

METABOLIC COSTS OF GROWTH AND MAINTENANCE IN THE TOAD, *BUFO BUFO*

BY C. BARKER JØRGENSEN

Zoophysiological Laboratory A, August Krogh Institute, Universitetsparken 13,
DK-2100 Copenhagen Ø, Denmark

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Summary

Metabolic costs of growth and maintenance were determined from the relationship M (metabolism) = $m + nG$ (growth), where m is the metabolic rate at the feeding level at which growth is zero. In the past, the slope n was interpreted as indicating the metabolic costs of growth, and the costs of maintenance that arise with the increase in body mass were disregarded. These costs are included in n . In female toads, *Bufo bufo*, feeding at different rates, the uncorrected value of n was 0.44, when metabolism and growth were expressed as kJ kJ^{-1} . After correction for increased metabolic maintenance expenditure with increased body mass, the value became 0.35, indicating that the physiological costs of growth were equivalent to about one-third of the body mass deposited. Metabolic costs of growth accounted for 80% of the increase in metabolism with growth, leaving 20% for costs of maintenance. At maximum growth rate the metabolic costs of growth amounted to about 60% of the total metabolism, total mass-specific metabolic rate being 2.5 times the rate at zero growth.

The physiological costs of growth in young toads were compared with the costs in teleosts. Recalculation of published data on the relationship between metabolism and growth in the African catfish *Clarias lazera* indicated that the metabolic costs of growth amounted to about 28% of body mass deposited. The costs represented about 80% of the increase in metabolism with growth.

The physiological costs of growth are several times higher than the net biochemical costs of synthesis of the macromolecules constituting the increase in body mass.

Introduction

Studies of metabolic rates in animals are generally concerned with the determination of the overall energy output as a function of internal and external factors, including body size, nutritional state, level of activity and temperature. Little attention has been given to how animals apportion their energy budgets between costs of growth, that is net synthesis of biomass, and costs of maintenance. The latter is the energy spent in keeping the organism alive and working. This neglect of the energetic costs of growth in animal energy budgets may be

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because they are generally thought to be relatively unimportant compared with the costs of maintenance and activity, or thermoregulation in the warm-blooded animals. However, recent studies indicate that the energetic costs of growth, including somatic growth and reproduction, may constitute substantial proportions of the overall energy output of an organism, e.g. in fish (Jobling, 1985; Kiørboe & Møhlenberg, 1987; Kiørboe *et al.* 1987), toads (Jørgensen & Wind-Larsen, 1987) and copepods (Kiørboe *et al.* 1985).

The distinction between energetic costs of growth and maintenance is to some extent arbitrary because costs of maintenance also include costs of synthesis of macromolecules to balance breakdown of body constituents, including turnover of proteins. The distinction is, however, biologically justified, particularly in animals that exhibit pronounced adaptability in growth, such as amphibians and many other cold-blooded animals. In contrast to warm-blooded vertebrates, i.e. birds and mammals, these animals are characterized by their tolerance towards varying availability of food. When food is in short supply, growth may subside, and even become negative, without ill effects on health and survival. Growth may be postponed until favourable conditions – high temperature and abundant food – return. During periods of net growth, the cost of growth thus constitutes a well-defined entry in the energy budget of the organism, and it becomes of interest to assess the physiological costs of growth and their relative importance when they reach maximum at maximum rates of growth.

The physiological costs of growth can be determined from the relationship between growth and metabolism in animals fed at different levels. These costs may be compared with net biochemical costs of growth as estimated from the costs of synthesis of the macromolecules that constitute growth/production (Atkinson, 1971, 1977). This paper deals with such studies in the toad *Bufo bufo*.

Materials and methods

The experiment was carried out on 15 juvenile female toads collected in the month of September and weighing 19 ± 5.9 g (s.d.). The toads were kept individually at 21°C in 36 cm × 55 cm × 22 cm plastic boxes divided in two by a partition. The bottoms of the boxes were covered with filter paper and the toads had access to water in a dish. They were offered mealworms either *ad libitum* for one 24-h period a week, or comparable amounts were administered in three rations a week (C. B. Jørgensen, in preparation). In the autumn, toads reduce feeding and discontinue growth in length when kept in the laboratory. To maintain feeding and growth at a high level the toads were injected subcutaneously 5 days a week with 10 µg of growth hormone (bovine growth hormone, USDA-bGH-B-1) (Wind-Larsen & Jørgensen, 1987).

