (Blaxter 1989, page 13):

$$\begin{aligned} \text{Heat production} &= 16.34 * \text{O}_2 \text{ (liters)} + 4.5 * \text{CO}_2 \text{ (liters)} - 3.292 \text{ N (grams)} \text{ or} \\ \text{Heat production} &= 16.34 * 89.66 \text{ (liters O}_2\text{)} + 4.5 * 246.55 \text{ (liters CO}_2\text{)} - 3.292 * 0 \text{ (grams)} = 2575 \text{ kJ} \end{aligned}$$

However, when we also take into account the 5 mol ATP that are generated:

4.5 mol glucose generates $4.5 * 2803 = 12614$ kJ energy and 1 mol palmitate generates 10039 energy and the energy used to produce 5 mol ATP = $(5/35.5) * 2803 = 394.8$ kJ (1mol glucose generates 2803 kJ or 35.5. mol ATP), thus:

12614 kJ (from glucose) results in ($10039 + 394.8 = 10433.8$ kJ)

The loss is $12614 - 10433.8 = 2180$ kJ or the loss is $2180/12614 = 17.3\%$

In terms of ATP:

4.5 mol glucose generates $4.5 * 35.5 \text{ ATP} = 159.75 \text{ ATP}$ and 1 mol palmitic acid generates 129 ATP (see Blaxter 1989, pg 76) and the yield of the reaction is 5 ATP, thus a yield of a total of $129 + 5 = 134 \text{ ATP}$.

The loss is $159.75 - 134 = 25.75 \text{ ATP}$ or the loss is $25.75/159.75 = 16.1\%$

The small difference in yield between the calculations in terms of energy and in terms of ATP is explained by the fact that the costs for the formation of ATP by means of palmitate are 78 kJ per mol ATP and by means of glucose are 79 kJ per mol ATP.

Glucose is converted into tripalmitic acid.

The biochemical pathway is (see page 80, Blaxter 1989):

14 glucose + 12 O₂ (22.414 * 12 = 268.97 liters) + 11 (ADP+Pi) → 1 tripalmitate + 33 CO₂ (22.414 * 33 = 739.66 liters) + 11 ATP (in mols). The respiration quotient = 739.66 / 268.97 = 2.75.

MW O₂ = 32 ; MW CO₂ = 44; 1 gram O₂ = 0.700 liter O₂; 1 gram CO₂ = 0.509 liters CO₂ 1 mol = 22.414 liters.

In terms of energy:

When we take only into account the starting (glucose) and end (tripalmitate) product:

14 mol glucose generates 14 * 2803 = 39242 kJ and 1 mol tripalmitate generates 31772 kJ, thus the loss is (39242 – 31772) = 7470 kJ or the loss is 7470 / 39242 = 19.0%

However, when we also take into account the 11 mol ATP that are generated:

14 mol glucose generates 14 * 2803 = 39242 kJ energy and 1 tripalmitate generates 31772 kJ energy and the energy used to produce 11 mol ATP = (11/35.5) * 2803 = 868.5 kJ (1 mol glucose generates 2803 kJ or 35.5 mol ATP), thus

39242 kJ (from glucose) results in (31772 + 868.5 = 32640.5 kJ).

The loss is 39242 – 32640.5 = 6601.5 kJ or the loss is 6601.5/39242 = 16.8%.

In terms of ATP:

14 mol glucose generates 14 * 35.5 ATP = 497 ATP and 1 mol tripalmitate acid generates 407 ATP and the yield of the reaction is 11 ATP, thus a yield of a total of 407 + 11 = 418 ATP..

The loss is 497 – 418 = 79 ATP or the loss is 79/497 = 15.9%.

The small difference in yield between the calculations in terms of energy and in terms of ATP is explained by the fact that the costs for the formation of ATP by means of tripalmitate are 78 kJ per mol ATP and by means of glucose are 79 kJ per mol ATP.

Further (see also van Milgen 2002, page 3201):

A mol glucose (2803 kJ/mol) has a yield of 35.5 ATP, thus the costs per mol ATP are (2803 / 35.5) = 78.96 kJ per mol ATP. A mol tripalmitate (31772 kJ / mol) has a yield of 407 ATP and the reaction also has a yield of 11 ATP, thus, the total yield is 407 + 11 = 418 ATP. Thus, the conversion of 14 mol glucose into 1 mol tripalmitate requires 14 mol glucose and yields 418 ATP and the costs per mol ATP are then (14 * 2803) / 418 = 93.89 kJ / mol ATP. Thus, the loss is: (93.96 – 78.96) / 93.96 = 15.9 %

Glucose is converted into glycogen.

(see Blaxter 1989 page 78 and 273, and van Milgen 2002 page 3201)

For the synthesis of glycogen, an average of 2.1 mol ATP is used for the coupling of 1 mol glucose. Neither of these 2.1 mol ATP are recovered when glycogen is hydrolysed. The loss in terms of ATP is thus 2.1 / 35.5 = 0.059 or 6%. Therefore, it is more efficient to store temporarily glucose in the form of glycogen than in the form of tripalmitate. (see also van Milgen 2002, page 3201)

These calculations indicate that it is more efficient to store glucose in the form of glycogen than in the form of tripalmitate. The less efficient storage of glucose in the form of lipid is, however, the price to store energy in a very dense form.

Synthesis of fat from other constituents.

Fat can also be synthesized from proteins and other compounds such as volatile fatty acids. Efficiencies of these various conversions are given for example by Green and Whitmore (2003, page 121), Millward (1976, page 344) and Reeds (1982, page 155) and Blaxter 1989, page 273.

The energy flow and the conversion routes of various nutrients is given in the diagram of Chwalibog (2005) below.

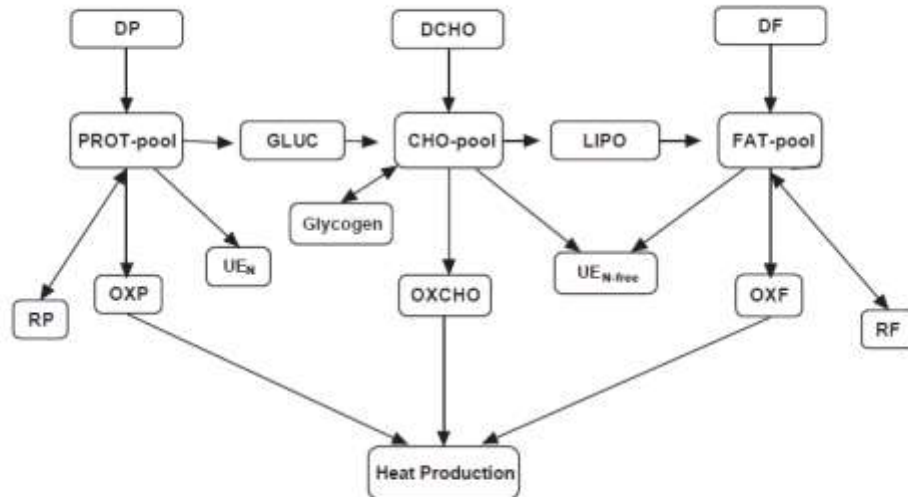


Fig. 1. Model of energy flow. DP: digested protein, RP: retained or mobilized protein, OXp: oxidized protein, UE_N: urinary energy from nitrogenous components, GLUC: energy transferred from protein to carbohydrate pool, DCHO: digested carbohydrate, Glycogen: carbohydrate retained or mobilized, OXCHO: oxidized carbohydrate, UE_{N-free}: urinary energy from nitrogen-free components, LIPO: energy transferred from carbohydrate to fat pool, DF: digested fat, OXF: oxidized fat, RF: retained or mobilized fat, HE: total heat production.

and in the diagram of Ferrannini (1988)

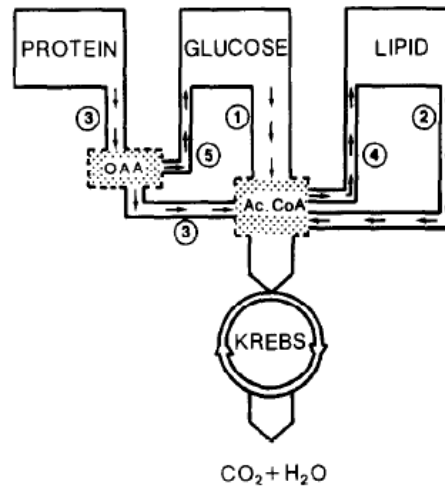


Fig 4. A simple scheme of glucose oxidation (1), lipid oxidation (2), protein oxidation (3), lipid synthesis (4), and gluconeogenesis from protein sources (5). OAA, oxaloacetic acid; Ac.CoA, -acetyl-CoA.

Appendix 12 (Text)

Derivation of the Formulae for the Calculations of Energy Expenditure by indirect Calorimetry (O₂ consumption and CO₂ production)

The Formula of Brouwer

The nutrients carbohydrates, fats and proteins are oxidized in the body and during this oxidation, oxygen (O₂) is consumed and carbondioxide (CO₂) is produced. The body can not completely oxidize the proteins and the nitrogen in the proteins is excreted into the urine in the form of energy rich compounds, such as ammonia, urea, uric acid, creatinine and creatine. In humans, most of the nitrogen is excreted in the form of urea, in birds in the form of uric acid and in fish in the form of ammonia. Formulae have been derived to calculate the energy expenditure from the amount of oxygen consumed, carbondioxide generated (gaseous exchange) and the amount of nitrogen excreted into the urine (see e.g. Ferrannini (1988, page 289 and 290) and Elia and Livesey (1992, page 94 and 95). For these calculations, we need the amount of energy that is released during the oxidation and the amount of oxygen consumed and CO₂ produced when carbohydrates, fats and proteins are oxidized. An overview of these data is given in the tabel below (see Appendix 3). These values were reported by Brouwer (1965).

	kJ/gram in body	liter O ₂ consumed per gram	liter CO ₂ produced per gram	kJ per liter O ₂	kJ per gram O ₂	RQ CO ₂ /O ₂
Carbohydrates	17,57	0,829	0,829	21,20	14,48	1,000
Fats	39,75	2,013	1,431	19,75	13,83	0,711
Proteins	18,41	0,957	0,774	19,24	13,48	0,809

Data from Brouwer (1965) as reviewed in J.A. McLean and G. Tobin (1987) Animal and Human Calorimetry Cambridge University Press. (pages 40, 41, 42, and 303).

We will use the values given in the Table above (values of Brouwer, 1965) for the derivation of the Formula of Brouwer. Slightly different values are given in the Appendices 1 (Values of Atwater) and 4 (values of Elia and Livesey)

Method of the derivation of the formula as described by Ferrannini (1988)

The procedure as described below for the derivation of the formulae to calculate the energy expenditure from the amount of consumed oxygen and amount of produced carbondioxide and the amount of nitrogen collected in the urine are essential as described by Ferrannini (1988).

The equations for the oxidation of carbohydrates, fat and proteins are according to Brouwer:

1 gram carbohydrate requires 0.829 liters O₂ and produces 0.829 liters CO₂ and 17.57 kJ and water.

1 gram fat + 2.013 liters of O₂ and produces 1.431 liters of CO₂ and 39.75 kJ and water.

1 grams of protein requires 0.957 liters of O₂ and produces 0.774 liters CO₂ and 18.41 kJ and water.

Proteins contain 16% nitrogen, thus when the proteins are expressed in terms of nitrogen:

1 grams of nitrogen requires (100/16) = 6.25 x 0.957 = 5.981 liters O₂ and produces 6.25 x 0.774 = 4.838 liters of CO₂ and produces 6.25 x 18.41 = 115.1 kJ and water.

First we will derive the formula for the oxidation of carbohydrates and fats and we will assume that only fats and carbohydrates are oxidized.

Oxidation of F gram of fat and C gram of carbohydrates:

$$\text{Total liters O}_2 \text{ consumed} = \text{VO}_2 = 0.829 \text{ C} + 2.013 \text{ F} \quad (1)$$

$$\text{Total liters CO}_2 \text{ produced} = \text{VCO}_2 = 0.829 \text{ C} + 1.431 \text{ F} \quad (2)$$

The volumes of O₂ and CO₂ are measured and then we have 2 equations with 2 unknowns, i.e the amounts of carbohydrate and fat being oxidized.

This set of 2 equations with 2 unknowns can be solved by subtracting the 2 equations from each other, thus

$$VO_2 - VCO_2 = 0.829C + 2.013 F - 0.829 C - 1.431 F = 0.582 F$$

or

$$F = 1/0.582 VO_2 - 1/0.582 CO_2 = 1.7182 VO_2 - 1.782 VCO_2 = 1.7182 (VO_2 - VCO_2)$$

$$F = 1.7182 (VO_2 - VCO_2) \quad (\text{grams of fat oxidized}) \quad (3)$$

Substitute now (3) in (1):

$$VO_2 = 0.829 C + 2.013 (1.7182 VO_2 - 1.7182 VCO_2)$$

$$0.829 C = -3.458 VO_2 - 3.458 CO_2 + VO_2 = -2.458 O_2 - 3.458 CO_2$$

$$C = -2.965 VO_2 + 4.171 VCO_2 \quad (\text{grams of carbohydrates oxidized})$$

Example: a reference man consumes per day 500 liters of O_2 and produces 425 liters of CO_2 . We assume that only carbohydrates and fats are oxidized. (See example in Elia and Livesey, 1992, page 106).
 gram fat oxidized = $1.7182 \cdot (500 - 425) = 128.9$ grams
 grams carbohydrates oxidized = $-2.965 \cdot 500 + 4.171 \cdot 425 = 290$ grams

Secondly, we will derive the formula for the oxidation of carbohydrates and fats and proteins.

These formulae can also be solved when we assume that besides carbohydrates and fat also proteins are oxidized. When we measure the VO_2 and the CO_2 , we cannot calculate the amount of fats and carbohydrates and proteins altogether, since we have only two equations (the amounts of VO_2 and VCO_2) and 3 unknown factors (the amounts of carbohydrate, fat and proteins. However, the amount of protein that has been oxidized can be calculated from the amount of nitrogen measured in the urine, and then we have again 2 equations with 2 unknowns (carbohydrates and fats).

Proteins contain 16% nitrogen, thus when the proteins are expressed in terms of nitrogen:

1 grams of nitrogen requires $(100/16) = 6.25 \times 0.957 = 5.981$ liters O_2 and produces $6.25 \times 0.774 = 4.838$ liters of CO_2 and water.

Thus, when C grams carbohydrates and F grams of fats are oxidized and N grams of nitrogen are measured (a measure of protein oxidation), then the total amount of O_2 consumed and CO_2 produced are:

$$\text{Total liters } O_2 \text{ consumed} = VO_2 = 0.829 C + 2.013 F + 5.981 N$$

$$\text{Total liters } CO_2 \text{ produced} = VCO_2 = 0.829 C + 1.431 F + 4.838 N$$

This system of 2 equations can be solved:

First we solve for F (the amount of fat oxidized) by subtracting the 2 equations from each other.

$$VO_2 = 0.829 C + 2.013 F + 5.981 N \quad (1)$$

$$VCO_2 = 0.829 C + 1.431 F + 4.838 N \quad (2)$$

Subtracting of (2) from (1) gives:

$$VO_2 - VCO_2 = (0.829 C + 2.013 F + 5.981 N) - (0.829 C + 1.431 F + 4.838 N) = 0.582 F + 1.143 N$$

or:

$$0.582 F = VO_2 - VCO_2 - 1.143 N$$

or:

$$F = (1/0.582) VO_2 - (1/0.582) VCO_2 - (1.143/0.582) N$$

or:

$F = 1.718 VO_2 - 1.718 VCO_2 - 1.964 N$ where F is the number of grams of fat oxidized and N is the grams of nitrogen collected in the urine.

Subsequently, we solve for C and use again the procedure of subtracting the two equations from each other.

First we multiply equation (2) with $(2.013 / 1.431 = 1.4067)$:

Thus:

$$1.4067 VCO_2 = (1.4067 \times 0.829) C + (1.4067 \times 1.431) F + (1.4067 \times 4.838) N$$

$$1.4067 VCO_2 = 1.166 C + 2.013 F + 6.806 N$$

Thus:

$$\text{VO}_2 = 0.829 \text{ C} + 2.013 \text{ F} + 5.981 \text{ N} \quad (1)$$

$$1.4067 \text{ VCO}_2 = 1.166 \text{ C} + 2.013 \text{ F} + 6.806 \text{ N} \quad (2')$$

Subtracting (2) from (1) gives:

$$\text{VO}_2 - 1.4067 \text{ VCO}_2 = (0.829 \text{ C} + 2.013 \text{ F} + 5.981 \text{ N}) - (1.166 \text{ C} + 2.013 \text{ F} + 6.806 \text{ N}) = -0.337 \text{ C} - 0.825 \text{ N}$$

Solving for C gives:

$$0.337 \text{ C} = -\text{VO}_2 + 1.4067 \text{ VCO}_2 - 0.825 \text{ N}$$

$$\text{C} = -(1/0.337) \text{VO}_2 + (1.4067/0.337) \text{VCO}_2 - (0.825/0.337) \text{N}$$

$\text{C} = -2.967 \text{VO}_2 + 4.174 \text{VCO}_2 - 2.448 \text{N}$ where C is the number of grams carbohydrate oxidized and N the grams of nitrogen collected in the urine.

Thus, we have now the following 2 equations:

$\text{F} = 1.718 \text{VO}_2 - 1.718 \text{VCO}_2 - 1.964 \text{N}$ where F is the number of grams of fat oxidized and N is the grams of nitrogen collected in the urine.

$\text{C} = -2.967 \text{VO}_2 + 4.174 \text{VCO}_2 - 2.448 \text{N}$ where C is the number of grams carbohydrate oxidized and N the grams of nitrogen collected in the urine.

When we measure the number of liters of O_2 consumed and the liters of CO_2 produced and the number of grams of nitrogen in the urine then we can calculate how many grams of carbohydrates, fats and proteins have been oxidized (see also the formulae derived above, when we assume that only fat and carbohydrates are oxidized).

Example: a reference man consumes per day 500 liters of O_2 and produces 425 liters of CO_2 and produces 12 grams of N in the urine. (See example in Elia and Livesey, 1992, page 106).

The amount of protein that has been oxidized is then $(100/16 = 6.25) \times 12 = 75$ grams of protein.

The amount of carbohydrates that has been oxidized is then:

$$\text{C} = -2.967 \text{VO}_2 + 4.174 \text{VCO}_2 - 2.448 \text{N} = -(2.967 \times 500) + (4.174 \times 425) - (2.448 \times 12) = 261 \text{ grams of carbohydrates}$$

The amount of fats that has been oxidized is then:

$$\text{F} = 1.718 \text{VO}_2 - 1.718 \text{VCO}_2 - 1.964 \text{N} = (1.718 \times 500) - (1.718 \times 425) - (1.964 \times 12) = 105 \text{ grams of fats}$$

The amount of H_2O that is produced can be calculated as following:

(see Table Appendix 4)

Proteins: oxidation of 75 grams of protein produces 75×0.40 grams $\text{H}_2\text{O} = 30.00$

Fats: oxidation of 105 grams of fat produces 105×1.07 grams $\text{H}_2\text{O} = 112.35$

Carbohydrates: 261 grams of carbohydrates produce 261×0.56 grams of $\text{H}_2\text{O} = 146.16$

Thus a total of $30 + 112 + 146 = 288$ grams of water.

Used energy is

Carbohydrates: $261.07 \times 17.57 = 4587 \text{ kJ}$ ($= 4587 / 10150 = 45\%$ of total energy used)

Fats: $105.28 \times 39.75 = 4185 \text{ kJ}$ ($= 4185 / 10150 = 41\%$ of total energy used)

Proteins: $75 \times 18.41 = 1380 \text{ kJ}$ ($= 1380 / 10150 = 14\%$ of total energy used)

A total of $4587 (45.2\%) + 4185 (41.2\%) + 1380 (13.6\%) = 10150 \text{ kJ}$ energy expenditure per day.

Further, we can derive a formula to calculate the energy expenditure with one formula.

The total energy production is the sum of the energy produced by the carbohydrates, the fats and the proteins.

Energy produced by the oxidation of the carbohydrates = the amount of carbohydrates oxidized x the energy density of carbohydrates (17.57 kJ per gram)

$$\text{Energy produced by the oxidation of the carbohydrates} = 17.57 \times (-2.967 \text{VO}_2 + 4.174 \text{VCO}_2 - 2.448 \text{N}) = -52.130 \text{VO}_2 + 73.337 \text{VCO}_2 - 43.011 \text{N}$$

When used 500 liters O_2 and produced 425 liters CO_2 and 12 grams nitrogen:

$$\text{Energy produced by the oxidation of the carbohydrates} = 17.57 \times [(-2.967 \times 500) + (4.174 \times 425) - (2.448 \times 12)] = (-52.130 \times 500) + (73.337 \times 425) - (43.011 \times 12) = 4587 \text{ kJ}$$

Energy produced by the oxidation of the fats = the amount of fats oxidized x the energy density of the fats (= 39.75 kJ per gram)

Energy produced by the oxidation of the fats = $39.75 \times (1.718 \text{ VO}_2 - 1.718 \text{ VCO}_2 - 1.964 \text{ N}) = 68.291 \text{ VO}_2 - 68.291 \text{ VCO}_2 - 78.069 \text{ N}$

When used 500 liters O_2 and produced 425 liters CO_2 and 12 grams nitrogen:

Energy produced by the oxidation of the fats = $39.75 \times (1.718 \text{ VO}_2 - 1.718 \text{ VCO}_2 - 1.964 \text{ N}) = 68.291 \times 500 - 68.291 \times 425 - 78.069 \times 12 = \mathbf{4185 \text{ kJ}}$.

Energy produced by the oxidation of the proteins = the amounts of proteins oxidized x the energy density of the proteins (= 18.41 kJ per gram).

Energy produced by the oxidation of the proteins = $18.41 \times (6.25 \times \text{N}) = 115.063 \text{ N} = 115.063 \times 12 = \mathbf{1380 \text{ kJ}}$

Thus the total energy expenditure is thus the sum of the energy produced by the carbohydrates, fats and proteins:

Total Energy Expenditure = $-52.130 \text{ VO}_2 + 73.337 \text{ VCO}_2 - 43.011 \text{ N} + 68.291 \text{ VO}_2 - 68.291 \text{ VCO}_2 - 78.069 \text{ N} + 115.063 \text{ N}$

Total Energy Expenditure = $16.161 \text{ VO}_2 + 5.046 \text{ VCO}_2 - 6.017 \text{ N}$

as derived in this article with the energy values of Brouwer.

Thus, this formula of allows us to calculate the energy expenditure when the total amounts of O_2 , CO_2 and the amounts of excreted N in the urine are known. Note that the formula can also be used for other reactions where O_2 is consumed and CO_2 is produced, e.g. when tripalmitate is synthesized from glucose (see Blaxter 1989 page 16-17 and 80 and Appendix 11, conversion of 4.5 mol glucose into 1 mol tripalmitate).

When consumed 500 liters O_2 (= $500 \times 1.428 = 714$ grams, 1 liter O_2 is 1.428 grams) and produced 425 liters CO_2 (= $425 \times 1.963 = 834$ grams of CO_2 , 1 liter of CO_2 is 1.963 grams) and 12 grams nitrogen (in an average human):

Energy expenditure = $(16.161 \times 500) + (5.046 \times 425) - (6.017 \times 12) = \mathbf{10153 \text{ kJ}}$

The formula as presented by Brouwer is (See McLean and Tobin (1987) page 30, Elia and Livesey (1992) page 106, Brockway (1987) page 464, Jéquier et al. (1987) page 191, and McLean and Tobin (1987) page 44):

Formula of Brouwer:

Total Energy Expenditure (kJ) = 16.175 VO_2 (liters) + 5.021 VCO_2 (liters) – 5.987 N (g)

And when only fats and carbohydrates are oxidized, the formula becomes:

Total Energy Expenditure (kJ) = 16.175 VO_2 (liters) + 5.021 VCO_2 (liters)

In our example of the reference man with 500 liter O_2 consumption and 425 liters of CO_2 production and 12 grams N excretion:

Total Energy expenditure = $16.175 \times 500 + 5.021 \times 425 - 5.987 \times 12 = \mathbf{10150 \text{ kJ}}$

The energy expenditure per liter O_2 is the EqO_2 of the fuel mixture (proteins, fats and carbohydrates) and is:

$\text{EqO}_2 \text{ Mixture} = \text{total energy Expenditure} / \text{total } \text{O}_2 \text{ consumption} = 16.175 + 5.021 (\text{CO}_2/\text{O}_2) - 5.987 \text{ N} / \text{O}_2$

And is in the example: $(10150 / 500 = 20.30 \text{ kJ} / \text{liter } \text{O}_2$

CO_2/O_2 is the respiration quotient (RQ) and is in this example: $425 / 500 = 0.85$. This is the RQ of the fuel mixture that has been oxidized in this example.

This formula of Brouwer differs slightly from the formula as derived by other authors, since different values for oxygen equivalents and energy densities of the carbohydrates, fats and proteins have been used. For an overview of the various formula derived by various authors, see: Elia and Livesey (1992) page 106 and Brockway (1987) page 464, Jéquier et al. (1987) page 191 and McLean and Tobin (1987) page 44. For an overview of the values for the various parameters used for the derivation of the formula by various authors, see McLean and Tobin (1987) Table 3.5 (page 40), table 3.6 (page 41) and Table 3.7 (page 42).

Thus, the formula of Brouwer allows us to calculate the energy expenditure when the amounts of O_2 , CO_2 and the amounts of excreted N in the urine are known and can be used when a mixture of carbohydrates, fats

and proteins are metabolized, but the formula is thus also true when only carbohydrates, fats, or proteins are metabolized.

For example, 1 gram of carbohydrates are metabolized and consume 0.829 liters of O₂ and produce 0.829 liters CO₂.

Energy expenditure = $16.175 \times 0.829 \text{ (liters O}_2\text{)} + 5.021 \times 0.829 \text{ (liters CO}_2\text{)} - 5.987 \times 0 \text{ (grams N)} = 17.57 \text{ kJ}$
(see Appendix 3)

Similarly, 1 gram of fats are catabolized and consume 2.013 liters of O₂ and produce 1.431 liters CO₂.

Energy expenditure = $16.175 \times 2.013 \text{ (liters O}_2\text{)} + 5.021 \times 1.431 \text{ (liters CO}_2\text{)} - 5.987 \times 0 \text{ (grams N)} = 39.75 \text{ kJ}$
(see Appendix 3)

Similarly 1 grams of proteins are catabolized and consume 0.957 liters O₂ and produce 0.774 liters of CO₂ and 0.16 grams of N (proteins contains 16% N).

Energy expenditure = $16.175 \times 0.957 \text{ (liters O}_2\text{)} + 5.021 \times 0.774 \text{ (liters CO}_2\text{)} - 5.987 \times 0.16 \text{ (grams N)} = 18.41 \text{ kJ}$
(see Appendix 3)

Thus, we could also have calculated the factors of the Brouwer formula from the following set of equations:

- (1) Energy expenditure = $X \times 0.829 \text{ (liters O}_2\text{)} + Y \times 0.829 \text{ (liters CO}_2\text{)} - Z \times 0 \text{ (grams N)} = 17.57 \text{ kJ}$
- (2) Energy expenditure = $X \times 2.013 \text{ (liters O}_2\text{)} + Y \times 1.431 \text{ (liters CO}_2\text{)} - Z \times 0 \text{ (grams N)} = 39.75 \text{ kJ}$
- (3) Energy expenditure = $X \times 0.957 \text{ (liters O}_2\text{)} + Y \times 0.774 \text{ (liters CO}_2\text{)} - Z \times 0.16 \text{ (grams N)} = 18.41 \text{ kJ}$

And this set of 3 equations with 3 unknowns could be solved for the 3 factors of the Brouwer formula.
(see Blaxter 1989, page 13)

Calculation of the energy expenditure with the formula of Brouwer by measuring the O₂ consumption and the CO₂ production and by estimating the rate of protein oxidation or N excretion

In order to calculate the total energy expenditure with the formula of Brouwer, we need to know the liters of O₂ uptake and the production of CO₂ and the amount of N excretion in the urine (which is related to the amount of protein that has been oxidized). However, when we only know the rate of O₂ consumption and the CO₂ production, but we do not know the rate of N excretion in the urine (due to the rate of protein oxidation), we can still make reasonable estimates of energy expenditure by making approximate assumptions about the rate of protein oxidation. The formula of Brouwer is:

$$\text{Total Energy Expenditure (kJ)} = EE = 16.175 \text{ VO}_2 \text{ (liters)} + 5.021 \text{ VCO}_2 \text{ (liters)} - 5.987 \text{ N (g)}$$

The factor 5.987 N (g) is a (correction) factor with the dimension of energy (kJ) and is related to the oxidation of the proteins as measured by the excretion of N in the urine. The oxidation of 1 grams of protein generates 18.410 kJ. Protein contains 16% N, thus 1 gram of N in the urine represents a quantity of $100/16 (=6.25) \times 18.410 = 115.0625 \text{ kJ}$. Thus N grams of N in the urine represents a total of $115.0625 \times \text{N(g)} \text{ kJ}$. The correction factor $5.987 \times \text{N (g)}$ can now be written as $0.0520 \times 115.0625 \text{ N(g)}$ (note: $0.0520 \times 115.0625 = 5.987$) where $115.0625 \times \text{N (g)}$ is the amount of energy (kJ) due to the oxidation of the protein. The formula of Brouwer becomes now:

$$\text{Total Energy Expenditure (kJ)} = EE = 16.175 \text{ VO}_2 \text{ (liters)} + 5.021 \text{ VCO}_2 \text{ (liters)} - 0.0520 \times 115.0625 \times \text{N (g)}$$

where $115.0625 \times \text{N (g)}$ is the energy produced by the oxidation of proteins.

Let us assume that the fraction of the total energy that is produced by the oxidation of the protein is p, then the energy produced by protein is $p \times EE$. (EE is the total energy expenditure that is produced by the oxidation of proteins, fats and carbohydrates all together). Substitution of $P \times EE$ for $115.0625 \times \text{N (g)}$ in the formula of Brouwer gives:

$$EE = 16.175 \text{ VO}_2 \text{ (liters)} + 5.021 \text{ VCO}_2 \text{ (liters)} - 0.0520 \times P \times EE$$

Solving for EE gives:

$$EE = (16.175 \text{ VO}_2 \text{ (liters)} + 5.021 \text{ VCO}_2 \text{ (liters)}) / (0.0520 + 0.0520 \times p)$$

The calculations of the energy expenditure of a reference man consuming 500 liters of O₂ and producing 425 liters of CO₂ and 12 grams of N in the urine indicated that the proportion of energy derived from the oxidation of the proteins is 13.6% and the energy expenditure was 10149 kJ (see calculations above). When we do not measure the rate of N excretion in the urine and do not know the rate of protein oxidation, we can make an estimate of the proportion of energy derived from the oxidation of the proteins. The error involved in an inaccurate estimation of the proportion of energy due to the oxidation of proteins is, however, rather small as the following examples will show.

Suppose that we estimated the the proportion of energy derived from the oxidation of proteins was 10%. Then:

$$EE = (16.175 * 500 + 5.021 * 425) / (0.0520 + 0.0520 * 0.10) = 10169 \text{ kJ (vs 10150 kJ)}$$

Thus the difference is $(10169 - 10150) / 10149 = 19 / 10150 = 0.19\%$

Suppose that we estimated the the proportion of energy derived from the oxidation of proteins was 20%. Then:

$$EE = (16.175 * 500 + 5.021 * 425) / (0.0520 + 0.0520 * 0.20) = 10118 \text{ kJ (vs 10150 kJ)}$$

Thus the difference is $(10118 - 10150) / 10118 = 32 / 10150 = 0.31\%$

Thus, still a good estimate of the energy expenditure can be made when we only measure the O₂ consumption and the CO₂ production and when we estimate that the proportion of energy derived from the oxidation of protein is about 15%.

Calculations of energy expenditure from VO₂ consumption alone.

We can calculate the total energy expenditure with the formula of Brouwer, or, if we know the Eeq O₂ of the fuel mixture, by multiplying the Eeq O₂ of the fuel mixture by the total O₂ consumption. In order to calculate the total energy expenditure with the Formula of Brouwer or with the Eeq O₂ of the fuel mixture that can be derived from the Formula of Brouwer, we need to know the liters of O₂ uptake and the production of CO₂ and the amount of N excretion in the urine (which is related to the amount of protein that has been oxydized).

It is also possible to calculate the EeqO₂ of the fuel mixture, if we know the percentages of energy derived from the proteins, fats and the carbohydrates that are oxidized e.g. from the energy partition in the diet. In the example of the reference man (consuming 500 liters of O₂ and producing 425 liters of CO₂ and 12 grams of N in the urine), we have calculated that the total energy expenditure and the partition of the energy expenditure was:

A total of 4587 (45.2% from carbohydrates) + 4185 (41.2% from fat) + 1380 (13.6% from proteins) = **10140** kJ energy expenditure per day.

If we know these percentages of the energy partition, then we can calculate the EeqO₂ of the fuel mixture as following:

$$\text{EeqO}_2 \text{ of fuel mixture} = \frac{\text{Total Energy Expenditure}}{\text{Total O}_2 \text{ consumption}}$$

$$\text{EeqO}_2 \text{ fuel mixture} = \frac{\text{Total Energy Expenditure} = 100}{\frac{\text{energy \% from protein}}{\text{EeqO}_2 \text{ protein}} + \frac{\text{energy \% derived from fat}}{\text{EeqO}_2 \text{ fat}} + \frac{\text{energy \% derived from carbohydrates}}{\text{EeqO}_2 \text{ carbohydrates}}}$$

$$\text{EeqO}_2 \text{ of fuel mixture} = \frac{100}{\frac{13.6}{19.24} + \frac{41.2}{19.75} + \frac{45.2}{21.20}} = 20.30 \text{ kJ per liter O}_2$$

If we know the EeqO₂ of the fuel mixture (e.g. derived from the diet composition or from the changes in body composition after fasting, from which data we can derive the amounts of fat and protein that have been oxidized), then we only have to measure the O₂ consumption and we can calculate the energy expenditure by multiplying the O₂ consumption by the EeqO₂ of the fuel mixture. This way, we do not have to measure the CO₂ production and the N excretion in the urine.

Example: the total O₂ consumption per day is 500 liters and the EeqO₂ of the fuel mixture is 20.30 (e.g. derived from the diet composition). The total energy expenditure is: $20.30 * 500 = 10150$ kJ per day.

The error that is being introduced is very small, when we do not use the correct and actual Eeq O₂, but an estimate that is derived from an estimate of the energy partition. Suppose that the actual energy partition is 45.2 energy % derived from carbohydrates, 41.2 energy % from fat, and 13.6 energy % from proteins, as in the example of the reference man and the calculated energy expenditure is $20.30 * 500 = 10150$ kJ. However, suppose that we estimate that the energy partition is 45.2 energy % from carbohydrates, 34.9 energy % from fat, and 20 energy % from proteins. The calculated EeqO₂ is then 20.26 and the total calculated energy expenditure is $20.26 * 500 = 10130$ kJ, thus an error of only 0.19%. When we estimate that the energy partition is 60 energy % from carbohydrates, 20 energy % from fat, and 20 energy % from proteins (which is very extreme), the calculated EeqO₂ is then 20.48 and the calculated energy expenditure is $20.48 * 500 = 10240$ kJ, thus an error of only 0.9%.

Calculations of energy expenditure from O₂ consumption alone in fish.

Many fish species are carnivorous and use predominantly proteins and fats as fuel. The energy equivalents of O₂ (Eeq O₂) for fats and proteins (for ammoniatelic animals such as fish) are 13.72 and 13.79 kJ per gram oxygen, respectively (values of Elia and Livesey 1992, see Table Appendix 4) The average of these two values is 13.75 kJ per liter oxygen or 13.75 * 1.428 = 19.64 kJ per gram oxygen (1 liter O₂ weighs 1.4258 grams) and a similar value of has been reported by Elliott (1975). Thus in fish, the heat production or energy expenditure can be estimated by multiplying the *grams* of oxygen consumption by 13.75 or the *liters* of oxygen consumption by multiplying the grams of oxygen consumption by 19.64.

Estimation of the O₂ consumption and the CO₂ production from the energy expenditure in fish.

The consumption of O₂ and the production of CO₂ in fish may be estimated when the energy expenditure is known, e.g. from growth models, where the energy expenditure can be calculated from the amount of food eaten, the deposition of fat and protein in the body and the energy expenditure of maintenance and the energy costs for fat and protein deposition (see energy budget chapter). This may be particularly useful in fish nutrition, since the amount of oxygen in the water may be a limiting factor. Most carnivorous fish utilize predominantly a mixture of fat and protein as fuel and the nitrogen in the protein is excreted in the form of ammonia. The EeqO₂ for the oxidation of protein (nitrogen excreted as ammonia) (19.68 kJ per liter oxygen or 13.78 kJ per gram oxygen (1 liter O₂ = 1.428 grams), see Elia and Livesey (1992) page 79) and fat (19.61 kJ per liter oxygen or 13.73 kJ per gram oxygen), see Elia and Livesey (1992) page 72) are comparable and an average value of 13.75 kJ per gram oxygen or 19.64 kJ per liter oxygen consumption can be used for the oxidation of a mixture of protein and fat. Thus, an energy expenditure of 1 kJ is associated with the consumption of (1/13.75) = 0.0727 grams of oxygen or 1/ 19.64 = 0.0509 liter oxygen.

The amount of CO₂ produced can also be roughly estimated when the respiration quotient or the ratio of (liters CO₂ produced / liters O₂ consumed) is known. The RQ of fats is 0.71 and that of protein 0.95 for ammoniatelic fish (see Table Appendix 4) and the average value is 0.83. When we use a RQ of 0.83, then the energy expenditure of 1 kJ is then associated with the production of 0.83 * 0.0509 = 0.0422 liters of CO₂ = 0.0215 grams of CO₂ (1 liter of CO₂ weighs 1.963 grams).

Derivation of the formula of Brouwer as described by Elia and Livesey (1992) (page 94) and Weir (1949)

A mixture of carbohydrates, fats and proteins are oxidized and assume that they consume together 1 liter of oxygen and the proportion of oxygen used for each nutrient is C, F, and P (expressed in liters).

$$\text{Oxygen used} = 1 \text{ liter} = C + F + P \quad \text{or } C \text{ (liters)} = 1 - F \text{ (liters)} - P \text{ (liters)} \quad (1)$$

The respiratory coefficients of carbohydrates are 1.00, of fats are 0.711 and of proteins 0.809. Then the total amount of CO₂ produced by the mixture is:

$$\text{Liters CO}_2 \text{ produced is : } 1 C + 0.711 F + 0.809 P \quad (\text{when 1 liter of O}_2 \text{ is used by the mixture}). \quad (2)$$

The energy equivalent (energy generated per liter oxygen) of carbohydrates is 21.20 kJ/L, for fats is 19.75 kJ/L and for proteins is 19.24 kJ/L.

The energy expenditure of the fuel mixture associated with the use of the total of 1 liter of O₂ is:

$$\text{Energy Expenditure} = 21.20 C + 19.75 F + 19.24 P \quad (3)$$

Substituting C of formula (1) in (2) and (3) gives:

$$\text{Total liters CO}_2 = 1 - F - P + 0.711 F + 0.809 P = 1 - 0.289 F - 0.191 P$$

$$\text{or } F = - (1/0.289) \text{ CO}_2 + (1/0.289) - (0.191/0.289) P$$

$$F = 3.460 \text{ CO}_2 + 0.3460 - 0.661 P \quad (4)$$

Substituting of (1) in (3) gives

$$\text{Energy expenditure} = 21.20 \times (1 - F - P) + 19.75 F + 19.24 P$$

$$\text{Energy Expenditure} = 21.20 - 1.45 F - 1.96 P \quad (5)$$

Substituting (4) into (5) gives:

$$\text{Energy Expenditure (per 1 liter O}_2) = 21.20 - 1.45 \times (3.460 \text{ CO}_2 + 3.460 - 0.661 P) - 1.96 P$$

or

$$\text{Energy expenditure (per liter O}_2\text{)} = \text{Eq O}_2 = 16.183 - 5.017 \text{ CO}_2 - 1.002 \text{ P} \quad (6)$$

The term P is the proportion of the O₂ consumption (of the total of 1 liter oxygen consumption) that is due to the oxidation of protein, or $P = (\text{liter O}_2 \text{ consumption due to protein oxidation}) / (\text{liter total O}_2 \text{ consumption})$. The term P can be transformed to the measured quantity of protein oxidized or the measured quantity of N excreted in the urine. An amount of 0.957 liters of O₂ is consumed for each gram of protein oxidized, protein contains 16% N and thus an amount of $6.25 \times 0.957 = 5.981$ liters O₂ is consumed for each gram of N excreted in the urine. Thus P is equal to $5.981 \times \text{N}$ and the equation (6) becomes:

$$\text{Energy expenditure (per liter O}_2\text{)} = \text{Eq O}_2 = 16.183 - 5.017 \text{ CO}_2/\text{liter O}_2 - 5.993 \text{ N(g)/liter O}_2$$

where N(g) is the quantity (grams) of N that is excreted during the time it takes to use 1 liter of O₂ and CO₂ is the quantity of CO₂ that is produced during the time it takes to use 1 liter of O₂.

When the total amount of O₂ used and the total amount of CO₂ and N produced is measured, then the energy expenditure formula (per liter O₂) has to be multiplied with the total amount of oxygen used and the formula is then:

$$\text{Energy Expenditure} = 16.183 \text{ O}_2 - 5.017 \text{ CO}_2 - 5.993 \text{ N.}$$

Where O₂ and CO₂ are in liters and N in grams nitrogen collected in the urine.

When 500 liters of O₂ are consumed and 425 liters of CO₂ produced and 12 grams of N collected in the urine, the energy expenditure is:

$$\text{Energy Expenditure} = 16.183 \times 500 - 5.017 \times 425 - 5.993 \times 12 = \mathbf{10152 \text{ kJ.}}$$

The formula as presented by Brouwer is (See McLean and Tobin (1987) page 30, Elia and Livesey (1992) page 106, Brockway (1987) page 464, Jéquier et al. (1987) page 191, and McLean and Tobin (1987) page 44.

$$\text{Total Energy Expenditure} = 16.175 \text{ VO}_2 + 5.021 \text{ VCO}_2 - 5.987 \text{ N}$$

$$\text{Total Energy expenditure} = 16.175 \times 500 + 5.021 \times 425 - 5.987 \times 12 = \mathbf{10149 \text{ kJ}}$$

Derivation of the formula of Brouwer as described by Blaxter (1989), page 13.

The formula of Brouwer allows us to calculate the energy expenditure when the amounts of O₂, CO₂ and the amounts of excreted N in the urine are known and can be used when a mixture of carbohydrates, fats and proteins are metabolized, but the formula is thus also true when only carbohydrates, fats, or proteins are metabolized.

For example, 1 gram of carbohydrates are metabolized and consume 0.829 liters of O₂ and produce 0.829 liters CO₂.

$$\text{Energy expenditure} = 16.175 \times 0.829 (\text{liters O}_2) + 5.021 \times 0.829 (\text{liters CO}_2) - 5.987 \times 0 (\text{grams N}) = 17.57 \text{ kJ}$$

(see Appendix 3)

Similarly, 1 gram of fats are catabolized and consume 2.013 liters of O₂ and produce 1.431 liters CO₂.

$$\text{Energy expenditure} = 16.175 \times 2.013 (\text{liters O}_2) + 5.021 \times 1.431 (\text{liters CO}_2) - 5.987 \times 0 (\text{grams N}) = 39.75 \text{ kJ}$$

(see Appendix 3)

Similarly 1 grams of proteins are catabolized and consume 0.957 liters O₂ and produce 0.774 liters of CO₂ and 0.16 grams of N (proteins contains 16% N).

$$\text{Energy expenditure} = 16.175 \times 0.957 (\text{liters O}_2) + 5.021 \times 0.774 (\text{liters CO}_2) - 5.987 \times 0.16 (\text{grams N}) = 18.41 \text{ kJ}$$

(see Appendix 3)

Thus, we could also have calculated the factors of the Brouwer formula from the following set of equations:

- (1) Energy expenditure = $X \times 0.829 (\text{liters O}_2) + Y \times 0.829 (\text{liters CO}_2) - Z \times 0 (\text{grams N}) = 17.57 \text{ kJ}$
- (2) Energy expenditure = $X \times 2.013 (\text{liters O}_2) + Y \times 1.431 (\text{liters CO}_2) - Z \times 0 (\text{grams N}) = 39.75 \text{ kJ}$
- (3) Energy expenditure = $X \times 0.957 (\text{liters O}_2) + Y \times 0.774 (\text{liters CO}_2) - Z \times 0.16 (\text{grams N}) = 18.41 \text{ kJ}$

And this set of 3 equations with 3 unknowns could be solved for the 3 factors of the Brouwer formula. (see Blaxter 1989, page 13).

Thus, this method can be used to calculate easily the factors for the formula of Brouwer when varying values of the combustion parameters are used for the carbohydrates, fats and proteins.

Appendix 13 (Text)

Scaling Laws or Allometry

Various parameters such as the metabolic rate, the body composition, the size of body parts such as size of the heart, intestines etc. and the length of humans and animals can be described as a function of the body weight. However, these relationships between these parameters and the body weight are allometric and follow allometric scaling laws which means that the relationship can be described by a function of the form:

$$Y = Y_0 M^b$$

where Y_0 is the normalisation constant (unit per M^b when $M = 1$) and b is the scaling exponent, scaling coefficient, or scaling function. An example of an allometric scaling law used in mathematics is the volume of a sphere as function of the radius (r) of that sphere: volume = $(2\pi)r^2$ where 2π is the normalisation constant (volume per unit of r^2 when $r = 1$) and 2 is the scaling exponent. The relationship is linear when the scaling factor is 1. Allometric scaling laws are frequently seen in biology and another example are the size of the organs in the body, chest circumference and body surface as functions of body weight. Scaling laws may for instance also apply to companies that merge. When two companies merge, it may well be that the required size of the administrative staff of the new company after the merger is not twice that large, but only 1.5 that large and the same may be true for the operating costs of the newly merged company.

Allometric scaling laws are described by the function:

$$Y = Y_0 M^b$$

and the logarithmic form is:

$$\log Y = \log (Y_0 M^b)$$

$$\log Y = \log Y_0 + b \log M$$

Suppose that various values for Y and M are observed or experimentally measured, then the various values of Y can be plotted vs the corresponding values of M (or the various values of $\log Y$ can be plotted versus various values for $\log M$) and a linear plot is generated. The slope and the intercept of this line can be calculated by linear regression. The slope of this linear plot is b in the formula $Y_0 BW^b$. The intercept of this linear plot is $\log Y_0$ and the anti – log of the value of $\log Y_0$ is Y_0 in the formula $Y_0 BW^b$.

Appendix 14 (Text)

Metabolic Rate as a Function of Body Weight

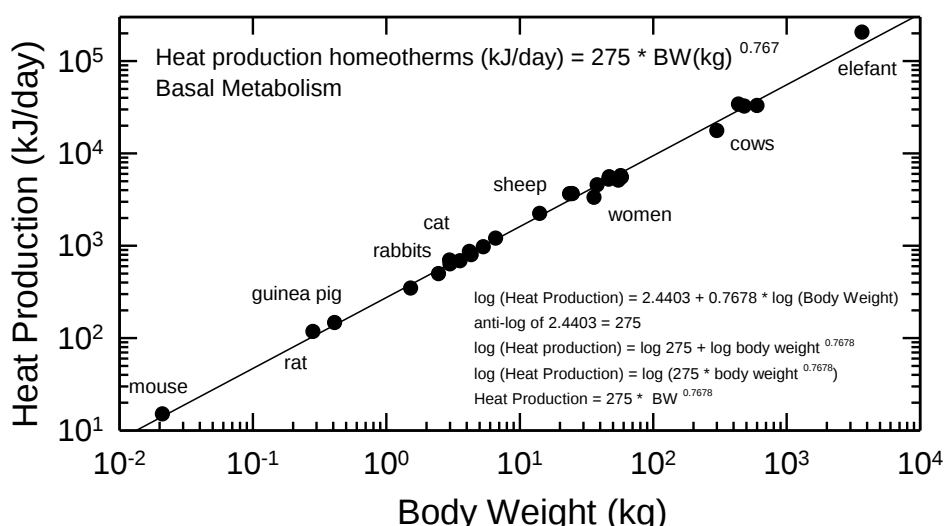
The oxidation of nutrients such as carbohydrates, fats and proteins results in the generation of energy and this energy is used for maintenance, work and growth. All the energy that is not retained in the body in the form of growth is eventually released as heat. This energy expenditure or metabolic rate can be expressed in kJ per day or in wats (W , rate of heat production in joules per second). The heat production is dependent on the body size with an allometric relationship of the form (White and Seymour, 2005):

$$\text{Heat Production (kJ/day)} = a * BW^b$$

where Heat Production is the metabolic rate in kJ/day, a is the normalisation constant (unit per BW^b when $BW = 1$), BW is the body weight in kg and b is the scaling exponent or coefficient. The total heat production (kJ per day) is plotted vs the body weights (kg) on double logarithmic graph paper (log – log) and a linear plot arises. The slope and the intercept of this linear plot can be calculated by linear regression. The slope is b in the formula aBW^b . The intercept is $\log a$ and the anti – log of the value of $\log a$ is a in the formula aBW^b .

Kleiber reported as far back as 1932 that the metabolic rate of various animal species as a function of their body weight follows allometric scaling laws (see Appendix 13 for details). He plotted the basal metabolic rate (BMR) of various animal species of different sizes vs their body weights on double logarithmic graph paper and observed a linear relationship. The graph below shows a data set of various animal species of different sizes (the so-called mouse – elephant graph) (the data in the figure are from Kleiber, 1975, The Fire of Life, page 203 and 207). The total heat production (kJ per day) is plotted vs the body weights (kg) on double logarithmic graph paper (log – log) and a linear plot arises. The slope and the intercept of this line can be calculated by linear regression. The slope of this linear plot is b in the formula $a * BW^b$. The intercept of this linear plot is $\log a$ and the anti – log of the value of $\log a$ is a of the formula $a * BW^b$.

Data from Kleiber (The Fire of Life, 1975 page 203 and 207)



Kleiber concluded (1975, The Fire of Life, page 214) that “for practical purposes, one may assume that the mean standard metabolic rate (kcal) of mammals is seventy times the three-fourth power of their body weight (in kg) per day”. Thus, the basal metabolic rate is:

$$\text{Basal Metabolic Rate (BMR) or Heat Production (kcal/day)} = 70 BW^{0.75}$$

$$\text{or in kJ (1 kcal = 4.184 kJ)}$$

$$\text{Basal Metabolic Rate (BMR) or Heat Production (kJ/day)} = 293 BW^{0.75} \text{ or about } 300 BW^{0.75}$$

Example:

The metabolic rate in the formula of Kleiber for various animal species is:

$$\text{Energy expenditure} = a * BW(kg)^b$$

where the body weights are expressed in kg. We can convert this formula into a formula where the body weights are expressed in gram. The formula is then:

$$\text{Energy Expenditure} = x * \text{BW(g)}^b$$

We can calculate the value of x as following:

$$\text{Energy Expenditure} = a * \text{BW(kg)}^b = x * [\text{BW(kg)} * 1000]^b$$

Solving for x gives:

$$x = [a * \text{BW(kg)}^b] / [x * \text{BW(kg)}^b * 1000^b] =$$

$$x = [a * \text{BW(kg)}^b] / x * \text{BW(kg)}^b * 1000^b = a / 1000^b$$

thus the formula becomes then:

$$\text{Energy Expenditure} = (a / 1000^b) * \text{BW(g)}^{0.75} \text{ where the body weights are now expressed in grams}$$

Thus:

Conversion from kg into grams: Divide a (the normalization constant) by 1000^b (b is scaling factor or coefficient)

Conversion from grams into kg: Multiply a (the normalization constant) by 1000^b (b is scaling factor or coefficient)

For example we have an animal of 150 grams and the energy expenditure is. $300 * \text{BW(kg)}^{0.75}$

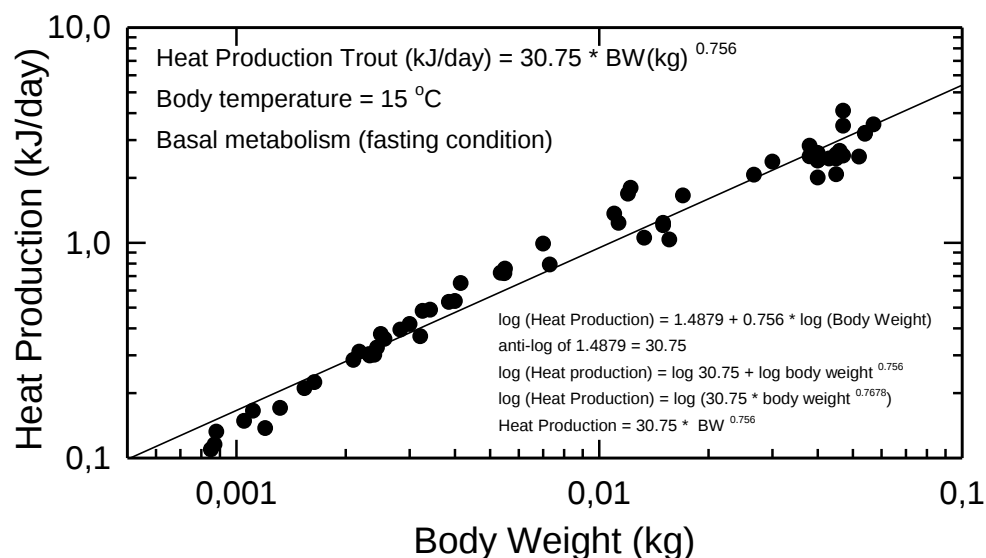
The energy expenditure of an animal of 150 grams = $300 * 0.15^{0.75} = 72.31$ kJ per day (weight in kilograms) or

The energy expenditure of an animal of 150 grams = $(300 / 1000^{0.75}) * 150^{0.75} = 72.31$ kJ per day (weight in grams)

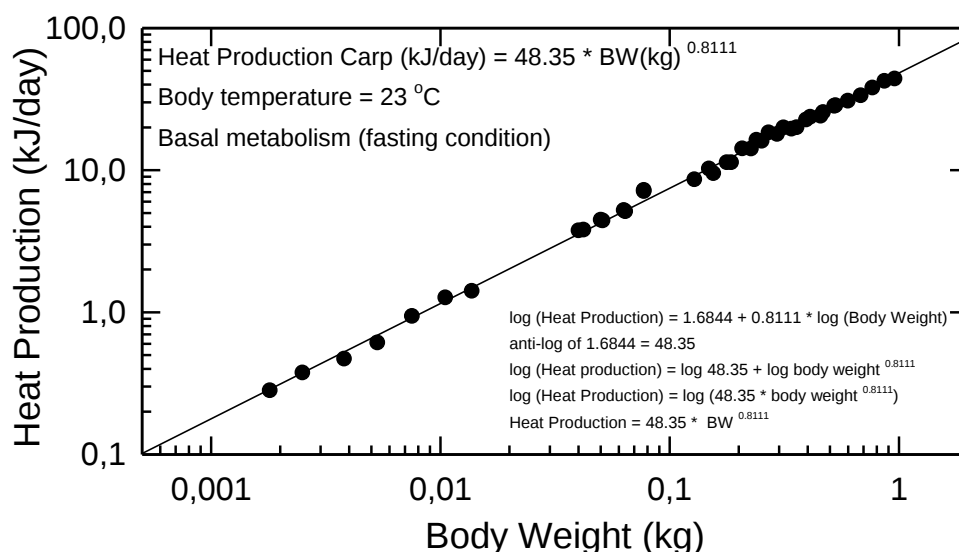
One may assume that the basal metabolic rate in animals is about 75% of the total metabolic rate (total metabolic rate comprises basal metabolic rate (BMR) or routine metabolism in fish, Specific Dynamic Action (SDA, heat production as a result of food consumption) and physical activity thermogenesis (AT).

Also within a particular animal species, the metabolic rate as a function of the body weight can be described according to a scaling formula. The example below shows a graph of the metabolic rate of trout of various sizes as described by Smith et al. (J. Nutr. 108: 1017 – 1024, 1978, page 1021) and a graph of the metabolic rate of carp of various sizes as described by Huisman (1974, Dissertation, Wageningen University, The Netherlands, the dissertation can be downloaded from the digital library of Wageningen University).

Data from Smith et al. (J. Nutr. 108: 1017 - 1024, 1978, page 1021)



Data from E.A. Huisman (Dissertation, 1974, page 58 and 59)



In the dissertation of Huisman (1974), the consumption of oxygen in ml per hour is given and the body weights are in grams. We converted the ml of oxygen per hour to kJ per day and the body weights in kg. 1 ml oxygen = 1.428 mg grams of oxygen and the energy equivalent of 1 gram oxygen is 13.75 kJ (see Table Appendix 4). Fish metabolize and oxidize predominantly fat and proteins and the average energy equivalent of oxygen (Eeq O₂) for fat (13.72 kJ per gram oxygen) and for protein (13.79 per gram oxygen in ammoniatic fish) (Appendix 4) is about 13.75 kJ per gram oxygen. Therefore, the energy expenditure or heat production of the fish can be calculated by multiplying the oxygen uptake (grams) of a fish by 13.75. Thus, the ml of oxygen (these data are given in the dissertation) has to be multiplied by: $1.428 \times 13.75 \times 24 / 1000$ (kJ) = 0.471.

The weight exponent for trout in the studies of Smith et al. (1978) was 0.756 and the weight exponent for carp in the studies of Huisman (1974) was 0.811. Carke and Johnston (1999) reported that the average weight exponent for fish is 0.80 and a weight exponent of 0.80 is now mostly used for fish.

Huisman (1974) calculated an oxygen consumption of $0.372 \text{ BW}^{0.816}$ where the oxygen consumption is expressed in ml per hour and the body weights in grams (at a temperature of 23 °C). We can also convert this formula into a formula where the body weights are expressed in kg and the heat production in kJ / day. The procedure is as following:

When the body weight is expressed in grams:
 oxygen consumption / hr = $0.372 * \text{BW(g)}^{0.816}$.

When the body weight is expressed in kg:
 oxygen consumption / hr = $x * (\text{BW(kg)}/1000)^{0.816}$

$$0.372 * \text{BW(g)}^{0.816} = x * (\text{BW(kg)}/1000)^{0.816} \text{ or}$$

$$x = (0.372 * \text{BW(g)}^{0.816}) / (\text{BW(kg)}/1000)^{0.816} = 0.372 * 1000^{0.816}$$

Further, 1 ml oxygen = 1.428 mgrams of oxygen and the energy equivalent of 1 mgram oxygen is 13.75 J for fish (see Table Appendix 4; the energy equivalent of 13.75 kJ per gram oxygen is the average of the energy equivalent for fat (13.72) and protein (13.79 for ammoniatic fish) and we assume that during fasting of the fish, only fats and proteins are

oxydized). Thus, the ml of oxygen / hr (these data are given in the dissertation) has to be multiplied by: $1000^{0.816} * 1.428 * 13.75 * 24 / 1000$ (kJ) = 132.20.

Thus the formula of Huisman

$$\text{oxygen consumption in ml / hr} = 0.372 * \text{BW (g)}^{0.816},$$

can be converted into $0.372 * 132.20$:

$$\text{Heat Production (kJ/day)} = 49.17 * \text{BW(kg)}^{0.816}$$

This formula is slightly different from the formula we calculated from the raw data of Huisman as given in the dissertation.

We used in this example the $^{10}\log$ values of the heat production and the body weights. However, we will get the same results when we use the $^e\ln$ values.

The metabolic rate or the rate of heat production is usually expressed in joules per day, but can also be expressed in watts (W). One watt is equivalent to the rate of heat production of 1 joule per second. Suppose that the heat production or metabolic rate of an animal is $400 \text{ kJ} * \text{BW}^{0.75}$ per day. The rate of heat production expressed in watts is then: $400 * 1000 / (24 \text{ (hours)} * 60 \text{ (minutes)} * 60 \text{ (seconds)}) = 4.63 \text{ watts} * \text{BW}^{0.75}$ (joule / second). The rate of heat production of an animal or human person of 75 kg is then $75^{0.75} * 4.63 = 118$ watts which is similar to the heat production of a light bulb of 118 watts. The rate of heat production of a carp of 0.5 kg is then: $[49.17 * 0.5^{0.81} * 1000] / [24 \text{ (hours)} * 60 \text{ (minutes)} * 60 \text{ (seconds)}] = 0.35$ watts which might be comparable to the heat production of a small LED light.

More graphs describing the relationship between body weight and heat production or energy expenditure in various fish species are given in Appendix 25 – 29. An overview of the metabolic rates of various animal species and fish are given in Appendix 9.

Example: The maintenance energy expenditure of humans is: $\text{HP} = 432 * \text{BW(kg)}^{0.75}$ kJ / day (see Appendix 9). The energy expenditure of a man of 70 kg is: $432 * 70^{0.75} = 10,455$ kJ per day. The energy expenditure expressed in watts (i.e. in kJ / sec) is: $(10,455 * 1000 \text{ (kJ into J)} / (24 \text{ (hours)} * 60 \text{ (minutes)} * 60 \text{ (seconds)})) = 121$ watts (kJ / second).

Example: The maintenance metabolic rate of a trout is $48.3 \text{ BW(kg)}^{0.80}$ kJ (Glencross, 2009) and the maintenance energy expenditure of a lean Zucker rat is $427 \text{ BW(kg)}^{0.75}$ kJ (Pullar and Webster 1977). Thus, the energy expenditure of a trout of 250 grams is $43.2 * 0.25^{0.80} = 14.3$ kJ and the energy expenditure of a rat of 250 grams is $427 * 0.25^{0.75} = 151.0$ kJ, thus a tenfold of that of a trout!

Appendix 15 (Text)

Exponential Effect of Temperature on Energy Metabolism or Metabolic Rate.

Fish are poikilotherm (poikilos means in greek variable) animals which means that their body temperature is similar to the temperature of the water they live in. The body temperature has an effect on the metabolism of the fish and the metabolic rate or heat production (and the feed intake) is lower at lower body temperatures. The effect of the temperature on the metabolic rate is exponential as explained below.

The various metabolic processes in the body that generate the metabolic rate or the heat production 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 velocity of a (monomolecular) (bio)chemical reaction or the change in the concentration of the reactant (dc) per unit of time (dt) is described by the formula:

$$\text{Reaction Velocity of a chemical reaction} = \frac{dc}{dt} = k c$$

where c is the concentration of the reactant and k is the velocity or reaction constant.

The velocity constant of a reaction (the reaction constant k) is dependent on the temperature in an exponential way according to the formula of Arrhenius:

$$k = A \cdot e^{-\alpha/RT}$$

where A and α are constants and R is the gas constant and T is the absolute temperature in degrees Kelvin. (0 °C is 273 degrees Kelvin). The logarithmic form of this formula is;

$$\ln(k) = \ln(A e^{-\alpha/RT}) = \ln A + \ln e^{-\alpha/RT}$$

$$\ln(k) = \ln A + (-\alpha/R) (1/T)$$

This is a regression line of the general form $y = a + bx$, where b represents $(-\alpha/R)$ and is the slope of the regression line and a represents $\ln A$ and is the intercept of the regression line.

Thus $\ln(k)$ can be plotted versus $1/T$ with T (absolute temperature) in degrees Kelvin when various values for k at various values for T are measured.

We have demonstrated above that the metabolic rate of a fish can be described by the scaling formula:

$$\text{Heat Production or Energy Expenditure} = a * BW^{0.80}.$$

where BW is body weight (kg), "a" is the normalization constant or the heat production per day per kg $BW^{0.80}$, and "b" is the scaling or exponential coefficient.

This formula for the metabolic rate is comparable to the formula for the reaction velocity of a chemical reaction:

$$\text{Reaction Velocity of a chemical reaction} = \frac{dc}{dt} = k c \quad (1)$$

The heat production or metabolic rate is comparable to the reaction velocity of a chemical reaction, the normalization constant "a" is comparable to the reaction constant "k" and the concentration "c" is comparable to the BW^b (metabolic body weight).

Further, the heat production in the body is the result of a series of (bio)chemical reactions and a higher heat production will be the result of a higher velocity of all these chemical reactions. The effect of the temperature on the velocity of all these various (bio)chemical reactions is described by the formula of Arrhenius and therefore, the effect of the body temperature on the metabolic rate can also be described by the formula of Arrhenius and therefore:

$$a = A \cdot e^{-\alpha/RT}$$

or the logarithmic form

$$\ln(a) = \ln A + (-\alpha/R) (1/T)$$

and the formula for the metabolic rate becomes then:

$$\text{Heat Production or Energy Expenditure} = A \cdot e^{-\alpha/RT} \cdot BW^b$$

(see Gillooly et al. (2001) and Clarke and Johnston (1999))

We can simplify the formula:

$$a = A \cdot e^{-\alpha/RT}$$

for our purposes into (Elliott (1976)):

$$a = c \cdot e^{\alpha \cdot T}$$

or in the logarithmic form:

$$\ln(a) = \ln c + \alpha T$$

since we found that plotting a vs T resulted in similar results as plotting a vs $1/RT$ (see also Clarke and Johnston, 1999).

This formula describes a regression line of the general form: $y = b + ax$ where $\ln c$ is the intercept and α is the slope of the regression line. This exponential function describes the effect of the temperature on the heat production or metabolic rate per kg BW^b

When we include the effect of the temperature on the heat production of the fish, then the formula becomes:

$$\text{Heat Production} = c \cdot e^{\alpha \cdot T} \cdot BW^b$$

Where $c \cdot e^{\alpha \cdot T}$ represents the normalization constant " a " (the heat production at $T = T$ per kg BW^b) and b is the weight exponent which is 0.80 (Clarke and Johnston, Journal of Animal Ecology 68: 893 – 905, 1999, page 896) for fish (see for this formula also Elliott, Animal Ecology 45: 923-948, 1976), Blaxter, Energy metabolism in animals and man, 1989, page 129 and Clarke and Johnston, Journal of Animal Ecology 68: 893 – 905, 1999).

Further,

$$\text{Heat Production (at } T=T_1) = c \cdot e^{\alpha \cdot T_1} \cdot BW^b$$

$$\text{Heat Production (at } T=T_2) = c \cdot e^{\alpha \cdot T_2} \cdot BW^b$$

$$\text{Heat Production (at } T=T_2) / \text{Heat Production (at } T=T_1) = (c \cdot e^{\alpha \cdot T_2} \cdot BW^b) / (c \cdot e^{\alpha \cdot T_1} \cdot BW^b)$$

$$\text{Heat Production per kg } BW^{0.80} \text{ (at } T=T_2) = \text{Heat Production per kg } BW^{0.80} \text{ (at } T=T_1) \cdot e^{\alpha \cdot (T_2 - T_1)}$$

With this formula we can now calculate the heat production at $T=T_2$ when we know the heat production at $T=T_1$. The term $e^{\alpha \cdot (T_2 - T_1)}$ of the exponential function $a = c \cdot e^{\alpha \cdot (T_2 - T_1)}$ represents essentially the (multiplication) factor by which the metabolic rate changes when the temperature changes with a defined number of degrees ($T_2 - T_1$).

Example: The heat production per kg $BW(kg)^{0.80}$ in a trout is 50 kJ/day at a temperature of 15 °C ($T=T_1 = 15$ °C) and $\alpha = 0.095$ (in trout as calculated from the data of Elliott, 1976, see below). Now we can calculate the heat production at a temperature of 10 °C ($T=T_2 = 10$ °C). The formula is: Heat Production per kg $BW(kg)^{0.80}$ (at $T=T_2$) = Heat Production per kg $BW(kg)^{0.80}$ (at $T=T_1$) * $e^{\alpha \cdot (T_2 - T_1)}$
 Heat Production per kg $BW(kg)^{0.80}$ (at $T=10$ °C) = 50 (at $T=15$ °C) * $e^{0.095 \cdot (10 - 15)} = 31.09$ kJ/day

We can also calculate how many degrees the body temperature has to increase to double the metabolic rate.

$$(\text{Heat Production at } T_2)/(\text{Heat Production at } T_1) = (c * e^{(\alpha * T_2)} * BW^b)/(c * e^{(\alpha * T_1)} * BW^b) = 2$$

$$(e^{(\alpha * T_2)}) / (e^{(\alpha * T_1)}) = 2$$

The logarithmic form is:

$$(\alpha * T_2) - (\alpha * T_1) = \ln 2$$

$$\alpha (T_2 - T_1) = \ln 2$$

$$T_2 - T_1 = \ln 2 / \alpha$$

Similarly, the required increase in body temperature to triple the metabolic rate is:

$$T_2 - T_1 = \ln 3 / \alpha$$

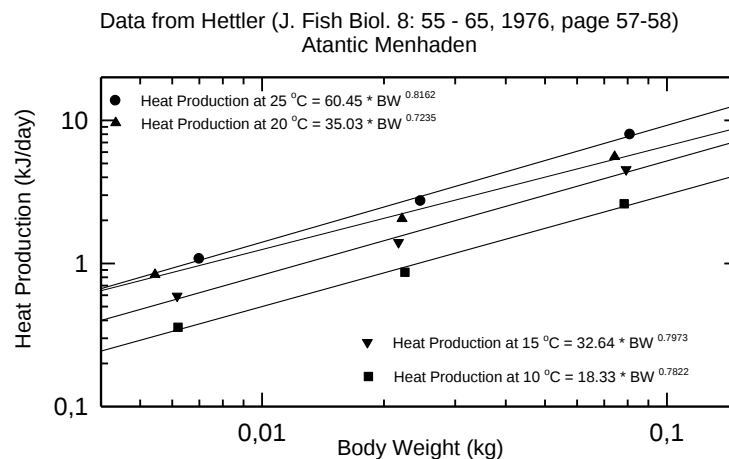
Examples of the (exponential) effect of temperature on the metabolic rate as calculated from data in various literature reports

1. Studies described by W.F. Hettler (Influence of temperature and salinity on routine metabolic rate and growth of young Atlantic Menhaden. *Journal of Fish Biology* 8: 55-65, 1976)

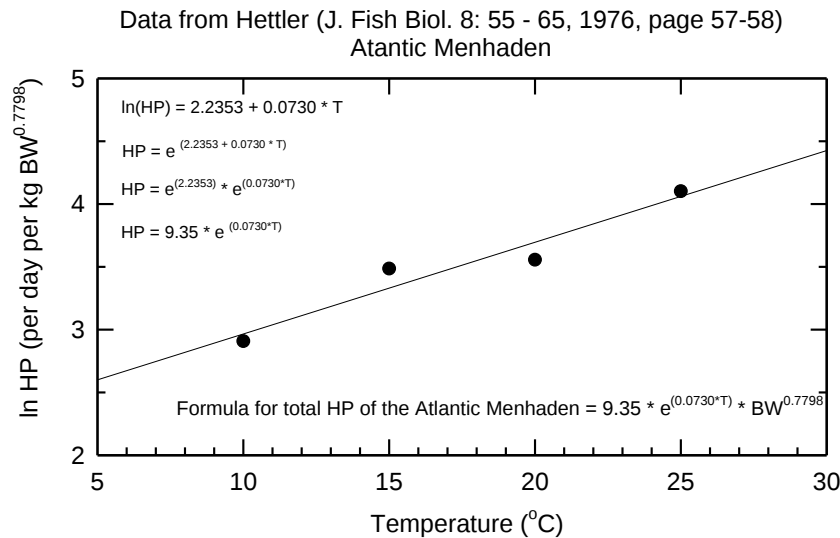
In this article, the effect of temperature on the basal or routine metabolism in the Atlantic Menhaden is described

The data are from Table 1 of the article of Hettler and the oxygen consumptions in this table were converted into kJ heat production (1 mg oxygen is the equivalent of 13.75 kJ heat production). First, we calculated the values of "a" (the normalization constant of the formula for heat production aBW^b at various water or body temperatures from 10 – 25 centigrades. "a" represents the heat production per kg BW^b (kg metabolic weight) at various temperatures and the heat production represents the basal metabolism or routine metabolism of the menhaden.

The heat production was plotted vs the body weight on double logarithmic graph paper and the heat production "a" per kg BW^b was calculated (see figure below) for the various temperatures. The results are given in the Figure below:



Subsequently, we plotted the $\ln$ values of the various values for “a” vs the temperature (figure below).



By linear regression, we can calculate that the heat production per kg BW^{0.7798} (the exponent 0.7798 is the average values of the exponents in the figure above) as function of the temperature is:

$$\text{Heat production per day per BW(kg)}^{0.7798} = 9.35 * e^{0.0730 * T}$$

The complete formula for calculating the heat production becomes then:

$$\text{Routine or Basal Heat Production (kJ/day)} = 9.35 * e^{0.0730 * T} * \text{BW(kg)}^{0.7798}$$

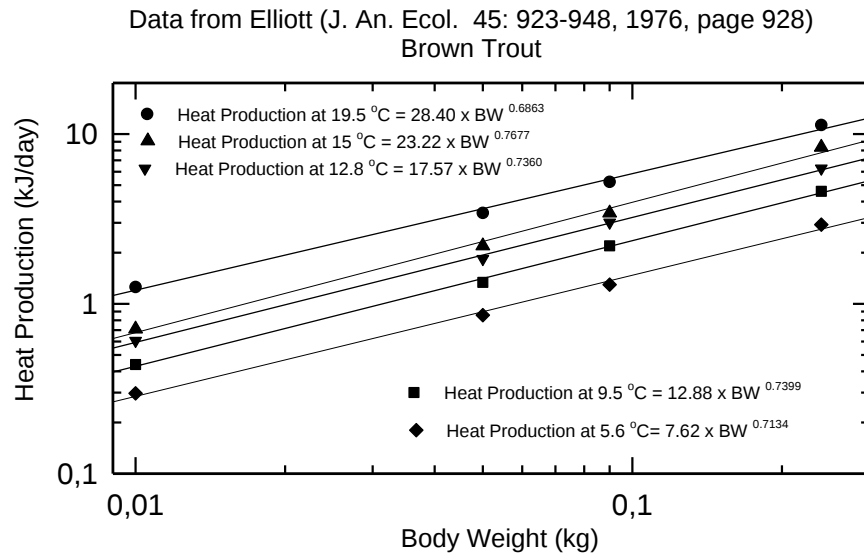
This formula represents the basal metabolic rate or the routine metabolism of the atlantic menhaden and includes the effect of the temperature on the heat production or metabolic rate.

The effect of the temperature on the heat production of metabolic rate can be described by the formula:

$$\text{Heat Production per kg BW}^{0.80} \text{ (at } T=T_2) = \text{Heat Production per kg BW}^b \text{ (at } T=T_1) * e^{0.0730 * (T_2 - T_1)}$$

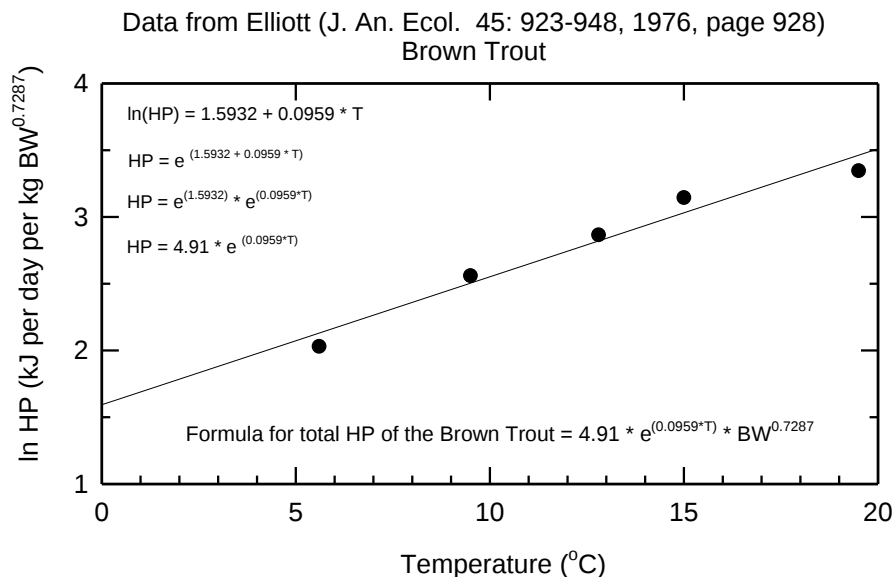
2. Studies described by J.M. Elliott (The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. *J Animal Ecology* 45: 923-948, 1976).

The values for the normalization constant “a” and the scaling coefficient “b” of the formula: heat production = $a * BW^b$ for different body (or water) temperatures can be experimentally determined as indicated above (i.e. by measuring the fasting heat production or fasting energy loss of trout or other animals of various body weights at various temperatures). In the present example we will use values of “a” at various temperatures that are derived from data of Elliott (Journal of Animal Ecology 45: 923 – 1976, 1976, graphs at page 928).



First, we calculate the values of “a” at various temperatures from 5 – 20 centigrees. “a” represents the heat production per kg BW(kg)^{0.75} (kg metabolic weight) at the various temperatures and the heat production represents the basal metabolism or routine metabolism of the brown trout. The data in the figure above are obtained from the graph on page 928 in the article of Elliott (1976).

Subsequently, we plot the ln values of the various values for “a” vs the temperature.



By linear regression, we can calculate that the heat production per kg BW(kg)^{0.7287} (the exponent 0.7287 is the average values of the exponents in the figure above) is:

$$\text{Heat production per day per kg BW(kg)}^{0.7287} = 4.91 \cdot e^{0.0959 \cdot T}$$

The complete formula for calculating the heat production becomes then:

$$\text{Routine or Basal Heat Production (kJ/day)} = 4.91 \cdot e^{0.0959 \cdot T} \cdot \text{BW(kg)}^{0.7287}$$

This formula represents the basal metabolic rate or the routine metabolism of the brown trout and includes the effect of the temperature on the heat production or metabolic rate.

Example: when the temperature is 15 °C, then the heat production per kg metabolic weight = 4.91 * $e^{0.0959 * 15} * BW(kg)^{0.7287} = 20.69 BW(kg)^{0.7287} kJ$

Elliott (1976, page 926, equation 9, temperature from 7.1 – 19.5 °C) calculated the following formula:

$$\text{Standard or Routine or Basal Heat Production (kcal/day)} = 8.277 * e^{0.0938 * T} * BW(g)^{0.731}$$

Where heat production is in calories and body weight in grams. We will convert the calories to joules and grams to kg body weight. 1 cal = 4.184 J, thus 8.277 x 4.184 = 34.63 J = 0.03463 kJ. The formula becomes then:

$$\text{Standard or Routine or Basal Heat Production (kJ/day)} = 0.03463 * e^{0.0938 * T} * BW(kg)^{0.731}$$

Where heat production is in kJ and body weights in grams. Further, we have to convert the body weight in grams to body weights in kg.

Let us take a fish of 100 grams:

When we express the body weight in grams:

$$\text{The heat production is then: } HP = 0.03463 * e^{0.0938 * T} * 100^{0.731}$$

When we express the body weight in kg:

$$\text{The heat production is then: } HP = x * e^{0.0938 * T} * 0.1^{0.731}$$

$$0.03463 * e^{0.0938 * T} * 100^{0.731} = x * e^{0.0938 * T} * 0.1^{0.731} \text{ or}$$

$$x = (0.03463 * e^{0.0938 * T} * 100^{0.731}) / (e^{0.0938 * T} * 0.1^{0.731}) = 34.63 * (100^{0.731}) / (0.1^{0.731}) = 5.4$$

The formula for the heat production, where the heat production is expressed in kJ per day and the BW in kg:

$$\text{Standard or Routine or Basal Heat Production (kJ/day)} = 5.40 * e^{0.0938 * T} * BW(kg)^{0.731}$$

which is slightly different from the formula we calculated from the data of Elliott; we used for the calculations the estimated data from the graphs of Elliott whereas Elliott used the original data.

Example: When the temperature is 15 °C, then the standard heat production per kg metabolic weight at a temperature of 15 °C is then: $5.4 * e^{0.0938 * 15} = 22.05 BW(kg)^{0.7287} kJ / day$.

Further, Elliott calculated that the maintenance metabolism of the brown trout was (Elliott , 1976 page 933 equation 12, temperature from 7.1 – 19.5 °C):

$$\text{Maintenance Heat Production (kcal/day)} = 11.866 * e^{0.0915 * T} * BW(g)^{0.721}$$

Where heat production is in calories and body weight in grams.

After conversion to kJ and kg, (see procedure above) the formula is:

$$\text{Maintenance Heat Production (kJ/day)} = 7.75 * e^{0.0915 * T} * BW(kg)^{0.721}$$

Example: when the temperature is 15 °C, then the maintenance heat production per kg metabolic weight = 30.58 BW(kg)^{0.721} kJ / day

Thus, the effect of the temperature on the maintenance metabolic rate or heat production can be described by the formula:

$$\text{Heat Production per kg BW}^{0.721} (\text{at } T=T_2) = \text{Heat Production per kg BW(kg)}^{0.721} (\text{at } T=T_1) * e^{0.0915*(T_2-T_1)}$$

Example: The heat production per day per kg BW(kg)^{0.80} of a trout is 40 kJ at a temperature of 10 °C, then the metabolic rate per kg BW(kg)^{0.80} at a temperature of 15 °C is:
 $40 * e^{0.0938*(15-10)} = 40 * e^{0.0938*5} = 63.9 \text{ BW(kg)}^{0.80} \text{ kJ / day}$

The formulas above are derived from data in the brown trout. However, we may assume that the relative effect of the temperature on the metabolic rate may be similar in other species of trout, although the absolute values for the heat production at various temperatures may be different.

3. Studies described by Andrew Clarke and Nadine M. Johnston (Scaling of metabolic rate with body mass and temperature in teleost fish. Journal of Animal Ecology 68: 893 – 905, 1999)

They reported that the effect of the temperature on the resting, routine or basal metabolic rate was:

$$\ln R = 15.7 - 5.02 * (1/T)$$

where T is degrees Kelvin (°C = 273 °Kelvin) and R is basal metabolism in mmol O₂ per hour for a 50 grams fish.

They expressed in their formula the temperature in °Kelvin, but the graph 3b on page 897 of their article indicates that similar effects on heat production were observed when the temperature was expressed in °C. From graph 3b of their article, we estimated that the slope of the graph 3b was 0.060 and the intercept -2.7. The formula is then:

$$\ln R = -2.7 + 0.060*T$$

$$\text{Resting oxygen consumption} = R = e^{(-2.7 + 0.060*T)} = e^{-2.7} * e^{0.060*T} = 0.0672 * e^{0.060*T}$$

where T is degrees Celsius and R is basal metabolism in mmol O₂ per hour for a 50 grams fish.

The metabolic weight of a fish of 50 grams is: $0.05^{0.80} = 0.091$

1 mmol O₂ = 0.001 mol, 1 mol O₂ is 32 grams, the energy equivalent of 1 gram of O₂ is 13.6 kJ, 1 day is 24 hours. Thus:

$(0.0672 * 0.001 * 32 * 13.6 * 24) / 0.091 = 7.69 \text{ kJ heat production per kg metabolic weight per day.}$

We converted the formula into:

$$\text{Resting Heat Production per kg BW(kg)}^{0.80} = 7.69 * e^{0.060 * T}$$

Where the temperature is in °C, BW in kg and heat production in kJ per kg BW^{0.80}.

The complete formula for the total resting heat production according to Clarke and Johnston is then:

$$\text{Resting Heat Production} = 7.69 * e^{(0.060 * T)} * \text{BW(kg)}^{0.80}$$

The standard heat production per kg metabolic weight (BW(kg)^{0.7287}) at a temperature of 15 °C = $7.69 * e^{(0.060 * 15)} = 18.91$ kJ per day.

The effect of the temperature on the heat production of metabolic rate can be described by the formula:

$$\text{Heat Production per kg BW(kg)}^{0.80} \text{ (at } T=T_2) = \text{Heat Production per kg BW(kg)}^{0.80} \text{ (at } T=T_1) * e^{0.060*(T_2-T_1)}$$

Example: the heat production per kg BW(kg)^{0.80} is 40 kJ/day at a temperature of 10 °C, then the metabolic rate per kg BW(kg)^{0.80} at a temperature of 15 °C is then:
 $40 * e^{0.0604*(15-10)} = 40 * e^{0.0604*5} = 54.1$ BW(kg)^{0.80} kJ/day.

4. Studies described by G.G. Winberg (Rate of metabolism and food requirements of fishes. Belorussian State University, Minsk, 1956. Translated from Russian by Fish. Res. Bd Can Transl Ser No 194, 1960, can be downloaded from the internet)

We calculated from the data of Winberg that the effect of the temperature on the heat production or metabolic rate of fish in general can be described by the formula:

$$\text{Heat Production per kg BW}^{0.80} \text{ (at } T=T_2) = \text{Heat Production per kg BW}^{0.80} \text{ (at } T=T_1) * e^{0.09602*(T_2-T_1)}$$

4. Other studies that describe the effect of temperature on the metabolic rate.

There are various studies that have described the exponential effect of the temperature on the heat production or the metabolic rate. The results of these studies are presented in Appendices 30 – 39. An overview of the results of these studies is given in the Table below.

The effect of the temperature on the energy expenditure or metabolic rate is described by the formula:

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

The values of α (the scaling exponent or coefficient) are given in the Table below. Routine metabolism of a fish is the basal or fasting metabolism.

Overview of studies on the exponential effect of the temperature on energy expenditure.

Reference	Species	Temperature Range (°C)	scaling exponent α	Condition
Winberg (1956)	General	5 - 30	0,0960	Routine
Clarke and Johnston (1999)	69 fish species	0 - 30	0,0600	Routine
Elliott (1976)	Brown trout	5,6 - 19,5	0,0959	Routine
Hettler (1976)	Atlantic Menhaden	10 - 25	0,0730	Routine
Job (1969)	Tilapia mosambica	15 - 40	0,0948	Routine
Lupatsch (2008)	Tilapia	22 - 28	0,0866	Routine
Lupatsch (2008)	Tilapia	22 - 28	0,0613	Maintenance
Lupatsch and Kissil (2005)	White grouper	22 - 27	0,1042	Routine
Lupatsch and Kissil (2005)	White grouper	23 - 27	0,0860	Maintenance

The routine metabolism is the basal or fasting metabolic rate and maintenance metabolic rate is the metabolic rate for maintenance or to maintain the body weight, thus the basal metabolic rate plus the SDA (specific dynamic action), but without any growth.

Appendix 16 (Text)

Basal Metabolic Rate as partitioned into the Loss of Body Fat and Body Protein.

The basal metabolic rate (i.e. the fasting metabolic rate or the routine metabolic rate) of a fish can be measured by either measuring the oxygen uptake (and convert the oxygen uptake into energy expenditure) or by measuring the loss of energy of the fasting fish (measured by carcass analysis). The uptake of 1 grams of oxygens is approximately the equivalent of 13.75 kJ heat production or energy expenditure. Fish oxydize predominantly fat and proteins and the average energy equivalent of oxygen for fat and protein is 13.75 kJ per gram oxygen uptake (Appendix 4). Thus, the energy expenditure or heat production of the fish can be calculated by multiplying the oxygen uptake (grams) of a fish by 13.75.

The loss of the body energy during fasting is also a measure of the basal or fasting energy expenditure or heat production. Fasting results in a loss of both body fat and body protein. Machiels and Henken (*Aquaculture* 56: 29 – 52, 1986) measured the loss of the total energy under fasting conditions in African Catfish and calculated the basal or fasting energy expenditure (see *Appendices 28 and 29*). Lupatsch et al. (1998) have measured the loss of both the total energy and the protein under fasting conditions in the European Seabass (*Aquaculture* 202: 289-302, 2001) the Gilthead Seabream (*Aquaculture Nutrition* 4: 165-173, 1998), the White Grouper (*Aquaculture* 248: 83-95, 2005, see *Appendices 36 - 38*) and the Tilapia (*Proceedings of the Seventh International Conference on recirculating aquaculture, Roanoke, Virginia 2008*, see *Appendices 33 - 35*) and calculated the fasting or basal energy expenditure. The scaling coefficient or the weight exponent of the energy loss (or energy expenditure or heat production) was about 0.80, whereas the weight exponent of the protein loss was about 0.70. This finding indicates that the loss of protein will increase less than the loss of the total energy when the size of the fish increases.

Example: The fasting energy loss of a tilapia at 22 °C is 25.88 BW(kg)^{0.80} kJ per day (Appendix 33) and the fasting protein loss is : 0.19 BW(kg)^{0.70} g per day (Appendix 35).

The energy loss of a tilapia of 50 grams (= 0.050 kg) is: 25.88 * 0.050^{0.80} = 2.36 kJ per day

The energy loss of a tilapia of 250 grams (= 0.25 kg) is: 25.88 * 0.250^{0.80} = 8.54 kJ per day

Thus the increase in energy loss is: 100% * (8.54 – 2.36) / 2.36 = **262%**

The protein loss of a tilapia of 50 grams (=0.050 kg) is: 0.19 * 0.050^{0.70} = 0.023 per day

The protein loss of a tilapia of 250 grams (=0.250 kg) is: $0.19 * 0.250^{0.70} = 0.075$ kJ per day
 Thus the increase in protein loss is: $100\% * (0.075 - 0.023) / 0.023 = 226\%$

Appendix 17 (Text)

Energy for Maintenance and Energy for Growth

In a growing animal, energy is used for maintenance and for growth. The energy expenditure or heat production under fasting or maintenance conditions is given by the formula $a \cdot BW^b$ as explained above (Appendix 14). Both the fasting energy expenditure as the maintenance energy expenditure can be measured. The fasting energy expenditure or the basal metabolic rate (i.e. the fasting metabolic rate) of an animal can be measured by either measuring the oxygen uptake (and convert the oxygen uptake into energy expenditure, the uptake of 1 grams of oxygens is the equivalent of 13.75 kJ heat production or energy expenditure (see Appendix 4) or by measuring the loss of energy of the fasting animal by carcass analysis. The energy needed for maintenance can be calculated by (1) measuring by oxygen uptake and CO₂ production (indirect calorimetry), (2) by measuring the heat production or energy expenditure (direct calorimetry), or (3) by measuring the energy intake and the loss of energy in the feces and the urine, while the animal is in energy balance. The energy needed for maintenance will be higher than the energy needed for the basal or fasting metabolic rate, since energy is also needed for the Specific Dynamic Action (SDA) or Thermic Effect of Feeding (TEF), i.e. the energy needed for the various metabolic processes such as de-amination of proteins, formation of amino acids into proteins etc. In pigs, the fasting metabolic rate is about 80% of the maintenance metabolic rate, an efficiency of 80%. The energy expenditure attributable to the SDA or TEF is thus 20% of the maintenance energy expenditure. Further, in growing animals, the deposition of energy in the form of fat and protein in the body can also be measured by carcass analysis and there is also energy (SDA or TEF) needed for growth or deposition of energy in the form of fat and protein. Thus, in a growing animal, the intake of digestible, or better, metabolizable energy, represents the energy used for maintenance and the energy used for growth:

$$\text{Metabolizable Energy Intake} = ME_m + (1/k_d) * ER$$

Where ME_m is the energy expenditure or heat production for maintenance ($a \cdot BW^b$), ER is the energy retained and k_d is the efficiency of energy deposition or fraction of the total energy used for growth that is retained in the body. Energy is predominantly deposited in the form of protein and fat and the energy for growth can be partitioned in energy for fat deposition and energy for protein deposition. The formula becomes then:

$$\text{Metabolizable Energy Intake} = ME_m + 1/k_p \text{ PD} + 1/k_f \text{ LD}$$

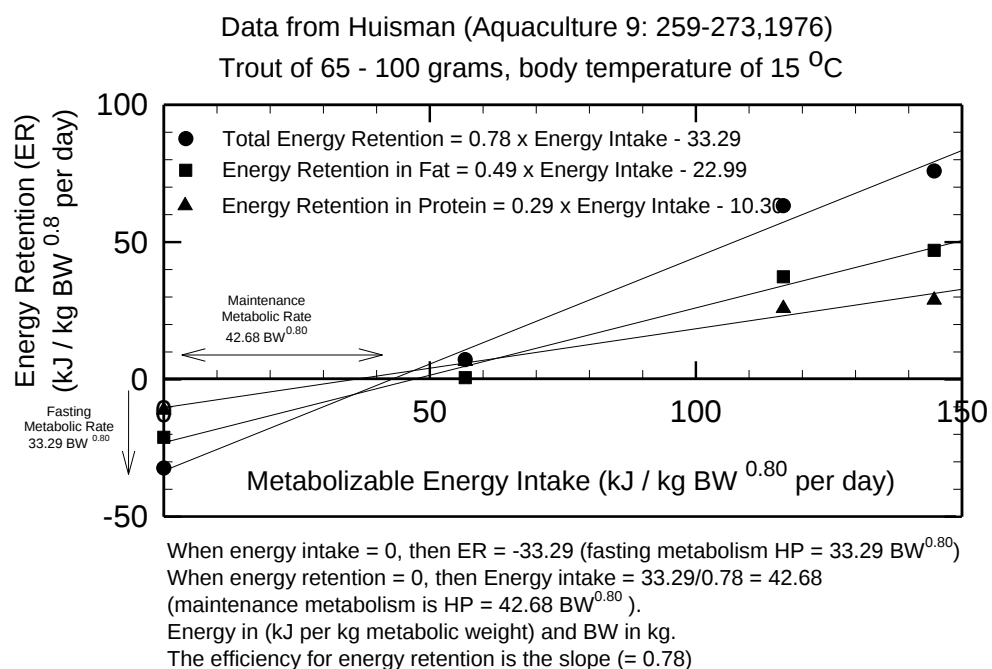
where PD and LD are the protein and lipid deposition (kJ/d), respectively, and k_p is the energetic efficiency of protein deposition and k_f the energetic efficiency of lipid deposition. Appendix 9 gives an overview of various reported values for ME_m and k_d and k_f and k_p in various animal species. There are considerable variations in reported values for k_p and k_f , but the k_p is typically smaller than k_f . For example, the NRC (1998) reports for pigs a k_p value of 0.53 and a k_f value of 0.75. Thus, for the deposition of 1 gram of protein (23.65 kJ) is needed $(1/0.53) * 23.65 = 45$ kJ of total energy and for the deposition of 1 grams of fat (39.6 kJ) is needed $(1/0.75) * 39.6 = 53$ kJ of total energy (the energy of the deposited 1 gram of fat and the energy needed for this deposition). Or, for the deposition of 1 kJ as protein is needed $(1/0.53) * 1 = 1.89$ kJ and for the deposition of 1 kJ as fat $(1/0.75) * 1 = 1.33$ kJ, thus more energy is needed for the deposition of 1 kJ as protein than as fat. Overviews of various reported k_d , k_p and k_f values in various animal species are given by Tess et al. (1984), Millward (1976), Nieto et al. (1995), Rattray and Joyce (1976), Roberts and Young (1988) and Sakomura (2004), see also Blaxter 1989, page 259 and 272-273. In animal nutrition, a

average value of about 0.65 for k_d (efficiency of energy deposition above maintenance) is mostly used for the efficiency of the deposition of the total energy in the body. The efficiency of the utilisation of metabolizable energy for maintenance is usually higher than the utilization of metabolizable energy for growth (Blaxter 1989, page 259, Sakomura 2004, Table 1).

Appendix 18 (Text)

Deposition of Energy as Fat and Protein for Growth

When an animal is fed more energy than is needed for maintenance, the excess of energy will be deposited in the form of protein and fat. Protein is essential for growth, since protein drives the growth. The amount of protein and fat that is deposited can be measured by carcass analysis. The Figure below shows the amount of protein and fat that are deposited when increasing amounts of metabolizable energy are fed to a trout.

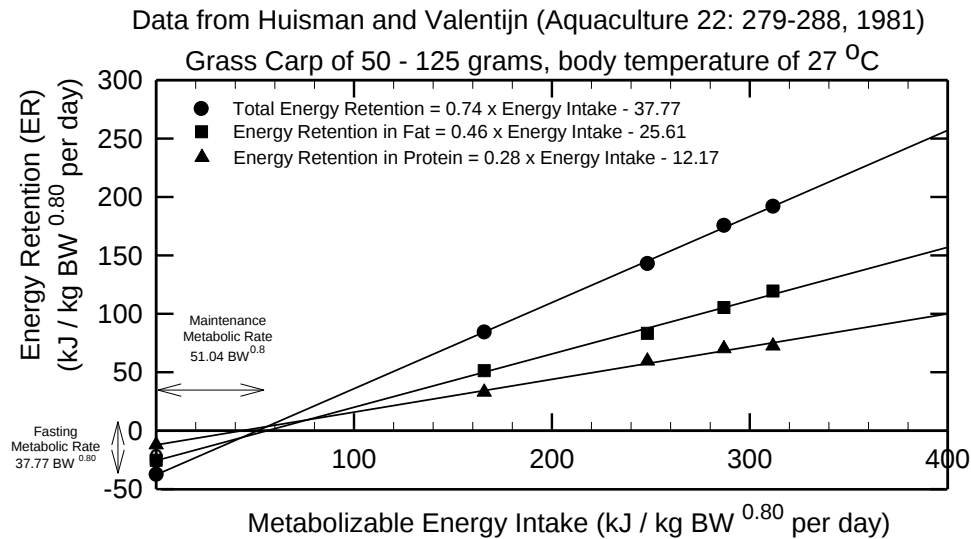


The equation for the retention of metabolizable energy in the body as a function of the intake of metabolizable energy intake (MEI) is:

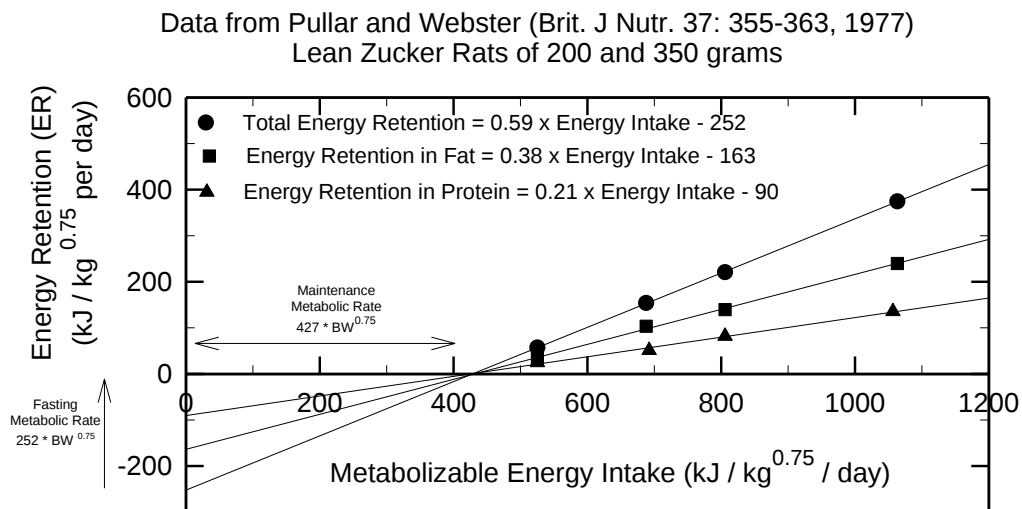
$$\text{Metabolizable Energy Retention} = -33.29 + 0.78 * \text{MEI}$$

When the intake of MEI = 0, then there is a loss of energy ($33.29 \text{ kJ/BW}^{0.80}$ per day) and this loss represents the basal metabolic rate. As indicated above, the basal metabolic rate can also be measured by measuring the energy expenditure (by direct calorimetry) or by measuring the oxygen uptake (indirect calorimetry). When the energy retention = 0, then we have the situation of maintenance and the equation becomes $0 = -33.29 + 0.78 \text{ MEI}$ or the MEI equals the energy intake needed for maintenance and is $33.29 / 0.78 = 42.68 \text{ kJ BW}^{0.80}$ per day. The energy intake above maintenance is deposited in the body with an efficiency of 0.78 or 78%. The efficiency of energy used either for maintenance or for growth in this example is 78%, but there may be differences in the efficiency of energy used for maintenance and growth. In order to find these possible differences in efficiencies, also measurements of energy losses between the situation of maintenance and complete starvation should be done.

The Figures below give the results of some other studies done in the Grass Carp and in Zucker rats.



When energy intake = 0, then ER = -37.77 (fasting metabolism HP = $37.77 \text{ BW}^{0.80}$)
 When energy retention = 0, then Energy intake = $37.77/0.74 = 51.04$
 (maintenance metabolism is HP = $51.04 \text{ BW}^{0.80}$).
 Energy in (kJ per kg metabolic weight) and BW in kg.
 The efficiency for energy retention is the slope (= 0.74)



When energy intake = 0, then ER = -252 (fasting metabolism HP = $252 \times \text{BW}^{0.75}$)
 When energy retention = 0, then Energy intake = $252/0.59 = 427$
 (maintenance metabolism is HP = $427 \times \text{BW}^{0.75}$).
 Energy in (kJ per kg metabolic weight) and BW in kg.
 The efficiency for energy retention is the slope (= 0.59)

More graphs are given in Appendix 40 – 44.

Appendix 19 (Text)

Feed Intake and Feeding Levels as a Function of Body Weight

We can express the feed intake in two different ways:

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

(a) Feed intake expressed in grams per kg metabolic weight (per $\text{BW}(\text{kg})^b$).

The maintenance energy expenditure of an animal is expressed in kJ per kg metabolic weight (per BW(kg)^b) and the maintenance metabolic rate or energy expenditure is described by the allometric scaling formula (see appendix 14):

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

Where a is the normalization constant (kJ per gram metabolic weight (per BW(kg)^{0.80})) and b the scaling coefficient. The scaling coefficient is for most terrestrial animal species 0.75 and for most fish species 0.80. The maintenance energy expenditure is a kJ per kg metabolic weight (per BW(kg)^b) and the animal should thus have a metabolizable energy intake of a kJ per BW(kg)^b or have a feed intake per BW(kg)^b that supplies this a kJ per per kg metabolic weight (per BW(kg)^b) for maintenance. Therefore, the (maintenance) feed intake should follow the same pattern as the (maintenance) energy expenditure and the feed intake (or energy intake) should thus also be expressed in grams per kg metabolic weight (per BW(kg)^b).

When the feed intake is c grams per kg metabolic weight (per BW(kg)^b), then the total feed intake is:

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

where BW is the body weight in kg and b is the scaling coefficient (0.80 for most fish species and 0.75 for most terrestrial animals).

When more feed and thus more metabolizable energy per kg metabolic weight (per BW(kg)^b) 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:

$$\frac{M_p}{M_m} = \frac{(\text{feed intake} * \text{energy density feed}) * \text{BW(kg)}^b - (\text{maintenance feed intake} * \text{energy density feed}) * \text{BW(kg)}^b}{(\text{maintenance feed intake} * \text{energy density feed}) * \text{BW(kg)}^b} \text{ or}$$

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

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

where the feed intake represents the feed intake per kg metabolic weight (per BW(kg)^b), the maintenance feed intake represents the maintenance feed intake per kg metabolic weight (per BW(kg)^b) (a constant quantity 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)^b) and changes when the feed intake per kilogram metabolic weight (per BW(kg)^b) changes. Each defined level of feed intake c (or metabolizable energy intake) per kg metabolic weight (per BW(kg)^b) above maintenance is associated with a defined ratio of metabolizable energy for production / metabolizable energy for maintenance (Mp/Mm).

Thus, when the same amount of feed per kg metabolic rate (per BW(kg)) is administered to different sizes animals, then also the ratio of Mp/Mm will be the same for all these different sizes animals (see e.g. Appendix 91, page 166). An increase or decrease of the feed intake per kg metabolic weight (per BW(kg)^b), however, will result in an increase or decrease of metabolizable energy available for growth or production and thus also result in an increase or decrease of the ratio Mp/Mm (see Appendix 90, page 165).