The experiment started on 20 October and lasted 16 weeks. The toads were weighed, after emptying of the bladder, at weekly intervals. At autopsy the fat bodies, liver and ovaries were excised and weighed separately. The water content of the carcass and other parts of the body was determined by drying to constant

weight at 80°C. The dry matter, excluding fat bodies, was pulverized using either a mortar or an impact mill. Samples of 10 mg were used for CHN-analysis in a Perkin-Elmer elemental analyser. The remainder was used to determine total organic matter from the loss on ignition in a muffle furnace at 450°C for about 7 h. Samples of mealworms and faeces, recovered quantitatively from eight toads over 4 weeks, were similarly analysed.

N was converted into protein, multiplying by the standard factor of 6.25. Assuming a protein carbon content of 50%, the remaining non-protein organic matter was apportioned between fat and glycogen, assuming fat to contain 76% C, typical of relatively long-chain fatty acids, and glycogen 44% C. Growth, food and faeces were converted into energy equivalents using the standard conversion factors of 5.65 kcal or 24 kJ g⁻¹ protein and 4.1 kcal or 17.2 kJ g⁻¹ glycogen. For fat the value of 8.5 kcal or 35.7 kJ g⁻¹ was adopted, as suggested by Nijkamp *et al.* (1974) and Jobling (1983). Gnaiger & Bitterlich (1984) found the conversion factor protein/nitrogen = 5.8 to apply in aquatic organisms, ranging from a fish to a bivalve and zooplankton, and they adopted a caloric equivalent for fat of 39.5 kJ g⁻¹. Recalculation of the present data based on these factors only slightly affected the results.

Metabolic expenditures of the individual toads were estimated from substrate used in the oxidative metabolism by subtracting deposited protein, fat and glycogen from absorbed protein, fat and carbohydrate, as determined from the efficiency of digestion and absorption of the ingested components. The caloric values of fat and glycogen also apply when these components serve as the substrate in oxidative metabolism, but in ureotelic animals, such as bufonids, the metabolic value of protein is reduced to 4.8 kcal or 20.2 kJ g⁻¹ (Elliott & Davison, 1975). Growth/production included both somatic growth and deposition of fat, as well as vitellogenic growth in the ovaries of most of the females (C. B. Jørgensen, in preparation).

Analysis of metabolic costs of growth

When metabolic and growth rates are measured in animals of the same initial body mass, but growing at different rates, the relationship between energy expenditure (M) and growth/production (G) can be described as a linear function $M = m + nG$. The slope n has been interpreted as indicating the cost per unit measure of growth, whereas the costs of maintenance are given by m , the energy expenditure at zero growth (Birkett, 1969; Jobling, 1985; Jørgensen & Wind-Larsen, 1987). This interpretation is correct when products are exported from the organism, e.g. as gametes (Kjørboe *et al.* 1985). When production constitutes an integral part of the body, as in somatic growth, the costs of maintenance that arise with the increase in body mass are included in the slope n , thus overestimating the true metabolic costs of growth. A correction was therefore made for the increased costs of maintenance with growth.

In the experiments, growth was approximately exponential (C. B. Jørgensen, in preparation), and the instantaneous, relative growth rate μ is given by the

equation $\mu = \ln(W_t/W_0)/t$, or $\ln W_t = \mu t + \ln W_0$. Thus $W_t = W_0 e^{\mu t}$, where W_0 and W_t are body masses at zero time and at time t . Body mass may be expressed as, for example, wet weight or energy equivalents.

Metabolic rate MR is usually related to body mass by the equation $MR = aW^b$. Thus metabolic rate at body mass W_t , $MR_t = aW_t^b$. By substitution we obtain $MR_t = a(W_0 e^{\mu t})^b = aW_0^b e^{b\mu t}$.

Total metabolic expenditure M during the period of growth is obtained from

$$M = \int_0^t MR dt = \int_0^t aW_0^b e^{b\mu t} dt$$

At a specific μ , aW_0^b is constant, so

$$M = aW_0^b \int_0^t e^{b\mu t} dt. \quad (1)$$

The calculations were based on weekly growth rates μ , and a was estimated by extrapolation of the relationship between mass-specific metabolism M and G to zero growth (Fig. 2), dividing the intercept m by 16, the duration of the experiment in weeks.