It is, however, more common and practical to express the feed intake as % of body weight. The feed intake per kg metabolic weight (per $BW(kg)^b$) 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 ($BW(kg)^b = c$), then the total feed intake is:

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

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

$$\text{Feed Intake (grams) per 100 gram trout} = (c * BW(kg)^{(b-1)}) / 10$$

$$\text{\% feed intake per day (or feed intake per 100 gram of fish)} = (c/10) * BW(kg)^{(b-1)} \quad (1)$$

where c (grams) is the feed intake per kg metabolic weight ($BW(kg)^b$) per day and the $BW(kg)$ is expressed in kg and the scaling coefficient is $(b - 1)$.

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

$$\text{\% feed intake per day} = (c/10) * BW(kg)^{(b-1)} \text{ or}$$

$$\text{Feed Intake per kg metabolic weight} = c = 10 * (\text{\% feed intake per day}) / (BW(kg)^{(b-1)}) \quad (2)$$

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 expressed in grams per kg metabolic weight (per $BW(kg)^b$)

(b is the scaling coefficient for metabolic weight, which is 0.75 for most terrestrial animals and 0.80 for most fish species and $(b - 1)$ are then - 0.25 and - 0.20, respectively).

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

$$\text{\% feed intake per day (or feed intake per 100 gram of fish)} = (c/10) * BW(kg)^{(b-1)} \quad (1)$$

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

$$\text{feed Intake per kg metabolic weight} = c = 10 * (\text{\% feed intake per day}) / (BW(kg)^{(b-1)}) \quad (2)$$

For the calculations of the total feed intake for a defined size animal, we have to know the feed intake per kg metabolic weight or the percentage feed intake for each defined size animal (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 $BW(kg)^b$) and the scaling factor $b = 0.80$ (for fish).

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

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):

$$\begin{aligned}\% \text{ feed intake per day (or feed intake per 100 gram of fish)} &= (c/10) * BW(kg)^{(b-1)} = 1.2 * BW(kg)^{-0.20} \\ \% \text{ feed intake of a fish of 300 grams} &= 1.2 * BW(kg)^{-0.20} = 1.2 * (0.3)^{-0.20} = 1.5267\%\end{aligned}$$

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

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

As shown above, the feed intake per kg metabolic weight (per $BW(kg)^b$) can be converted into the feed intake expressed as % of body weight, and the feed intake expressed as % of body weight can be described by an allometric scaling feeding formula of the general form $x * BW(kg)^p$ and where x is the normalization constant and p the scaling coefficient:

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

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 $BW(kg)^b$), then:

$$\text{feed Intake per kg metabolic weight} = c = 10 * (\% \text{ feed intake per day}) / (BW(kg)^{(b-1)})$$

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

$$\text{feed Intake (g) per kg metabolic weight} = c = 10 * (x * BW(kg)^p) / (BW(kg)^{(b-1)}) \text{ or}$$

$$\text{feed intake (g) per kg metabolic weight (per } BW(kg)^b = c = x * 10 * BW(kg)^{(p-(b-1))}$$

where c is the feed intake per kg metabolic weight (per $BW(kg)^b$) and b is the scaling coefficient which is 0.75 for most terrestrial animal species and 0.80 for most fish species.

Thus, the feed intake per kg metabolic weight (per $BW(kg)^b$) can also be described by an allometric scaling formula. When the general allometric scaling formula to describe the feed intake per kg metabolic weight (per $BW(kg)^b$) is:

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

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

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

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

$$\% \text{ feed intake per day (or feed intake per 100 gram of fish)} = (z * BW(kg)^w / 10) * BW(kg)^{(b-1)}$$

or

$$\% \text{ feed intake per day (or feed intake per 100 gram of fish)} = z/10 * BW(kg)^{w+(b-1)}$$

Thus, both the feed intake expressed in % of body weight and the feed intake expressed in gram per kg metabolic weight (per $BW(kg)^b$) are functions of the body weights and can be calculated for each different size trout. Further, the allometric scaling formula describing the feed intake either expressed as % of body weight or in grams per kg metabolic weight (per $BW(kg)^b$) can be converted from one to another (see below).

Conversion 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)^b)

(where b is the scaling coefficient which is 0.75 for most terrestrial animal species and 0.80 for most fish species and $(b - 1)$ are then - 0.25 and - 0.20, respectively.)

When the feed intake in grams per kg metabolic weight (per BW(kg)^b) (as a function of body weight) is described by the general allometric scaling formula:

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

$$\% \text{ feed intake} = z/10 BW(kg)^{(w + (b - 1))} \quad (3)$$

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

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

$$\text{feed intake per kg metabolic weight (per BW(kg)^b)} = x * 10 * BW(kg)^{(p - (b - 1))} \quad (4)$$

Where b is the scaling coefficient for metabolic weight (0.75 for most terrestrial animals and 0.80 for most fish species and $(b - 1)$ are then - 0.25 and - 0.20, respectively.

Example 1:

The formula for the feed intake expressed in % of body weight is described by the formula:

% feed intake = $x * BW(kg)^p = 1.2 * BW(kg)^{-0.25}$ per day and the scaling coefficient for metabolic weight $b = 0.80$ (for fish) and $(b - 1) = - 0.20$

The formula for the feed intake expressed in grams per kg metabolic weight is then:

$$\text{feed intake in grams per BW(kg)}^{0.80} = x * 10 * BW(kg)^{(p - (b - 1))} = 10 * 1.2 * BW(kg)^{(-0.25 - (-0.20))} = 12 BW(kg)^{-0.05}$$

feed intake in grams (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.

Example 2:

The formula for the feed intake expressed in grams per kg metabolic weight is:

feed intake per BW(kg)^b = $z * BW(kg)^w = 12 * BW(kg)^{-0.05}$ per day and the scaling factor $b = 0.80$ (for fish)

The formula for the feed intake expressed in % of body weight is then:

$$\text{feed intake as \% body weight} = z/10 BW(kg)^{(w + (b - 1))} = 1.2 * BW(kg)^{(-0.05 + (0.8 - 1))} = 1.2 * BW(kg)^{-0.25}$$

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.

However, when the scaling coefficient p of the formula % feed intake = $x * BW(kg)^p$ that expresses the feed intake in % of the body weight is $(b - 1)$ or % feed intake = $x * BW(kg)^{(b - 1)}$ (where b is the scaling coefficient for metabolic weight of 0.75 for most terrestrial animals and 0.80 for most fish species and $(b - 1)$ is then - 0.25 and - 0.20, respectively), then conversion of this formula into grams per kg metabolic weight (per BW(kg)^{0.80}) with formula 4:

$$\text{feed intake (g) per kg metabolic weight (per BW(kg)}^{0.80} = c = x * 10 * BW(kg)^{(b - 1) - (b - 1)} \text{ or}$$

$$\text{feed intake (g) per kg metabolic weight (per BW(kg)}^b = c = a * 10$$

and the feed intake per kg metabolic weight (per BW(kg)^b) 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). Thus, when the scaling coefficient of the formula that describes the feed intake as % of body weight is $(b - 1)$, then both the feed intake per kg metabolic weight (per BW(kg)^b) 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 fish size (see graph in Appendix 91). Some examples are given below and in Appendix 90 and 91, pages 165 and 166.

Example 1:

When we have a feeding curve: % feed intake = $x \cdot BW(kg)^p = 1.2 \cdot BW(kg)^{-0.20}$ for a fish and the scaling factor b for the fish is 0.80, 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:

$$\text{feed Intake (g) per kg metabolic weight (per } BW(kg)^{0.80}) = c = 10 \cdot (\% \text{ feed intake per day}) / (BW(kg)^{(b-1)})$$

$$\text{feed Intake (g) per kg metabolic weight (per } BW(kg)^{0.80}) = c = 10 \cdot (x \cdot BW(kg)^p) / (BW(kg)^{(b-1)})$$

$$\text{feed intake (g) per kg metabolic weight (per } BW(kg)^{0.80}) = c = 10 \cdot (x \cdot BW(kg)^{(p+(b-1))})$$

$$\text{feed intake (g) per kg metabolic weight (per } BW(kg)^{0.80}) = c = 10 \cdot (1.2 \cdot BW(kg)^{(-0.20-(0.80-1))} = 12 \cdot BW(kg)^0$$

$$\text{feed intake (g) per kg metabolic weight (per } BW(kg)^{0.80}) = c = 12.$$

and this is true for all sizes of fish and is independent on the body weight.

When we have a feeding curve: feed intake per kg metabolic weight (per $BW(kg)^{0.80}$) = $c = 12$ grams (which is a constant value for all body weights) for a fish and the scaling factor b for fish is 0.80, then we can convert this feeding level into the feed intake as % of body weight with the conversion formula 1 :

$$\% \text{ feed intake per day (or feed intake per 100 gram of fish)} = (c/10) \cdot BW(kg)^{(b-1)}$$

$$\% \text{ feed intake per day (or feed intake per 100 gram of fish)} = (12/10) \cdot BW(kg)^{(0.80-1)} = 1.2 \cdot BW(kg)^{-0.20}$$

Example 2: we have for example a trout feed with a metabolizable energy density of 19.64 kJ / gram (feed in Table 5) 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 $1.2 \cdot BW(kg)^{-0.20}$ (thus the scaling factor is -0.20).

The maintenance energy expenditure of trout is about $50 \cdot BW(kg)^{0.80}$ at 15 °C (see Appendix 9).

The energy expenditure of a trout of 200 grams is: $50 \cdot (0.2)^{0.8} = 13.79$ kJ per day. The intake of energy from the feed is $12 \cdot 19.64 \cdot BW(kg)^{0.80} = 12 \cdot 19.64 \cdot (0.2)^{0.80} = 65.03$ kJ. The ratio $Mp/Mm = (65.03 - 13.79) / 13.79 = 3.72$.

The maintenance energy expenditure of a trout of 400 grams is $50 \cdot (0.4)^{0.80} = 24.02$ kJ and the intake of energy from the feed is $12 \cdot 19.64 \cdot BW(kg)^{0.80} = 12 \cdot 19.64 \cdot (0.4)^{0.80} = 113.23$ kJ. The ratio of metabolizable energy for production / metabolizable energy for maintenance or $Mp/Mm = (113.23 - 24.02) / 24.02 = 3.71$.

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 Appendix 91 and compare with Appendix 90, pages 165 and 166).

Example 3:

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 14):

For example, the formula for a feeding curve (see above), expressed as % of body weight is:

$$\% \text{ feed intake (gram feed per 100 gram trout)} = a \cdot BW(kg)^b$$

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:

$$\% \text{ feed intake (gram feed per 100 gram trout)} = x \cdot BW(g)^b$$

We can calculate the value of x as following:

$$\% \text{ feed intake} = a \cdot BW(kg)^b = x \cdot [BW(kg) \cdot 1000(g)]^b$$

Solving for x gives:

$$x = [a \cdot BW(kg)^b] / [BW(kg) \cdot 1000(g)]^b =$$

$$x = [a \cdot BW(kg)^b] / BW(kg)^b \cdot 1000^b = a / 1000^b$$

thus the formula becomes then:

$$\% \text{ feed intake} = (a / 1000^b) \cdot BW(g)^b \text{ where the body weights are now expressed in grams.}$$

Thus:

Conversion from kg into grams: Divide a (the normalization constant) by 1000^b (b is scaling factor or coefficient)

Conversion from grams into kg: Multiply a (the normalization constant) by 1000^b (b is scaling factor or coefficient)

Appendix 20 (Text)

The Effect of the Temperature on the Feeding Level in Fish

The effect of temperature on the feeding level is of particular interest in fish since fish are poikilothermic and the metabolic rate of a fish is dependent on the water and body temperature. Feeding per kg metabolic weight involves that the amount of feed (and energy) parallels or follows the heat production or metabolic rate of different size fish. Therefore, the

effect of the temperature on the feed intake should be the same as the effect on the heat production or metabolic rate in fish. The general 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 (see Appendix 15) and is:

$$\text{Feeding level at } T=T_2 \text{ (in grams per BW(kg))}^{0.80} = (\text{feeding level at } T=T_1) * e^{\alpha(T_2-T_1)}$$

Studies of Winberg (1956) have indicated that the value for α in the formula describing the effect of the temperature on the heat production in fish (see Appendix 15) and thus also on the feed intake is in general about 0.095 and a similar value for α has been reported by Elliott (1976) in the Brown Trout at a temperature range of 6 – 20 °C. Various values for other fish species have been reported and calculated (Appendix 30 – 39). These values for α should thus also be used to calculate the effect of the temperature on the feeding level in grams per kg BW^{0.80}.

Example: We have a feeding level of 15 grams per kg metabolic weight (BW(kg)^{0.80}) for the trout at a temperature of 15 °C. We want to calculate the feeding level at a temperature of 10 °C.
 Formula: Feeding level at $T=T_2 = (\text{feeding level at } T=T_1) * e^{\alpha(T_2-T_1)}$
 We can use the value of 0.095 for α for trout as reported by Elliott (1976).
 Feeding level at ($T=10$ °C) = $15 * e^{0.095*(10-15)} = 9.33$ grams of feed per kg metabolic weight.
 We can also calculate the feeding level at a temperature of 5 °C. There are two ways for these calculations.
 1. The feeding level at 15 °C is 15 grams. Thus:
 Feeding level at ($T=5$ °C) = $15 * e^{0.095*(5-15)} = 5.80$ grams of feed per kg metabolic weight.
 2. The feeding level at 10 °C is 9.10 grams. Thus:
 Feeding level at ($T=5$ °C) = $9.1 * e^{0.095*(5-10)} = 5.80$ grams of feed per kg metabolic weight.

Now we can also easily construct feeding curves (% feed intake) for trout at different temperatures.

Example: We have a feeding level of 20 grams per kg metabolic weight (BW^{0.80}) at 15 °C for all the body weights of trout.

Feeding level at 15 °C = 20 gram / BW(kg)^{0.80}

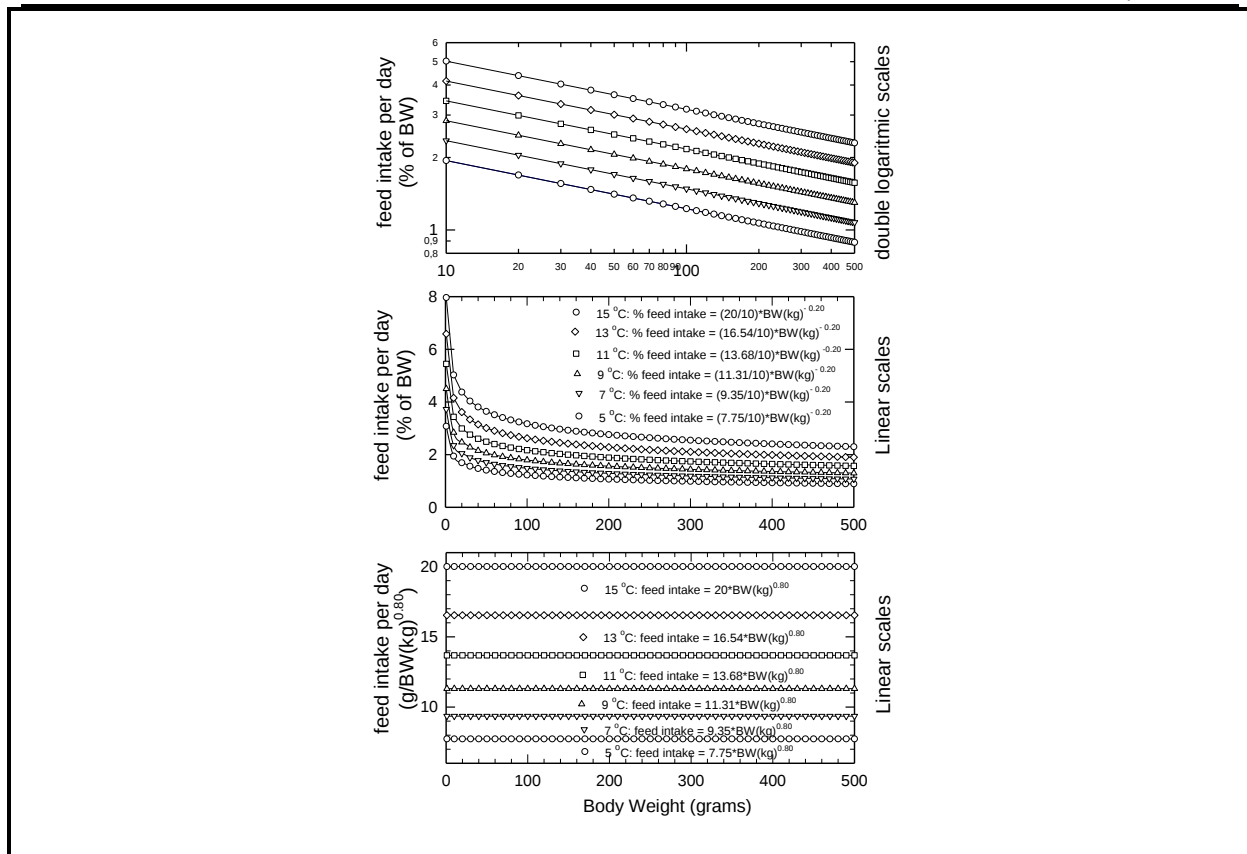
Formula is: Feeding level at $T=T_2$ (in grams per BW(kg)^{0.80}) = (feeding level at $T=T_1$) * $e^{\alpha(T_2-T_1)}$

Feeding level at 13 °C	= $20 * e^{0.095*(13-15)}$	= $20 * e^{-0.19}$	= $20 * 0.827$	= 16.54 gram / BW(kg) ^{0.80}
Feeding level at 11 °C	= $20 * e^{0.095*(11-15)}$	= $20 * e^{-0.38}$	= $20 * 0.684$	= 13.68 gram / BW(kg) ^{0.80}
Feeding level at 9 °C	= $20 * e^{0.095*(9-15)}$	= $20 * e^{-0.57}$	= $20 * 0.566$	= 11.31 gram / BW(kg) ^{0.80}
Feeding level at 7 °C	= $20 * e^{0.095*(7-15)}$	= $20 * e^{-0.76}$	= $20 * 0.468$	= 9.35 gram / BW(kg) ^{0.80}
Feeding level at 5 °C	= $20 * e^{0.095*(5-15)}$	= $20 * e^{-0.95}$	= $20 * 0.387$	= 7.73 gram / BW(kg) ^{0.80}

Now we can calculate the % of feed intake at the various temperatures for the various sizes of fish:
 Formula is: % feed intake per day = $(c/10) * BW(kg)^{-0.20}$
 where c is the feed intake in grams per BW(kg)^{0.80} and BW is expressed in kg.

$$\begin{aligned} 15\text{ °C: \% feed intake} &= (20/10) * BW(kg)^{-0.20} \\ 13\text{ °C: \% feed intake} &= (16.54/10) * BW(kg)^{-0.20} \\ 11\text{ °C: \% feed intake} &= (13.68/10) * BW(kg)^{-0.20} \\ 9\text{ °C: \% feed intake} &= (11.31/10) * BW(kg)^{-0.20} \\ 7\text{ °C: \% feed intake} &= (9.35/10) * BW(kg)^{-0.20} \\ 5\text{ °C: \% feed intake} &= (7.73/10) * BW(kg)^{-0.20} \end{aligned}$$

The graph below shows the feeding levels for trout at various temperatures.



Appendix 21 (Text)

Body Composition

The major components of the body are water, protein, fat and ash. The % of water in mammals is approximately 70 -75%, protein 16%, ash 2-4% and the percentage of fat 10 – 20%. The percentage of protein in the body is rather constant (about 16%) and the same is true for the ash content (about 4% in mammals and about 2.5% in fish). However, the percentage of fat can strongly vary 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. 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 lean body mass (LBM) is the whole body minus the body fat and comprises the protein, ash and water. The composition of the lean body mass appears to be rather constant, as we will see below.

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

$$\text{amount (grams)} = a \cdot BW(g)^b$$

where a is the normalization constant, BW is the body weight in grams and b is the scaling coefficient. The Figure below shows the body composition of the trout.

For example, the total amount of body fat (grams) in trout is plotted vs the corresponding body weights (grams) on double logarithmic graph paper (log – log) (data from

Appendices 68 and 69), and a linear plot arises (Figure below, bottom panel). A linear regression line can be constructed:

$$^{10}\log \text{ fat (grams)} = -1.4789 + 0.1776 \cdot ^{10}\log \text{ BW(g)}$$

$$\text{anti-log of } -1.4789 = 0.0332$$

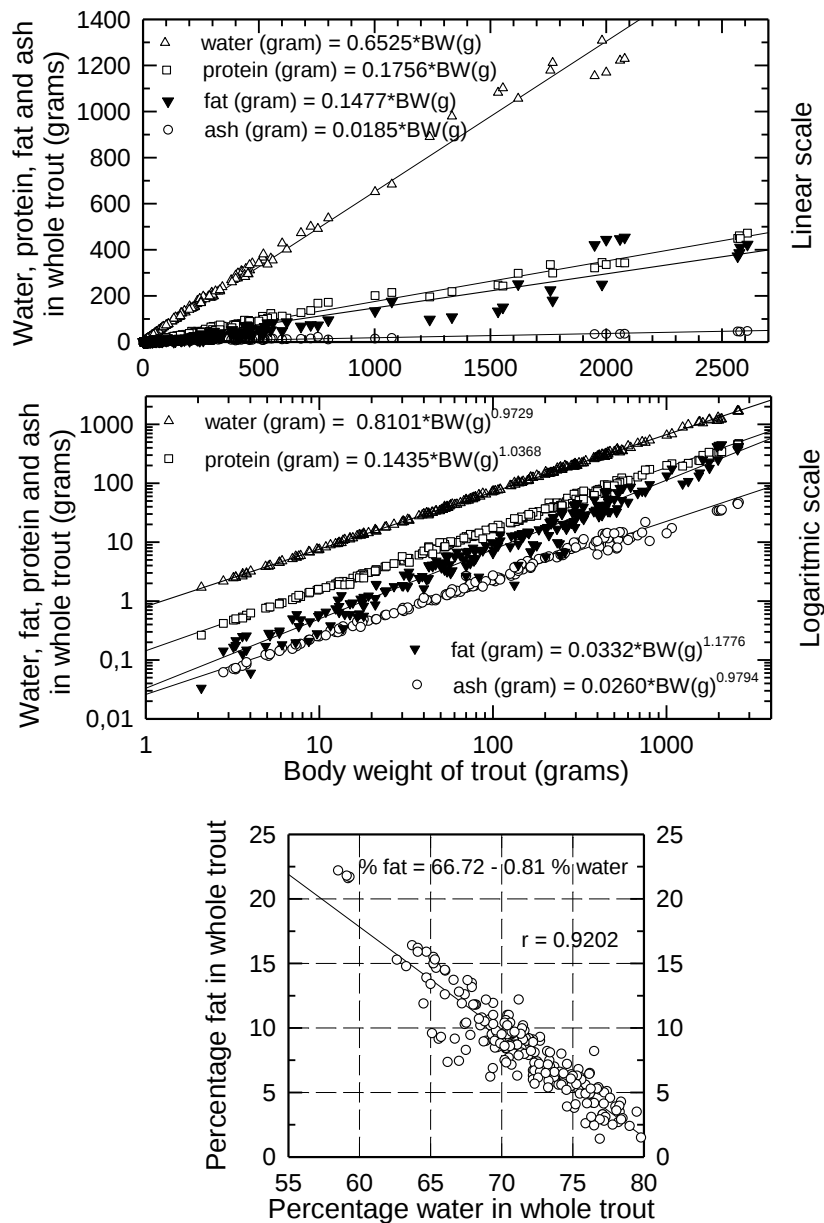
$$^{10}\log \text{ fat (grams)} = ^{10}\log 0.0332 + 0.1776 \cdot ^{10}\log \text{ BW(g)}$$

$$^{10}\log \text{ fat (grams)} = ^{10}\log 0.0332 + ^{10}\log \text{ BW(g)}^{0.1776}$$

$$^{10}\log \text{ fat (grams)} = ^{10}\log (0.0332 \cdot \text{BW(g)}^{0.1776})$$

$$\text{gram body fat in whole body} = 0.0332 \cdot \text{BW(g)}^{0.1776}$$

Thus, the slope of the regression line is 0.1776 and represents the scaling coefficient b and the anti-log of the intercept of the regression is 0.0332 and represents the normalization constant a of the formula $a \cdot \text{BW}^b$.



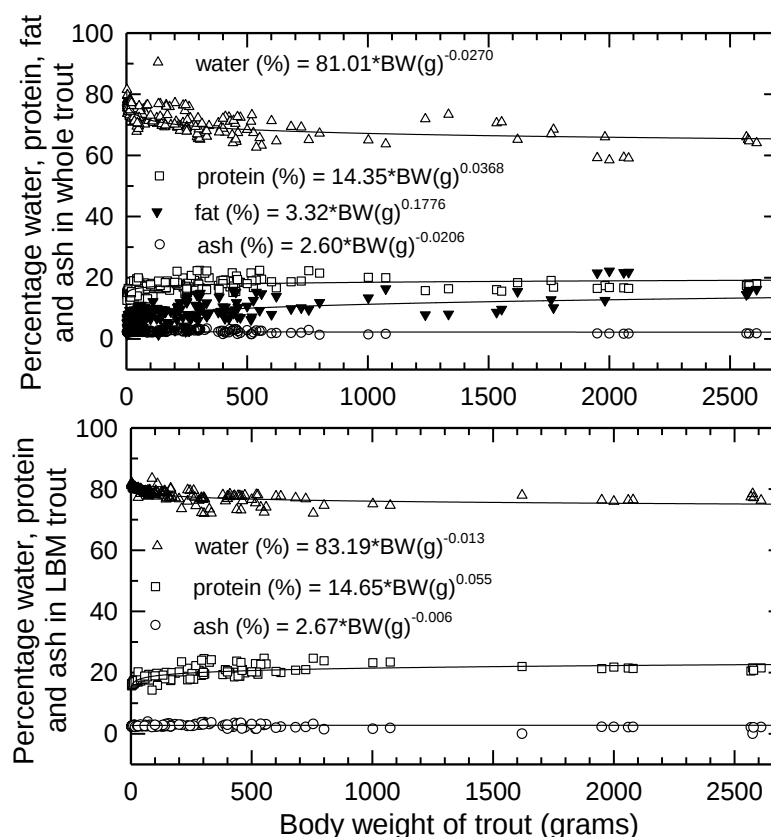
The middle panel of the figure above gives the allometric formulae that describe the amount of protein, fat, ash and water expressed in grams as a function of the body weight in grams of the trout.

The bottom panel of the graph above indicates that there is a strong correlation between the percentage of water and percentage of fat. An increase of 1% water in the trout was associated with the decrease of 0.81% fat.

Further, the percentage of fat in the trout is the absolute amount of fat in grams divided by the body weight in grams and multiplied by 100%. Thus:

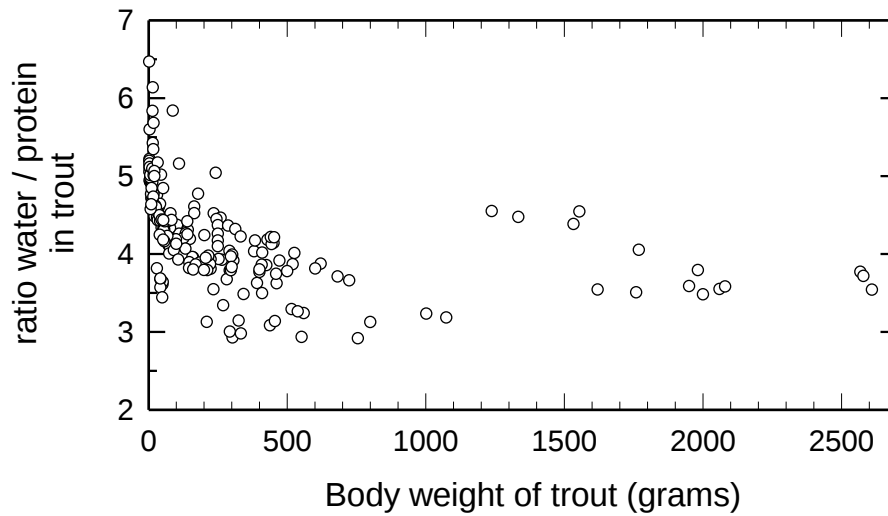
$$\% \text{ fat} = 0.0332 * (\text{BW(g)}^{0.1776} / \text{BW(g)}) * 100\% = 3.32 * \text{BW(g)}^{(1.1776 - 1)} = 3.32 * \text{BW(g)}^{0.1776}$$

Similarly, the formulas for the percentage of protein, fat and ash can be derived. The Figure below shows the composition of the trout in percentages as a function of the body weight and shows also the composition of the lean body mass (LBM) or the fat free mass of the trout.

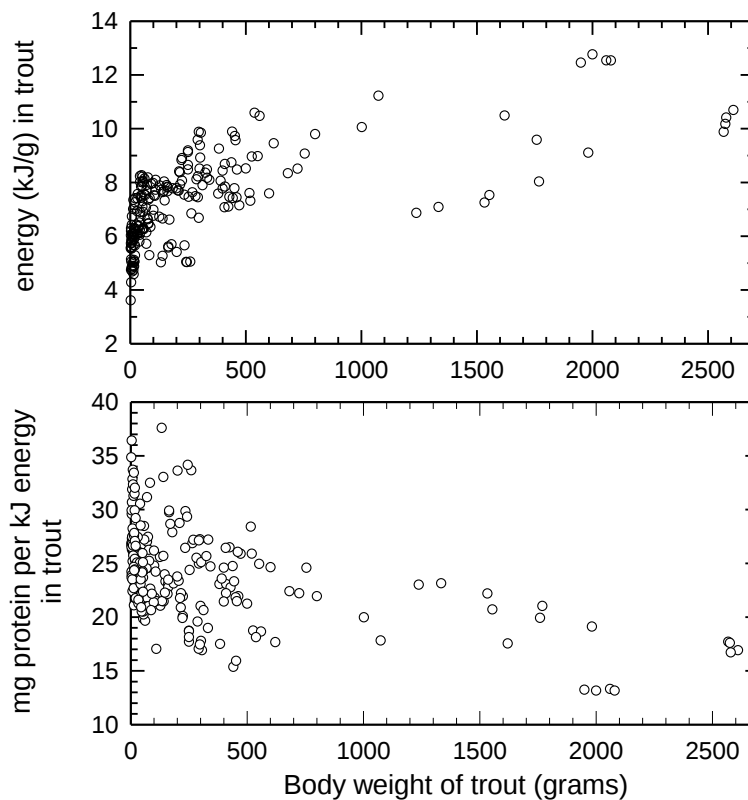


The data of the Figure above (bottom panel) indicates that the % water in the LBM decreases and the % protein increases during the early growth, but remain rather constant later on (trout larger than about 200 grams). These findings suggest that after the early growth, the composition of the LBM is rather constant and that the fat in the body may then be considered as a diluent of the LBM. Similar observations have been reported in other animal species (Pace and Rathbun 1945).

The percentage of water and protein in the LBM of trout after early growth (trout larger than about 200 grams) is thus rather constant and as a consequence, the amount of water associated with the protein should then also be rather constant. The figures below indicates that 1 gram of protein is associated with about 3 – 4 grams of water. Similar results were found in other fish species (Appendices 45 – 73) and terrestrial animal species, such as the pig (Appendix 82).



The energy densities (kJ/g) of trout as a function of the body weights are given in the Figure below. The Figure indicates that particularly during the early growth, the energy density of the trout increases and the ratio mg protein per kJ energy decreases.



We analyzed the composition of both the whole body and the lean body mass (LBM) of various fish species and in pigs (Appendices 45 – 83). The following, general observations were done:

Ash: Inspection of the compositional data indicated that the percentage of ash as a function of the body weight was constant in all the various species studied and this observation was

true for both the whole body mass and the lean body mass and during and after the early growth.

Protein: The percentage of protein as a function of body weight after early growth was also rather constant. During the early growth, however, the percentage of protein appears to be somewhat lower. These observations were true for both the whole and lean body mass.

Water and fat in whole body mass: The compositional data of the whole body mass indicated that the percentage of fat and water in the whole body mass varied sometimes considerably, either between individual animals of comparable body weights or as a function of the body weight (see for example Appendices 53 (pike perch), 64 (carp), 70 (trout), 82 (pig)); a higher percentage of fat was mostly associated with a lower percentage of water. As a consequence, there was a strong correlation between the percentage of body fat and the percentage of body water. A strong correlation between the percentage of body fat and the percentage of body water has also been reported in mice (Terpstra 2002), hamsters (Kadoma 1971) and guinea pigs (Pace and Rathbun 1945).

Water in lean body mass: However, the percentage of water in the lean body mass after early growth appeared to be rather constant (see Appendices 53 (pike perch), 64 (carp), 70 (trout), 82 (pig)). For example, the Figure of the whole body composition of the pig in Appendix 82 indicated that there was a strong decrease in whole body water which was associated with a increase in whole body fat when the pigs grew larger. Further, there were sometimes also large differences in body water together with differences in fat between individual pigs of comparable body weights. However, no such fluctuations in the percentages of body water were observed in the lean body mass and similar observations have been reported in various other animal species (Pace and Rathbun, 1945). Thus, the composition of the lean body mass after early growth appears to be rather constant and the body fat can be considered as a diluent of the lean body mass.

Ratio of water to protein: As discussed above, the composition of the lean body mass is rather constant after early growth. As a consequence, the ratio of water to protein will also be rather constant and about 3 – 5 grams of water is associated with 1 gram of protein. However, during the early growth, the percentage of water was generally higher and the percentage of protein lower (see for example Appendices 53, 64, 70, 82) which also resulted in a somewhat higher ratios of water to protein during the early growth compared with the ratios after the early growth. A higher percentage water and a lower percentage protein in the lean body mass during the early growth has also been reported in humans (Fomon 1982 and 2002).

Appendix 22 (Text)

Growth Curves

The growth can be described by various types of growth curves. The major types of growth curves are (see also K.W. Kaufmann (1981) *Fitting and using growth curves. Oecologia (Berl)* 49: 293 – 299):

1. The exponential growth curve
2. The power growth curve
3. The Gompertz growth curve
4. The Logistic growth curve
5. The Bertalanffy growth curve
6. The Brody growth curve

and various other (related) models.

We will only discuss here the exponential growth curve and the power growth curve.

The exponential growth curve (specific growth rate, SGR).

The exponential growth curve is described by an exponential function and the change in growth or the growth rate is proportional to the body weight at each time point of the growth curve, a property of the exponential function. Thus:

$$\frac{dBW}{dt} = \alpha BW$$

The change in body weight or the growth rate is proportional to the body weight.

$$\frac{1}{BW} dBW = \alpha dt$$

Integration of this differential equation:

$$\int_{BW_0}^{BW_1} \frac{1}{BW} dBW = \int_{t_0}^{t_1} \alpha dt$$

$$\ln BW_1 - \ln BW_0 = \alpha (t_1 - t_0)$$

$$\ln BW_1 - \ln BW_0 = \alpha t_1 - \alpha t_0$$

$$\text{when } t_0 = 0$$

$$\ln BW_1 - \ln BW_0 = \alpha t_1$$

$$\alpha = (\ln BW_1 - \ln BW_0) / t_1$$

$$\ln \frac{BW_1}{BW_0} = \alpha t_1$$

and per definition:

$$\frac{BW_1}{BW_0} = e^{\alpha t_1}$$

$$BW_1 = BW_0 e^{\alpha t_1}$$

Thus, the general form of the exponential growth curve is:

$$BW_1 = BW_0 e^{\alpha t}$$

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

$$\ln (BW_1) = \ln (BW_0 * e^{\alpha t}) = \ln BW_0 + \alpha t \ln e = \ln BW_0 + \alpha t$$

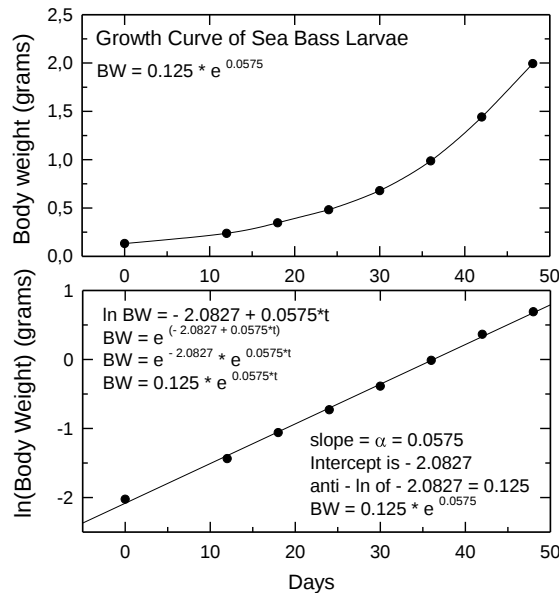
The $\ln$ values of the body weights are plotted vs the time (days). A growth curve fits an exponential growth curve when a linear plot arises when the $\ln$ values of the body weights are plotted vs the time. The slope α and the intercept ($\ln BW_0$) of this linear plot can be calculated by linear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

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

$$\alpha = \ln BW_{t=t_2} - \ln BW_{t=t_1}$$

When we have calculated α , we can calculate the body weights at each time point with the formula for any value of BW_0 .

The curve below shows an exponential growth curve of fish larvae (Sea Bass larvae).



Example: Suppose that we calculated from the experimental data that the exponent $\alpha = 0.05$ and suppose the body weight at time $t=t_0$ is 10 grams. We want to calculate now the body weights after 20 days. Then:

$$BW_{t_1} = BW_{t_0} e^{\alpha t}$$

$$BW_{t_{20}} = 10 e^{0.05 \cdot 20} = 27.18 \text{ grams}$$

Note: $e^{0.05 \cdot 20}$ is the anti-ln of $(0.05 \cdot 20)$

Example: The growth of trout larvae is for example described by the exponential function:

$$BW_1 = BW_0 * e^{\alpha t} = 0.2507 * e^{0.06588t}$$

where BW_0 is the BW at $t = 0$ and is in this example 0.2507 grams

The body weight at $t = 10$ days is:

$$BW_1 = 0.2507 * e^{0.06588 \cdot 10} = 0.4845 \text{ grams.}$$

The body weight after another 10 days is:

Method 1:

$$BW_1 = BW_0 * e^{\alpha t} = 0.4845 * e^{0.06588 \cdot 10} = 0.936 \text{ grams}$$

Method 2:

$$BW_1 = BW_0 * e^{\alpha t} = 0.2507 * e^{0.06588 \cdot 20} = 0.936 \text{ grams.}$$

Further,

$$BW_1 \text{ (at } t=t_1) = BW_0 * e^{\alpha t_1}$$

$$BW_2 \text{ (at } t=t_2) = BW_0 * e^{\alpha t_2}$$

$$(BW_2 \text{ (at } t=t_2)) / (BW_1 \text{ (at } t=t_1)) = (BW_0 * e^{\alpha t_2}) / (BW_0 * e^{\alpha t_1})$$

$$BW_2 = BW_1 * e^{\alpha(t_2 - t_1)}$$

With this formula we can now calculate the body weight at $t=t_2$ when we know the body weight at $t=t_1$. The term $e^{\alpha(t_2 - t_1)}$ of the exponential function $BW_2 = BW_1 * e^{\alpha(t_2 - t_1)}$ represents essentially the (multiplication) factor by which the body weight changes when the time or number of days changes with a defined number of units $(t_2 - t_1)$.

Example: The body weight at $t=5$ is 100 grams and the exponent α is 0.05. The body weight at $t = 20$ is then:
 $BW_{t=20} = 100 * e^{0.05 * (20 - 5)} = 211.7$ grams

In addition, it is possible to calculate the time (e.g. days) that is needed to double the body weights when we know the growth rate factor α .

$$BW_1 = BW_0 e^{\alpha(t_2-t_1)}$$

$$BW_1 = 2 BW_0$$

$$2BW_0 = BW_0 e^{\alpha(t_2-t_1)} \text{ or } 2 = e^{\alpha(t_2-t_1)}$$

$$\ln 2 = \alpha (t_2-t_1)$$

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

Similarly, it can be shown that, for example, how many units x has to increase in order to triple the value of the body weights:

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

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

Example: Suppose that we calculated from the experimental data that the exponent $\alpha = 0.05$. We want to calculate now how long it takes to double the body weights.

$$t_2 - t_1 = 2 = (\ln 2 / \alpha)$$

$$t_2 - t_1 = 2 = (\ln 2 / 0.05) = 13.86 \text{ days}$$

Further, we can calculate the percentage of growth per unit of time, e.g. the percentage of growth per day or per 2, or 3 days (when the time is expressed in days).

$$BW_1 = BW_0 e^{\alpha t}$$

The general formula for the % growth for a defined time span is:

$$\% \text{ growth per time unit of } t_1-t_0 = 100\% * [(BW_1 - BW_0) / BW_0]$$

$$\% \text{ growth per time unit of } t_1-t_0 = 100\% * [(BW_0 e^{\alpha(t_1-t_0)} - BW_0) / BW_0]$$

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

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

And the % growth per day is

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

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

Example: Suppose that we calculated from the experimental data that $\alpha = 0.05$ we want to calculate the % growth per day, thus $t_1-t_0 = 1$ day.

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

$$\% \text{ growth per day} = 100\% * (e^{(0.05 * 1)} - 1) = 5.157 \% \text{ per day}$$

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.

The percentage 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.

The exponential growth curve can be used to describe the growth rate of e.g. fish larvae and the growth rate of bacteria.

The Power Growth Function (Daily Growth Coefficient, DGC)

The power growth curve is frequently used as a growth curve for fish. The change on body weight or the growth rate is now proportional to the power of the body weight, thus BW^b , thus:

$$\frac{dBW}{dt} = \alpha BW^b$$

Note: when $b = 1$, then the function becomes identical to the exponential function, see above).

$$\frac{dBW}{BW^b} = \alpha dt$$

or

$$BW^{-b} dBW = \alpha dt$$

$$\int_{BW_0}^{BW_1} BW^{-b} dBW = \int_{t_0}^{t_1} \alpha dt$$

Note:

when e.g. $y = x^3$, then: $y' = 3x^{(3-1)}$, and thus similarly:
 when $y = \frac{1}{(1-b)} BW^{(1-b)}$, then: $y' = [(1-b)/(1-b)] BW^{(1-b-1)} = BW^{-b}$

$$\left[\frac{1}{(1-b)} BW^{(1-b)} \right]_{BW_{t=0}}^{BW_{t=1}} = \alpha t$$

$$BW^{(1-b)}_{t=1} - BW^{(1-b)}_{t=0} = (1-b) \alpha t$$

$$BW^{(1-b)}_{t=1} = BW^{(1-b)}_{t=0} + (1-b) \alpha t$$

$$BW_1^{(1-b)} = BW_0^{(1-b)} + (1-b) \alpha t$$

Note:

when $b = 1$, then the differential equation:

$$\frac{dBW}{dt} = \alpha BW^b$$

becomes equal to the differential equation:

$$\frac{dBW}{dt} = \alpha BW$$

and integration of this differential equation results in an exponential function (see above)

The power growth function is less steep than an exponential growth function when $0 < b < 1$.

b	(1-b)
0.3	0.7
0.5	0.5
0.7	0.3
0.9	0.1

The closer the value for b approaches the value of 1 and (1-b) the value of 0, the steeper the power growth functions will be and the more the power growth function will approach the exponential growth function. For fish larvae, the exponential curve can be used to describe the growth curve, but it is also possible to use the power function and using an exponent of about 0.20, thus an exponent close to 0 (See figures of Appendix 84 - 87).

If we substitute c for (1-b) α and d for (1-b) in the formula:

$$BW_1^{(1-b)} = BW_0^{(1-b)} + (1-b) \alpha t$$

Then:

$$BW^d_{day=1} = BW^d_{day=0} + c t$$

which is a linear function and where BW is body weight, t is time (days), c is the slope of the graph, c multiplied by 100 is called the Daily Growth Coefficient (DGC, see: *Iwama, G.K. & Tautz, F.A. (1981) A simple growth model for salmonids in hatcheries. Can. J. Fish. Aquat. Sci 38: 649-656*) and $BW^d_{day=0}$ is the body weight when t=0. The slope c of this linear plot and the intercept $BW^d_{day=0}$ can be calculated with linear regression. The growth curve fits a power growth curve when a linear plot arises when the values of the body weights raised to the power d are plotted vs the time.

This is a linear regression line where $BW^d_{day=0}$ is the intercept, i.e. the value for BW^d when t=0, and where c is the slope of the line. The slope c of this line x100 is called the Daily Growth Coefficient (DGC).

$$BW^d_{day=1} = BW^d_{day=0} + c \cdot \text{days} \text{ or}$$

$$BW_{day=1} = [BW^d_{day=0} + (DGC/100) \cdot \text{days}]^{1/d}$$

The DGC is expressed as % (weight gain or growth)^d per day.

With this formula we can now calculate the body weight at day = 1 when we know the body weight at day = 0.

Further, we can calculate the percentage of growth after a defined number of days (see examples below).

$$BW_{day=1} = [BW^d_{day=0} + (DGC/100) \cdot \text{days}]^{1/d}$$

The general formula for the % growth for a defined time span is:

$$\% \text{ growth per time unit of } t_1-t_0 = 100\% * (BW_{\text{day}=1} - BW_{\text{day}=0}) / BW_{\text{day}=0}$$

$$\% \text{ growth per time unit of } t_1-t_0 = 100\% * ([BW_{\text{day}=0}^d + (DGC/100)*\text{days}]^{1/d} - BW_{\text{day}=0}) / BW_{\text{day}=0}$$

$$\text{And the \% growth per day} = 100\% * ([BW_{\text{day}=0}^d + (DGC/100)*1]^{1/d} - BW_{\text{day}=0}) / BW_{\text{day}=0}$$

Note that the % growth after a defined number of days is dependent on the (initial) body weights as shown in the examples below (the % growth for a defined number of days for an exponential growth curve is independent of the (initial) body weight).

Example: the Daily Growth Coefficient is 4.656 and the $BW_{\text{day}=0}$ is 50 grams and the power coefficient $d = 0.33$.

$$\text{The \% growth per time unit of } t_1-t_0 = 100\% * ([BW_{\text{day}=0}^d + (DGC/100)*\text{days}]^{1/d} - BW_{\text{day}=0}) / BW_{\text{day}=0}$$

$$\text{The \% growth per day is: } 100\% * ([50^{0.33} + (4.645/100)*1]^{1/0.33} - 50) / 50 = 3.93\%$$

When the $BW_{\text{day}=0}$ is 200 grams, then:

$$\text{The \% growth per day is: } 100\% * ([200^{0.33} + (4.645/100)*1]^{1/0.33} - 200) / 200 = 2.48\%$$

Thus, the percentage growth per day is dependent on the initial body weight.

How to calculate the the DGC:

Method 1.

When a set of growth data are given (various time points with various body weights), then all the $(\text{body weights})^d$ 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 ($\times 100 = \text{DGC}$) 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 $(\text{body weights})^d$ 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.

Method 2.

When only the body weights at two time points are known and one is sure 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:

$$BW_{\text{day}=1}^d = BW_{\text{day}=0}^d + c * \text{days}$$

$$c = (BW_{\text{day}=1}^d - BW_{\text{day}=0}^d) / \text{days}$$

This 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.

$$\text{Daily Growth Coefficient} = \text{DGC} = 100\% * (BW_{\text{day}=1}^d - BW_{\text{day}=0}^d) / \text{days}$$

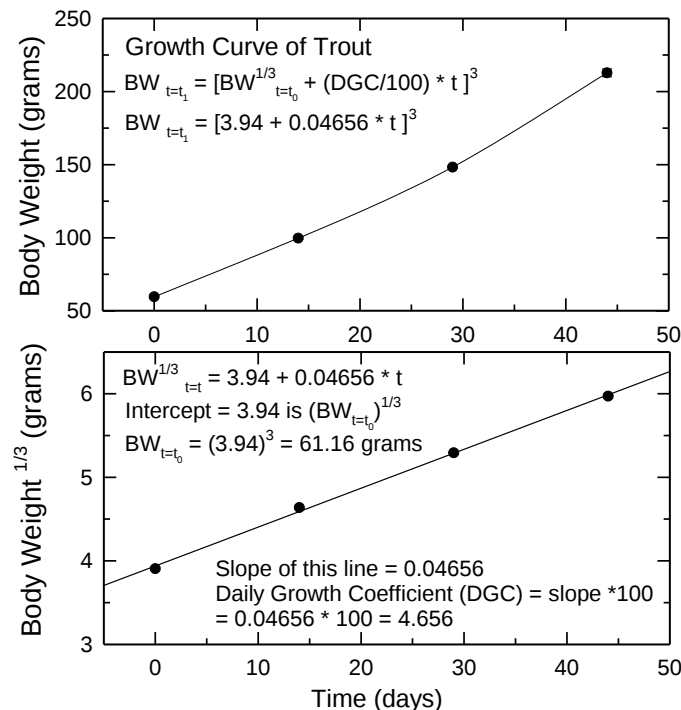
The curve below shows a power growth function of trout. The best fit value of d (the exponent of the body weight) was $1/3 = 0.33$. This value was found by trial and error, i.e. a linear graph is generated when the body weights raised to this power are plotted vs the time (see Figure below, bottom panel).

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

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

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

$$\text{Initial Body Weight} = [(\text{Final Body Weight})^d] - [(\text{DGC}/100) * (\text{days on diet})]^{1/d}$$



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:

$$\text{Days on Diet} = 100 * [(\text{Final Body Weight})^d - (\text{Initial Body Weight})^d] / (\text{DGC})$$

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:

$$\text{DGC} = 100\% * (BW_{\text{day}=1}^d - BW_{\text{day}=0}^d) / \text{days}$$

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

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

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

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

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

$$\text{Initial Body Weight} = [(\text{Final Body Weight})^d] - [(\text{DGC}/100) * (\text{days on diet})]^{1/d}$$

$$\text{Initial Body Weight} = [(73.4)^{1/3}] - [(2.54/100) * (20)]^{1/0.33} = 49.8 \text{ grams}$$

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?

$$\text{Days on Diet} = 100 * [(\text{Final Body Weight})^d - (\text{Initial Body Weight})^d] / (\text{DGC})$$

$$\text{Days on Diet} = 100 * [(100)^{1/3} - (50)^{1/3}] / (2.54) = 37.7 \text{ days}$$

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?

$$\text{Days on Diet} = 100 * [(\text{Final Body Weight})^d - (\text{Initial Body Weight})^d] / (\text{DGC})$$

$$\text{Days on Diet} = 100 * [(200)^{1/3} - (100)^{1/3}] / (2.54) = 47.5 \text{ days}$$

Examples of exponential and power growth curves are given in Appendices 84 - 89

Appendix 23 (Text)

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):

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

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:

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

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.

The graphs below show the relationship between the body weights and the body lengths in trout and pike perch. Data were collected by the author. The body weights in grams are plotted vs the body lengths in centimeter 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 $a * BW^b$.

The graphs show that the relationship between the body weights and the body lengths can also be described by a second order polynomial function (bottom panels of the figures). Further, the experimental results from trout and pike perch indicate that the value of the normalization constant a is somewhat higher than 3, the value of the scaling coefficient used for the calculation of the condition factor. The experimentally found values of the normalization constant a were 3.2394 for pike perch and 3.3807 for trout. The value of 3 for b is chosen to calculate the condition factor, since this value appears to be the median of the normalization constant of a large number of fish species (Froese 2006).

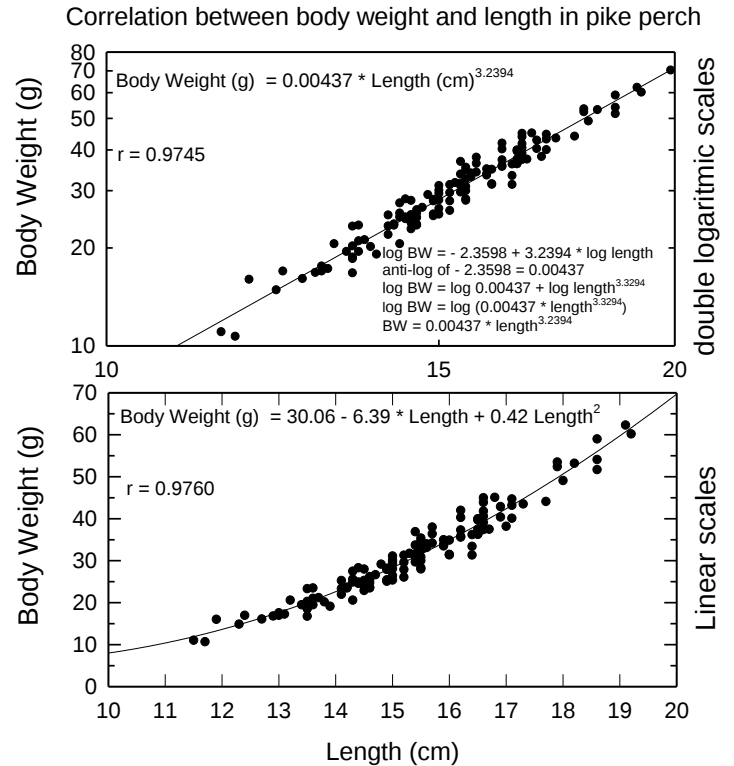
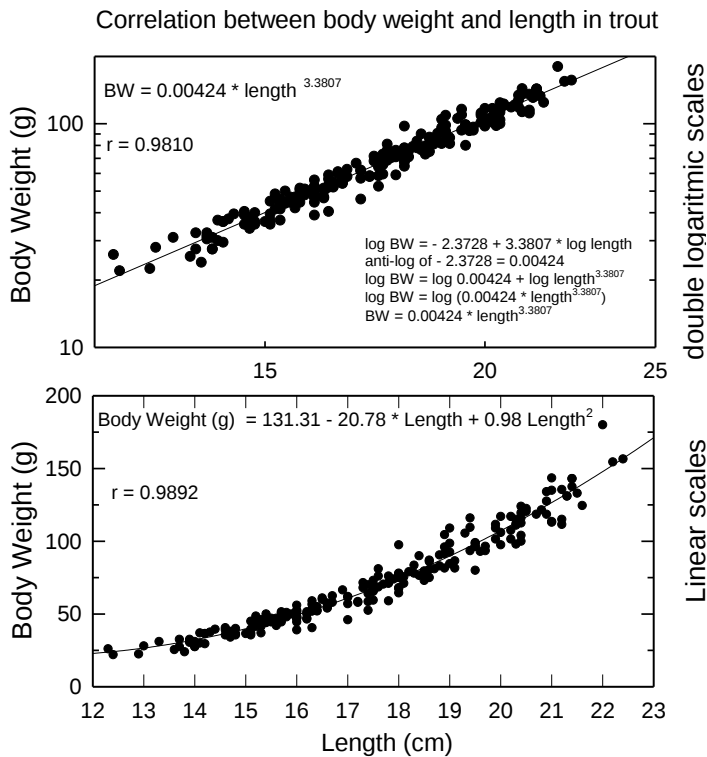
Example: We can calculate from the graph above that describes the correlation between the body weight and body length in trout, that the body weight of a trout with a length of 15 centimeter is:
Body weight = $0.00424 * 15^{3.3807} = 40.8$ grams.
The condition factor of this trout of 40.8 grams and 15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

The condition factor used in fish biology and fish nutrition is comparable to the Body Mass Index (BMI) in humans. The relationship between body weight and length in humans can also be described by the allometric equation: body weight (kg) = a length (meters)^b where the scaling coefficient or exponent is 2. The body mass index in humans is defined as:

$$\text{BMI} = a = (\text{body weight (kg)} / \text{length}^2).$$

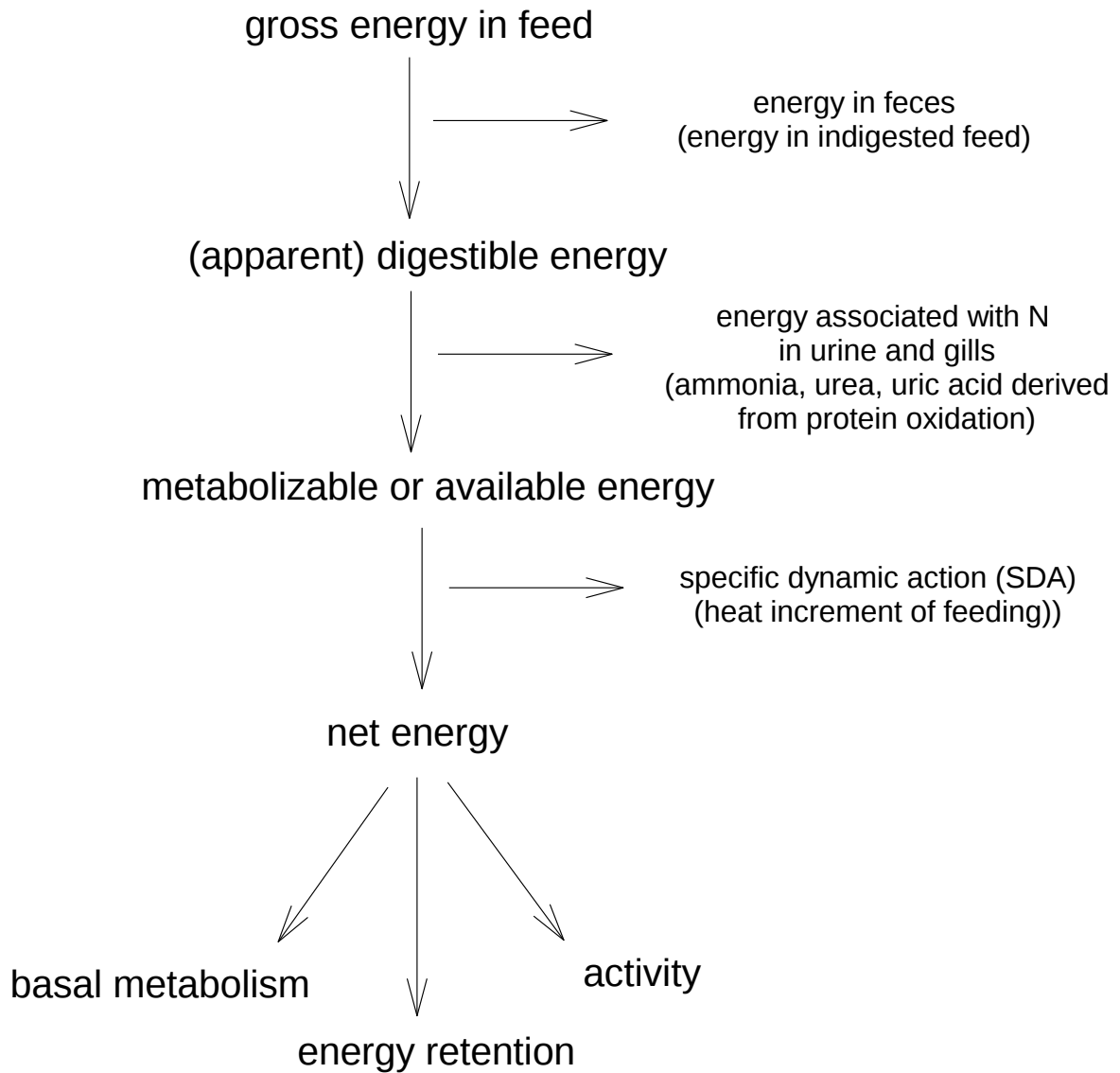
The body mass Index in humans should be between 20 and 25, values larger than 25 indicates a tendency to obesity and should be considered as undesirable.

This BMI index is used to describe the degree of overweight or obesity in humans, thus a condition factor for humans. Similar factors can probably be described in other (animal) species, but we have no further information about this issue.



Appendix 24 (Figure)

Gross, digestible, metabolizable and net energy

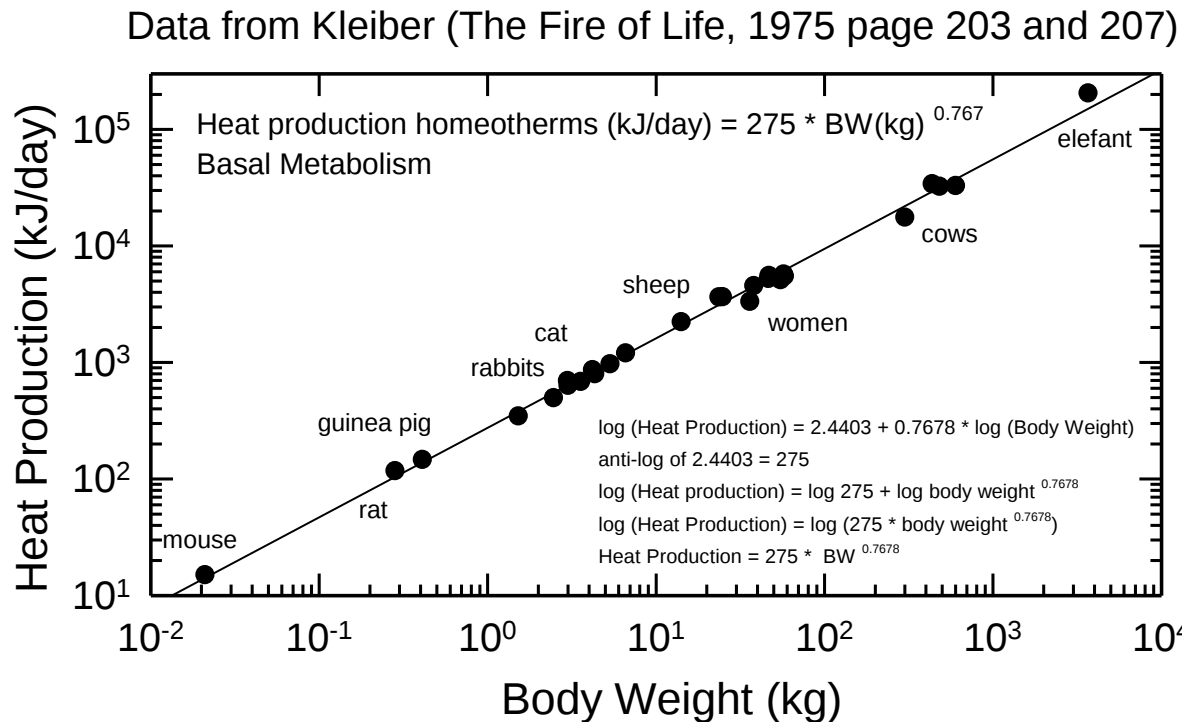


Appendix 25 (Figure)

Metabolic rate as a function of body weight in various species (mouse – elephant graph)

Max Kleiber. (1975) *The fire of life.* Robert E. Krieger Publishing Company. Huntington, New York, ISBN 0 – 88275 – 161 - 1

This graph shows the total metabolic rate of various animal species as a function of body weight, the so-called “mouse – elephant” graph



Kleiber concluded (1975, The Fire of Life, page 214) that “for practical purposes, one may assume that the mean standard metabolic rate (kcal) of mammals is seventy times the three-fourth power of their body weight (in kg) per day”. Thus, the basal metabolic rate is:

$$\text{Basal Metabolic Rate (BMR) or Heat Production (kcal/day)} = 70 BW^{0.75}$$

or in kJ (1 kcal = 4.184 kJ):

$$\text{Basal Metabolic Rate (BMR) or Heat Production (kJ/day)} = 293 BW^{0.75} \text{ or about } 300 BW^{0.75}$$

One may assume that the basal metabolic rate in animals is about 75% of the total metabolic rate (total metabolic rate comprises basal metabolic rate (BMR) or routine metabolism in fish, Specific Dynamic Action (SDA, heat production as a result of food consumption) and physical activity thermogenesis (AT).

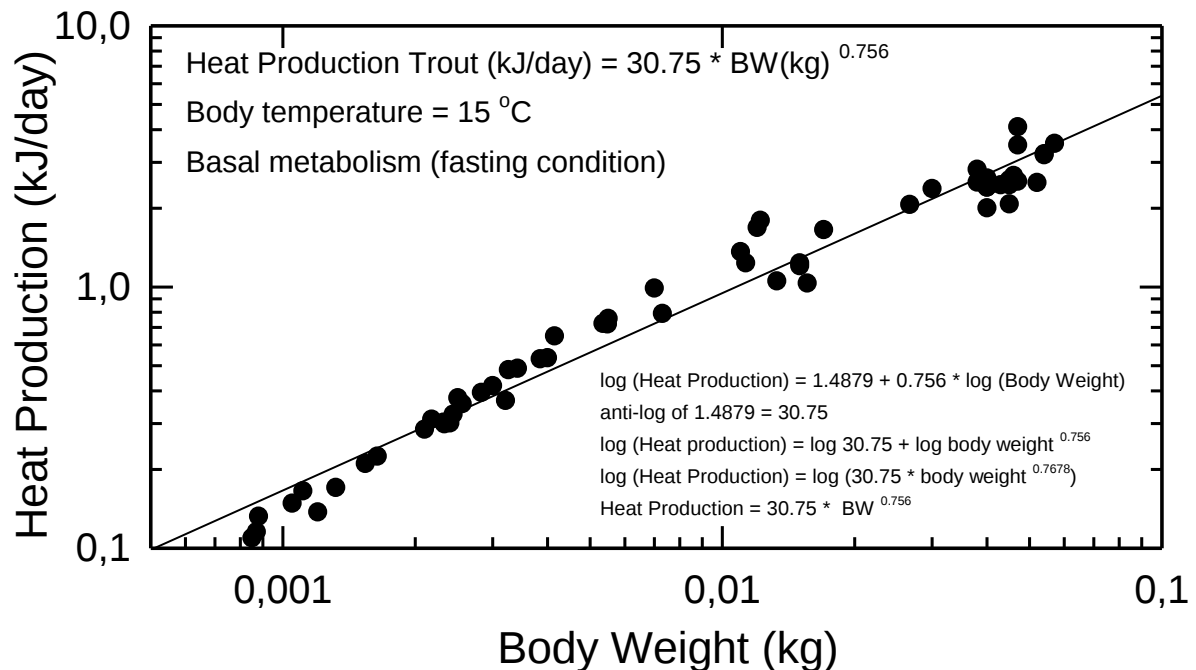
Appendix 26 (Figure)

Metabolic rate as a function of body weight in trout.

R.R. Smith, G.L. Rumsey, and M.L. Scott (1978) Net energy maintenance requirements of salmonids as measured by direct calorimetry: Effect of body size and environmental temperature. Journal of Nutrition 108: 1017 – 1024.

This graph shows the total metabolic rate as a function of the body weights in trout. The heat production was measured by direct calorimetry.

Data from Smith et al. (J. Nutr. 108: 1017 - 1024, 1978, page 1021)



The body weights of the trout ranged from 0.85 – 57 grams

Figure 27 (Figure)

Metabolic rate as a function of body weight in carp

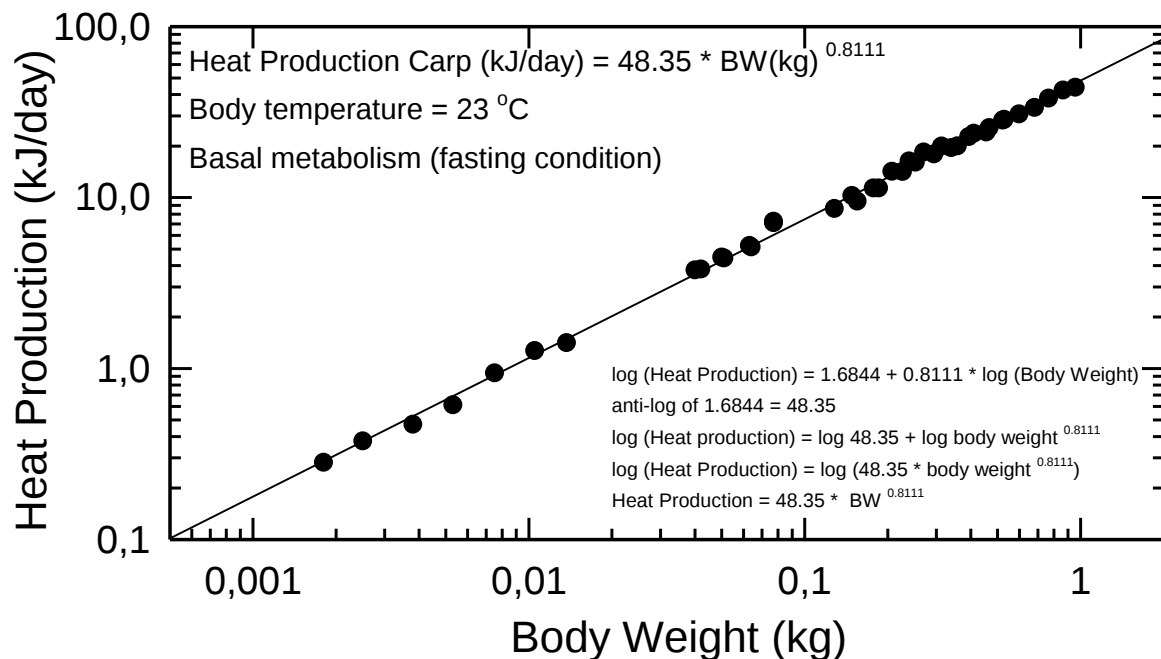
E.A. Huisman (1974) *Optimalisering van de groei van de karper. Dissertation, Wageningen University, the Netherlands.*

This dissertation can be downloaded from the website of Wageningen University and Research (WUR) the Netherlands.

In the dissertation of Huisman (1974), the consumption of oxygen in ml per hour is given and the body weights are in grams. We converted the ml of oxygen per hour to kJ per day and the body weights in kg. 1 ml oxygen = 1.428 mg grams of oxygen (see Table Appendix 8) and the energy equivalent of 1 gram oxygen is 13.75 kJ (see Table Appendix 4), i.e. the average of the energy equivalents of oxygen (E_{eqO_2}) for fat (13.72) and protein (13.79, ammonia as end product for nitrogen). Thus, the ml of oxygen (these data are given in the dissertation) has to be multiplied by: $1.428 * 13.75 * 24 / 1000$ (kJ) = 0.466.

The body weights of the Carp ranged from 2 – 1000 grams

Data from E.A. Huisman (Dissertation, 1974, page 58 and 59)



Appendix 28 (Figure)

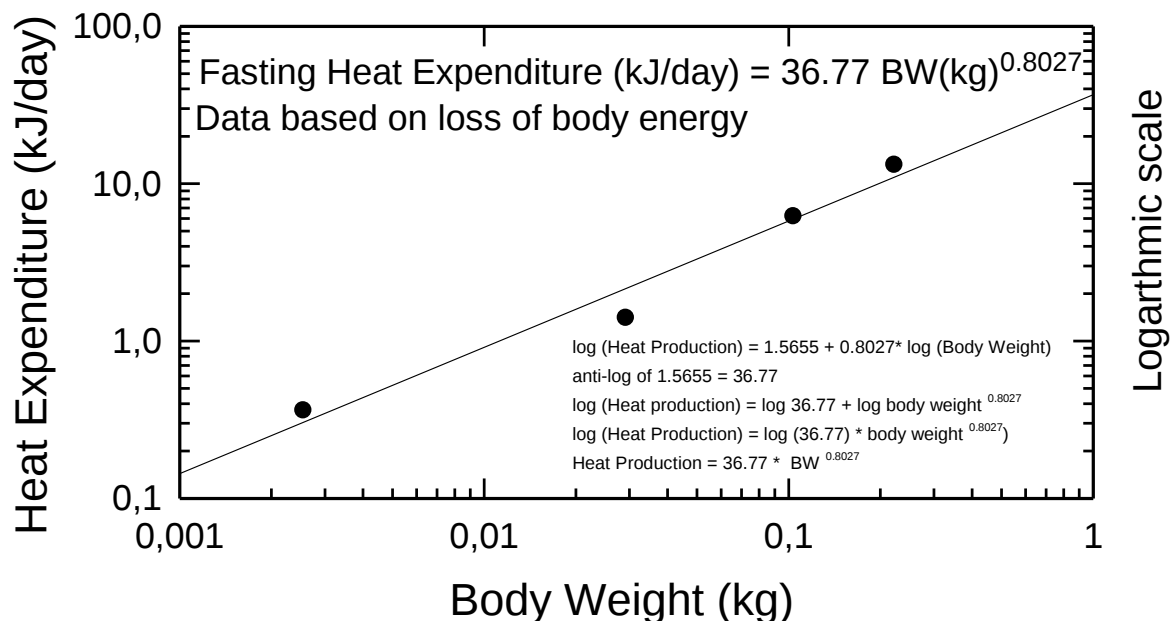
Metabolic rate as a function of body weight in African Catfish

M.A.M. Machiels and A.M. Henken (1986) A dynamic simulation model for growth of the African Catfish (*Clarias gariepinus*) Burchell 1822. I Effect of feeding level on growth and energy metabolism. *Aquaculture* 56: 29 – 52.

This graph shows the total metabolic rate as a function of the body weights in African Catfish, *Clarias Gariepinus*.

The body weights of the African Catfish ranged from 3 – 300 grams

Data from Machiels (1986) *Aquaculture* 56: 29-52)
 (African catfish, 30 °C)



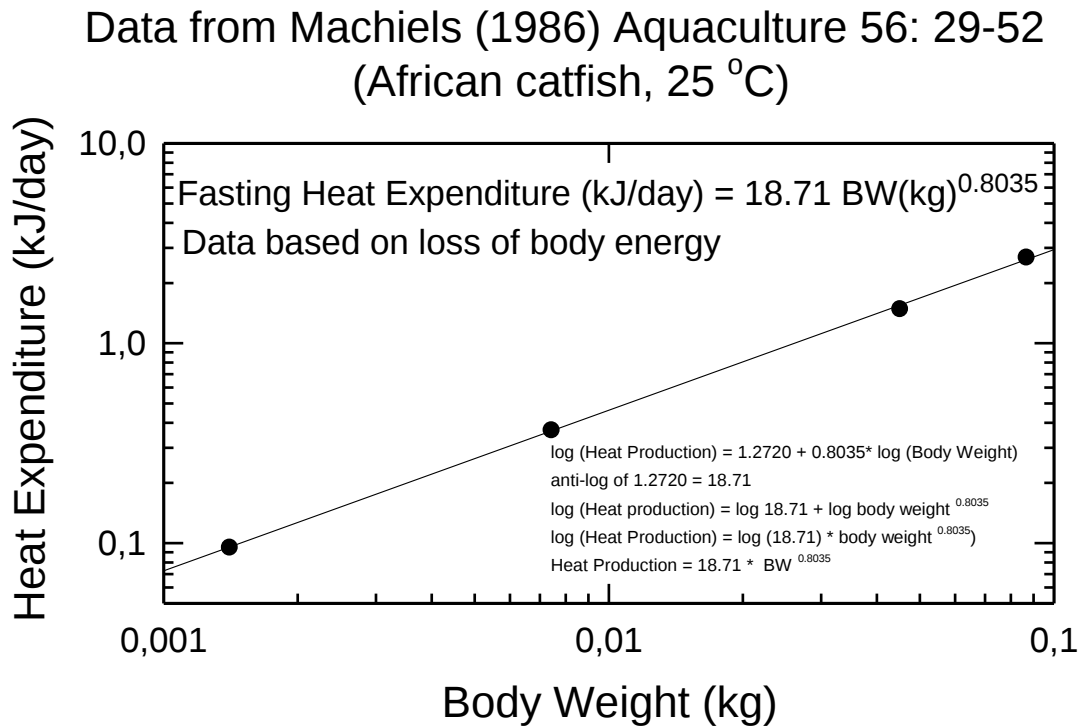
We also calculated the fasting heat expenditure with an alternative method (see Appendix 42) and was then $39.26 \cdot \text{BW}^{0.80}$ kJ/day. The value of $39.26 \cdot \text{BW}^{0.80}$ is reported in Appendix 9

Appendix 29 (Figure)

Metabolic rate as a function of body weight in African Catfish

M.A.M. Machiels and A.M. Henken (1986) A dynamic simulation model for growth of the African Catfish (*Clarias gariepinus*) Burchell 1822. I Effect of feeding level on growth and energy metabolism. *Aquaculture* 56: 29 – 52.

Body weights 1.5 – 100 grams.



We also calculated the fasting heat expenditure with an alternative method (see Appendix 43) and was then $22.04 \cdot \text{BW}^{0.80}$ kJ/day. The value of $22.04 \cdot \text{BW}^{0.80}$ is reported in Appendix 9.

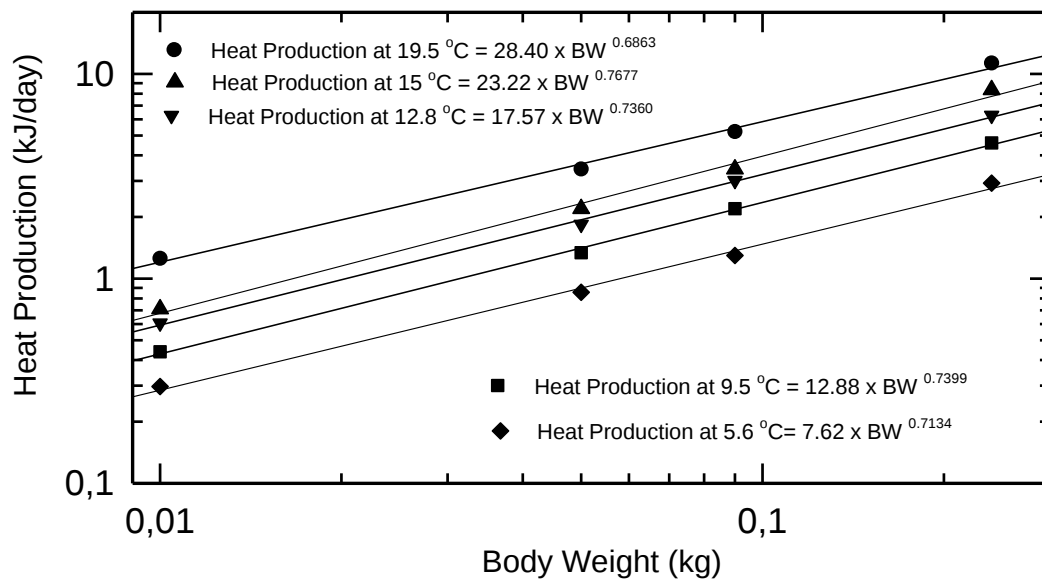
Appendix 30 (Figure)

Metabolic rate as a function of temperature in trout

J.M. Elliott (1976) The energetics of feeding, metabolism and growth of Brown Trout (Salmo trutta L.) in relation to body weight, water temperature and ration size. The Journal of Animal Ecology 45: 923 – 948.

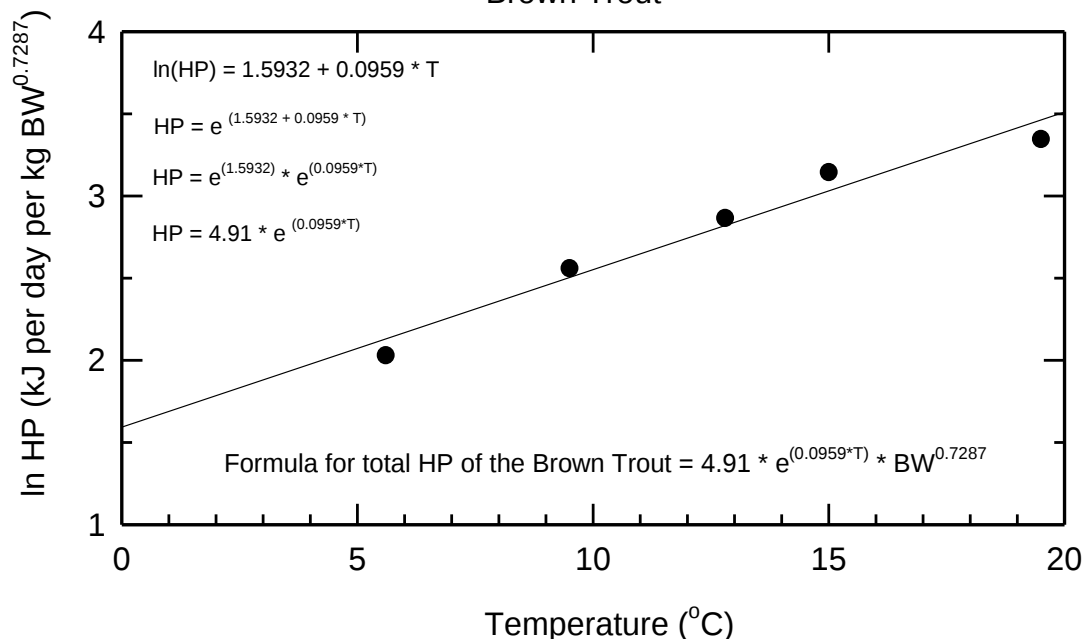
In this article, the effect of temperature on the routine or basal metabolic rate in the Brown trout is described. The data are from Figure 2 of the article of Elliott. The heat production was plotted vs the body weights on double logarithmic graph paper and the heat production per kg metabolic weight ($BW(kg)^b$) was calculated. The results are given in the Figure below:

Data from Elliott (J. An. Ecol. 45: 923-948, 1976, page 928)
 Brown Trout



We plotted the $\ln$ values of these basal metabolic rates (per $BW(kg)^b$) vs the temperature.

Data from Elliott (J. An. Ecol. 45: 923-948, 1976, page 928)
 Brown Trout



By linear regression, we can calculate that the heat production per kg BW^{0.7287} (the exponent 0.7261 is the average values of the 5 exponents in the figure above) :

$$\text{Fasting Heat production per day per BW(kg)}^{0.7287} = 4.91 * e^{0.0959*T}$$

The complete formula for calculating the heat production becomes then:

$$\text{Routine or Basal Heat Production (kJ/day)} = 4.91 * e^{0.0959*T} * \text{BW(kg)}^{0.7287}$$

This formula represents the basal metabolic rate or the routine metabolism of the Brown trout and includes the effect of the temperature on the maintenance heat production or metabolic rate.

The effect of the temperature on the routine heat production or metabolic rate can thus be described by the fomula:

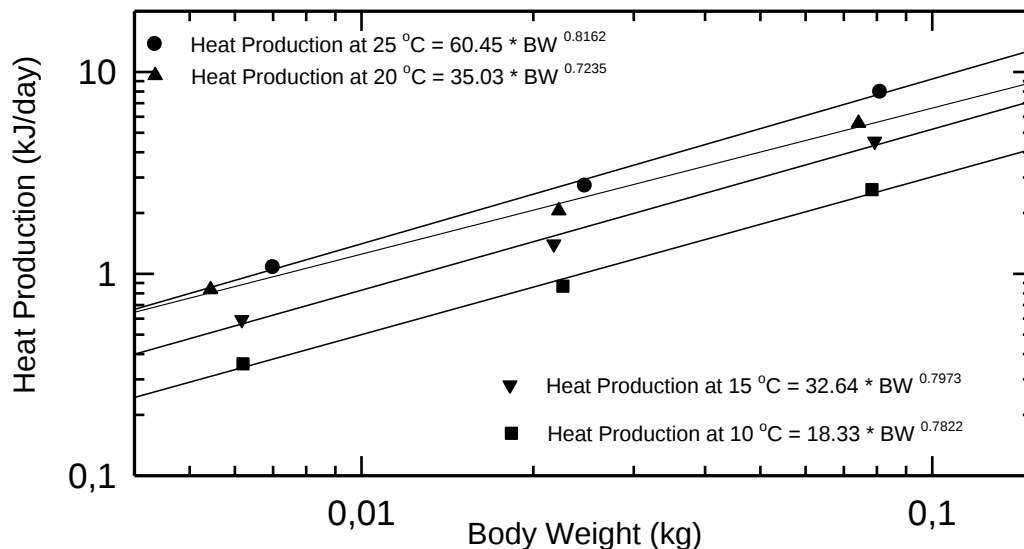
$$\text{Heat Production per kg BW}^b \text{ (at } T=T_2) = \text{Heat Production per kg BW}^b \text{ (at } T=T_1) * e^{0.0959*(T_2-T_1)}$$

Appendix 31 (Figure)

Metabolic rate as a function of temperature in Atlantic Menhaden
W.F. Hettler (1976) Influence of temperature and salinity on routine metabolic rate and growth of young Atlantic menhaden. Journal of Fish Biology 8: 55 - 65.

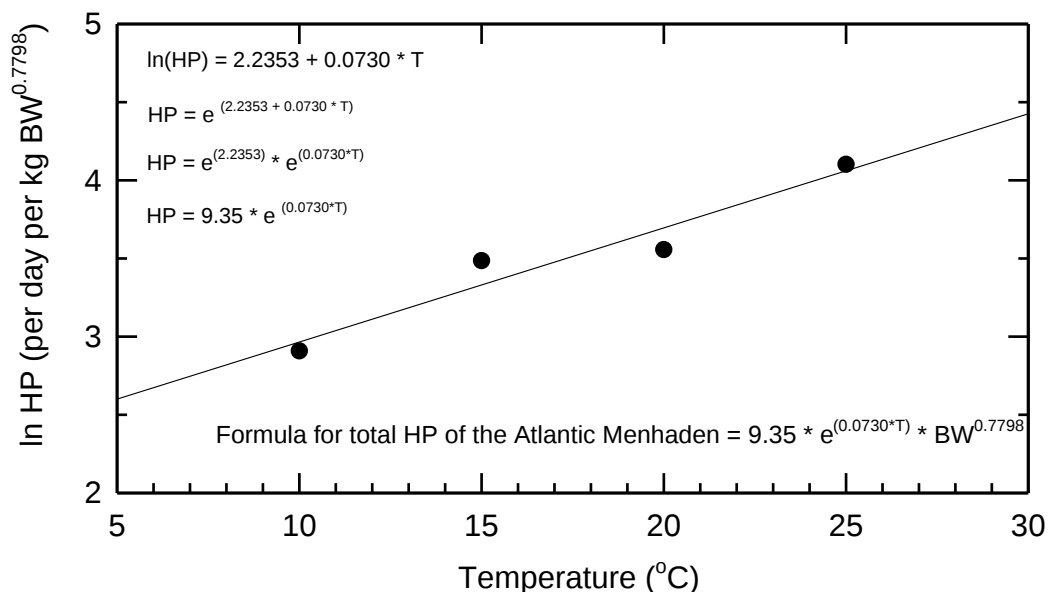
In this article, the effect of temperature on the basal or routine metabolism in the Atlantic Menhaden is described. Data are from Table 1 of the article of Hettler and the oxygen consumptions in this table were converted into kJ heat production (1 mg oxygen is the equivalent of 13.75 kJ heat production). The heat production was plotted vs the body weight on double logarithmic graph paper and the heat production per kg BW^b was calculated (see figure below) for the various temperatures. The results are given in the Figure below:

Data from Hettler (J. Fish Biol. 8: 55 - 65, 1976, page 57-58)
 Atlantic Menhaden



Subsequently, we plotted the $\ln$ values of these basal metabolic rates (per BW(kg)^b) vs the temperature.

Data from Hettler (J. Fish Biol. 8: 55 - 65, 1976, page 57-58)
 Fasting heat production of the Atlantic Menhaden
 as a function of temperature



By linear regression, we can calculate that the heat production per kg BW^{0.7798} (the exponent 0.7798 is the average values of the 4 exponents in the figure above) is:

$$\text{Fasting Heat production per day per BW(kg)}^{0.7798} = 9.35 * e^{0.0730 * T}$$

The complete formula for calculating the heat production becomes then:

$$\text{Routine or Basal Heat Production (kJ/day)} = 9.35 * e^{0.0730 * T} * \text{BW(kg)}^{0.7798}$$

This formula represents the basal metabolic rate or the routine metabolism of the Atlantic Menhaden and includes the effect of the temperature on the basal heat.

The effect of the temperature on the routine heat production or metabolic rate can thus be described by the formula:

$$\text{Heat Production per kg BW}^b \text{ (at } T=T_2) = \text{Heat Production per kg BW}^b \text{ (at } T=T_1) * e^{0.0730 * (T_2 - T_1)}$$

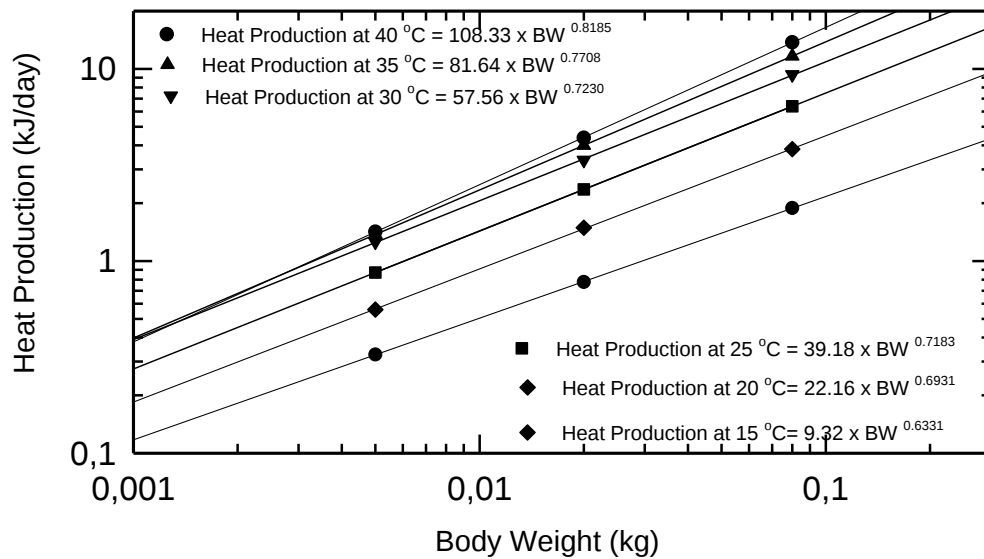
Appendix 32 (Figure)

Metabolic rate as a function of temperature in *Tilapia mossambica*

S.V. Job (1969) The respiratory metabolism of Tilapia mossambica (Teleostei). I. the effect of size, temperature and salinity. Marine Biology 2: 121 – 128.

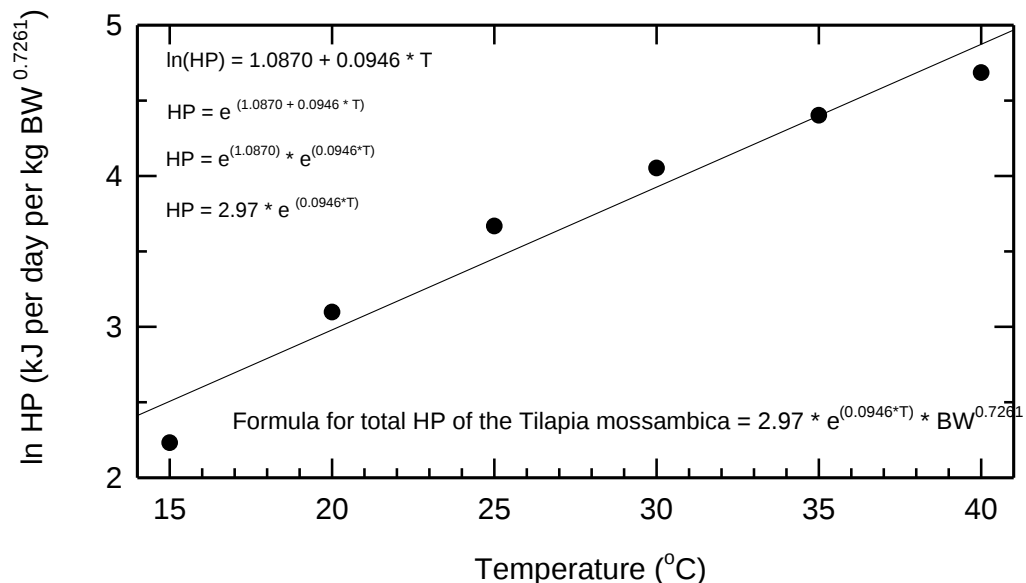
In this article, the routine or basal metabolic rate (oxygen consumption) of *Tilapia* at 6 temperatures is described. We used the data from Table 1 (fresh water) of the article of Job and the oxygen uptake in ml/hr were converted in mg/hr (1 ml oxygen = 1.428 mg oxygen) and subsequently in heat production in kJ per day (1 mg of oxygen consumption represents the heat production of 13.75 kJ). Body weights were plotted vs the heat production on double logarithmic graph paper and the heat production per kg BW^b was calculated (see figure below) for the various temperatures

Data from Job (Marine Biol. 2: 121-126, 1969, page 928)
Tilapia mossambica



We plotted the $\ln$ values of these basal metabolic rates (per BW(kg)^b) vs the temperature.

Data from Job (Marine Biol. 2: 121-126, 1969, page 928)
 Maintenance heat production of *Tilapia mossambica*
 as a function of the temperature



By linear regression, we can calculate that the heat production per kg BW^{0.7261} (the exponent 0.7261 is the average values of the 6 exponents in the figure above):

$$\text{Fasting Heat production per day per BW(kg)}^{0.7261} = 5.65 * e^{0.0946 * T}$$

The complete formula for calculating the heat production becomes then:

$$\text{Routine or Basal Heat Production (kJ/day)} = 4.91 * e^{0.0946 * T} * \text{BW(kg)}^{0.7267}$$

This formula represents the basal metabolic rate or the routine metabolism of the Atlantic Menhaden and includes the effect of the temperature on the basal heat production or metabolic rate.

The effect of the temperature on the basal heat production or metabolic rate can thus be described by the formula:

$$\text{Heat Production per kg BW}^b \text{ (at } T=T_2) = \text{Heat Production per kg BW}^b \text{ (at } T=T_1) * e^{0.0946 * (T_2 - T_1)}$$

Appendix 33 (Figure)

Fasting metabolic rate as a function of temperature in Tilapia

Ingrid Lupatsch (2008) Predicting growth, feed intake, and waste production of intensively reared Tilapia based on nutritional bioenergetics. Proceedings of the Seventh Conference on Recirculating aquaculture in Roanoke, Virginia, USA, July 25-27, 2008, Downloaded from the internet November, 2008)

In this article, the routine or basal or fasting metabolic rate for Tilapia at 4 temperatures is described

Fasting Heat Production (kJ per day):

Fasting Heat Production at 22 °C (kJ/day) = 25.88 * BW(kg)^{0.80}

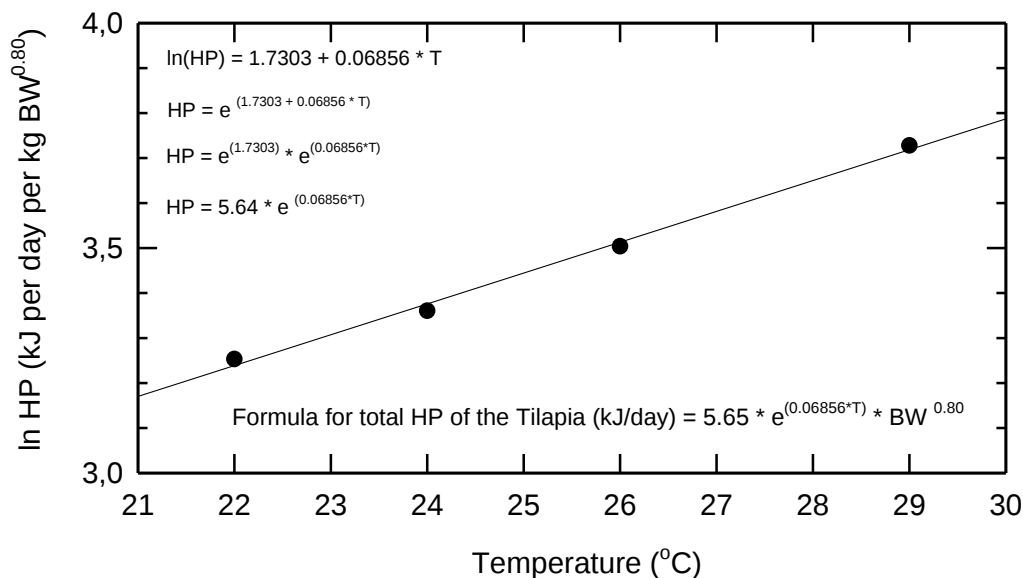
Fasting Heat Production at 24 °C (kJ/day) = 28.81 * BW(kg)^{0.80}

Fasting Heat Production at 26 °C (kJ/day) = 33.25 * BW(kg)^{0.80}

Fasting Heat Production at 28 °C (kJ/day) = 41.60 * BW(kg)^{0.80}

We plotted the ln values of these maintenance metabolic rates vs the temperature, see figure below:

Data from I. Lupatsch (Proc. Int. Conference in Roanoke, USA, 2008)
Fasting Heat Production of the Tilapia as function of the temperature



By linear regression, we can calculate that the fasting heat production per kg BW^{0.80} is:

$$\text{Fasting Heat production per day per BW(kg)}^{0.80} = 5.65 * e^{0.06856 * T}$$

The complete formula for calculating the fasting heat production becomes then:

$$\text{Routine or Basal Heat Production (kJ/day)} = 5.65 * e^{0.06856 * T} * \text{BW(kg)}^{0.80}$$

This formula represents the basal metabolic rate or the routine metabolism of the Tilapia and includes the effect of the temperature on the fasting heat production or metabolic rate.

The effect of the temperature on the basal heat production or metabolic rate can thus be described by the formula:

$$\text{Heat Production per kg BW}^b \text{ (at } T=T_2) = \text{Heat Production per kg BW}^b \text{ (at } T=T_1) * e^{0.06856 * (T_2 - T_1)}$$

Appendix 34 (Figure)

Maintenance metabolic rate as a function of temperature in Tilapia

Ingrid Lupatsch (2008) Predicting growth, feed intake, and waste production of intensively reared Tilapia based on nutritional bioenergetics. Proceedings of the Seventh Conference on Recirculating aquaculture in Roanoke, Virginia, USA, July 25-27, 2008, Downloaded from the internet November, 2008)

In this article, the maintenance metabolic rate for Tilapia at 4 temperatures is described
 Maintenance Heat Production (kJ per day):

Maintenance Heat Production at 22 °C (kJ/day) = $43.13 \cdot \text{BW}(\text{kg})^{0.80}$

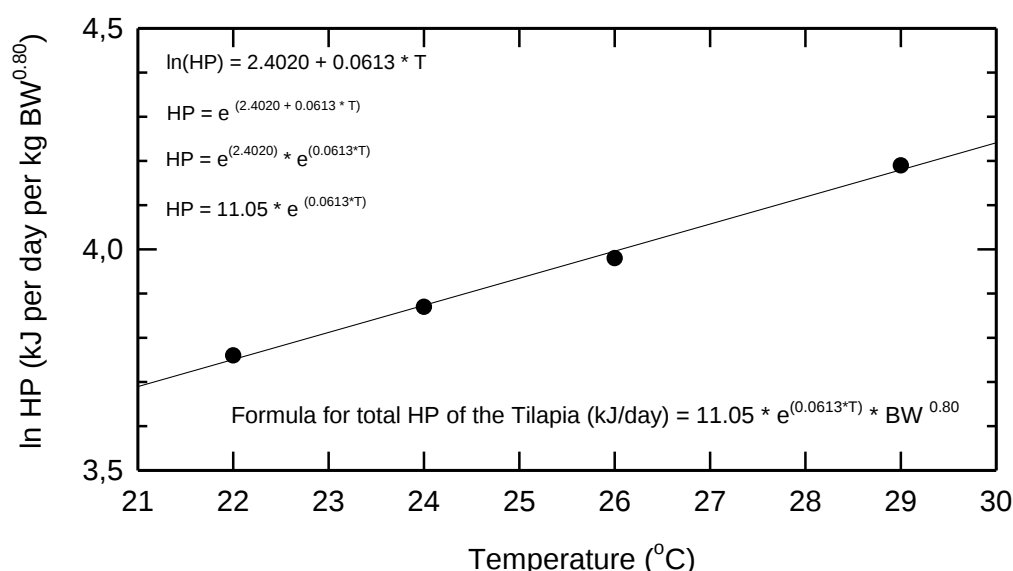
Maintenance Heat Production at 24 °C (kJ/day) = $48.02 \cdot \text{BW}(\text{kg})^{0.80}$

Maintenance Heat Production at 26 °C (kJ/day) = $53.63 \cdot \text{BW}(\text{kg})^{0.80}$

Maintenance Heat Production at 28 °C (kJ/day) = $66.03 \cdot \text{BW}(\text{kg})^{0.80}$

We plotted the ln values of these maintenance metabolic rates vs the temperature, see figure below:

Data from I. Lupatsch (Proc. Int. Conference in Roanoke, USA, 2008)
 Maintenance Heat Production of the Tilapia as function of the temperature



By linear regression, we can calculate that the heat production per kg BW^{0.80} is:

$$\text{Maintenance Heat Production per day per BW}(\text{kg})^{0.80} = 11.05 \cdot e^{0.0613 \cdot T}$$

The complete formula for calculating the heat production becomes then:

$$\text{Maintenance Heat Production (kJ/day)} = 11.05 \cdot e^{0.0613 \cdot T} \cdot \text{BW}(\text{kg})^{0.80}$$

This formula represents the maintenance metabolism of the Tilapia and includes the effect of the temperature on the maintenance heat production or metabolic rate.

The effect of the temperature on the basal heat production or metabolic rate can thus be described by the formula:

$$\text{Heat Production per kg BW}^b \text{ (at } T=T_2) = \text{Heat Production per kg BW}^b \text{ (at } T=T_1) \cdot e^{0.0946 \cdot (T_2 - T_1)}$$

Appendix 35 (Figure)

Fasting protein loss as a function of temperature in Tilapia

Ingrid Lupatsch (2008) Predicting growth, feed intake, and waste production of intensively reared Tilapia based on nutritional bioenergetics. Proceedings of the Seventh Conference on Recirculating aquaculture in Roanoke, Virginia, USA, July 25-27, 2008, Downloaded from the internet November, 2008)

In this article, the protein loss for the fasting Tilapia at 4 temperatures is described
Fasting protein loss (grams per day):

$$\text{Fasting protein loss at } 22^{\circ}\text{C (g/day)} = 0.19 * \text{BW(kg)}^{0.70}$$

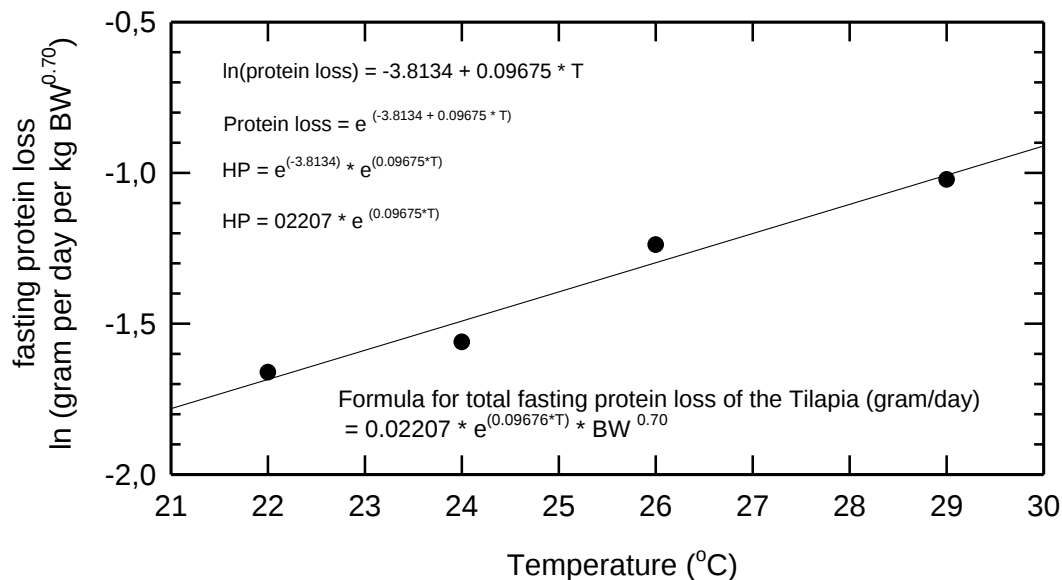
$$\text{Fasting protein loss at } 24^{\circ}\text{C (g/day)} = 0.21 * \text{BW(kg)}^{0.70}$$

$$\text{Fasting protein loss at } 26^{\circ}\text{C (g/day)} = 0.29 * \text{BW(kg)}^{0.70}$$

$$\text{Fasting protein loss at } 28^{\circ}\text{C (g/day)} = 0.36 * \text{BW(kg)}^{0.70}$$

We plotted the ln values of these fasting protein losses vs the temperature, see figure below:

Data from I. Lupatsch (Proc. Int. Conference in Roanoke, USA, 2008)
Fasting protein loss of the Tilapia as a function of the temperature



By linear regression, we can calculate that the fasting protein loss per kg BW^{0.70} is:

$$\text{Fasting protein loss per day per BW(kg)}^{0.70} = 0.02207 * e^{0.09675 * T}$$

The complete formula for calculating the fasting protein loss becomes then:

$$\text{Fasting protein loss (grams/day)} = 0.02207 * e^{0.09675 * T} * \text{BW(kg)}^{0.70}$$

This formula represents the fasting protein loss of the Tilapia and includes the effect of the temperature on the fasting protein loss.