The actual value of b in the relationship $MR = aW^b$ may vary with the relative importance of the metabolic costs of growth and maintenance. The energetic costs of growth are constant, independent of body mass (Jørgensen & Wind-Larsen, 1987). The value of b is thus 1 in the relationship $MR_G = a_G W^b$, whereas b in the maintenance relationship $MR_M = a_M W^b$ may attain a value around 0.67–0.75, typical of standard metabolic rates in vertebrates (Heusner, 1982, 1987). The resulting value of b cannot be mathematically derived, but the value will approach 1 when metabolic costs of growth predominate and 0.75 when costs of maintenance predominate. We should therefore estimate the range through which the values of b may vary with varying rates of growth to see the effects on the apportioning of total metabolism on costs of maintenance and growth.

In *Bufo terrestris*, in the postabsorptive state, the value of b relating energy expenditure to body mass was found to be 0.78 (Smith, 1976). The postabsorptive metabolic rate is presumably representative of the maintenance metabolic rate, being the metabolic rate at the transition between discontinuation of growth based on the previous meal and starvation. The value of 0.78 was therefore adopted in the present study. When body mass is expressed in energy equivalents, the value should, however, be adjusted because during the experiment the caloric value increased from 4.9 kJ g^{-1} body mass to $6.1 \pm 0.34 \text{ kJ g}^{-1}$ (s.d.). In the African catfish, *Clarias lazera*, the value of b at zero growth declined from 0.81 when body mass was expressed in grams to 0.74 when expressed in units of energy, corresponding to an increase in energy per unit body mass from 4.2 to 6.2 kJ g^{-1} (data from Hogendoorn, 1983). Assuming an approximate inverse proportionality between increase in caloric value with decline in the value of the exponent b , this relationship would correspond to a decline in the value of b in the toads from 0.78 to 0.73. Calculations were, therefore, also made using the conservative estimate of

$b = 0.70$. As will be shown, the use of different b values did not substantially affect the estimated costs of growth.

Results

The relationships between ingestion, absorption, growth (production) and metabolism were established from the basic data listed in Table 1. The apportioning of terminal contents of nitrogen and carbon in the toad bodies provides reliable values for protein and lipid, but not for glycogen. However, because glycogen constitutes such a small fraction of the organic matter, even large errors in its determination are of negligible importance.

The amounts of organic matter deposited as protein and lipid were calculated by subtraction of the amounts present in the body at the start of the experiment. These amounts are not precisely known but they were computed from a standard composition of the toad body in the autumn, amounting to 16% protein, 2.4% lipid and 1.6% glycogen (Jørgensen & Wind-Larsen, 1987). Because of the large increase in organic mass during the experiment, the results were little affected by inaccuracies in the initial values used in the calculations. The increase in body mass ranged from 2.3 to 5.5 times, mean 3.6 times.

Food ingested during the experiment could be accurately determined by weighing the mealworms eaten. Two samples of mealworms, analysed during the experiment, were of similar composition and contained 19.2% protein, 14.4% lipid and 5.6% glycogen, as percentages of the fresh weight. The proportions of ingested matter that were absorbed could be accurately determined as the differences between amounts ingested and amounts egested with the faeces. 100% of the fat was absorbed, 92.5% of the protein and 74.2% of the carbohydrate.

It may be noted that the high terminal lipid contents in the toads are correlated with a high content of lipid in the mealworms. The lipid content in the toads increased with the rate of growth. As mentioned, the increase in fatness with body mass reduces the value of the exponent b in the relationships between metabolic rate and body size, when body size is expressed in energy equivalents instead of mass.

The relationship between growth G and ingestion I , expressed in energy equivalents per gram body mass, could be described by the equation $G = -1.6 + 0.63I$ ($r = 0.986$) (Fig. 1).

The apportioning of the absorbed matter, expressed in energy equivalents, to growth and metabolism is shown in Fig. 2. The relationship could be described by the equation $M = 0.61 + 0.44G$ ($r = 0.869$).

The proportions of total metabolism M that constituted the costs of maintenance M_M were calculated by means of equation 1. Subtraction of M_M from M , expressed as kJ kJ^{-1} initial body mass, provided the metabolic costs of growth M_G . When a value of $b_M = 0.7$ was used as the exponent in the equation $MR_M = a_M W^{b_M}$ the relationship between M_G and G could be described by the equation $M_G = -0.11 + 0.35G$ ($r = 0.811$) (Fig. 2). When a value of $b_M = 0.78$ was adopted,

Table 1. *Bufo bufo*: growth, terminal body composition, ingestion, absorption and deposition of organic matter (g)