The effect of the temperature on the fasting protein loss can thus be described by the formula:

$$\text{Protein loss per kg BW}^b \text{ (at } T=T_2) = \text{Protein loss per kg BW}^b \text{ (at } T=T_1) * e^{0.09675 * (T_2 - T_1)}$$

Appendix 36 (Figure)

Fasting metabolic rate as a function of temperature in the White grouper

Ingrid Lupatsch and George Wm. Kissil (2005) Feed formulations based on energy and protein demands in the White Grouper (Ephinephelus aeneus). Aquaculture 248: 83-95 (2005)

In this article, the fasting metabolic rate for the White Grouper at 3 temperatures is described
 Fasting Heat Production (kJ per day) (body weights about 12 – 120 grams)

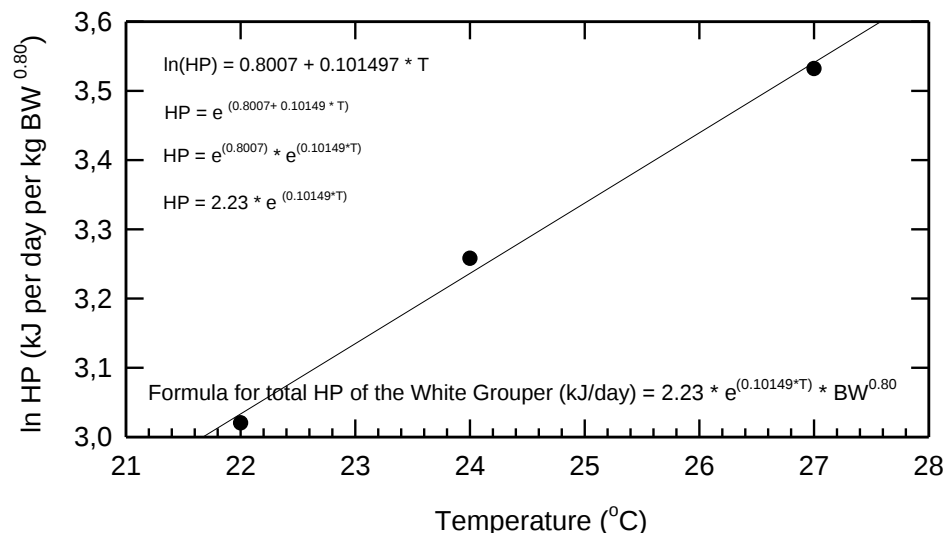
Fasting Heat Production at 22 °C (kJ/day) = 20.5 * BW(kg)^{0.80}

Fasting Heat Production at 24 °C (kJ/day) = 26.0 * BW(kg)^{0.80}

Fasting Heat Production at 27 °C (kJ/day) = 34.2 * BW(kg)^{0.80}

We plotted the ln values of these maintenance metabolic rates vs the temperature, see figure below:

Data from I. Lupatsch (Aquaculture 248: 83-95, 2005)
 Fasting heat production of the White grouper as a function of the temperature



By linear regression, we can calculate that the fasting heat production per kg BW^{0.80} is:

$$\text{Fasting Heat Production per day per BW(kg)}^{0.80} = 2.23 * e^{0.10149 * T}$$

The complete formula for calculating the fasting heat production becomes then:

$$\text{Routine or Basal Heat Production (kJ/day)} = 2.23 * e^{0.10149 * T} * \text{BW(kg)}^{0.80}$$

This formula represents the basal metabolic rate or the routine metabolism of the Tilapia and includes the effect of the temperature on the fasting heat production or metabolic rate.

The effect of the temperature on the basal heat production or metabolic rate can thus be described by the formula:

$$\text{Heat Production per kg BW}^b \text{ (at } T=T_2) = \text{Heat Production per kg BW}^b \text{ (at } T=T_1) * e^{0.10149 * (T_2 - T_1)}$$

Appendix 37 (Figure)

Maintenance metabolic rate as a function of temperature in the White Grouper

Ingrid Lupatsch and George Wm. Kissil (2005) Feed formulations based on energy and protein demands in the White Grouper (Ephinephelus aeneus). Aquaculture 248: 83-95 (2005)

In this article, the maintenance metabolic rate for the White Grouper at 3 temperatures is described.

Fasting Heat Production (kJ per day) (body weights about 12 – 120 grams):

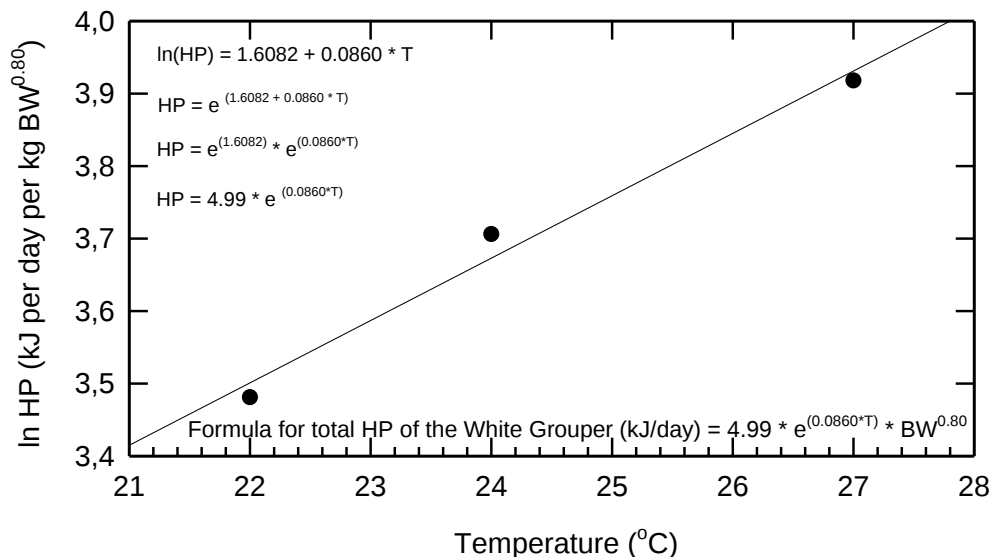
Maintenance Heat Production at 22 °C (kJ/day) = $32.5 * BW(kg)^{0.80}$

Maintenance Heat Production at 24 °C (kJ/day) = $40.7 * BW(kg)^{0.80}$

Maintenance Heat Production at 27 °C (kJ/day) = $50.3 * BW(kg)^{0.80}$

We plotted the ln values of these maintenance metabolic rates vs the temperature, see figure below:

Data from I. Lupatsch (Aquaculture 248: 83-95, 2005)
 Maintenance heat production of the White grouper as a function of the temperature



By linear regression, we can calculate that the heat production per kg $BW^{0.80}$ is:

$$\text{Maintenance Heat Production per day per } BW(kg)^{0.80} = 4.99 * e^{0.0860 * T}$$

The complete formula for calculating the heat production becomes then:

$$\text{Maintenance Heat Production (kJ/day)} = 4.99 * e^{0.0860 * T} * BW(kg)^{0.80}$$

This formula represents the maintenance metabolism of the White grouper and includes the effect of the temperature on the maintenance heat production or metabolic rate.

The effect of the temperature on the maintenance heat production or metabolic rate can thus be described by the formula:

$$\text{Heat Production per kg } BW^b \text{ (at } T=T_2) = \text{Heat Production per kg } BW^b \text{ (at } T=T_1) * e^{0.0860 * (T_2 - T_1)}$$

Appendix 38 (Figure)

Fasting protein loss as a function of temperature in the White Grouper

Ingrid Lupatsch and George Wm. Kissil (2005)

Feed formulations based on energy and protein demands in the White Grouper (Ephinephelus aeneus). Aquaculture 248: 83-95 (2005)

In this article, the protein loss for the fasting White Grouper at 3 temperatures is described
 Fasting protein loss (grams per day) (body weights about 12 – 120 grams):

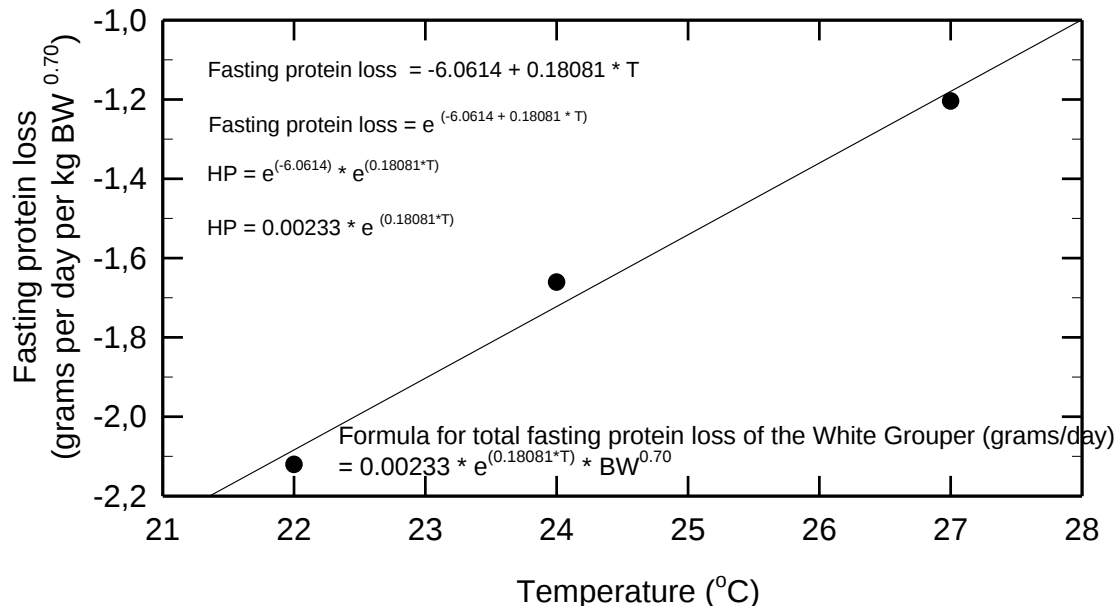
$$\text{Fasting protein loss at } 22^{\circ}\text{C (g/day)} = 0.12 * \text{BW(kg)}^{0.70}$$

$$\text{Fasting protein loss at } 24^{\circ}\text{C (g/day)} = 0.19 * \text{BW(kg)}^{0.70}$$

$$\text{Fasting protein loss at } 27^{\circ}\text{C (g/day)} = 0.30 * \text{BW(kg)}^{0.70}$$

We plotted the ln values of these fasting protein losses vs the temperature, see figure below:

Data from I. Lupatsch (Aquaculture 248: 83-95, 2005)
 Fasting protein losses of the White grouper as a function of the temperature



By linear regression, we can calculate that the fasting protein loss per kg BW^{0.70} is:

$$\text{Fasting protein loss per day per BW(kg)}^{0.70} = 0.00233 * e^{0.18081 * T}$$

The complete formula for calculating the fasting protein loss becomes then:

$$\text{Fasting protein loss (grams/day)} = 0.00233 * e^{0.18081 * T} * \text{BW(kg)}^{0.70}$$

This formula represents the fasting protein loss of the White Grouper and includes the effect of the temperature on the fasting protein loss.

The effect of the temperature on the fasting protein loss can thus be described by the formula:

$$\text{Protein loss per kg BW}^b \text{ (at } T=T_2) = \text{Protein loss per kg BW}^b \text{ (at } T=T_1) * e^{0.18081 * (T_2 - T_1)}$$

Appendix 39 (Figure)

Overview of studies on the exponential effect of the temperature on energy expenditure.

Reference	Species	Temperature Range (°C)	scaling exponent α	Condition
Winberg (1956)	General	5 - 30	0,0960	Routine
Clarke and Johnston (1999)	69 fish species	0 - 30	0,0600	Routine
Elliott (1976)	Brown trout	5,6 - 19,5	0,0959	Routine
Hettler (1976)	Atlantic Menhaden	10 - 25	0,0730	Routine
Job (1969)	Tilapia mosambica	15 - 40	0,0948	Routine
Lupatsch (2008)	Tilapia	22 - 28	0,0866	Routine
Lupatsch (2008)	Tilapia	22 - 28	0,0613	Maintenance
Lupatsch and Kissil (2005)	White grouper	22 - 27	0,1042	Routine
Lupatsch and Kissil (2005)	White grouper	23 - 27	0,0860	Maintenance

The routine metabolism is the basal or fasting metabolic rate and maintenance metabolic rate is the metabolic rate for maintenance or to maintain the body weight, thus the basal metabolic rate plus the SDA (specific dynamic action), but without any growth.

The effect of the temperature on the energy expenditure or metabolic rate is described by the formula:

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

The values of α (the scaling exponent or coefficient) are given in the Table above . Routine metabolism of a fish is the basal or fasting metabolism.

Example: Suppose that the routine heat production of a White grouper at a temperature of 25 °C is 50 * BW^{0.80} kJ / day. The heat production at a temperature at 20 °C is then: 50 * e^{0.1042*(20 - 25)} = 29.7 * BW^{0.80} kJ/ day

Appendix 40 (Figure)

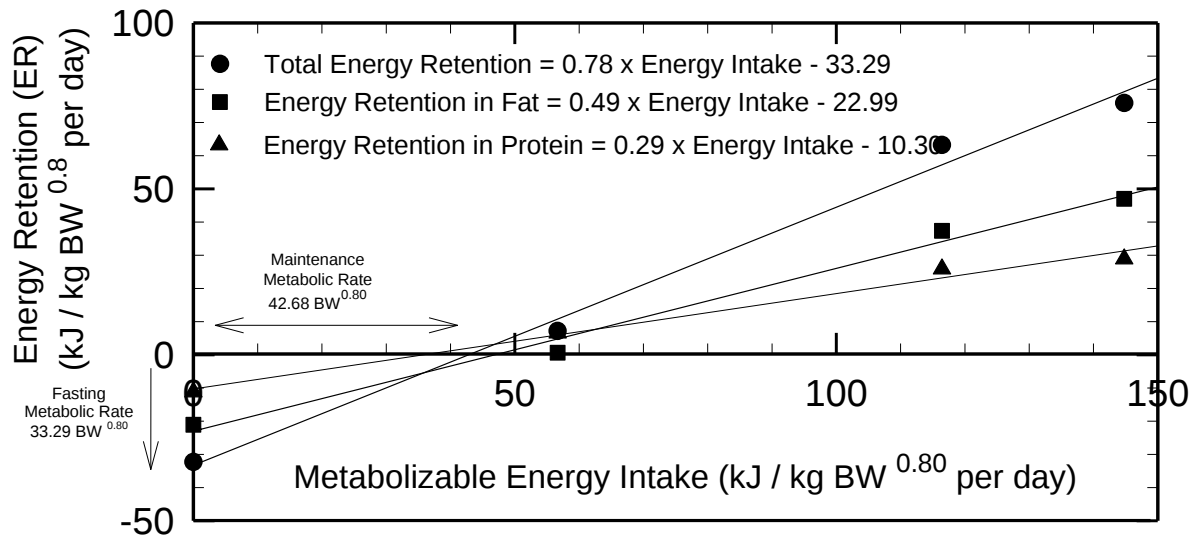
Energy, protein and fat retention as a function of energy intake in the trout

E.A. Huisman (1976) Food conversion efficiencies at maintenance and production levels for carp, *Cyprinus carpio* L., and Rainbow trout, *Salmo gairdneri* Richardson. *Aquaculture* 9: 259-273.

Body weights 65 – 100 grams.

Data from Huisman (Aquaculture 9: 259-273,1976)

Trout of 65 - 100 grams, body temperature of 15 °C



When energy intake = 0, then ER = -33.29 (fasting metabolism HP = 33.29 BW^{0.80})

When energy retention = 0, then Energy intake = 33.29/0.78 = 42.68

(maintenance metabolism is HP = 42.68 BW^{0.80}).

Energy in (kJ per kg metabolic weight) and BW in kg.

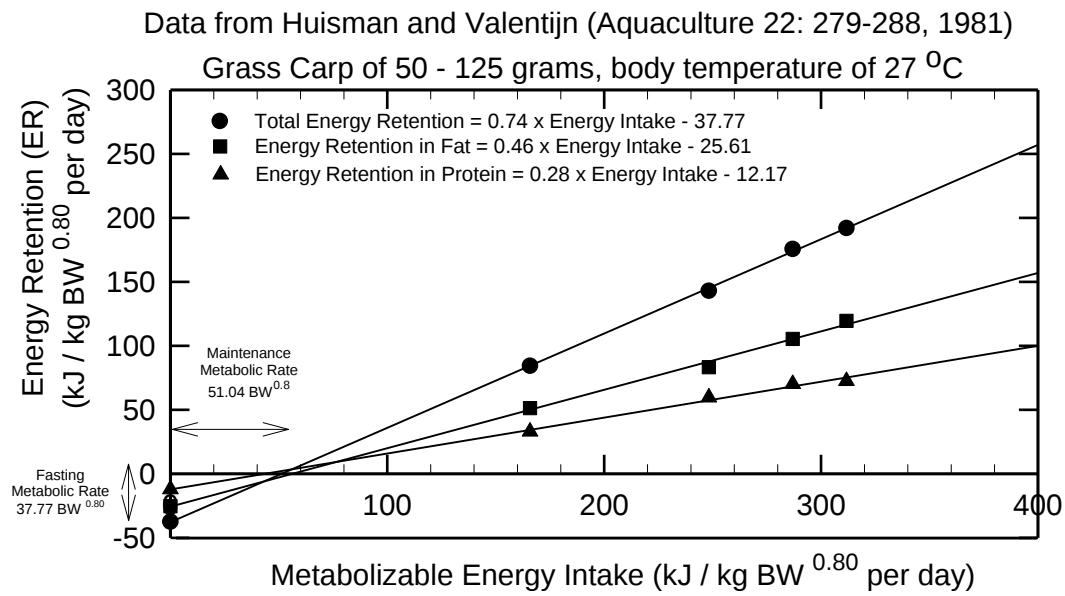
The efficiency for energy retention is the slope (= 0.78)

Appendix 41 (Figure)

Energy, protein and fat retention as a function of energy intake in the grass carp

E.A. Huisman and P. Valentijn (1981) Conversion efficiencies in grass carps (*Ctenopharyngodon Idella* Val.) using a feed for commercial production *Aquaculture* 22: 279-288.

Body weights 50 – 125 grams.



When energy intake = 0, then ER = -37.77 (fasting metabolism HP = 37.77 BW^{0.80})

When energy retention = 0, then Energy intake = 37.77/0.74 = 51.04

(maintenance metabolism is HP = 51.04 BW^{0.80}).

Energy in (kJ per kg metabolic weight) and BW in kg.

The efficiency for energy retention is the slope (= 0.74)

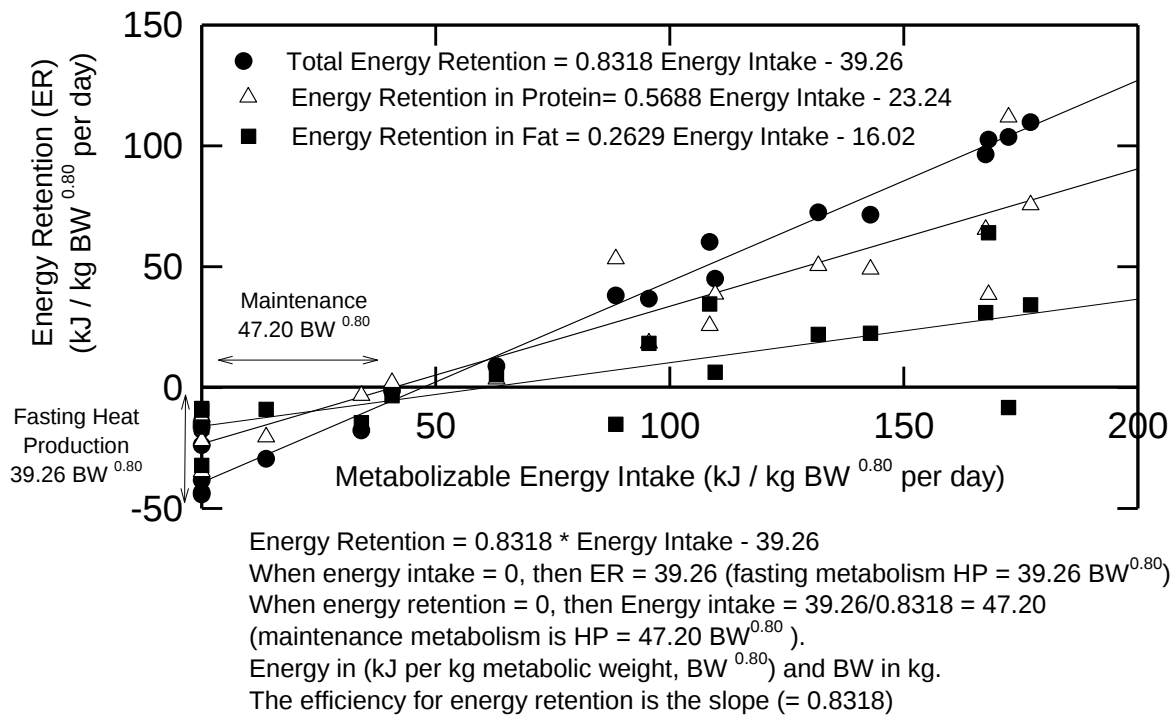
Appendix 42 (Figure)

Energy, protein and fat retention as a function of energy intake in the African Catfish

M.A.M. Machiels and A.M. Henken (1986) A dynamic simulation model for growth of the African Catfish (Clarias gariepinus) Burchell 1822. I Effect of feeding level on growth and energy metabolism. Aquaculture 56: 29 – 52.

Body weights 3 – 300 grams.

Data from Machiels (1986) Aquaculture 56: 29-56
 (African catfish, 30 °C)



With this method, the fasting heat production was 39.26 BW^{0.80}. These data are reported in Appendix 9

The fasting heat production as calculated with the alternative method i.e. from the loss of total body energy under fasting conditions (Appendix 27) was 36.77 BW^{0.8027}

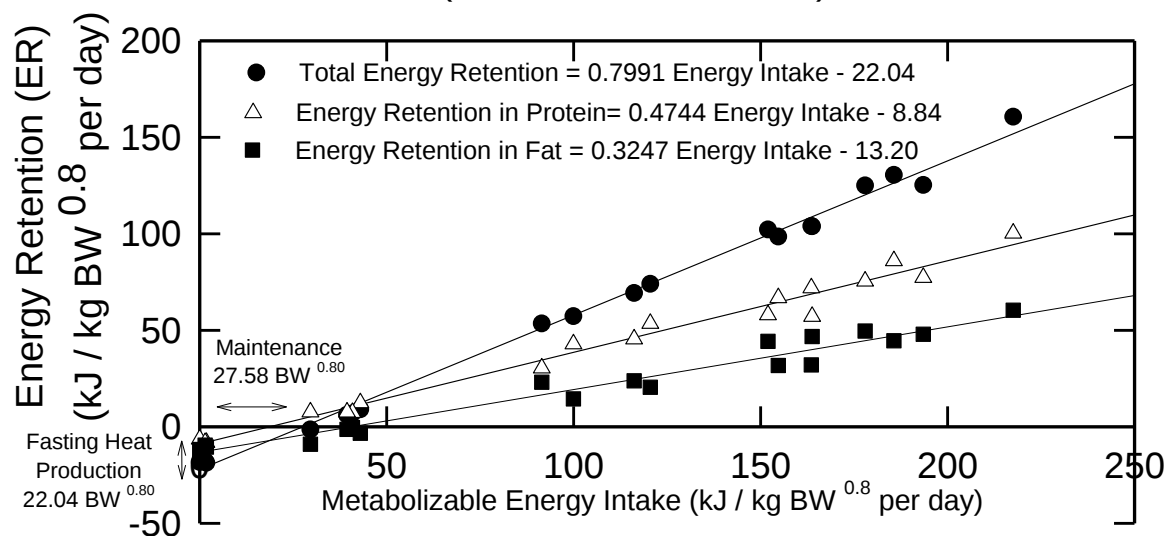
Appendix 43 (Figure)

Energy, protein and fat retention as a function of energy intake in the African Catfish

M.A.M. Machiels and A.M. Henken (1986) A dynamic simulation model for growth of the African Catfish (Clarias gariepinus) Burchell 1822. I Effect of feeding level on growth and energy metabolism. Aquaculture 56: 29 – 52.

Body weights 3 – 300 grams.

Data from Machiels (1986) 56: 29-52
 (African catfish, 25 °C)



Energy Retention = 0.7991 * Energy Intake - 22.04
 When energy intake = 0, then ER = 22.04 (fasting metabolism HP = 22.04 BW^{0.80})
 When energy retention = 0, then Energy intake = 22.04/0.7991 = 27.58
 (maintenance metabolism is HP = 27.58 BW^{0.80}).
 Energy in (kJ per kg metabolic weight, BW^{0.80}) and BW in kg.
 The efficiency for energy retention is the slope (= 0.7991)

With this method, the fasting heat production was 22.04 BW^{0.80} (these data are reported in Appendix 9)

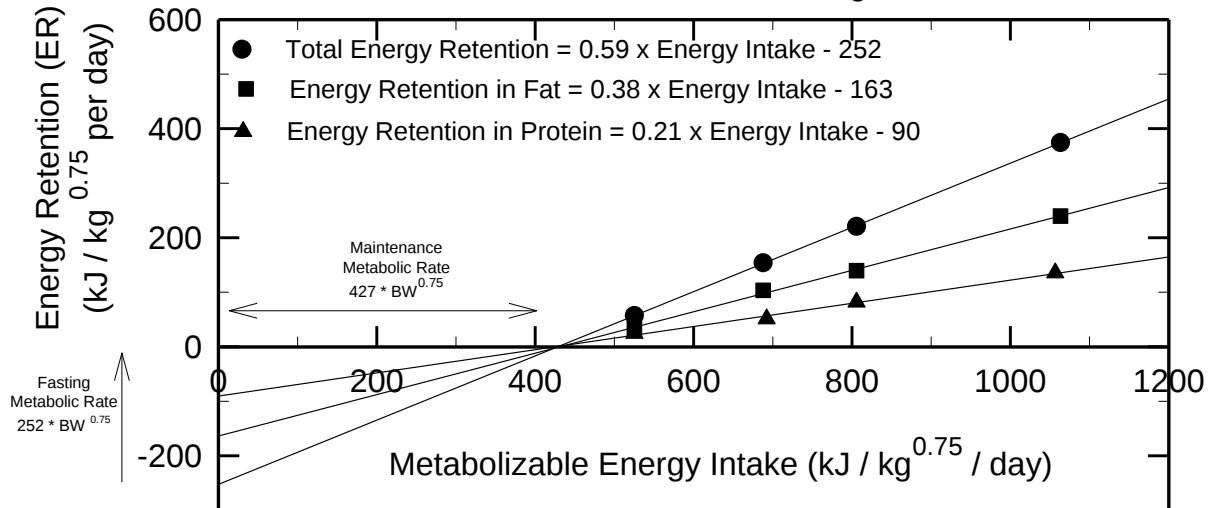
The fasting heat production as calculated with the alternative method, i.e. from the loss of body energy under fasting conditions (Appendix 28) was 18.71 BW^{0.8035}

Appendix 44 (Figure)

Energy, protein and fat retention as a function of energy intake in the obese and lean rat

J.D. Pullar and A.J.F. Webster (1977) The energy cost of fat and protein deposition in the rat. British Journal of Nutrition 37: 355 – 363.

Data from Pullar and Webster (Brit. J Nutr. 37: 355-363, 1977)
Lean Zucker Rats of 200 and 350 grams



When energy intake = 0, then ER = -252 (fasting metabolism HP = $252 \times \text{BW}^{0.75}$)

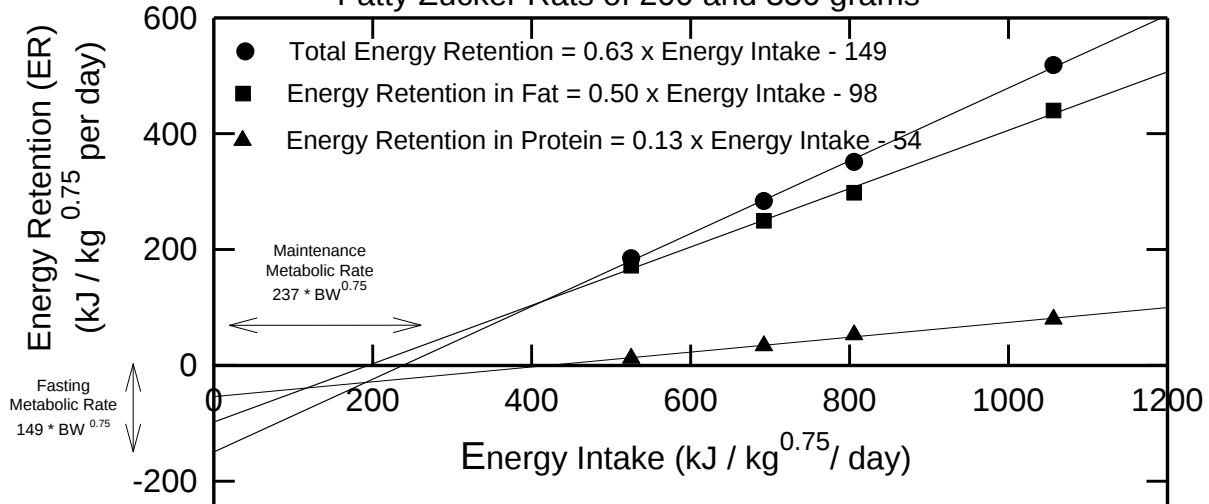
When energy retention = 0, then Energy intake = $252/0.59 = 427$

(maintenance metabolism is HP = $427 \times \text{BW}^{0.75}$).

Energy in (kJ per kg metabolic weight) and BW in kg .

The efficiency for energy retention is the slope (= 0.59)

Data from Pullar 1977 (Brit. J Nutr. 37, page 355-363)
Fatty Zucker Rats of 200 and 350 grams



When energy intake = 0, then ER = -149 (fasting metabolism HP = $149 \times \text{BW}^{0.75}$)

When energy retention = 0, then Energy intake = $149/0.63 = 237$

(maintenance metabolism is HP = $237 \times \text{BW}^{0.8}$).

Energy in (kJ per kg metabolic weight) and BW in kg .

The efficiency for energy retention is the slope (= 0.63)

Appendix 45 (Figure)

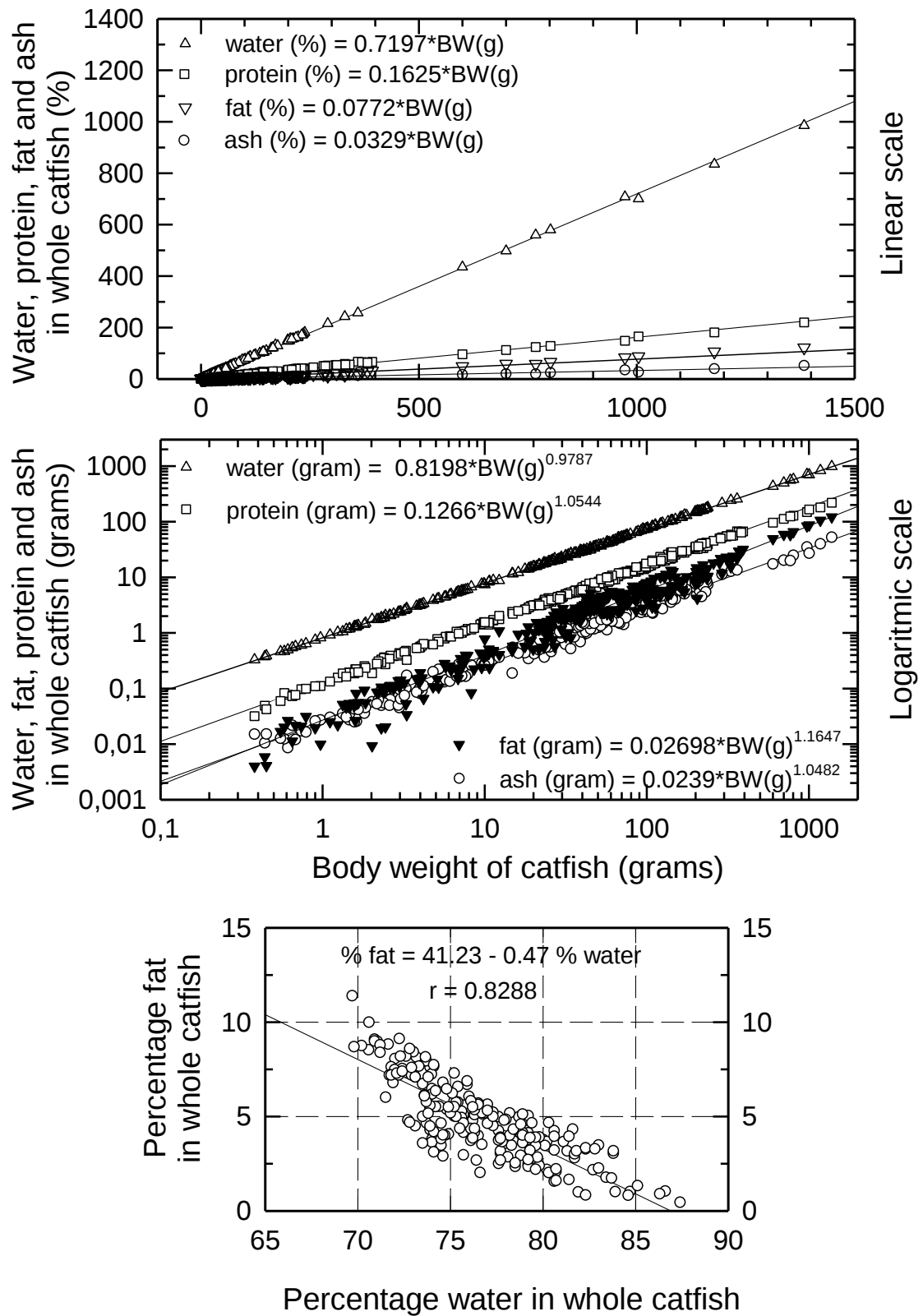
Body Composition of the African Catfish

For the body composition of the African Catfish (*Clarias gariepinus*), the compositional data of the following articles have been used:

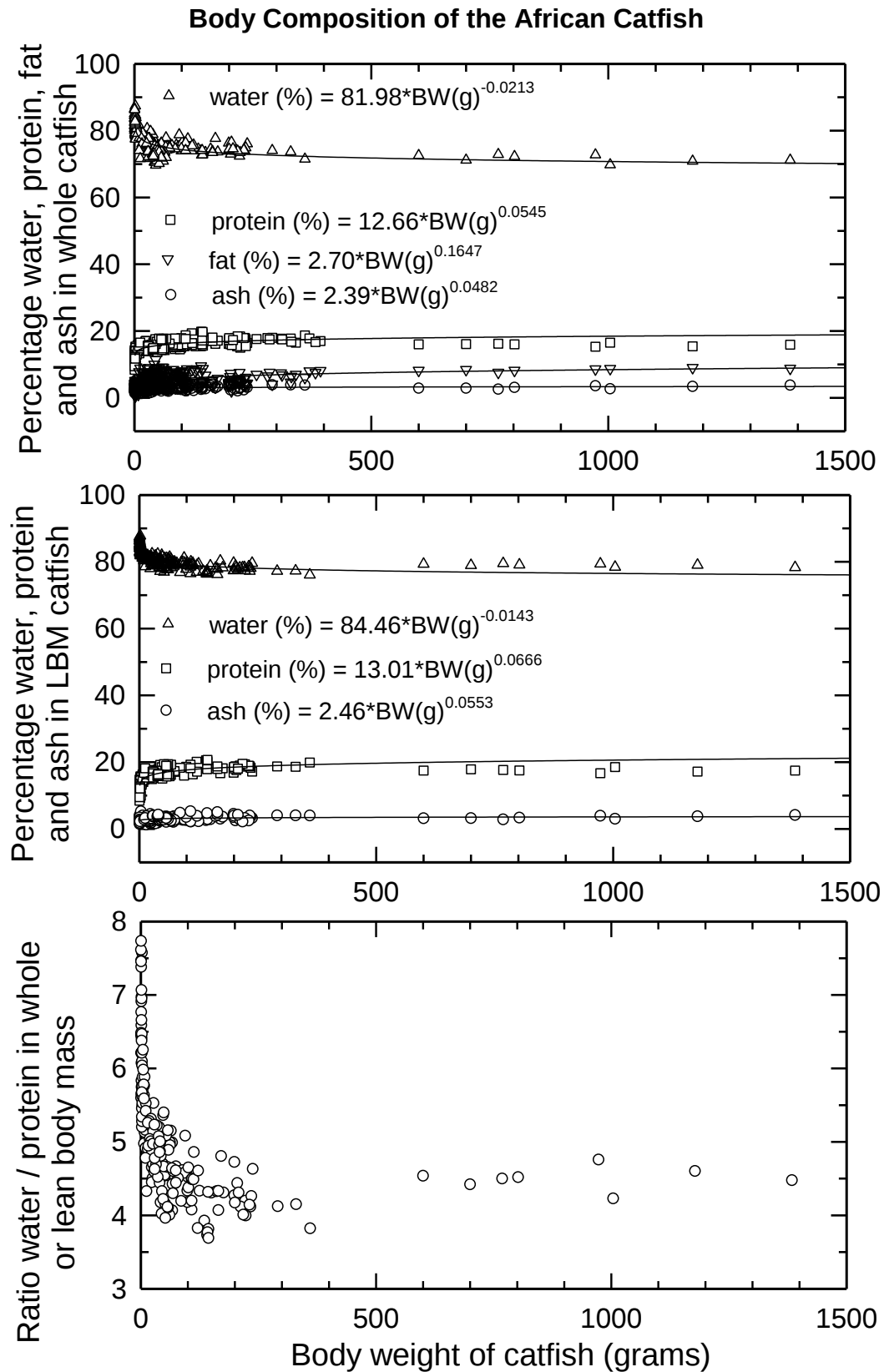
- Machiels, M.A.M. & Henken, A.M. (1986) A dynamic simulation model for growth of the African Catfish, *Clarias Gariepinus* (Burchell 1822). I Effect of feeding level on growth and energy metabolism. *Aquaculture* 56: 29-52
- Machiels, M.A.M. (1987) A dynamic simulation model for growth of the African Catfish, *Clarias Gariepinus* (Burchell 1822). IV Effect of feed formulation on growth and feed utilization. *Aquaculture* 64: 305-323.
- Hogendoorn, H.F. (1983) Growth and production of the African Catfish *Clarias lazera* (C&V). II Effects of body weight, temperature and feeding level in intensive tank culture. *Aquaculture* 34: 265-285.
- Lim, P.-K., Boey, P.-L. and Ng, W.-K (2002) Dietary palm oil level affects growth performance, protein retention and tissue vitamin E concentration of African catfish, *Clarias gariepinus*. *Aquaculture* 202: 101-112.
- Ali, M.Z. and Jauncey, K. (2005) Approaches to optimizing dietary protein to energy ratio for African catfish *Clarias gariepinus* (Burchell 1822). *Aquaculture Nutrition* 11: 95-101.
- Ali, M.Z. and Jauncey, K. (2004) Optimal dietary carbohydrate to lipid ratio in African catfish *Clarias gariepinus* (Burchell 1822) *Aquaculture International* 12: 169-180.
- Ng, W.-K., Wang, Y., Ketchimenin, P. and Yuen, K.-H. (2004) Replacement of dietary fish oil with palm oil fatty acid distillate elevates tocopherol and tocotrienol concentrations and increases oxidative stability in the muscle of African catfish, *Clarias gariepinus*. *Aquaculture* 223: 423-437.
- Ng, W.-K., Lim, P.-K. and Boey, P.-L. (2003) Dietary lipid and palm oil source affects growth, fatty acid composition and muscle α -tocopherol concentration of African catfish, *Clarias gariepinus*. *Aquaculture* 215: 229-243.

Appendix 46 (Figure)

Body Composition of the African Catfish

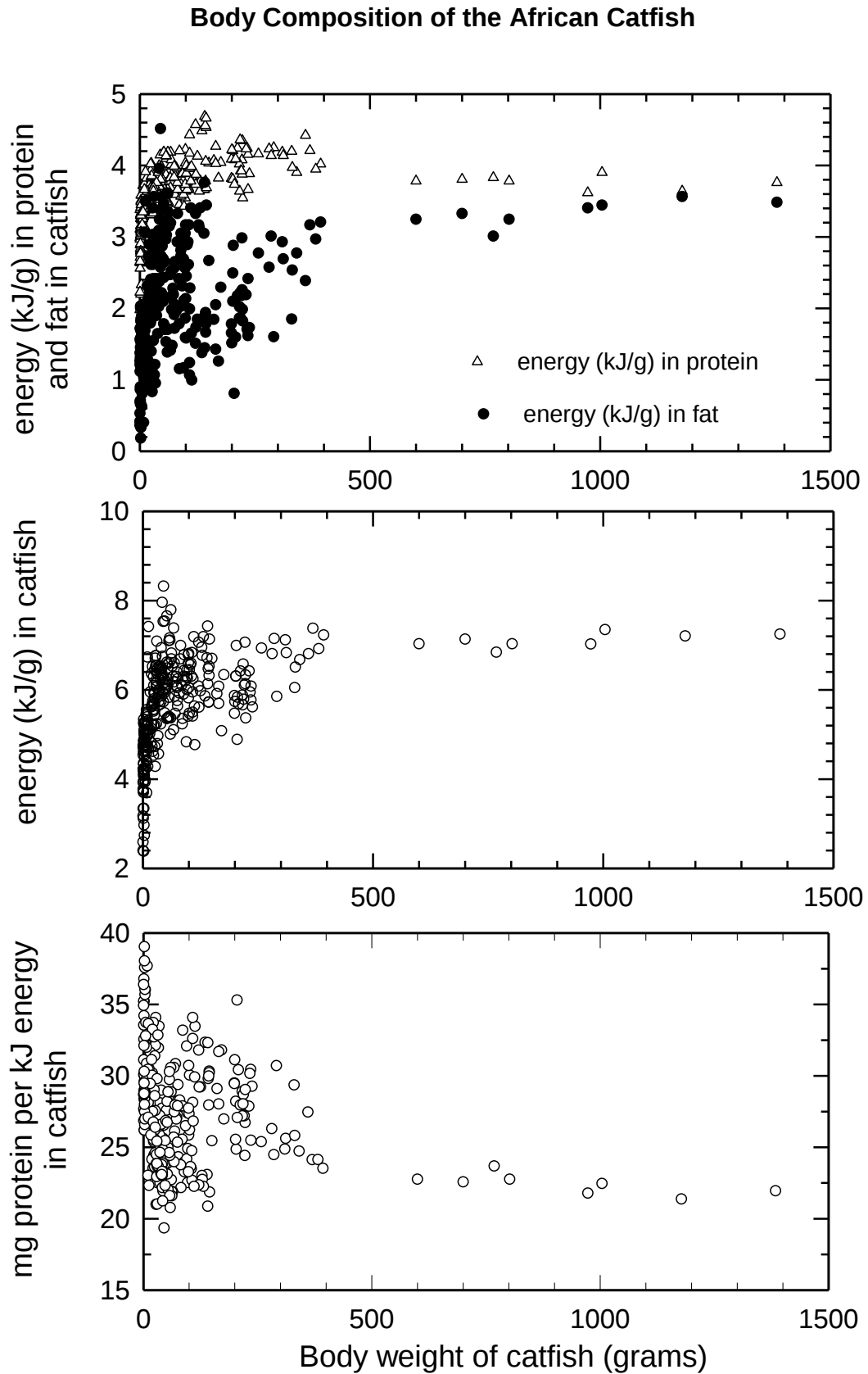


Appendix 47 (Figure)



LMB, lean body mass or fat-free body mass.

Appendix 48 (Figure)



The energy values of 23.65 kJ / gram protein and 39.6 kJ per gram fat were used

Appendix 49 (Figure)

Body Composition of the African Catfish

The graphs on the next page are a summary of the previous graphs with all the individual data from the various articles that describe the body composition of the African catfish.

Compositional data in the graphs were derived from African catfish in the weight range of about 0 – 1400 grams (see previous graphs).

The formula below were derived from the previous graphs

$$\begin{aligned}\text{Moisture (\%)} &= 81.98 \text{ BW(g)}^{-0.0213} \\ \text{Protein (\%)} &= 12.66 \text{ BW(g)}^{0.0545} \\ \text{Fat (\%)} &= 2.70 \text{ BW(g)}^{0.1647} \\ \text{Ash (\%)} &= 2.39 \text{ BW(g)}^{0.0482} \\ \text{Energy (kJ/gram)} &= 3.929 \text{ BW}^{0.0975}\end{aligned}$$

$$\text{mg protein / kJ} = 32.22 \text{ BW}^{-0.0431}$$

$$\begin{aligned}\text{Moisture (g)} &= 0.8198 \text{ BW(g)}^{0.9787} \\ \text{Protein (g)} &= 0.1266 \text{ BW(g)}^{1.0545} \\ \text{Fat (g)} &= 0.027 \text{ BW(g)}^{1.1647} \\ \text{Ash (g)} &= 0.0239 \text{ BW(g)}^{1.0482} \\ \text{Energy (kJ)} &= 3.929 \text{ BW}^{1.0975}\end{aligned}$$

The formulas for the calculation of the energy / kJ and the mg protein / kJ were derived from the formula describing the protein and fat content of the body that were calculated from the individual data from the various articles.

When the formula is known that gives the absolute amount of moisture, fat, protein or ash (in grams) in the body as a function of the body weight, then the formula that gives the percentage of moisture, fat, protein or ash (in percentages) in the body as function of the body weight can be derived.

Similarly, when the formula is known that gives the percentage of moisture, fat, protein or ash (in percentages) in the body as a function of the body weight, then the formula that gives the absolute amount of moisture, fat, protein or ash (in grams) in the body as function of the body weight can be derived.

For example:

Suppose that the amount of protein (grams) in the body as a function of the body weight is $0.1336 \text{ BW(g)}^{1.036}$.

Then the percentage of protein in the fish is:

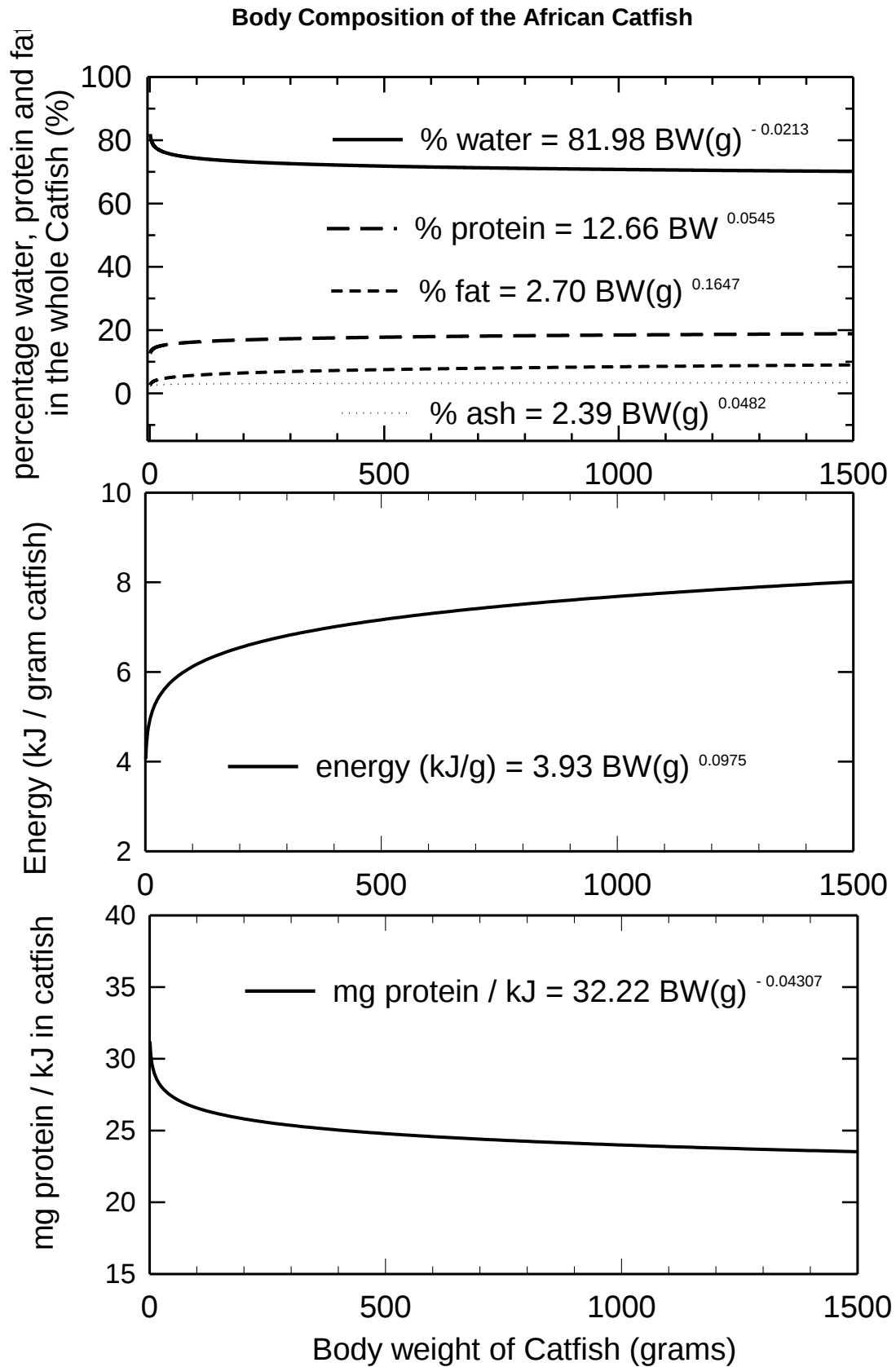
$$\% \text{ of protein} = 100\% * 0.1336 \text{ BW(g)}^{1.036} / \text{BW} = 13.36 \text{ BW}^{1.036 - 1} = 13.36 \text{ BW(g)}^{0.036}$$

On the other hand, suppose that the percentage of protein in the body as a function of the body weight is $13.36 \text{ BW(g)}^{0.036}$

Then, the absolute amount of protein (in grams) is:

$$= (13.36 / 100) \text{ BW}^{0.036} * \text{BW} = 0.1336 \text{ BW}^{(0.036+1)} = 0.1336 \text{ BW}^{1.036}$$

Appendix 50 (Figure)



The gross energy values of 23.65 kJ / gram protein and 39.6 kJ per gram fat were used

Appendix 51 (Figure)

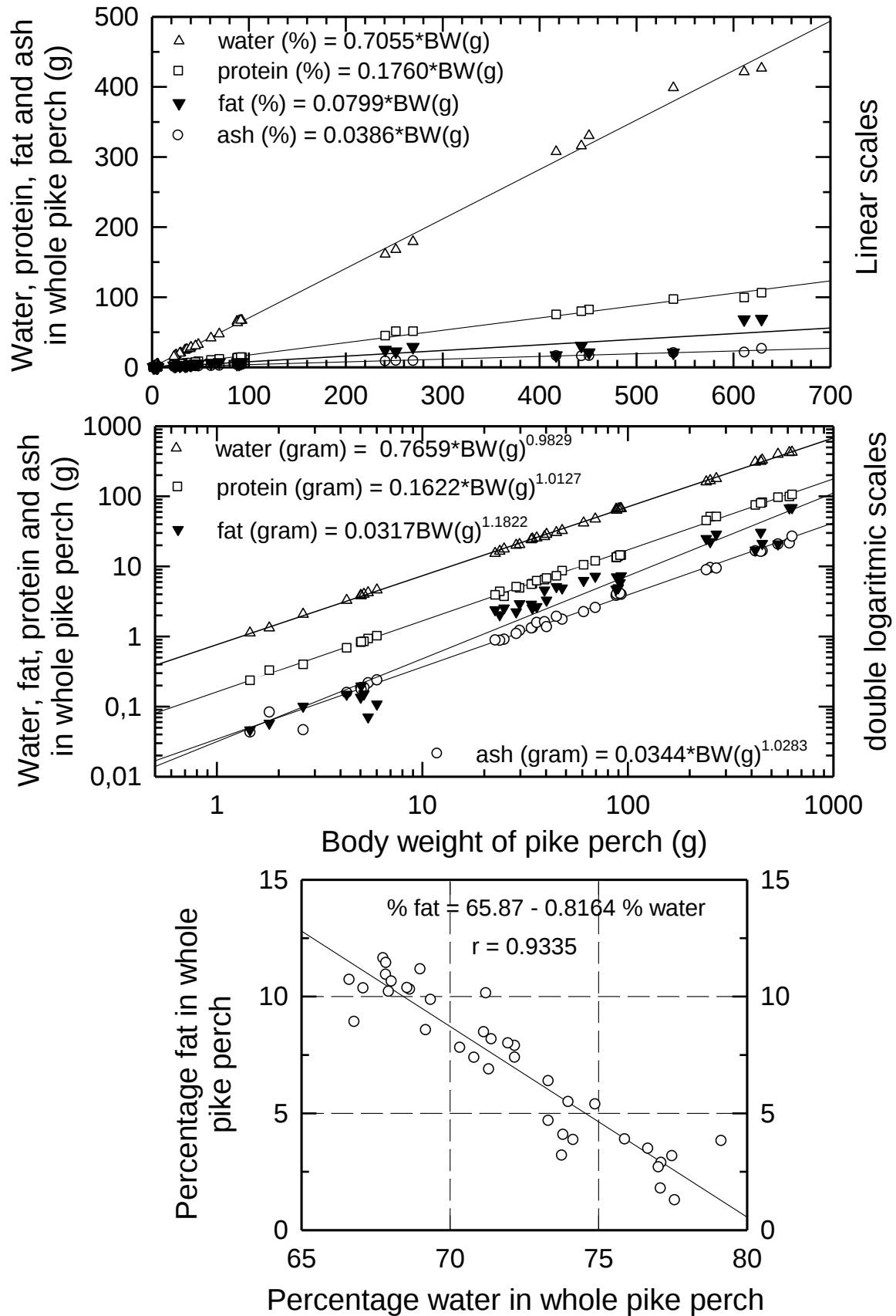
Body Composition of the Pike Perch, *Sander Lucioperca*

For the body composition of the Pike Perch, the compositional data of the following articles have been used:

- Kowalska, A., Zakes, Z., Jankowska, B. and Demska-Zakes, K. (2011) Effect of different dietary lipid levels on growth, performance, slaughter yield, chemical composition and histology of liver and intestine of pike perch, *Sander lucioperca*. Czech Journal of Animal Science 56: 136-149.
- Molnar, T., Szabo, A., Szabo, G., Szabo, C. & Hancz, C. (2006). Effect of different dietary fat content and fat type on the growth and body composition of intensively reared pike perch *Sander lucioperca* (L.). Aquaculture Nutrition 12: 173-182 (2006). (PDF)
- Nyina-Wamwiza, L., Xu, G.T., Blanchard, G & Kestemont, P. (2005) Effect of dietary protein lipid and carbohydrate ratio on growth, feed efficiency and body composition of pike perch *Sander Lucioperca* fingerlings. Aquaculture Research 35: 486-492. (PDF)
- Schulz, C., Böhm, M., Wirth, M. & Rennert, B. (2007) Effect of dietary protein on growth, feed conversion, body composition and survival of Pike Perch fingerlings (*Sander lucioperca*). Aquaculture Nutrition 13: 373-380 (PDF).
- Zakes, Z., Przybyl, A., Wozniak, M., Szczepkowski, M. & Mazurkiewicz, J. (2004) Growth performance of juvenile pike perch *Sander Lucioperca* (L) fed graded levels of dietary lipids. Czech Journal of Animal Science 49:156-2004. (PDF)
- Zakes, Z., Szkudlarek, M., Wozniak, M., Demska-Zakes, K. and Czerniak, S. (2003) Effects of feeding regimes on growth, within group weight variability, and chemical composition of the juvenile Zander, *Sander lucioperca* (L), body. Electronic Journal of Polish Agricultural Universities. Volume 6.

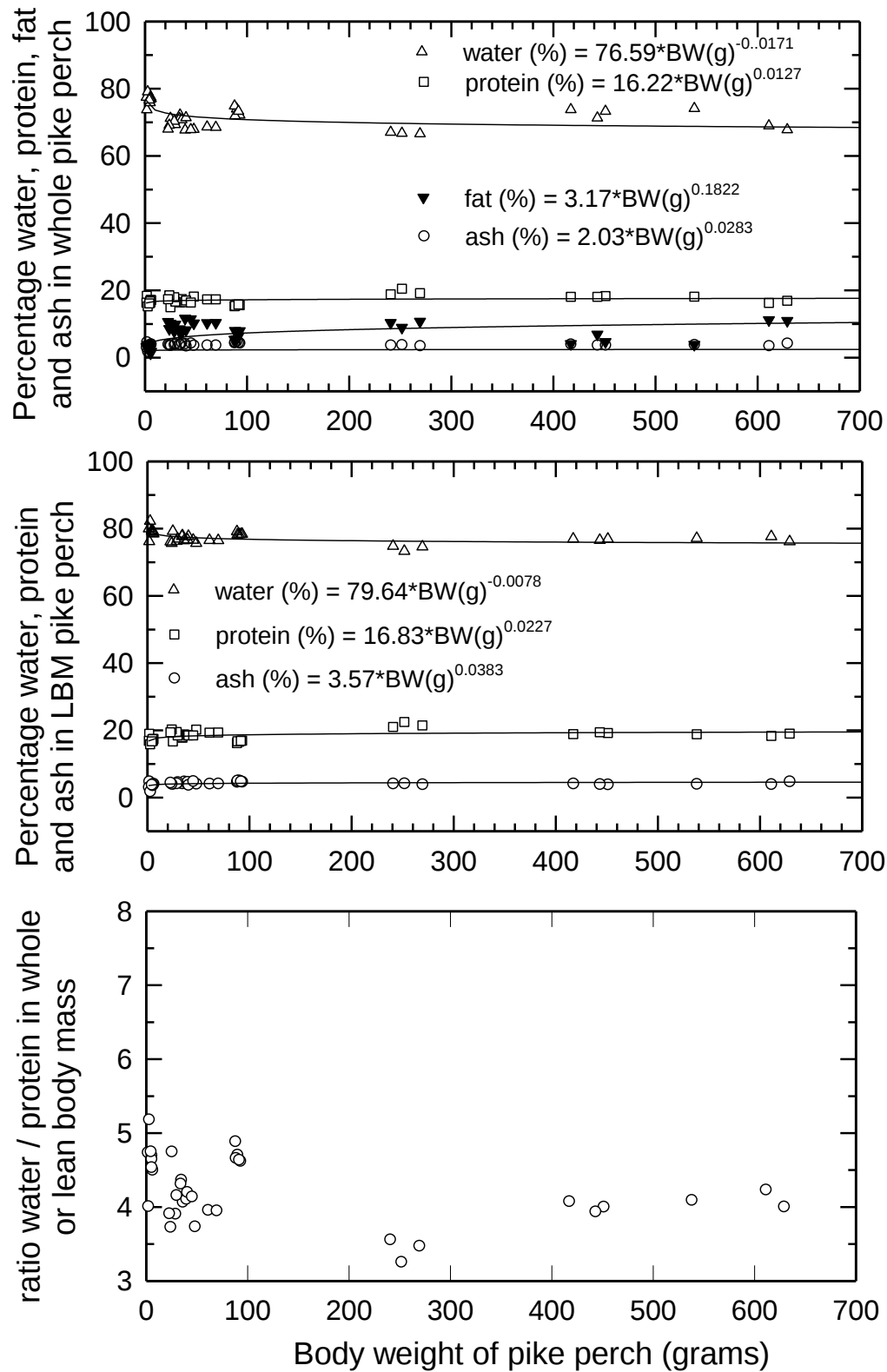
Appendix 52 (Figure)

Body Composition of the Pike Perch



Appendix 53 (Figure)

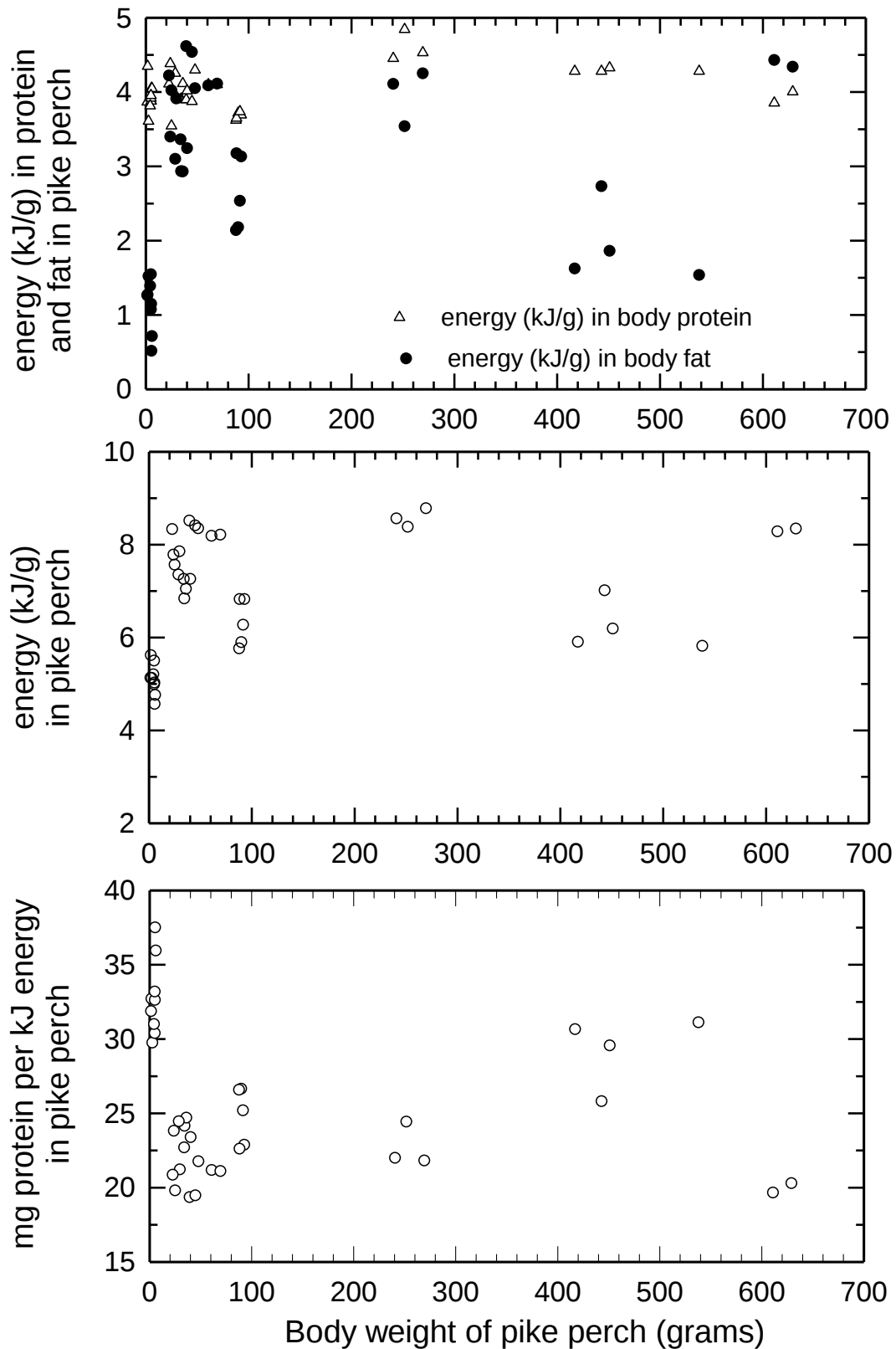
Body Composition of the Pike Perch



LBM, lean body mass or fat-free body mass.

Appendix 54 (Figure)

Body Composition of the Pike Perch



The energy values of 23.65 kJ / gram protein and 39.6 kJ per gram fat were used

Appendix 55 (Figure)

Body Composition of the Pike Perch

The graphs on the next page are a summary of the previous graphs with all the individual data from the various articles that describe the body composition of the Pike Perch.

Compositional data in the graphs were derived from Pike Perch in the weight range of about 0 – 650 grams (see previous graphs).

The formula below were derived from the previous graphs

$$\begin{aligned}\text{Moisture (\%)} &= 76.59 \text{ BW(g)}^{-0.0171} \\ \text{Protein (\%)} &= 16.22 \text{ BW(g)}^{0.0127} \\ \text{Fat (\%)} &= 3.17 \text{ BW(g)}^{0.1822} \\ \text{Ash (\%)} &= 2.03 \text{ BW(g)}^{0.0283} \\ \text{Energy (kJ/gram)} &= 4.8834 \text{ BW}^{0.08749} \\ \text{mg protein / kJ} &= 33.21 \text{ BW}^{-0.06048}\end{aligned}$$

$$\begin{aligned}\text{Moisture (g)} &= 0.7659 \text{ BW(g)}^{0.9829} \\ \text{Protein (g)} &= 0.1622 \text{ BW(g)}^{1.01271} \\ \text{Fat (g)} &= 0.0317 \text{ BW(g)}^{1.1822} \\ \text{Ash (g)} &= 0.0203 \text{ BW(g)}^{1.0283} \\ \text{Energy (kJ)} &= 4.8834 \text{ BW}^{1.08749}\end{aligned}$$

The formulas for the calculation of the energy / kJ and the mg protein / kJ were derived from the formulas describing the protein and fat content of the body that were calculated from the individual data from the various articles.

When the formula is known that gives the absolute amount of moisture, fat, protein or ash (in grams) in the body as a function of the body weight, then the formula that gives the percentage of moisture, fat, protein or ash (in percentages) in the body as function of the body weight can be derived.

Similarly, when the formula is known that gives the percentage of moisture, fat, protein or ash (in percentages) in the body as a function of the body weight, then the formula that gives the absolute amount of moisture, fat, protein or ash (in grams) in the body as function of the body weight can be derived.

For example:

Suppose that the amount of protein (grams) in the body as a function of the body weight is $0.1336 \text{ BW(g)}^{1.036}$.

Then the percentage of protein in the fish is:

$$\% \text{ of protein} = 100\% * 0.1336 \text{ BW(g)}^{1.036} / \text{BW} = 13.36 \text{ BW}^{1.036-1} = 13.36 \text{ BW(g)}^{0.036}$$

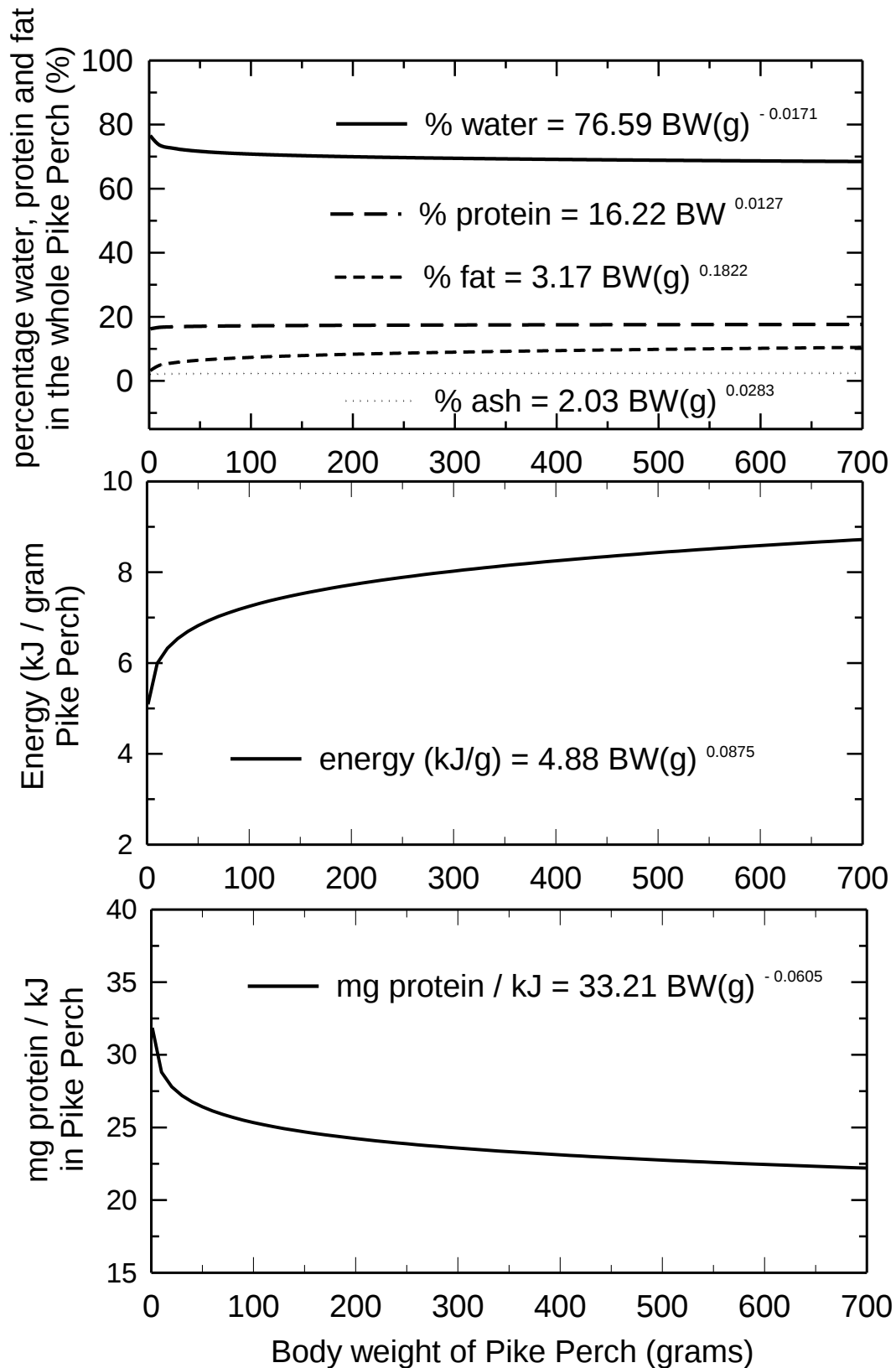
On the other hand, suppose that the percentage of protein in the body as a function of the body weight is $13.36 \text{ BW(g)}^{0.036}$

Then, the absolute amount of protein (in grams) is:

$$= (13.36 / 100) \text{ BW}^{0.036} * \text{BW} = 0.1336 \text{ BW}^{(0.036+1)} = 0.1336 \text{ BW}^{1.036}$$

Appendix 56 (Figure)

Body Composition of the Pike Perch

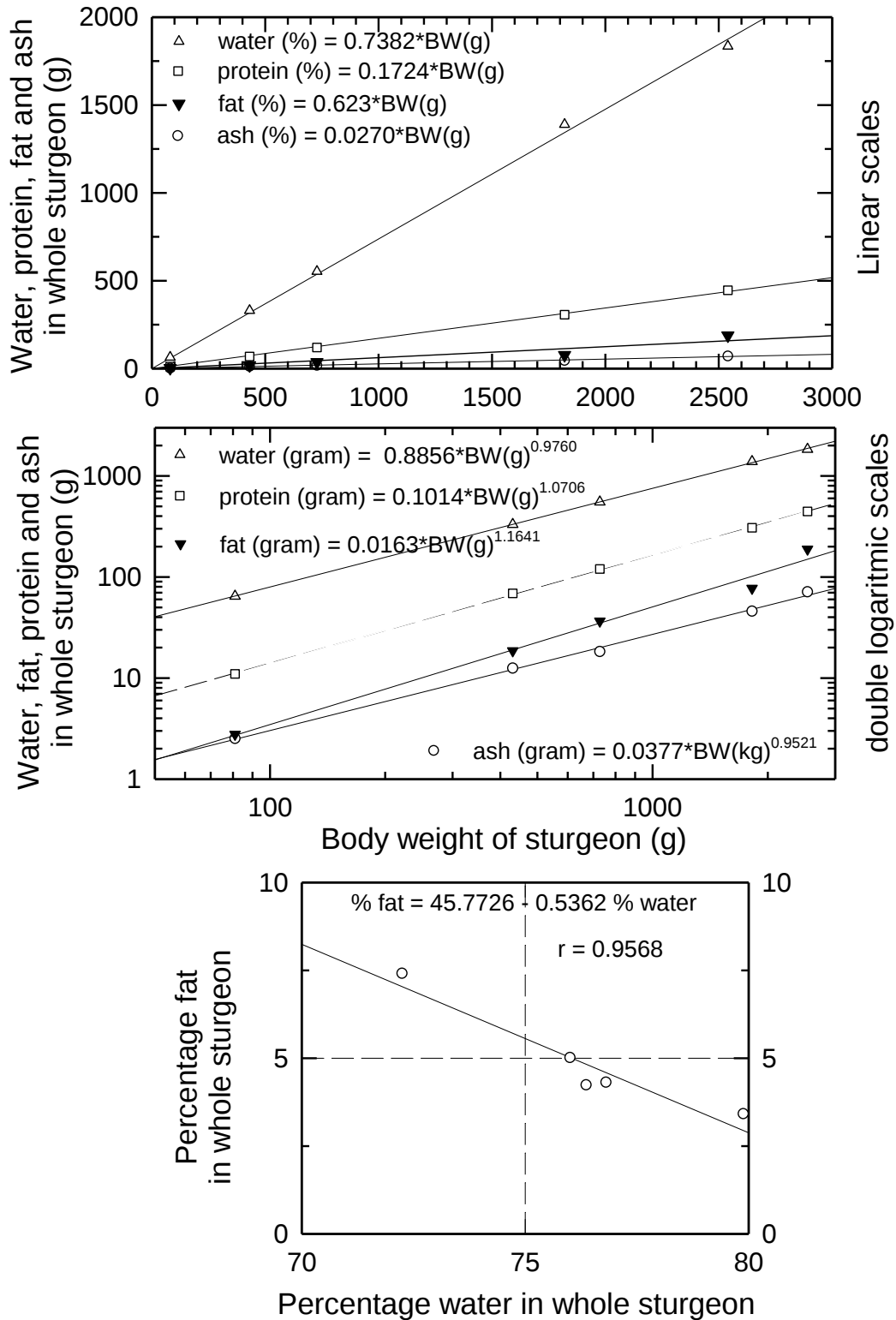


The energy values of 23.65 kJ / gram protein and 39.6 kJ per gram fat were used

Appendix 57 (Figure)

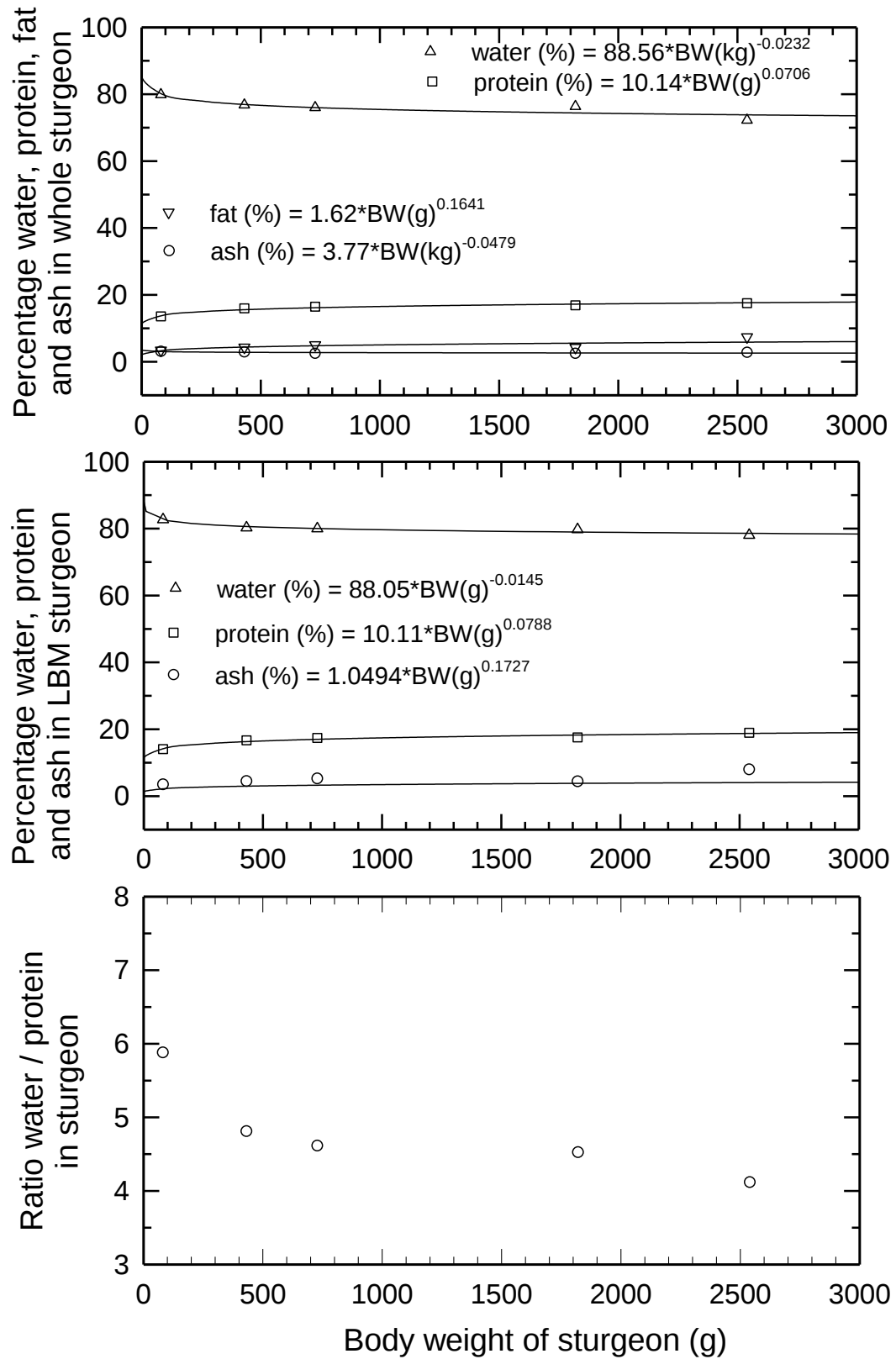
Body Composition of the Sturgeon (*Acipenser Transmontanus*)

Data from: Hung, S.S.O., Lutes, P.B. and Conte, F.S. (1987) Carcass proximate composition of juvenile white sturgeon (*Acipenser transmontanus*). Comparative Biochemistry and Physiology 88B: 269-272.



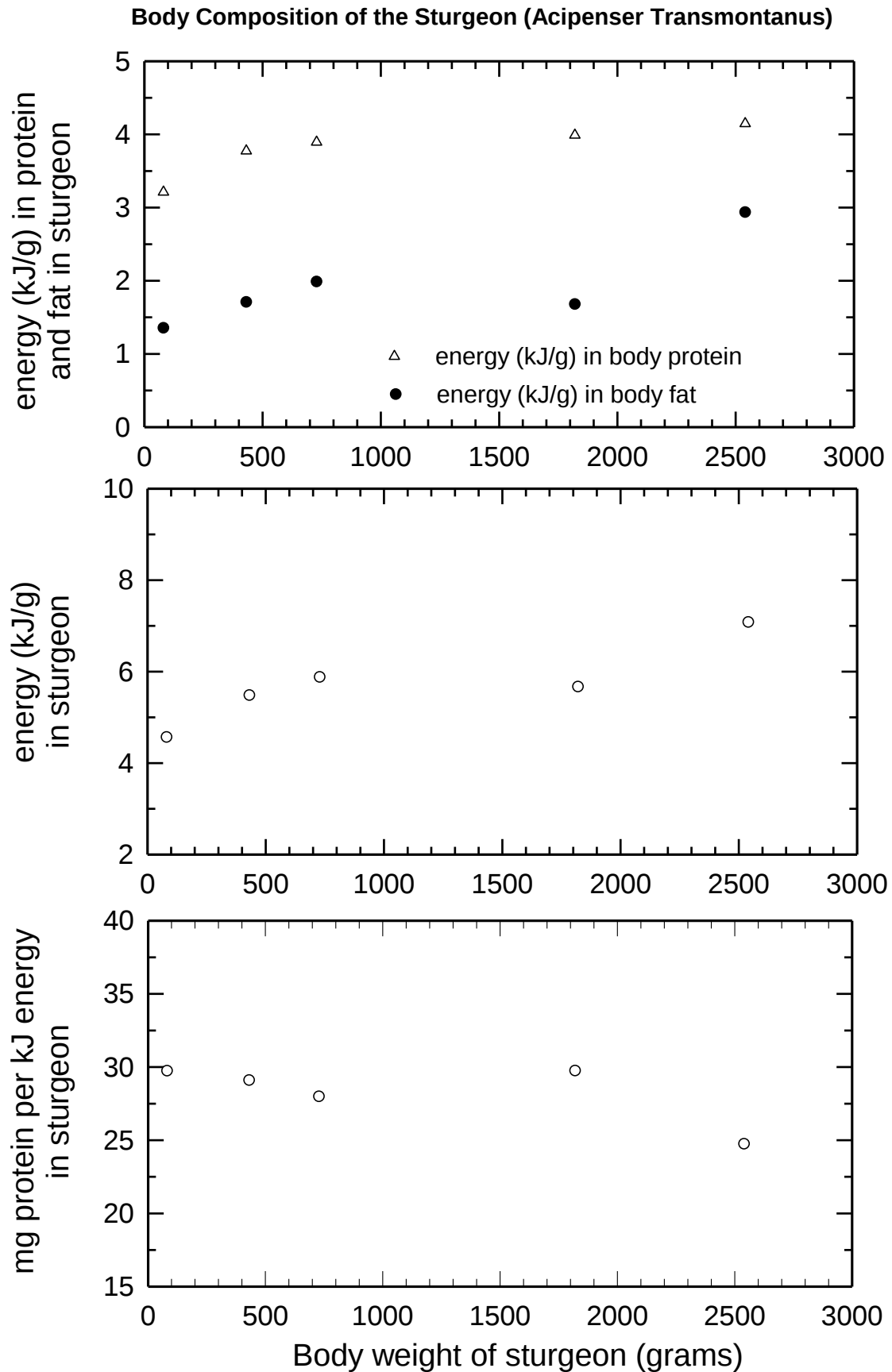
Appendix 58 (Figure)

Body Composition of the Sturgeon (*Acipenser Transmontanus*)



LBM, lean body mass or fat-free body mass.

Appendix 59 (Figure)



The energy values of 23.65 kJ / gram protein and 39.6 kJ per gram fat were used

Appendix 60 (Figure)

Body Composition of the Sturgeon (*Acipenser Transmontanus*)

The graphs on the next page are a summary of the previous graphs with all the individual data from the various articles that describe the body composition of the Sturgeon.

Compositional data in the graphs were derived from Sturgeon in the weight range of about 0 – 2500 grams (see previous graphs).

The formula below were derived from the previous graphs.

$$\begin{aligned}\text{Moisture (\%)} &= 88.56 \text{ BW(g)}^{-0.0232} \\ \text{Protein (\%)} &= 10.14 \text{ BW(g)}^{0.0706} \\ \text{Fat (\%)} &= 1.62 \text{ BW(g)}^{0.1641} \\ \text{Ash (\%)} &= 3.77 \text{ BW(g)}^{-0.0479} \\ \text{Energy (kJ/gram)} &= 2.942 \text{ BW}^{0.1011}\end{aligned}$$

$$\text{mg protein / kJ} = 34.46 \text{ BW}^{-0.0305}$$

$$\begin{aligned}\text{Moisture (g)} &= 0.8856 \text{ BW(g)}^{0.9768} \\ \text{Protein (g)} &= 0.1014 \text{ BW(g)}^{1.0706} \\ \text{Fat (g)} &= 0.0162 \text{ BW(g)}^{1.1641} \\ \text{Ash (g)} &= 0.0377 \text{ BW(g)}^{0.952} \\ \text{Energy (kJ)} &= 2.942 \text{ BW}^{1.01011}\end{aligned}$$

The formulas for the calculation of the energy / kJ and the mg protein / kJ were derived from the formula describing the protein and fat content of the body that were calculated from the individual data from the various articles.

When the formula is known that gives the absolute amount of moisture, fat, protein or ash (in grams) in the body as a function of the body weight, then the formula that gives the percentage of moisture, fat, protein or ash (in percentages) in the body as function of the body weight can be derived.

Similarly, when the formula is known that gives the percentage of moisture, fat, protein or ash (in percentages) in the body as a function of the body weight, then the formula that gives the absolute amount of moisture, fat, protein or ash (in grams) in the body as function of the body weight can be derived.

For example:

Suppose that the amount of protein (grams) in the body as a function of the body weight is $0.1336 \text{ BW(g)}^{1.036}$.

Then the percentage of protein in the fish is:

$$\% \text{ of protein} = 100\% * 0.1336 \text{ BW(g)}^{1.036} / \text{BW} = 13.36 \text{ BW}^{1.036 - 1} = 13.36 \text{ BW(g)}^{0.036}$$

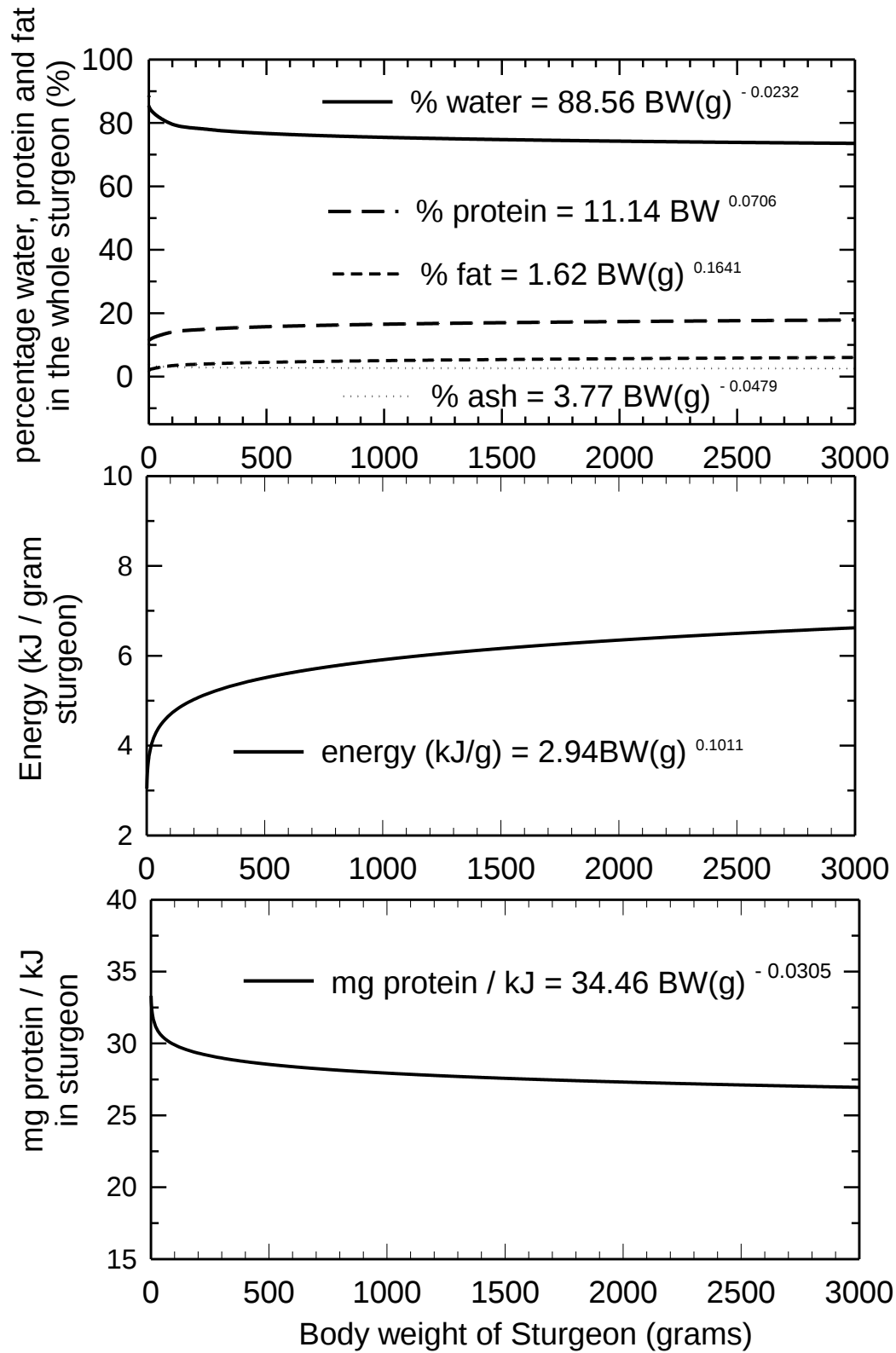
On the other hand, suppose that the percentage of protein in the body as a function of the body weight is $13.36 \text{ BW(g)}^{0.036}$

Then, the absolute amount of protein (in grams) is:

$$= (13.36 / 100) \text{ BW}^{0.036} * \text{BW} = 0.1336 \text{ BW}^{(0.036+1)} = 0.1336 \text{ BW}^{1.036}$$

Appendix 61 (Figure)

Body Composition of the Sturgeon (*Acipenser Transmontanus*)



The gross energy values of 23.65 kJ / gram protein and 39.6 kJ per gram fat were used

Appendix 62 (Figure)

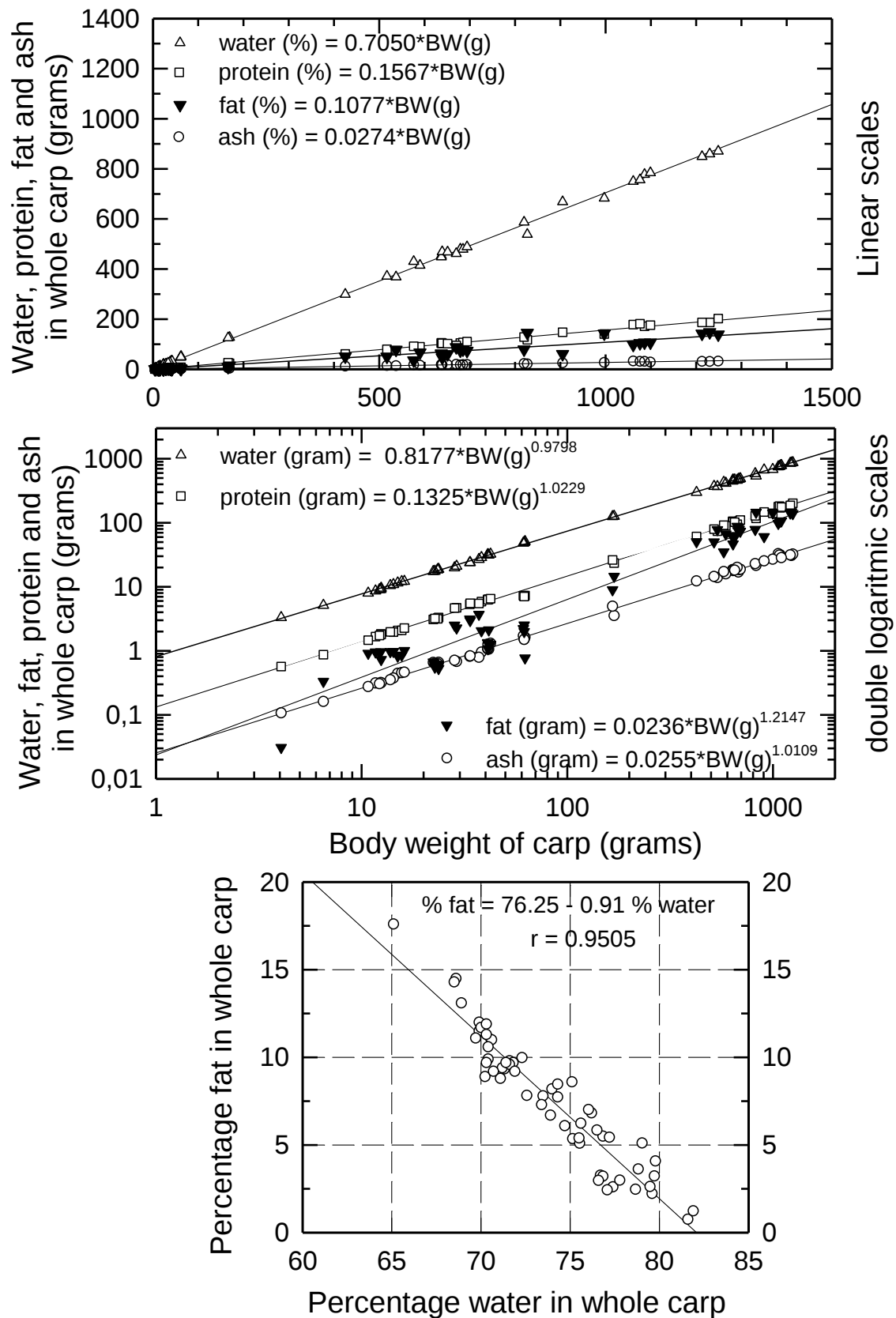
Body Composition of the Carp

For the body composition of the Carp, the compositional data of the following articles have been used:

- Du, Z.-Y., Liu, Y.-J., Tian, L.-X, Wang, J.-T., Wang, Y. and Liang, G.-Y. (2005) Effect of dietary lipid level on growth, feed utilization and body composition by juvenile grass carp. *Aquaculture Nutrition* 11: 139-146.
- Du, Z.-Y., Clouet, P., Zheng, W.-H., Degrace, P., Tian, L.-X. and Liu, Y.-J. (2006) Biochemical hepatic alterations and body lipid composition in the herbivorous grass carp (*Ctenopharyngodon idella*), fed high-fat diets. *The British Journal of Nutrition* 95: 905-915.
- Keshavanath, P., Manjappa, K. and Gangadhara, B. (2002) Evaluation of carbohydrate rich diets through common carp culture in manured tanks. *Aquaculture Nutrition* 8: 169-174.
- Nandeesh, M.C., Gangadhar, B., Varghese, T.J. and Keshavanath, P. (1998) Effect of *Spirulina platensis* on the growth, proximate composition and organoleptic quality of common carp, *Cyprinus carpio* L. *Aquaculture Research* 29: 305-312.
- Nandeesh, M.C., Gangadhar, B., Manissery, J.K. and Venkataraman, L.V. (2001) Growth performance of two Indian major carps, catla (*Catla catla*) and rohu (*Labeo rohita*) fed diets containing different levels of *Spirulina platensis*. *Bioresource Technology* 80: 117-120.
- Zeitler, M.H., Kirchgessner, M. and Schwarz, F.J. (1984) Effects of different protein and energy supplies on carcass composition of carp (*Cyprinus carpio* L.) *Aquaculture* 36: 37-48.

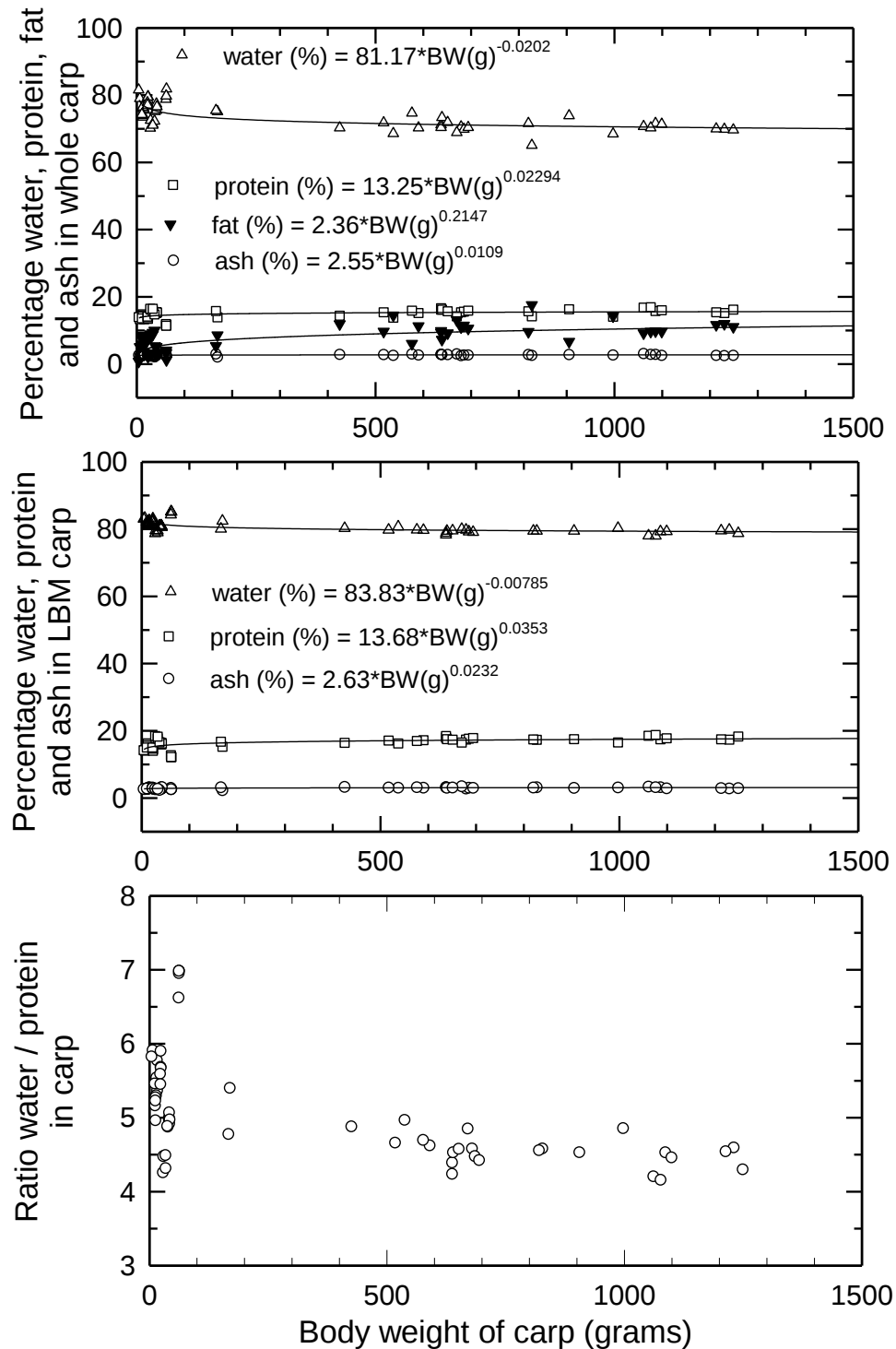
Appendix 63 (Figure)

Body Composition of the Carp



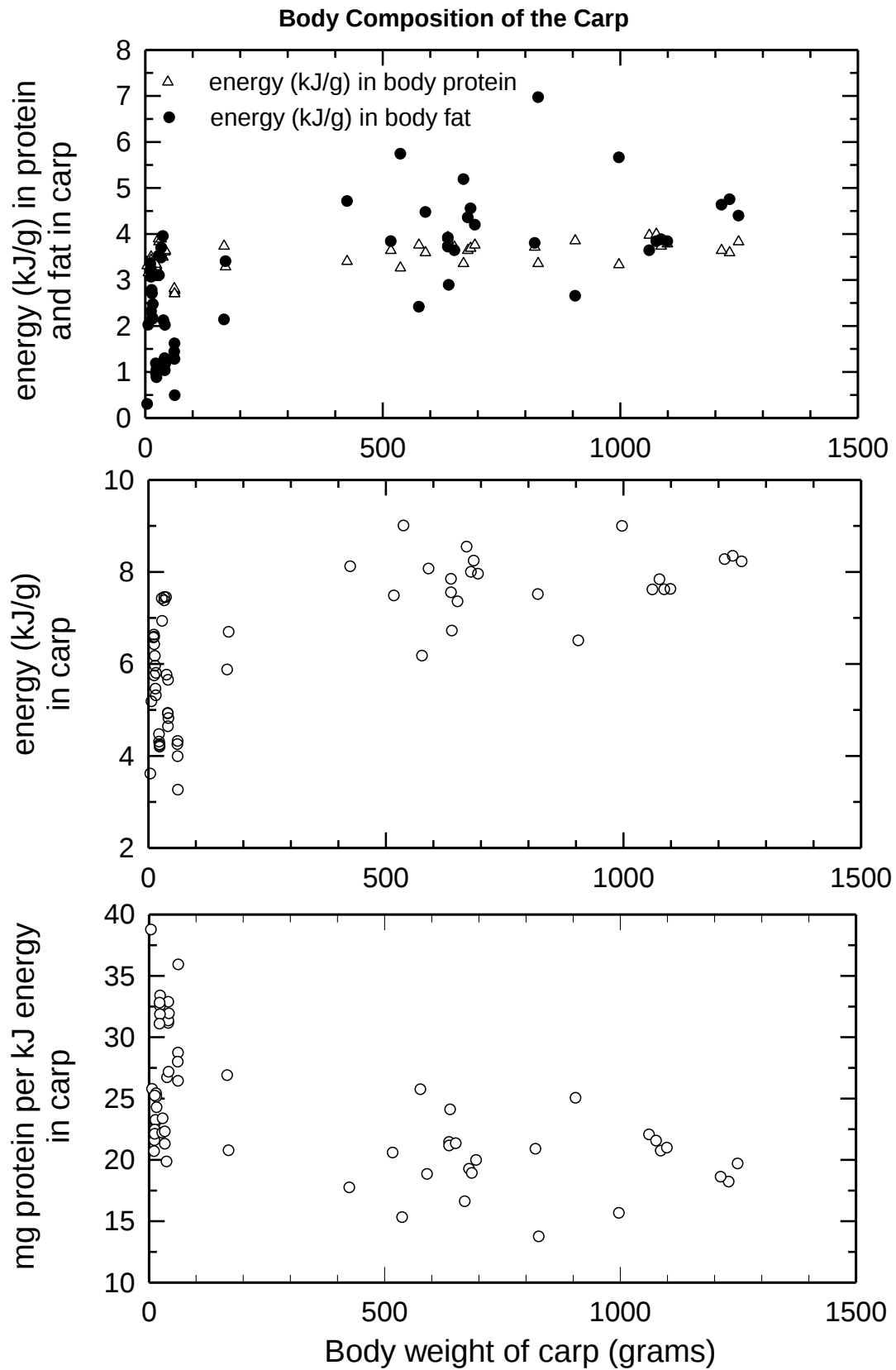
Appendix 64 (Figure)

Body Composition of the Carp



LBM, lean body mass or fat-free body mass.

Appendix 65 (Figure)



The gross energy values of 23.65 kJ / gram protein and 39.6 kJ per gram fat were used

Appendix 66 (Figure)

Body Composition of the Carp

The graphs on the next page are a summary of the previous graphs with all the individual data from the various articles that describe the body composition of the Carp.

Compositional data in the graphs were derived from Carp in the weight range of about 0 – 1250 grams (see previous graphs).

The formula below were derived from the previous graphs.

$$\begin{aligned}\text{Moisture (\%)} &= 81.17 \text{ BW(g)}^{-0.0202} \\ \text{Protein (\%)} &= 13.25 \text{ BW(g)}^{0.02294} \\ \text{Fat (\%)} &= 2.36 \text{ BW(g)}^{0.2147} \\ \text{Ash (\%)} &= 2.55 \text{ BW(g)}^{0.0109} \\ \text{Energy (kJ/gram)} &= 3.6015 \text{ BW}^{0.1114} \\ \text{mg protein / kJ} &= 36.79 \text{ BW}^{-0.0885}\end{aligned}$$

$$\begin{aligned}\text{Moisture (g)} &= 0.8117 \text{ BW(g)}^{0.9798} \\ \text{Protein (g)} &= 0.1325 \text{ BW(g)}^{1.02294} \\ \text{Fat (g)} &= 0.0236 \text{ BW(g)}^{1.2147} \\ \text{Ash (g)} &= 0.0255 \text{ BW(g)}^{1.0109} \\ \text{Energy (kJ)} &= 3.6015 \text{ BW}^{1.1114}\end{aligned}$$

The formulas for the calculation of the energy / kJ and the mg protein / kJ were derived from the formula describing the protein and fat content of the body that were calculated from the individual data from the various articles.

When the formula is known that gives the absolute amount of moisture, fat, protein or ash (in grams) in the body as a function of the body weight, then the formula that gives the percentage of moisture, fat, protein or ash (in percentages) in the body as function of the body weight can be derived.

Similarly, when the formula is known that gives the percentage of moisture, fat, protein or ash (in percentages) in the body as a function of the body weight, then the formula that gives the absolute amount of moisture, fat, protein or ash (in grams) in the body as function of the body weight can be derived.

For example:

Suppose that the amount of protein (grams) in the body as a function of the body weight is $0.1336 \text{ BW(g)}^{1.036}$.

Then the percentage of protein in the fish is:

$$\% \text{ of protein} = 100\% * 0.1336 \text{ BW(g)}^{1.036} / \text{BW} = 13.36 \text{ BW}^{1.036-1} = 13.36 \text{ BW(g)}^{0.036}$$

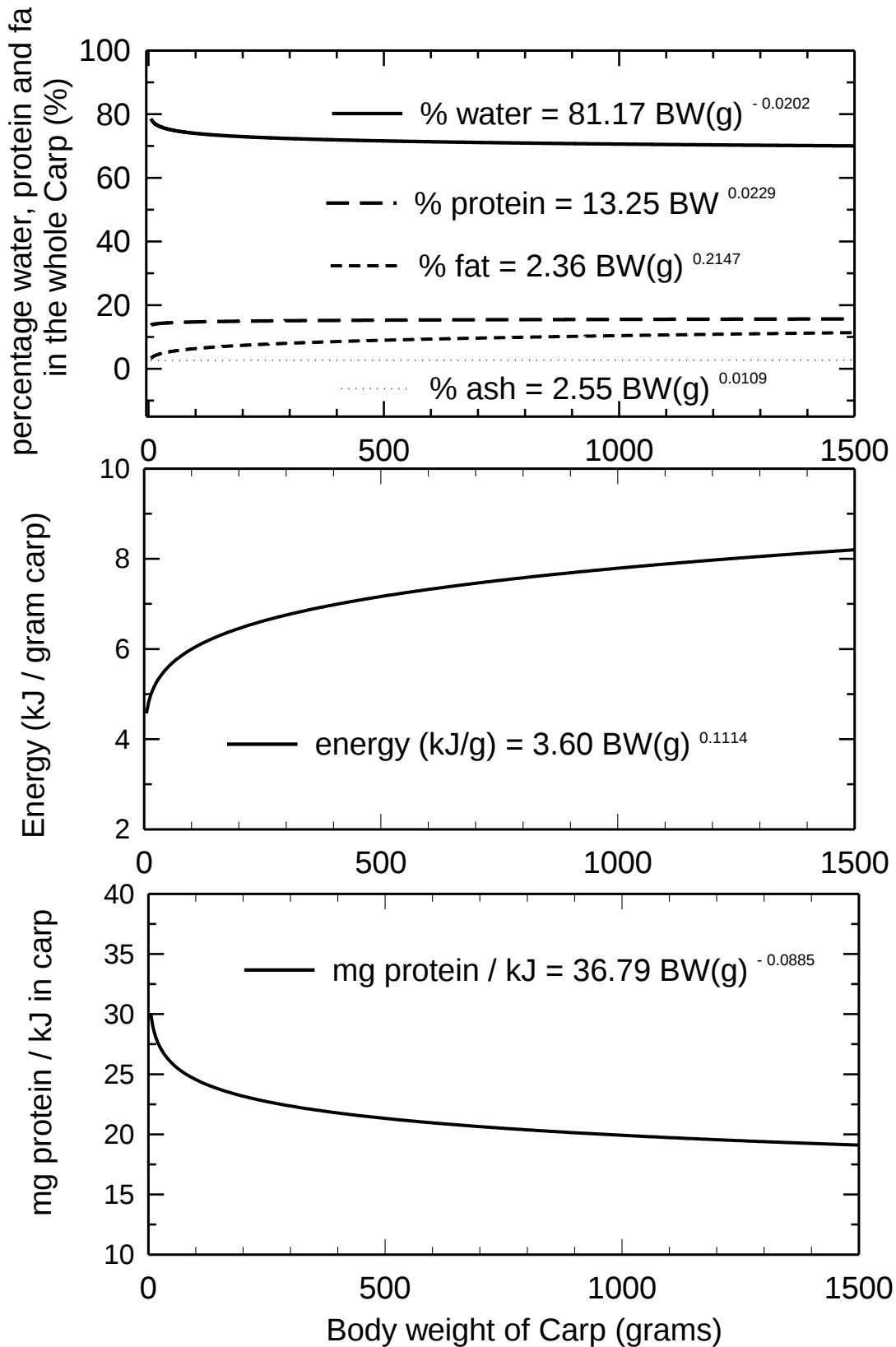
On the other hand, suppose that the percentage of protein in the body as a function of the body weight is $13.36 \text{ BW(g)}^{0.036}$

Then, the absolute amount of protein (in grams) is:

$$= (13.36 / 100) \text{ BW}^{0.036} * \text{BW}^{(0.036+1)} = 0.1336 \text{ BW}^{1.036}$$

Appendix 67 (Figure)

Body Composition of the Carp



The gross energy values of 23.65 kJ / gram protein and 39.6 kJ per gram fat were used

Appendix 68 (Figure)

Body Composition of the Rainbow trout (*Oncorhynchus mykiss*)

For the body composition of the Rainbow trout (*Oncorhynchus mykiss*), the compositional data of the following articles have been used:

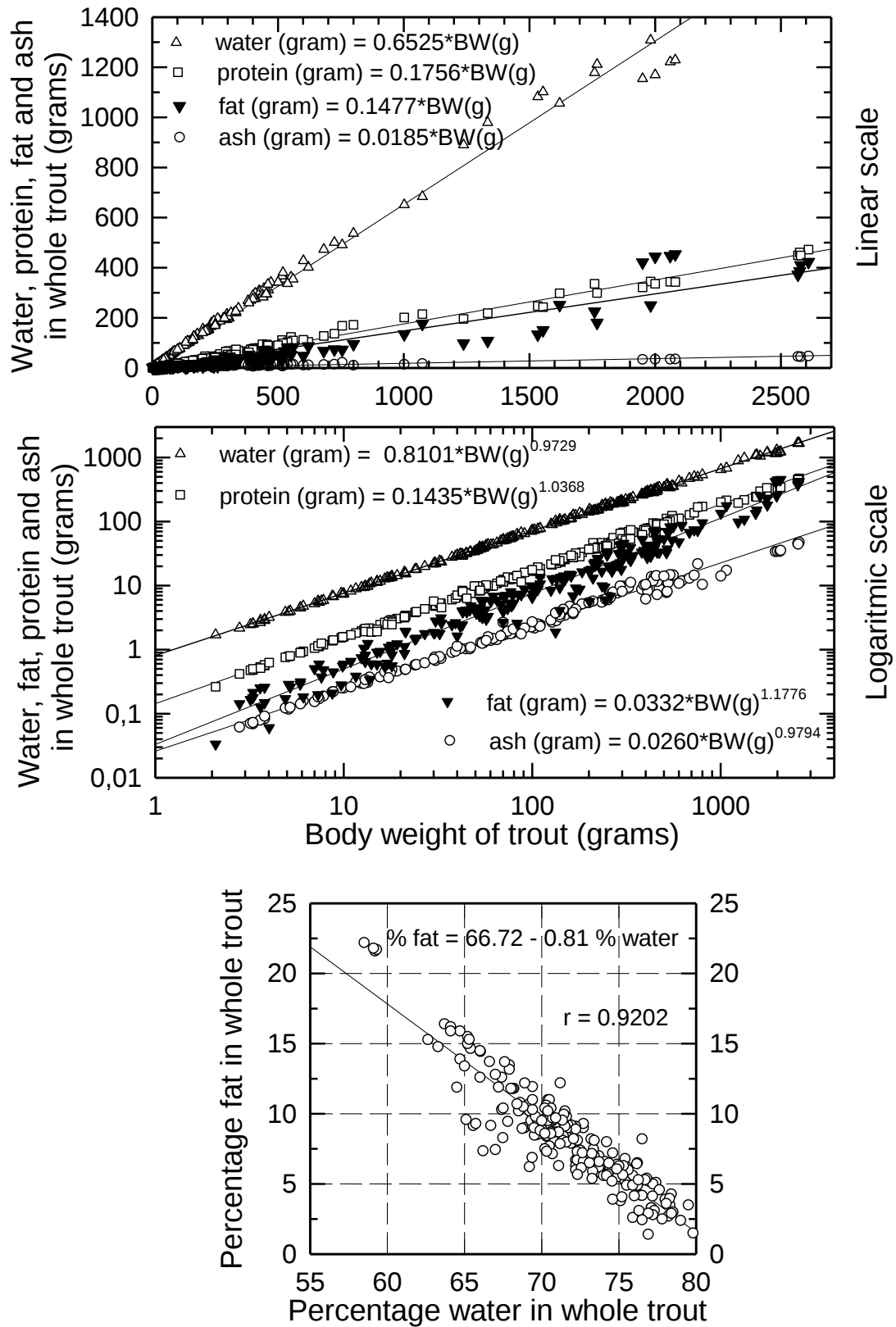
- Alexis, M.N., Theochari, V. and Papaparaskeva, E. (1986) Effect of diet composition and protein level on growth, body composition, haematological characteristics and cost of production of rainbow trout (*Salmo Gairdneri*). *Aquaculture* 58: 75-85.
- Alvarez, M.J., Lopez-Bote, C.J., Diez, A., Corraze, G., Arzel, J., dias, J., Kaushik, S.J. and Bautista, J.M. (1999) The partial substitution of digestible protein with gelatinized starch as an energy source reduces susceptibility to lipid oxidation in rainbow trout (*Oncorhynchus mykiss*) and sea bass (*Dicentrarchus labrax*) Muscle. *Journal of Animal Science* 77: 3322-3329.
- Arzel, J., Martinez-Lopez, F.X., Métailler, R., Stéphan, G., Viau, M., Grandemer, G. and Guillaume, J. (1994) Effect of dietary lipid on growth performance and body composition of brown trout (*Salmo trutta*) reared in seawater. *Aquaculture* 123: 361-375.
- Austreng, E., Risa, S., Edwards, D.J. and Hvidsten, H. (1977) Carbohydrate in rainbow trout diets II. Influence of carbohydrate levels on chemical composition and feed utilization of fish from different families. *Aquaculture*, 11: 39-50.
- Beamish, F.W.H., Hilton, J.W., Niimi, E. and Slinger, S.J. (1986) Dietary carbohydrate and growth, body composition and heat increment in rainbow trout (*Salmo gairdneri*). *Fish Physiology and Biochemistry* 1: 85-91.
- Bergot, B. (1979) Carbohydrate in rainbow trout diets: effects of the level and source of carbohydrate and the number of meals on growth and body composition. *Aquaculture*, 18: 157-167.
- Brauge, C., Medale, F. and Corraze, G. (1994) effect of dietary carbohydrate levels on growth, body composition and glycaemia in rainbow trout, *Oncorhynchus mykiss*, reared in seawater. *Aquaculture*, 123: 109-120.
- Bureau, D.P., Hua, K. and Cho, C.Y. (2006) Effect of feeding level on growth and nutrient deposition in rainbow trout (*Oncorhynchus mykiss* Walbaum) growing from 150-600 grams. *Aquatic Resources* 37: 1090 – 1098.
- Grayton, B.D. and Beamish, F.W.H. (1977) Effect of feeding frequency on food intake, growth and body composition of rainbow trout (*Salmo gairdneri*). *Aquaculture* 11: 159-172.
- Huisman, E.A. (1976) Food conversion efficiencies at maintenance and production levels for carp, *Cyprinus Carpio* L, and Rainbow trout, *Salmo Gairdneri* Richardson. *Aquaculture* 9: 259-273.
- Kaushik, S.J., Cravedi, J.P., Lalles, J.P., Sumpter, J., fauconneau, B. and Laroche, N.M. (1995) Partial or total replacement of fish meal by soybean protein on growth, protein utilization, potential estrogenic or antigenic effects, cholesterolemia and flesh quality in rainbow trout, *Oncorhynchus mykiss*. *Aquaculture*, 133; 257-274.

- Mambrini, M., Roem, A.J., Cravedi, J.P., Lalles, J.P. and Kaushik, S.J. (1999) Effects of replacing fish meal with soy protein concentrate and of DL-methionine supplementation in high-energy, extruded diets on the growth and nutrient utilization of rainbow trout, *Oncorhynchus mykiss*. Journal of Animal Science 77: 2990-2999.
- Moyano, F.-J., Cardenete, G. and De La Higuera, M. (1992) Nutritive value of diets containing a high percentage of vegetable proteins for trout, *Oncorhynchus mykiss*. Aquatic Living Resources 5: 23-29.
- Popoutsoglou, S.E. and Papaparaskeva-Papoutsoglou, E.G. (1978) Comparative studies on body composition of rainbow trout (*Salmo Gairdneri* R.) in relation to type of diet and growth rate. Aquaculture, 13: 235-243.
- Rasmussen, R.S., Rønsholdt, B., Ostensfeld, T.H., McLean, E. and Byatt, J.C. (2001) growth, feed utilization, carcass composition and sensory characteristics of rainbow trout treated with recombinant bovine placental lactogen and growth hormone. Aquaculture 195: 367-384.
- Refstie, T. and Austreng, E. (1981) Carbohydrate in rainbow trout diets III. Growth and chemical composition of fish from different families fed four levels of carbohydrate in the diet. Aquaculture 25: 35-49.
- Reinitz, G. (1983) Relative effect of age, diet, and feeding rate on the body composition of young rainbow trout (*Salmo gairdneri*). Aquaculture 35: 19-27.
- Smith, R.S., Kincaid, H.L., Regenstein, J.M. and Rumsey, G. (1988) growth, carcass composition, and taste of rainbow trout of different strains fed diets containing primarily plant and animal protein. Aquaculture, 70: 309-321.
- Staples, D.J. and Nomura, M. (1976) Influence of body size and food ration on the energy budget of rainbow trout *Salmo Gairdneri* Richardson. Journal of Fish biology 9: 29-43.
- Storebakken, T. and Austreng, E. (1987) Ration level for salmonids II. Body composition, and feed conversion in rainbow trout weighing 0.5 – 1.0 kg. aquaculture 60: 207-221.
- Storebakken, T., Hung, S.S.O., Calvert, C.C. and Plisetskaya, E.M. (1991) Nutrient partitioning in rainbow trout at different feeding levels. Aquaculture 96: 191-203.
- Vilema, J., Mäkinen, T., Ekhol, P. and Koskela, J. (2000) Influence of dietary soy and phytase levels on performance and body composition of large rainbow trout (*Oncorhynchus mykiss*) and algal availability of phosphorus load. Aquaculture 183: 349-362.
- Weatherup, R.N. and McCracken, K.J. (1999). Changes in rainbow trout, *Oncorhynchus mykiss* (Walbaum), body composition with weight. Aquaculture Research 30: 305-307.

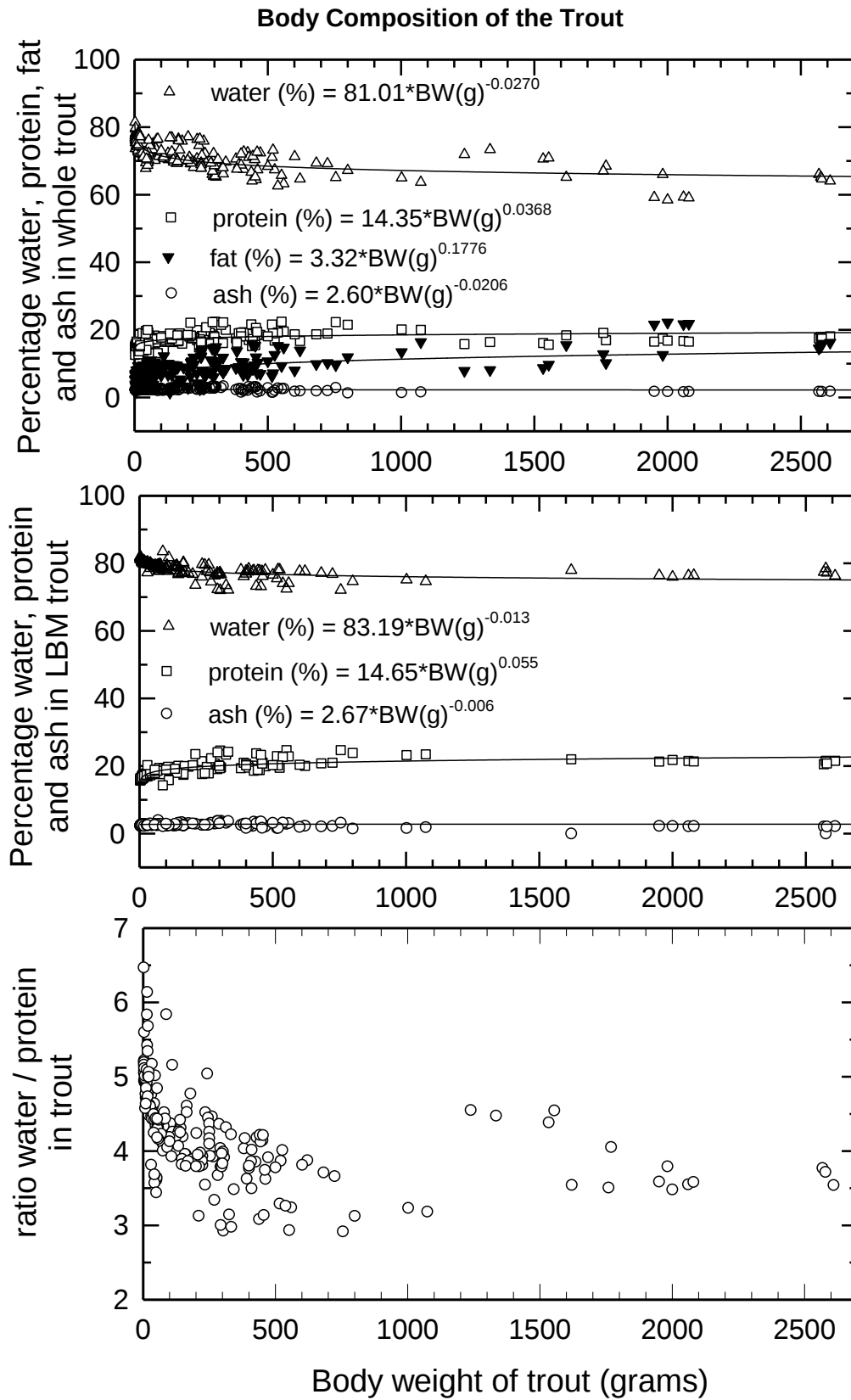
There are, however, many more articles that have described the body composition of the trout. In the article of Dumas et al. (2007) the compositional data of a larger numbers of articles have been used to describe the composition of the trout (see below)

Appendix 69 (Figure)

Body Composition of the Trout



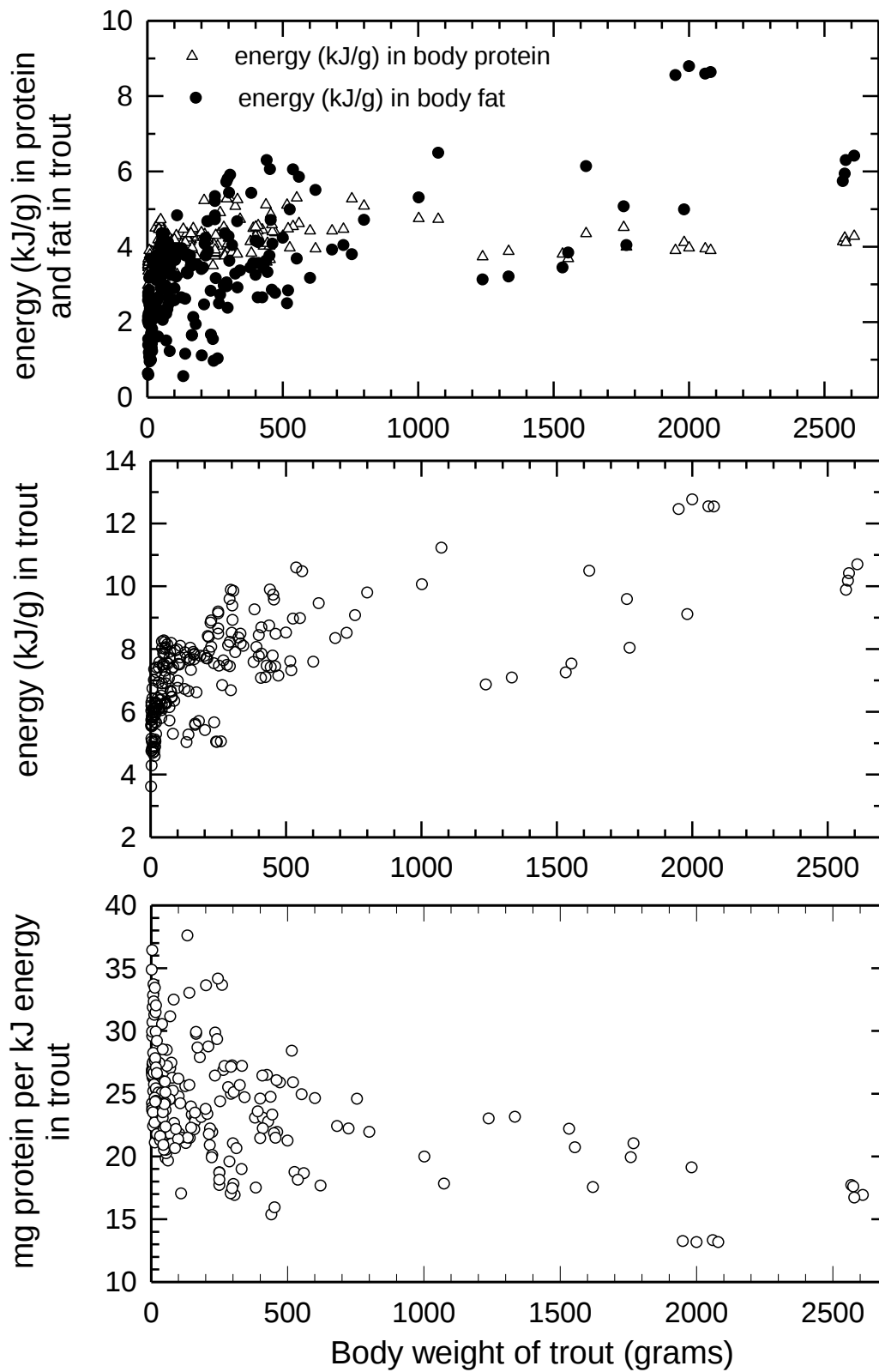
Appendix 70 (Figure)



LB, lean body mass or fat-free mass.

Appendix 71 (Figure)

Body Composition of the Trout



The gross energy values of 23.65 kJ / gram protein and 39.6 kJ per gram fat were used

Appendix 72 (Figure)

Body Composition of the Trout

The graphs on the next page are a summary of the previous graphs with all the individual data from the various articles that describe the body composition of the trout.

Compositional data in the graphs were derived from trout in the weight range of about 0 – 2600 grams (see previous graphs).

The formula below were derived from the previous graphs

$$\text{Moisture (\%)} = 81.01 \text{ BW(g)}^{-0.0270}$$

$$\text{Protein (\%)} = 14.35 \text{ BW(g)}^{0.0368}$$

$$\text{Fat (\%)} = 3.32 \text{ BW(g)}^{0.1776}$$

$$\text{Ash (\%)} = 2.60 \text{ BW(g)}^{-0.0206}$$

$$\text{Energy (kJ/gram)} = 2.45 \text{ BW}^{0.1003}$$

$$\text{mg protein / kJ} = 32.25 \text{ BW}^{-0.0636}$$

$$\text{Moisture (g)} = 0.8101 \text{ BW(g)}^{0.9730}$$

$$\text{Protein (g)} = 0.1435 \text{ BW(g)}^{1.0368}$$

$$\text{Fat (g)} = 0.0332 \text{ BW(g)}^{1.1776}$$

$$\text{Ash (g)} = 0.026 \text{ BW(g)}^{0.9794}$$

$$\text{Energy (kJ)} = 2.45 \text{ BW}^{1.1003}$$

The formulas for the calculation of the energy / kJ and the mg protein / kJ were derived from the formula describing the protein and protein content of the body that were calculated from the individual data from the various articles.

When the formula is known that gives the absolute amount of moisture, fat, protein or ash (in grams) in the body as a function of the body weight, then the formula that gives the percentage of moisture, fat, protein or ash (in percentages) in the body as function of the body weight can be derived.

Similarly, when the formula is known that gives the percentage of moisture, fat, protein or ash (in percentages) in the body as a function of the body weight, then the formula that gives the absolute amount of moisture, fat, protein or ash (in grams) in the body as function of the body weight can be derived.

For example:

Suppose that the amount of protein (grams) in the body as a function of the body weight is $0.1336 \text{ BW(g)}^{1.036}$.

Then the percentage of protein in the fish is:

$$\% \text{ of protein} = 100\% * 0.1336 \text{ BW(g)}^{1.036} / \text{BW} = 13.36 \text{ BW}^{1.036-1} = 13.36 \text{ BW(g)}^{0.036}$$

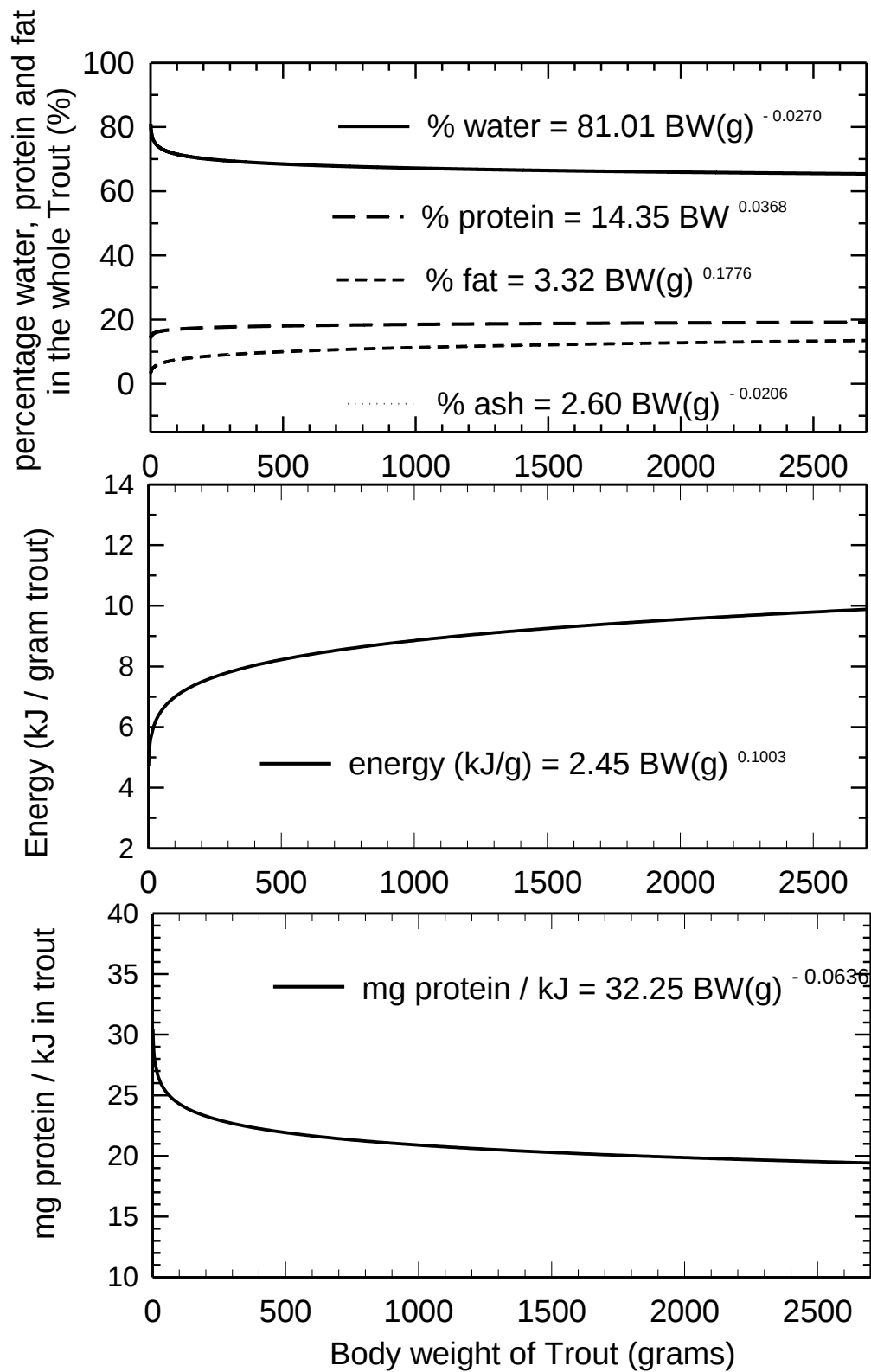
On the other hand, suppose that the percentage of protein in the body as a function of the body weight is $13.36 \text{ BW(g)}^{0.036}$

Then, the absolute amount of protein (in grams) is:

$$= (13.36 / 100) \text{ BW}^{0.036} * \text{BW} = 0.1336 \text{ BW}^{(0.036+1)} = 0.1336 \text{ BW}^{1.036}$$

Appendix 73 (Figure)

Body Composition of the Trout



The gross energy values of 23.65 kJ / gram protein and 39.6 kJ per gram fat were used

Appendix 74 (Figure)

Body Composition of the Trout (Dumas et al. 2007)

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.

Compositional data were derived from Trout in the weight range of about 0 – 1600 grams

The formula below were derived from the data and formula as reported by Dumas et al.

Expressed as percentage of body weight:

$$\text{Moisture (\%)} = 92.25 \text{ BW(g)}^{-0.0543}$$

$$\text{Fat (\%)} = 3.235 \text{ BW(g)}^{0.243}$$

$$\text{Protein (\%)} = 13.36 \text{ BW(g)}^{0.036}$$

$$\text{Ash (\%)} = 2.1978 \text{ BW(g)}^{-0.004}$$

$$\text{Energy (kJ/g)} = 3.84 \text{ BW(g)}^{0.1510}$$

Expressed in total weight:

$$\text{Moisture (g)} = 0.9225 \text{ BW(g)}^{0.9458}$$

$$\text{Fat (g)} = 0.03235 \text{ BW(g)}^{1.243}$$

$$\text{Protein (g)} = 0.1336 \text{ BW(g)}^{1.036}$$

$$\text{Ash (g)} = 0.021978 \text{ BW(g)}^{0.996}$$

$$\text{Energy (kJ/g)} = 3.84 \text{ BW(g)}^{1.1510}$$

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

When the formula is known that gives the absolute amount of moisture, fat, protein or ash (in grams) in the body as a function of the body weight, then the formula that gives the percentage of moisture, fat, protein or ash (in percentages) in the body as function of the body weight can be derived.

Similarly, when the formula is known that gives the percentage of moisture, fat, protein or ash (in percentages) in the body as a function of the body weight, then the formula that gives the absolute amount of moisture, fat, protein or ash (in grams) in the body as function of the body weight can be derived.

For example:

Suppose that the amount of protein (grams) in the body as a function of the body weight is $0.1336 \text{ BW(g)}^{1.036}$.

Then the percentage of protein in the fish is:

$$\% \text{ of protein} = 100\% * 0.1336 \text{ BW(g)}^{1.036} / \text{BW} = 13.36 \text{ BW}^{1.036-1} = 13.36 \text{ BW(g)}^{0.036}$$

On the other hand, suppose that the percentage of protein in the body as a function of the body weight is $13.36 \text{ BW(g)}^{0.036}$

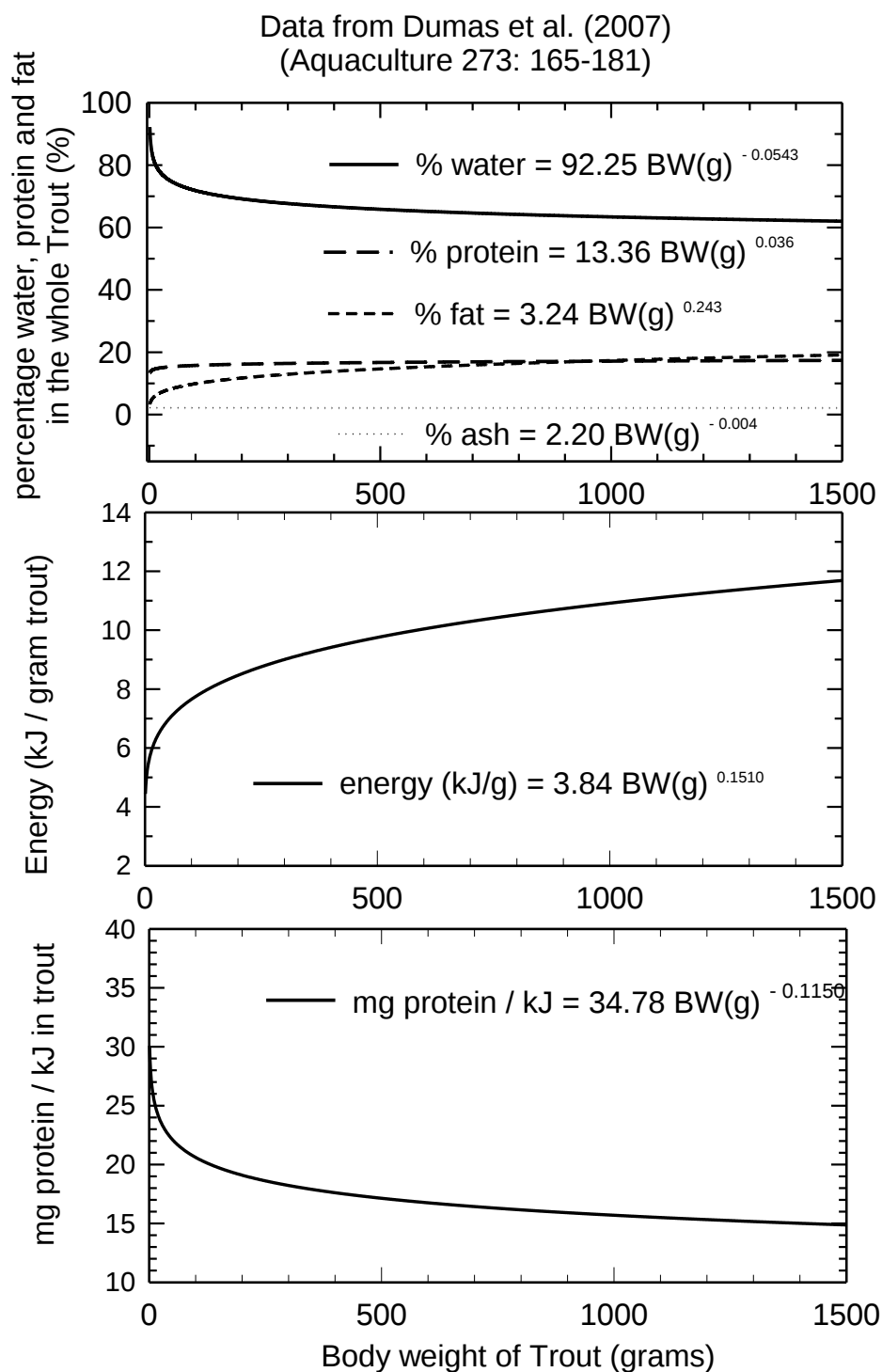
Then, the absolute amount of protein (in grams) is:

$$= (13.36 / 100) \text{ BW}^{0.036} * \text{BW} = 0.1336 \text{ BW}^{(0.036+1)} = 0.1336 \text{ BW}^{1.036}$$

Appendix 75 (Figure)

Body Composition of the Trout (Dumas et al. 2007)

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.



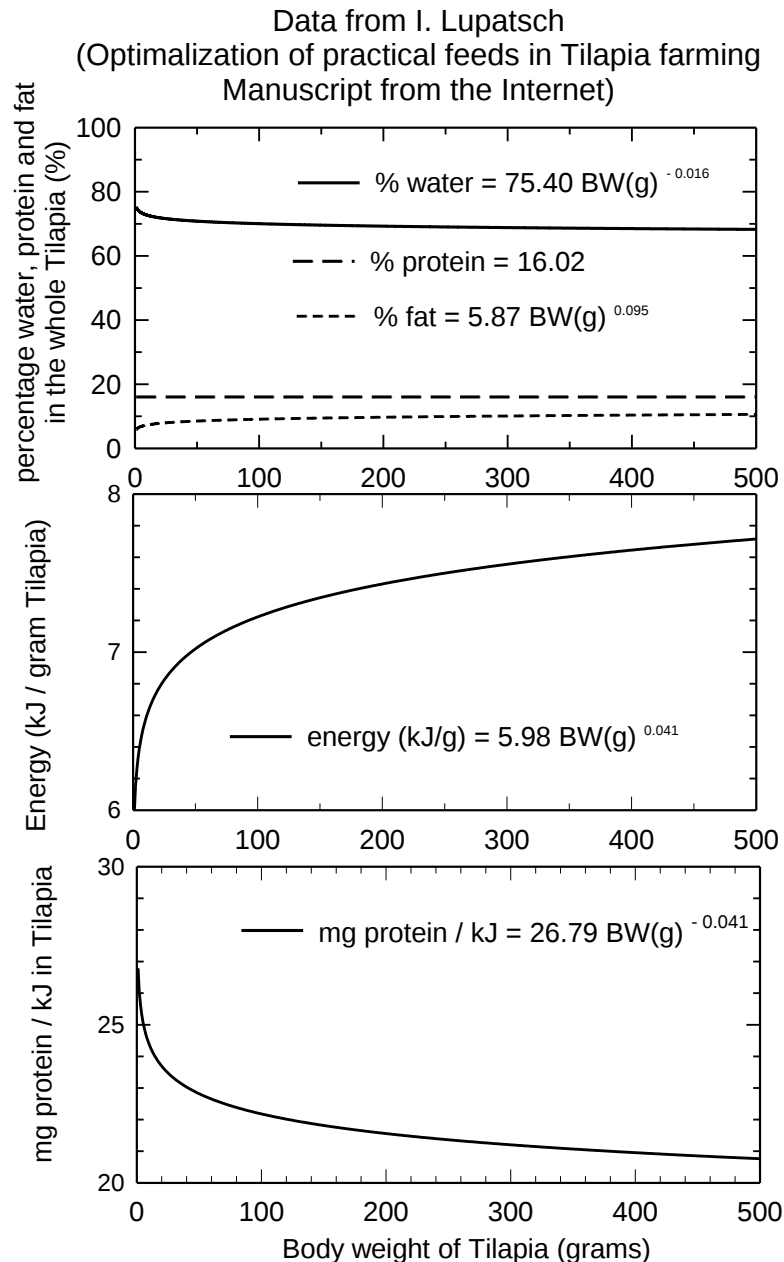
The gross energy values of 23.65 kJ / gram protein and 39.6 kJ per gram fat were used.

Appendix 76 (Figure)

Body Composition of the Tilapia

Ingrid Lupatsch (2008) Optimization of practical feeds in Tilapia farming. Manuscript from the Internet.

The mg protein / kJ data were calculated from the body energy and the body protein data.



Data derived from Tilapia in the weight range of about 0 – 450 grams

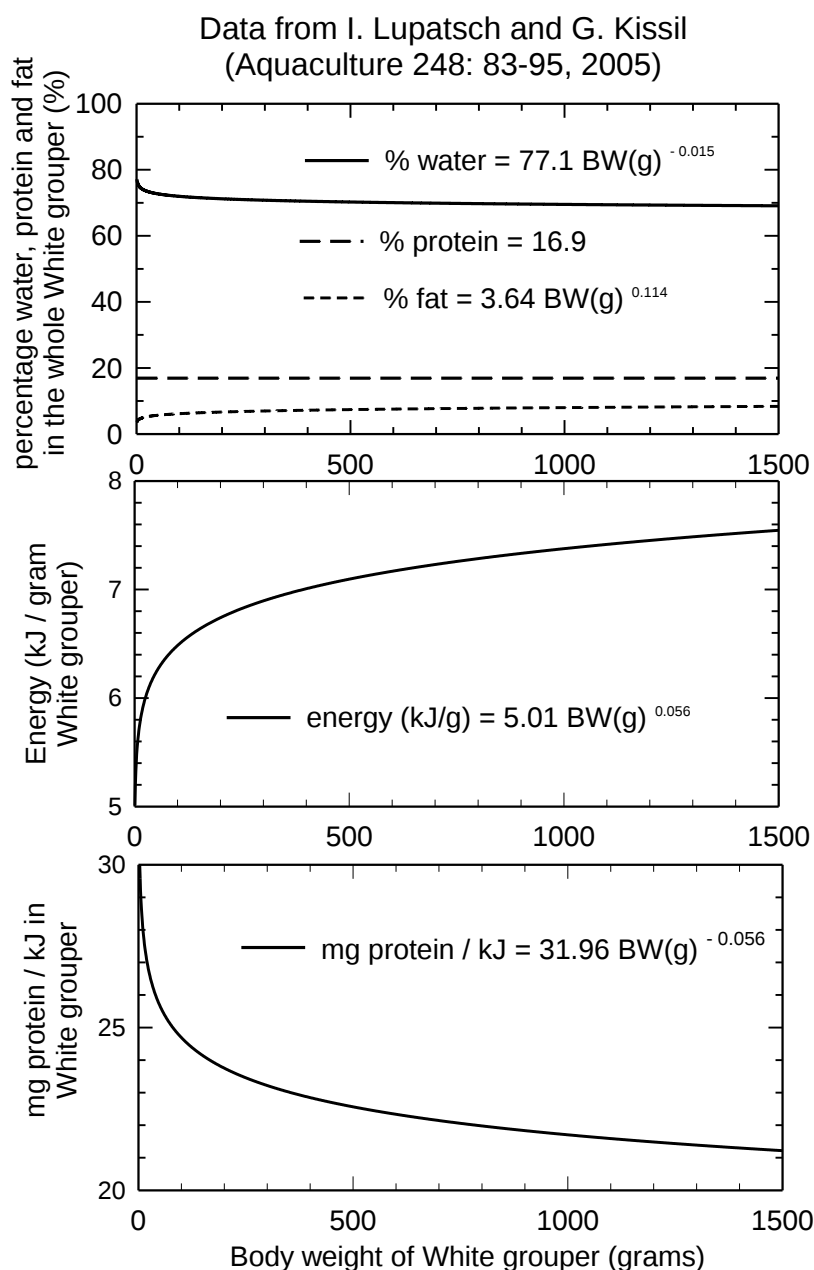
Moisture (%) = 75.40 BW(g)^{-0.016}
 Fat (%) = 5.87 BW(g)^{0.095}
 Protein (%) = 16.02
 Ash (%) = 4.28
 Energy (kJ/g) = 5.98 BW(g)^{0.041}

Moisture (g) = 0.754 BW(g)^{0.984}
 Fat (g) = 0.0587 BW(g)^{1.095}
 Protein (g) = 0.1602 BW (g)
 Ash (g) = 0.0428 BW (g)
 Energy (kJ) = 5.98 BW(g)^{1.041}

Appendix 77 (Figure)

Body Composition of the White grouper

Ingrid Lupatsch and George Wm. Kissil (2005) Feed formulations based in energy and protein demands in white grouper (*Epinephelus aeneus*). Aquaculture 248: 83 – 95.
 The mg protein / kJ data were calculated from the body energy and the body protein data.



Data derived from white grouper in the weight range of about 0 – 1700 grams

Moisture (%) = $77.1 \text{ BW(g)}^{-0.015}$
 Fat (%) = $3.64 \text{ BW(g)}^{0.114}$
 Protein (%) = 16.9
 Ash (%) = 4.45
 Energy (kJ/gram) = $5.01 \text{ BW(g)}^{0.056}$

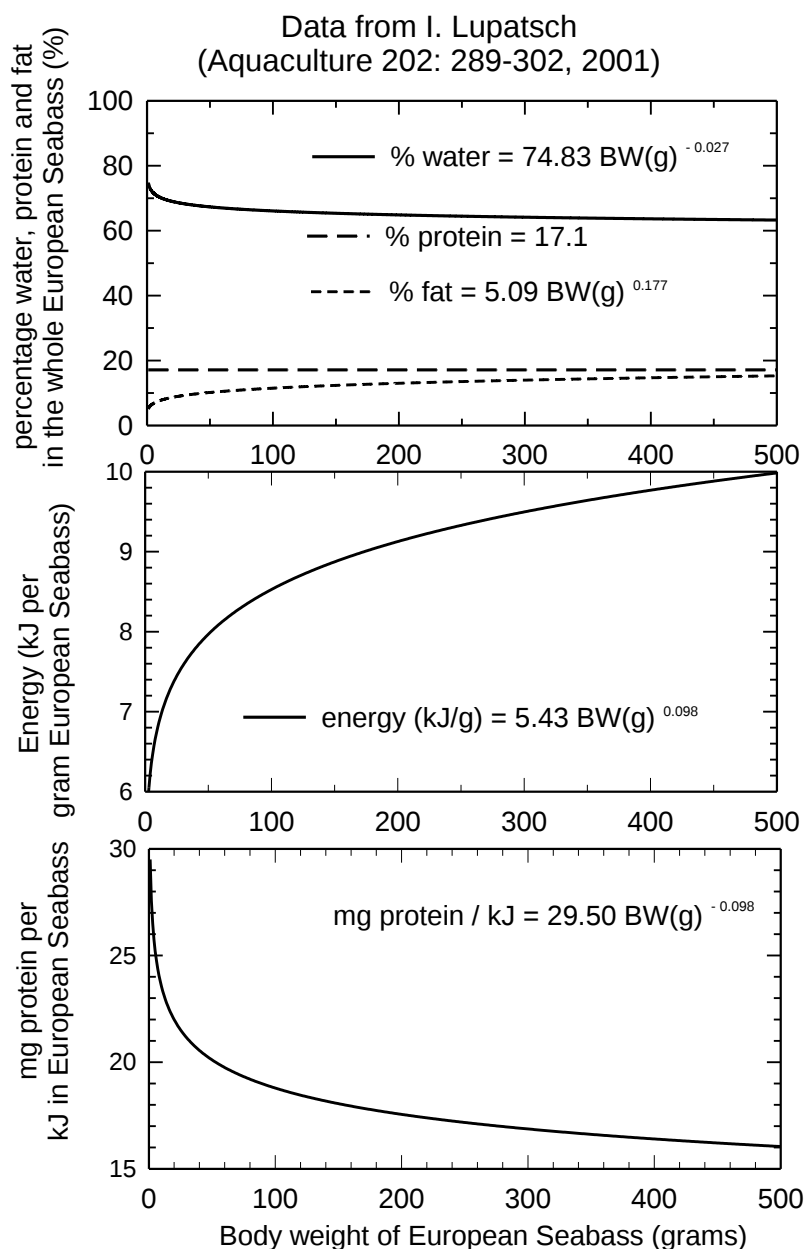
Moisture (g) = $0.771 \text{ BW(g)}^{0.984}$
 Fat (g) = $0.0364 \text{ BW(g)}^{1.095}$
 Protein (g) = 0.169 BW (g)
 Ash (g) = 0.0445 BW (g)
 Energy (kJ) = $5.01 \text{ BW(g)}^{1.056}$

Appendix 78 (Figure)

Body Composition of the European Seabass

Ingrid Lupatsch, George Wm. Kissil and David Sklan (2001) Optimization of feeding regimes for European sea bass *Dicentrarchus labrax*: a factorial approach. Aquaculture 202: 289 – 302.

The mg protein / kJ data were calculated from the body energy and the body protein data.



Data derived from European seabass in the weight range of about 0 – 450 grams

Moisture (%) = $74.83 \text{ BW(g)}^{-0.027}$
 Fat (%) = $5.09 \text{ BW(g)}^{0.177}$
 Protein (%) = 17.1
 Ash (%) = 4.63
 Energy (kJ/gram) = $5.43 \text{ BW(g)}^{0.098}$

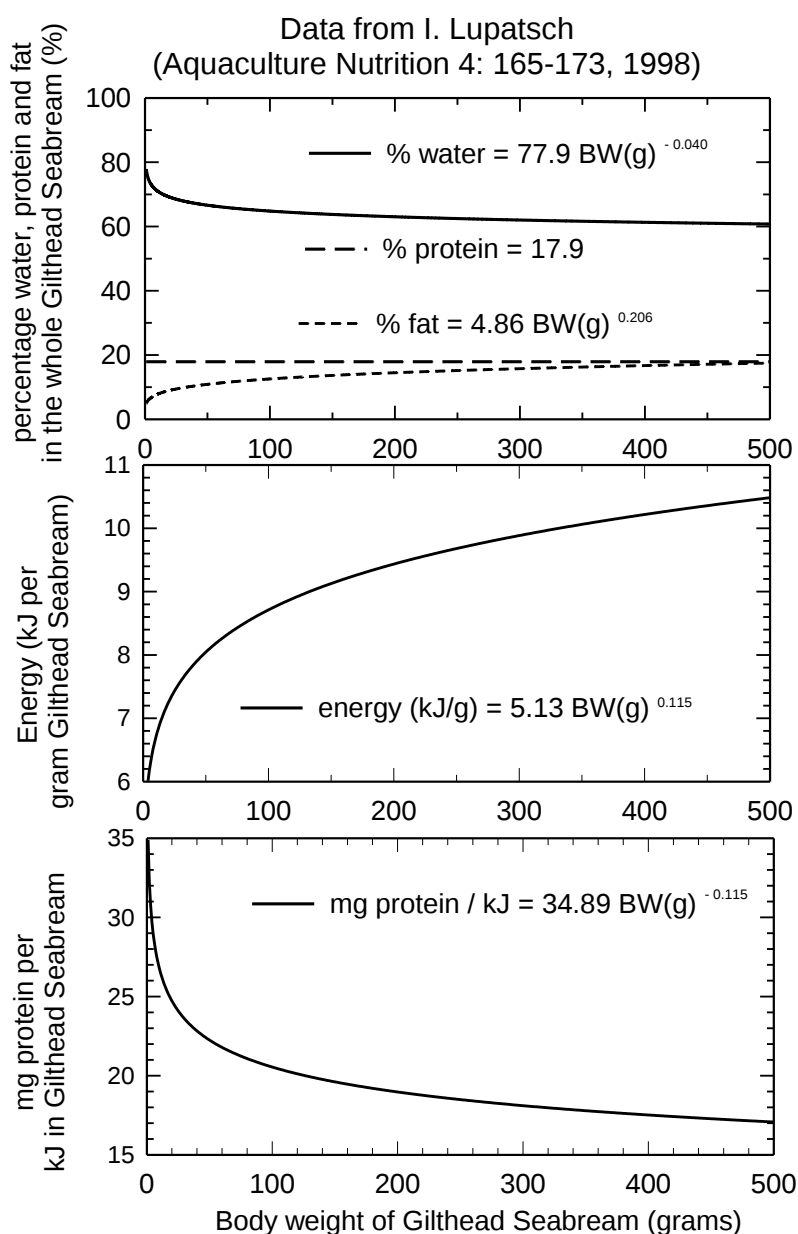
Moisture (g) = $0.748 \text{ BW(g)}^{0.973}$
 Fat (g) = $0.0509 \text{ BW(g)}^{1.177}$
 Protein (g) = 0.171 BW(g)
 Ash (g) = 0.0463 BW(g)
 Energy (kJ) = $5.43 \text{ BW(g)}^{1.098}$

Appendix 79 (Figure)

Body Composition of the Gilthead Seabream

Ingrid Lupatsch, George Wm. Kissil, David Sklan and E. Pfeffer (1998). Energy and protein requirements for maintenance and growth in gilthead seabream (*Sparus aurata* L.)
 Aquaculture Nutrition 4: 165 – 173.

The mg protein / kJ data were calculated from the body energy and the body protein data.



Data derived from gilthead seabream in the weight range of 0 – 250 grams

Moisture (%) = $77.9 \text{ BW(g)}^{-0.040}$
 Fat (%) = $4.86 \text{ BW(g)}^{0.206}$
 Protein (%) = 17.9
 Ash (%) = 4.50
 Energy (kJ/gram) = $5.13 \text{ BW(g)}^{0.115}$

Moisture (g) = $0.779 \text{ BW(g)}^{0.960}$
 Fat (g) = $0.0486 \text{ BW(g)}^{1.206}$
 Protein (g) = 0.179 BW (g)
 Ash (g) = 0.0450 BW (g)
 Energy (kJ) = $5.13 \text{ BW(g)}^{1.115}$

Appendix 80 (Figure)

Body Composition of the Pig

For the body composition of the pig, the compositional data of the following articles have been used:

De Lange, C.F.M., Morel, P.C.H. and Birkett, S.H. (2003) Modeling chemical and physical body composition of the growing pig. *Journal of Animal Science* 81: E159-165.

Shields, R.G., Mahan, D.C. and Graham, P.L. (1983) changes in swine body composition from birth to 145 kg, *Journal of Animal Science* 57: 43-54.

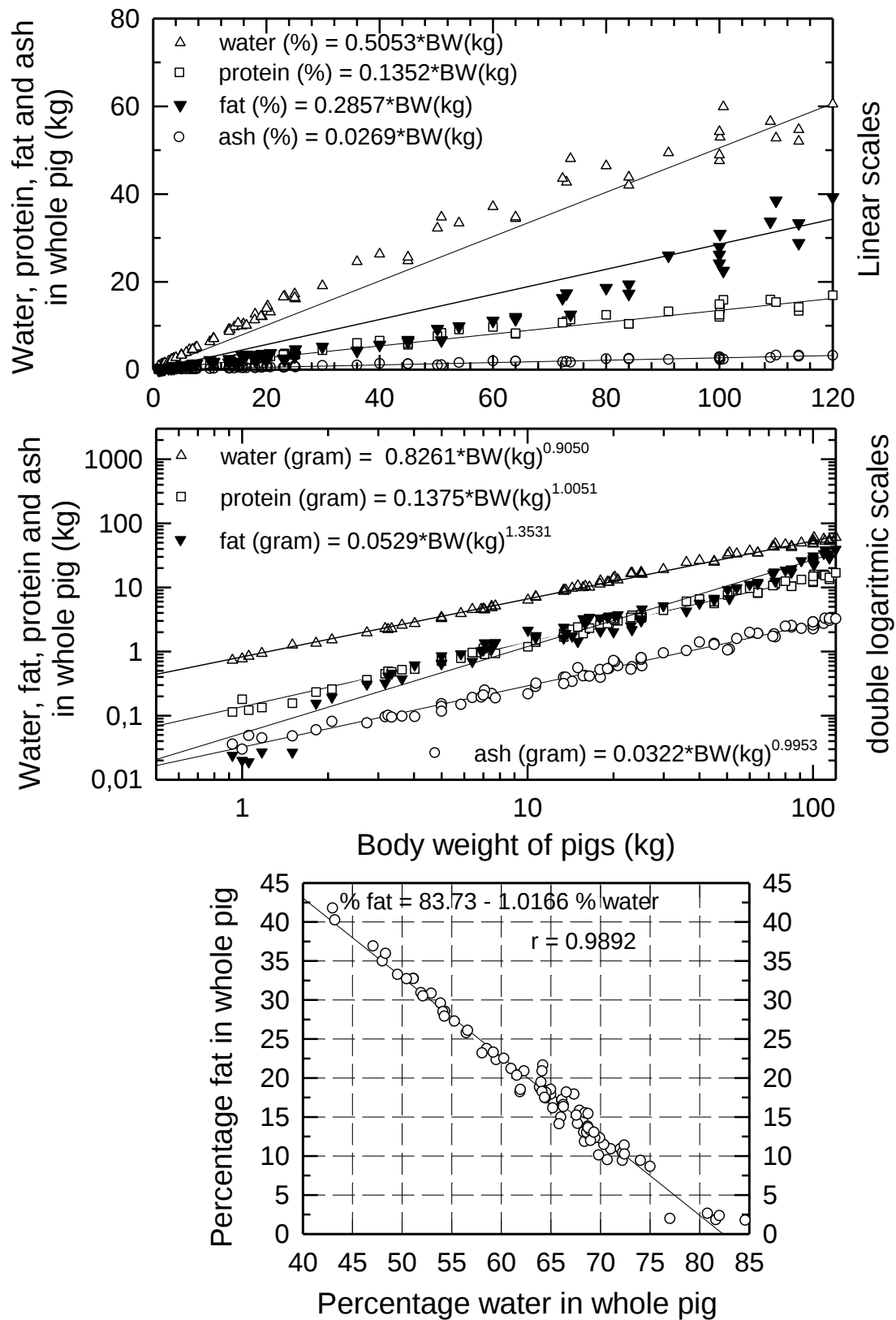
Wagner, J.R., Schinckel, A.P., Chen, W., Forrest, J.C. and Coe, B.L. (1999) Analysis of body composition changes of swine during growth and development. *Journal of Animal Science* 77: 1442-1466.

Wiseman, T.G., Mahan, D.C., Peters, J.C., Fastinger, N.D., Ching, S. and Kim, Y.Y. (2007) Tissue weights and body composition of two genetic lines of barrows and gilts from twenty to one hundred twenty-five kilograms of body weight. *Journal of Animal Science* 85: 1825-1835.

Wood, A.J. and Groves, T.D.D. (1965) Body composition studies on the suckling pig. 1. Moisture, chemical fat, total protein, and total ash in relation to age and body weight. *Canadian Journal of Animal Science* 45: 8-13

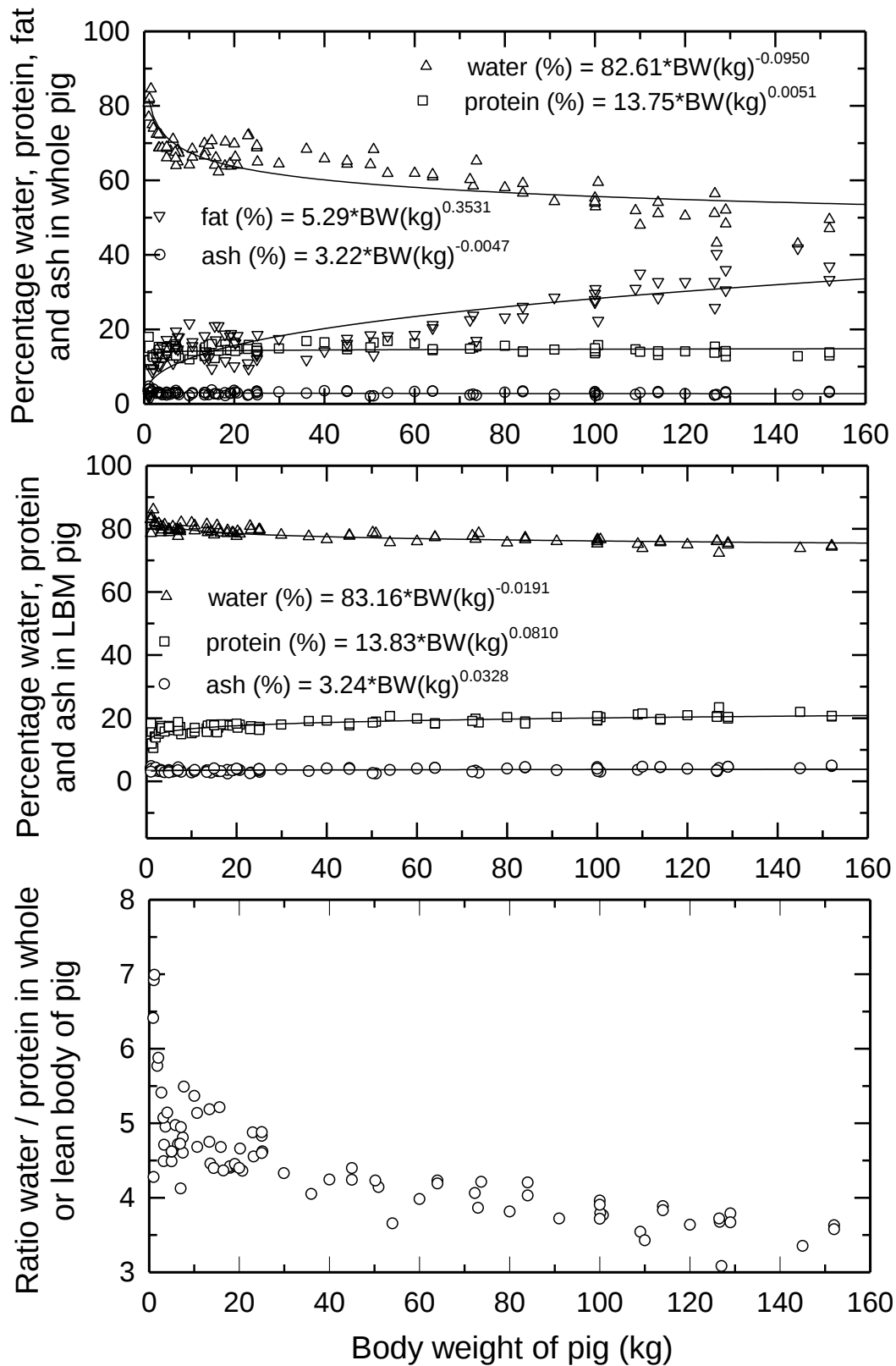
Appendix 81 (Figure)

Body Composition of the Pig



Appendix 82 (Figure)

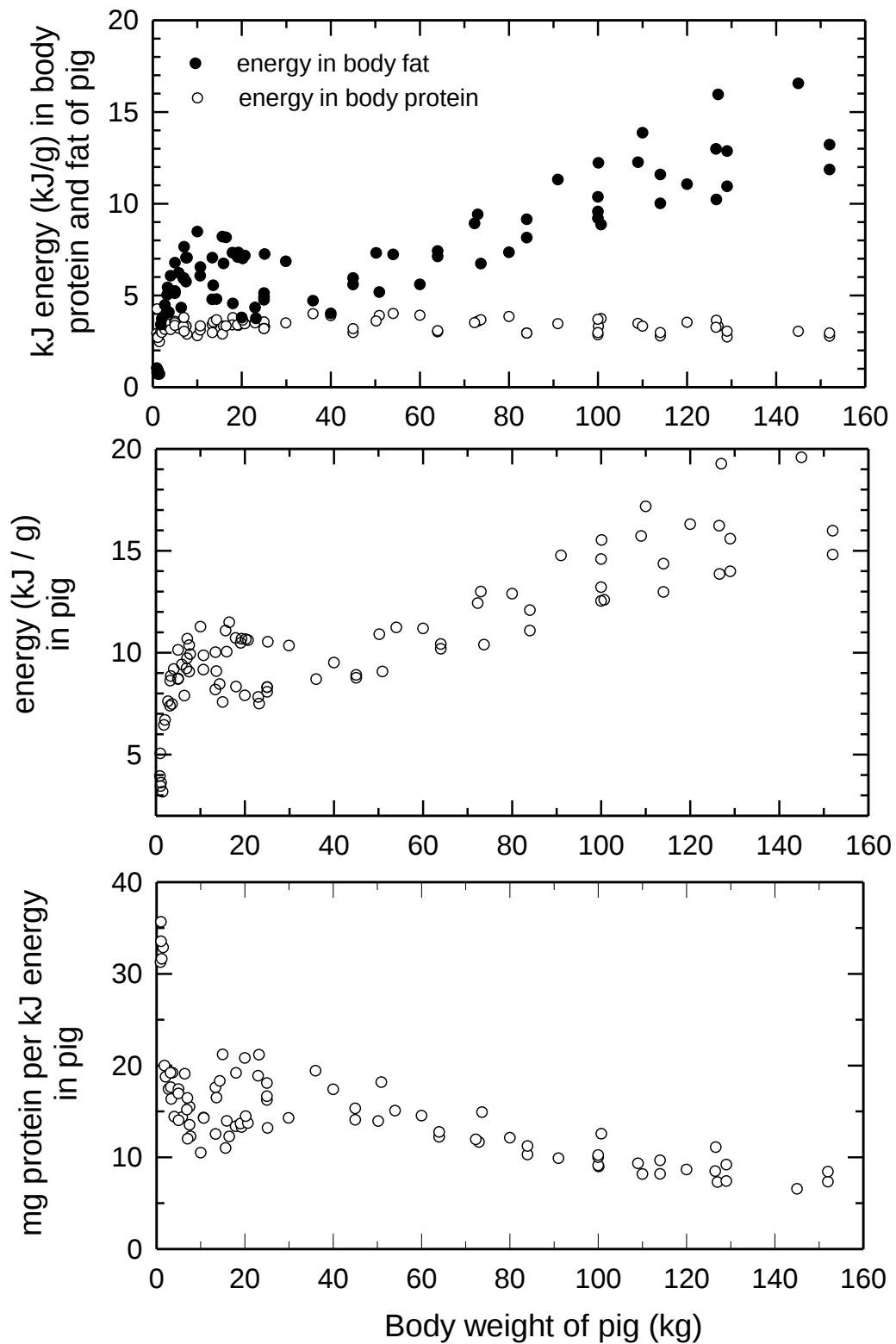
Body Composition of the Pig



LMB, lean body mass or fat-free body mass.

Appendix 83 (Figure)

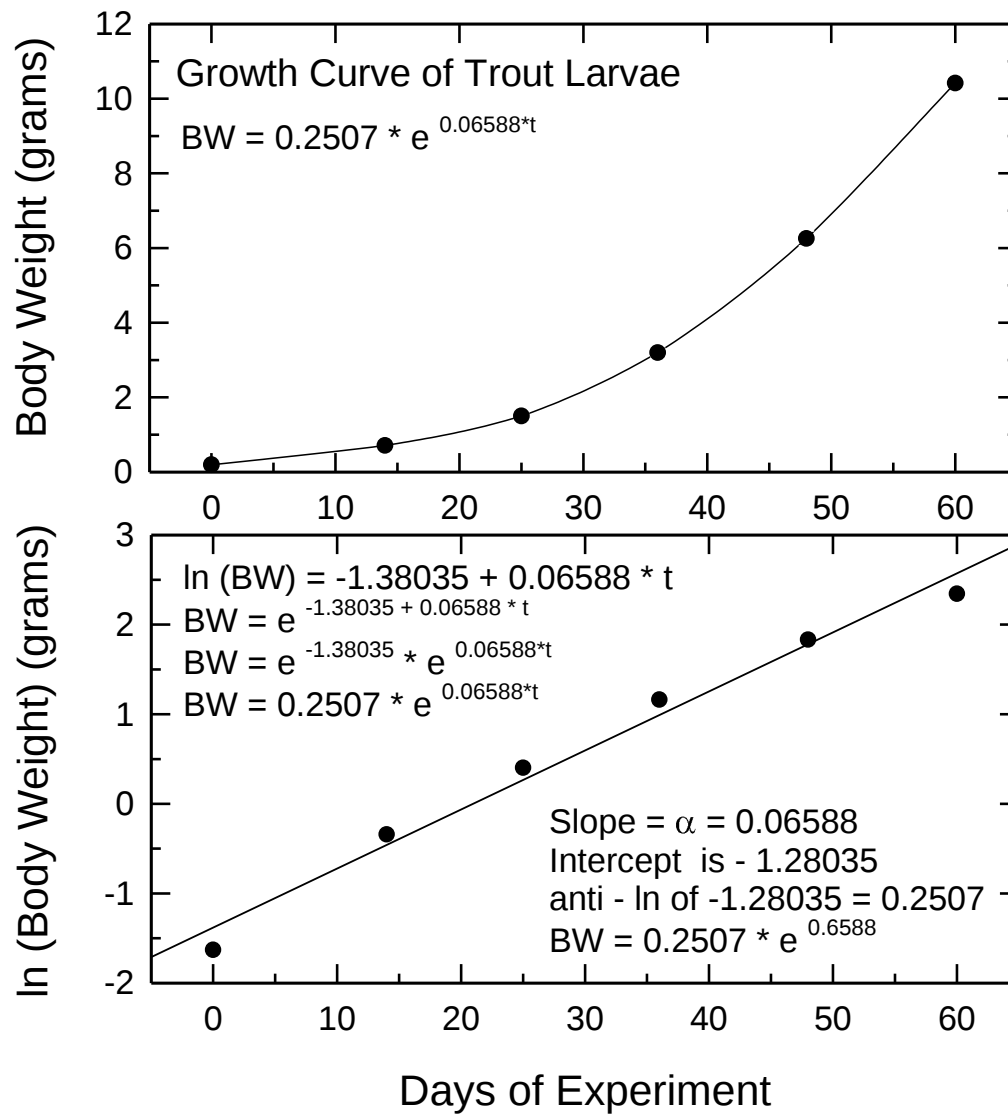
Body Composition of the Pig



The gross energy values of 23.65 kJ / gram protein and 39.6 kJ per gram fat were used

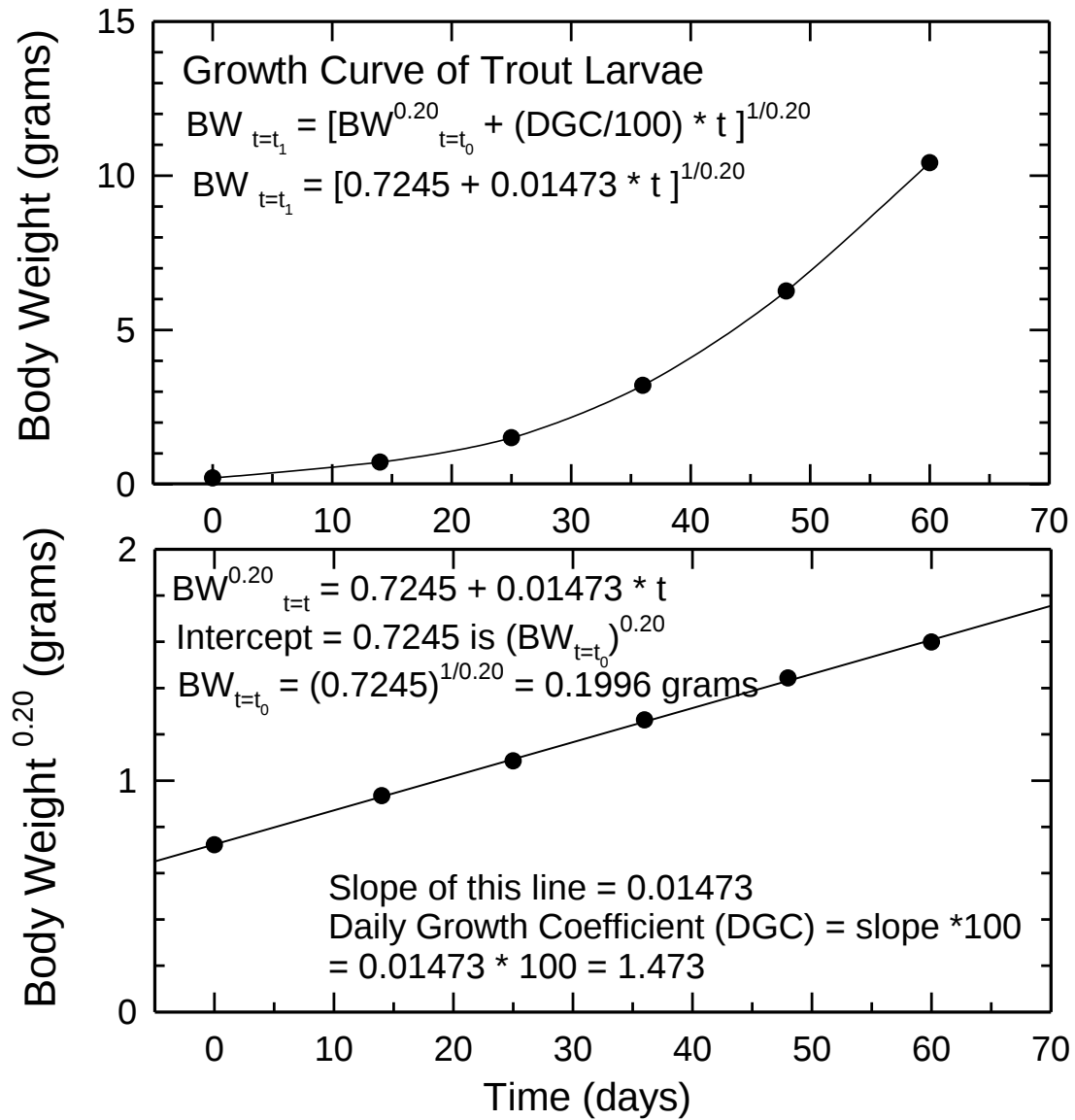
Appendix 84 (Figure)

Growth curve of trout larvae. The data were fitted an exponential growth curve.



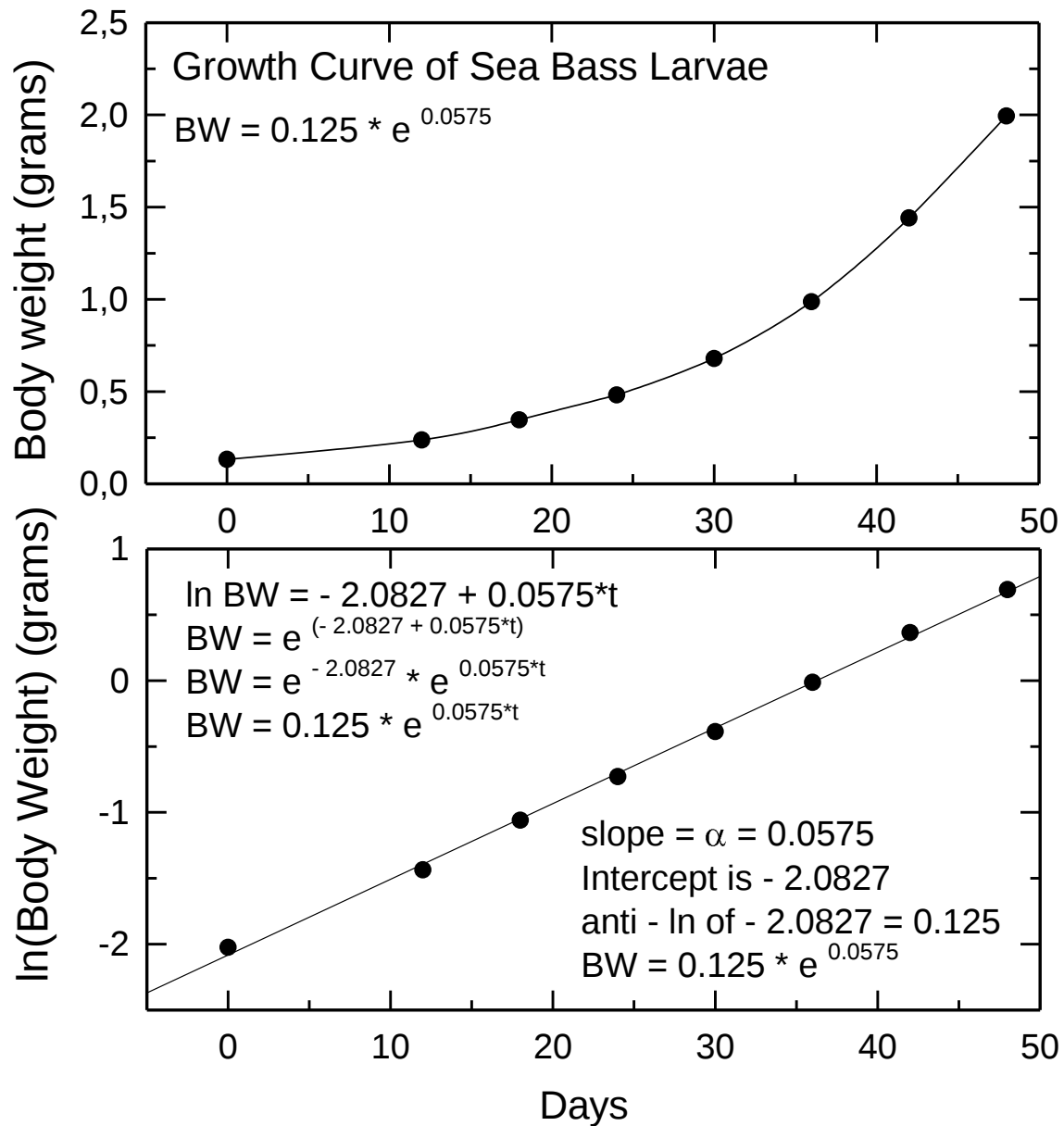
Appendix 85 (Figure)

Growth curve of trout larvae. The data were fitted a power growth curve.



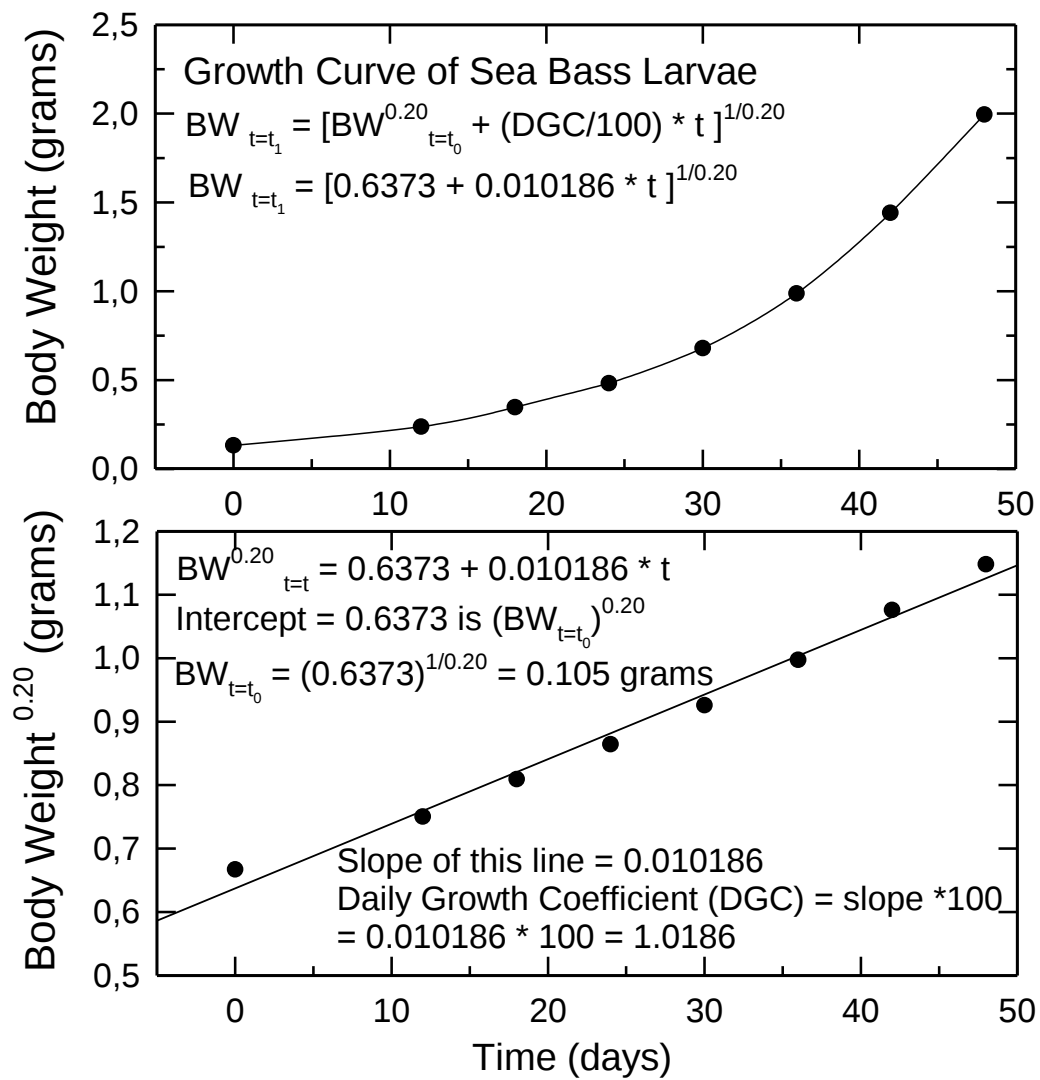
Appendix 86 (Figure)

Growth curve of Sea Bass larvae. The data were fitted an exponential growth curve.



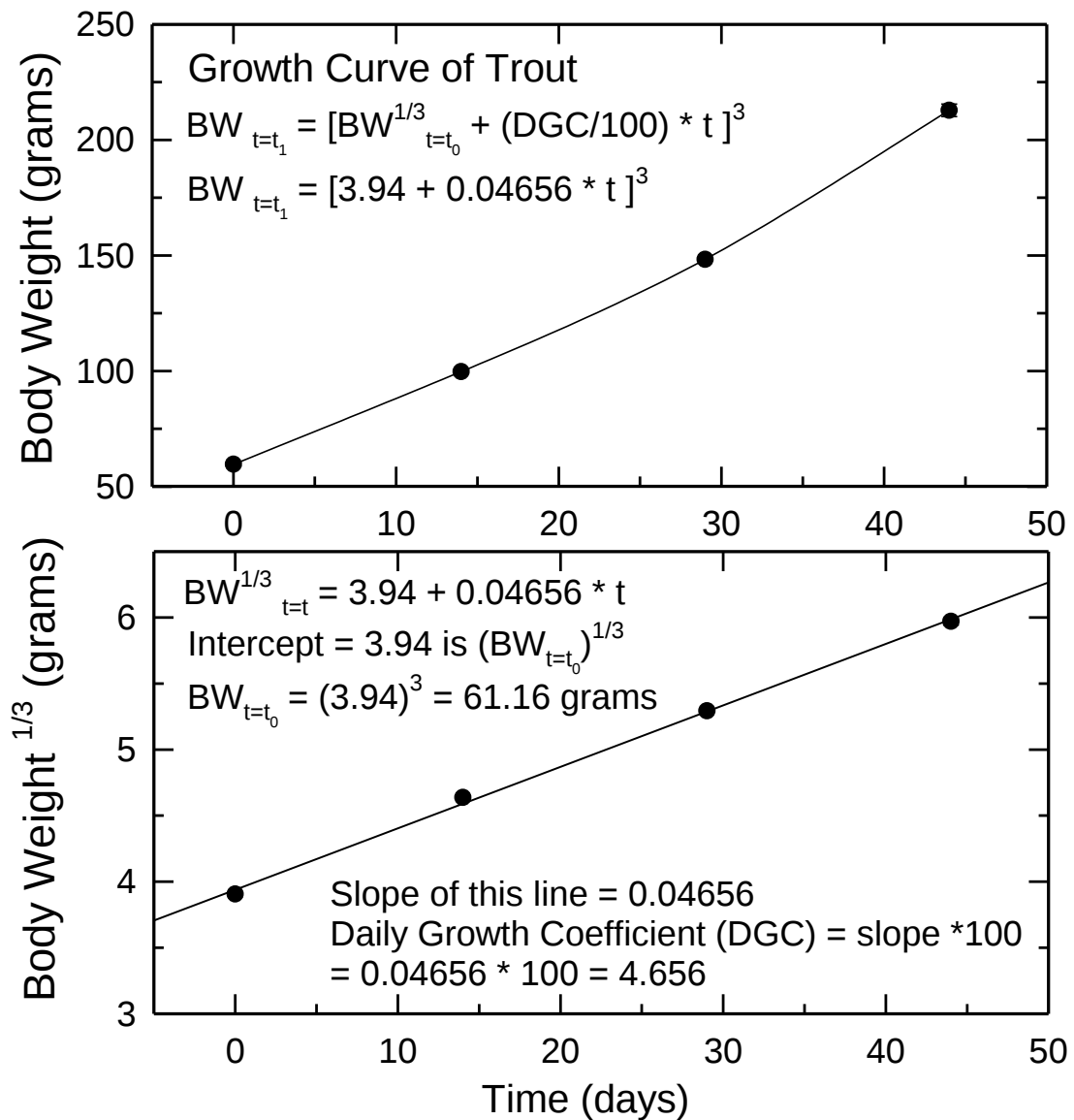
Appendix 87 (Figure)

Growth curve of Sea Bass larvae. The data were fitted a power growth curve.



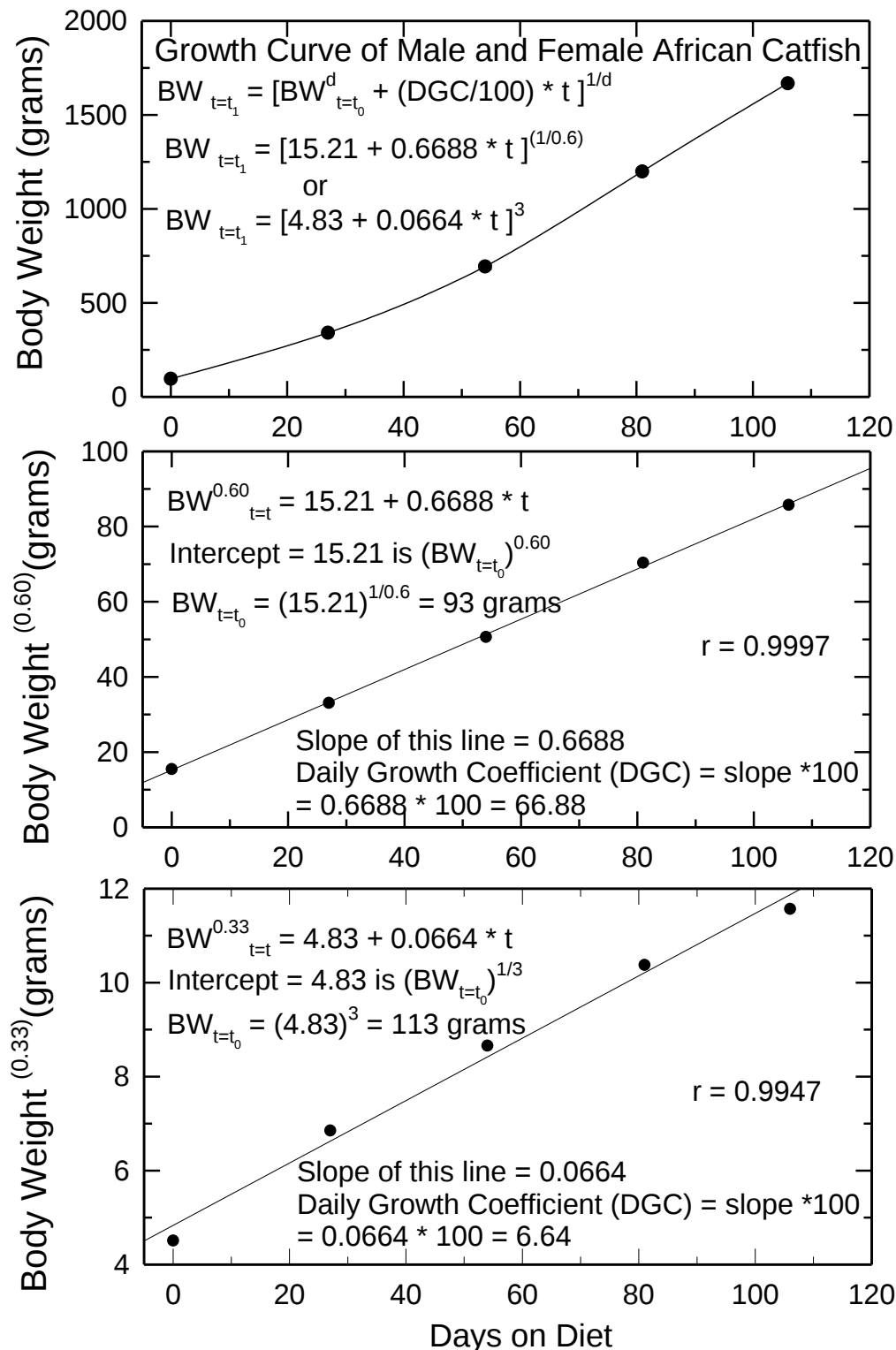
Appendix 88 (Figure)

Growth curve of Trout. The data were fitted a power growth curve.



Appendix 89 (Figure)

Growth curve of African Catfish. The data were fitted a power growth curve.



The data were fitted a power function. By trial and error we found that the power exponent of 0.60 fitted the data the best, better than the conventional 0.33 exponent (see middle and bottom panel).

Appendix 90 (Figure)

Feeding curves for trout

We can express the feed intake in trout in:

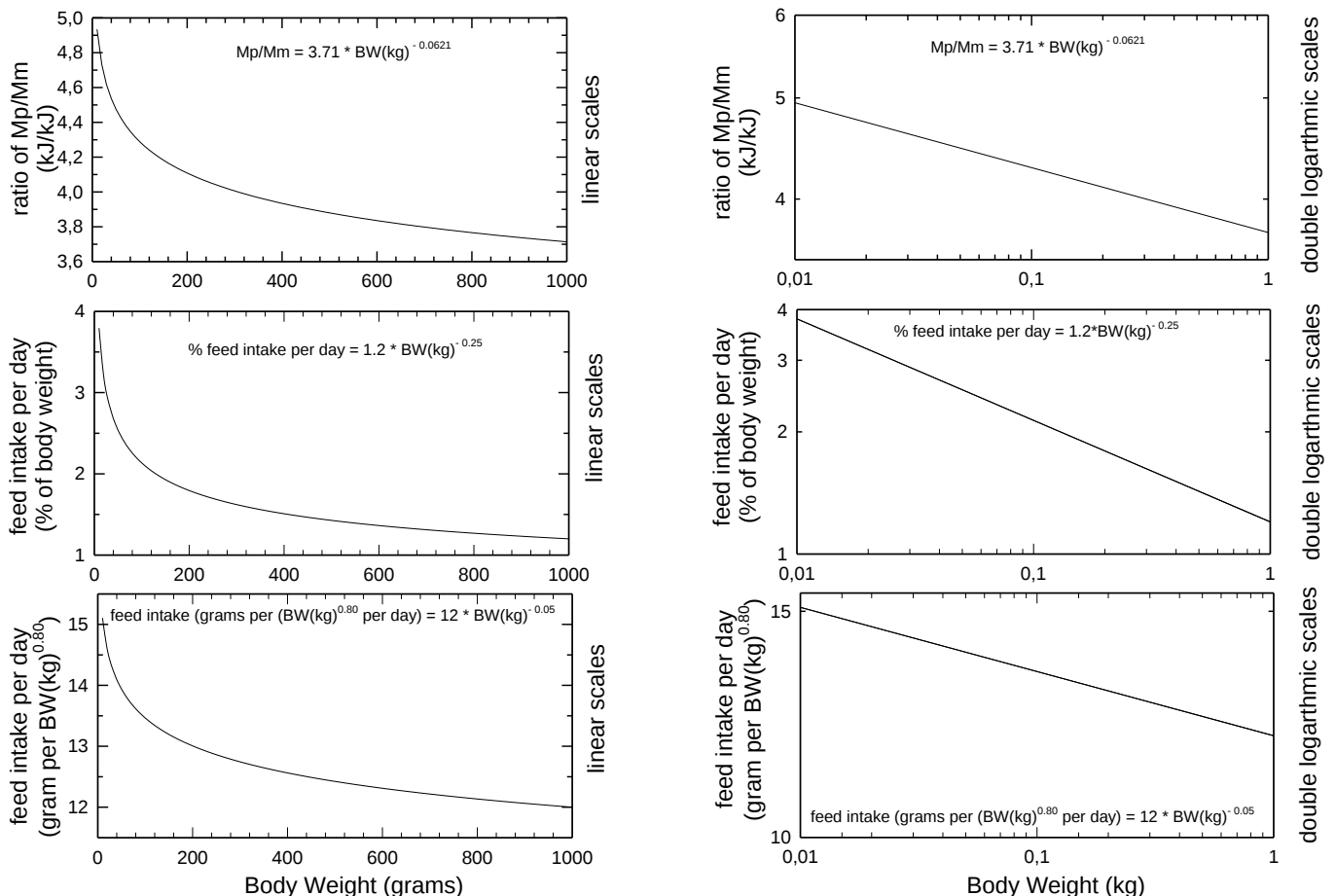
- (a) in percentage of body weight (most commonly used way) or
- (b) in grams per kg metabolic weight (per $BW(kg)^{0.80}$) (scaling coefficient for metabolic weight of trout is 0.80).

Both ways of feed intake can be described by allometric scaling formulae and both ways of expressing the feed intake can be converted into each other with formulae 1 and 2 of Appendix 19:

For example, we have the feeding curve:

- (a) Feed intake in % body weight = $1.2 * BW(g)^{-0.25}$ or
- (b) Feed intake in grams per kg metabolic weight = $12 * BW^{-0.05}$

The feeding curves are given in the graphs below.



The ratio of metabolizable energy for production / metabolizable energy for maintenance (Mp/Mm) was calculated as described in Example 2 on page 79.

Appendix 91 (Figure)

Feeding curves for trout

When the scaling coefficient p of the formula ($\% \text{ feed intake} = x * BW(kg)^p$) that expresses the feed intake in % of the body weight is $(b - 1)$ or $\% \text{ feed intake} = x * BW(kg)^{(b-1)}$ (where b is the scaling coefficient for metabolic weight of 0.75 for most terrestrial animals and 0.80 for most fish species and $(b - 1)$ is then - 0.25 and - 0.20, respectively), then conversion of this formula into grams per kg metabolic weight (per $BW(kg)^{0.80}$) with formula 4, Appendix 19, page 78:

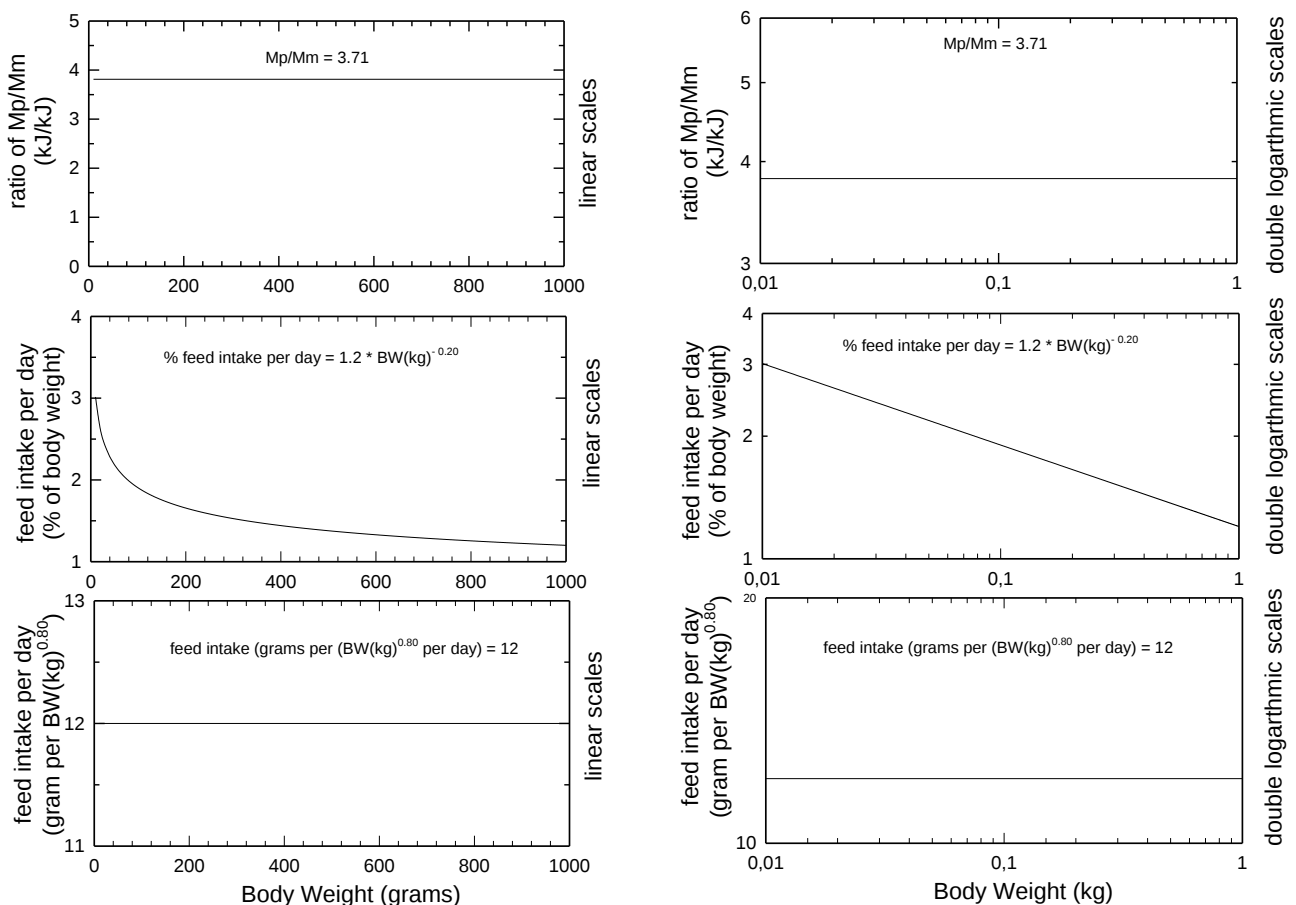
$$\text{feed intake (g) per kg metabolic weight (per } BW(kg)^{0.80} = c = x * 10 * BW(kg)^{(b-1) - (b-1)} \text{ or}$$

and for trout (scaling coefficient b is 0.80)

$$\text{feed intake (g) per kg metabolic weight (per } BW(kg)^{0.80} = c = x * 10 * BW(kg)^{(0.80-1) - (0.80-1)} \text{ or}$$

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

and the feed intake per kg metabolic weight (per $BW(kg)^{0.80}$) of trout is now independent of the body weight and is now the same for all the various body weights. As discussed earlier (Appendix 19), 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). Thus, when the scaling coefficient of the formula that describes the feed intake as % of body weight is $(b-1)$ and in trout $(0.80 - 1) = - 0.20$, 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 fish size as seen in the graph below.



The ratio of metabolizable energy for production / metabolizable energy for maintenance (Mp/Mm) was calculated as described in Example 2 on page 79.

Appendix 92 (Text)

Properties of logarithms

Properties of logarithms:

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

$$\ln (a) - \ln (b) = \ln (a/b)$$

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

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

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

proof: ${}^g\log a = {}^g\log a$, and thus, per definition: $g \wedge ({}^g\log a) = a$

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

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

proof:

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

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

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

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

or

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

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

proof:

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

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

$$10^1 = 10$$

$$10^0 = 1$$

$$1^a = 1$$

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

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

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

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

The logarithms of 0 and negative numbers do not exist.

The logarithms of values $0 < \text{value} < 1$ are negative.

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

Further:

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

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

$$a/b = c/d \text{ then: } a*d = b*c \text{ (cross-wise multiplication)}$$

$$\sqrt[3]{10} = 10^{(1/2)} \text{ root is the inverse of the power}$$

$$10 / 2 = 10 * (1/2)$$

$$2^{\log 50} = a, \text{ then } 2^a = 50$$

$${}^a\log a = 1 \text{ (} a^1 = a \text{)}$$

$${}^a\log 1 = 0 \text{ (} a^0 = 1 \text{)}$$

The number e = 2.71:

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

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

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

Proof that the derivative of $^{10}\log x = (1/x) * ^{10}\log (2.71)$ and the number e is 2.71.

$$y = {}^a\log x$$

$$y + \Delta y = {}^a\log (x + \Delta x)$$

substitute in this formula: $y = {}^a\log x$

$${}^a\log x + \Delta y = {}^a\log (x + \Delta x)$$

$$\Delta y = {}^a\log (x + \Delta x) - {}^a\log x \quad (\text{note that } \log a - \log b = \log (a/b))$$

$$\Delta y = {}^a\log \frac{(x + \Delta x)}{x} = {}^a\log \left(1 + \frac{\Delta x}{x}\right)$$

$$\frac{\Delta y}{\Delta x} = \frac{1}{\Delta x} {}^a\log \left(1 + \frac{\Delta x}{x}\right)$$

$$\frac{\Delta y}{\Delta x} = \frac{1}{x} \frac{x}{\Delta x} {}^a\log \left(1 + \frac{\Delta x}{x}\right)$$

$$\frac{\Delta y}{\Delta x} = \frac{1}{x} {}^a\log \left(1 + \frac{\Delta x}{x}\right)^{\left(\frac{x}{\Delta x}\right)} \quad (\text{note that } 2 \log x = \log x^2)$$

$$\frac{dy}{dx} = \lim_{\Delta x \rightarrow 0} \left(\frac{\Delta y}{\Delta x}\right) = \frac{1}{x} {}^a\log \lim_{\Delta x \rightarrow 0} \left(1 + \frac{\Delta x}{x}\right)^{\left(\frac{x}{\Delta x}\right)}$$

$$\lim_{\Delta x \rightarrow 0} \left(1 + \frac{\Delta x}{x}\right)^{\left(\frac{x}{\Delta x}\right)}$$

$$\text{When } x = 1 \text{ and } \Delta x = 1, \text{ then } \left(1 + \frac{1}{1}\right)^{\frac{1}{1}} = (1 + 1) = 2$$

$$\text{When } x = 1 \text{ and } \Delta x = 0.1, \text{ then } \left(1 + \frac{0.1}{1}\right)^{\frac{1}{0.1}} = (1 + 0.1)^{10} = 2.594$$

$$\text{When } x = 1 \text{ and } \Delta x = 0.01, \text{ then } \left(1 + \frac{0.01}{1}\right)^{\frac{1}{0.01}} = (1 + 0.01)^{100} = 2.7048$$

$$\text{When } x = 1 \text{ and } \Delta x = 0.001, \text{ then } \left(1 + \frac{0.001}{1}\right)^{\frac{1}{0.001}} = (1 + 0.001)^{1000} = 2.717$$

Note that all different values for x can be taken, e.g.

$$\text{When } x = 10 \text{ and } \Delta x = 0.001, \text{ then } \left(1 + \frac{0.001}{10}\right)^{\frac{10}{0.001}} = 2.718$$

$$\text{When } x = 100 \text{ and } \Delta x = 0.001, \text{ then } \left(1 + \frac{0.001}{100}\right)^{\frac{100}{0.001}} = 2.718$$

Thus, when Δx approaches to 0, $\frac{x}{\Delta x}$ approaches to 2.71828, the number e.

Thus, the derivative of the function $y = {}^a\log x$ is then $= \frac{1}{x} {}^a\log 2.718$

When $a = e$, then the derivative becomes $\frac{1}{x} \log 2.71 = \frac{1}{x}$

Thus, the derivative of $\ln x = \frac{1}{x}$

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