Toad	Body mass			Organic constituents			Meal-worms eaten	Absorbed			Deposited		
	Initial	Terminal		Protein	Lipid	Glycogen		Protein	Lipid	Glycogen	Protein	Lipid	Glycogen
15	30	90		9.6	9.9	1.0	66	11.7	9.5	2.6	4.8	8.5	1.5
17	25	92		10.9	7.9	1.0	71	12.6	10.2	2.8	6.9	7.5	0.1
19	33	94		11.3	8.4	1.0	73	12.9	10.5	2.9	6.0	7.7	0.8
20	14	77		7.5	6.3	0.7	54	9.8	7.9	2.2	5.3	6.0	0.8
21	20	68		7.5	5.1	0.7	46	8.4	6.8	2.9	4.3	4.4	0.5
22	17	73		8.5	6.3	0.8	56	10.0	8.1	2.2	5.8	5.6	0.8
23	19	70		8.2	5.7	0.8	54	9.6	7.8	2.2	5.1	5.5	0.7
24	11	60		7.6	5.8	0.7	55	9.8	7.9	2.2	5.8	5.4	0.5
25	13	50		6.1	4.3	0.5	42	7.4	6.0	2.7	4.0	4.1	0.3
26	17	65		7.7	6.3	0.7	53	9.4	7.6	2.1	5.0	5.7	0.7
27	15	55		7.2	5.1	0.6	49	8.7	7.0	1.9	4.8	4.8	0.5
28	22	75		8.5	6.6	0.7	56	9.9	8.0	2.2	5.0	5.5	0.7
30	15	73		8.2	7.6	0.8	65	11.5	9.3	2.6	5.8	7.0	0.9
31	19	43		5.8	2.8	0.5	35	6.2	5.0	1.4	2.7	2.2	0.3
32	18	59		6.2	4.8	0.6	38	6.7	5.4	1.5	3.3	4.1	0.5
$\bar{x} \pm$ s.d.	19.2 ± 5.9	69.6 ± 14.5					54.2 ± 10.9						

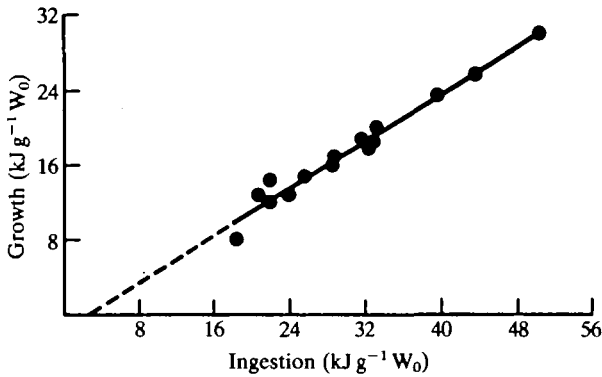


Fig. 1. Relationship between ingestion and growth, expressed in kJ g^{-1} initial body mass, in young female toads, *Bufo bufo*.

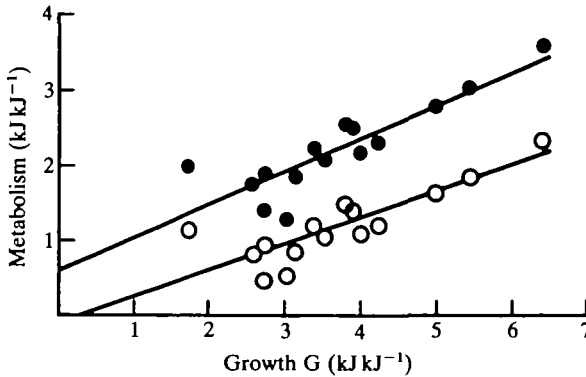


Fig. 2. Relationship between mass-specific growth and metabolism in young female toads. (●) Total metabolism M ; (○), metabolic costs of growth $M_G = M - M_M$ (M_M = metabolic costs of maintenance). Calculations of M_M are based on a value of $b_M = 0.7$ in the relationship $M_M = aW^b$ (see text).

the slope of the relationship $M_G = m + nG$ became 0.33. At the extreme situation of both b_M and b_G being 1, the slope declined to 0.28.

The mean value (\pm s.d.) of the ratios M_G/G calculated individually were 0.32 ± 0.12 and 0.30 ± 0.12 , at values of $b_M = 0.70$ and 0.78 , respectively. As expected, the individual values are similar to the slopes of the regressions of M_G on G , and it can be seen that the relationship between M_G and G is only moderately affected by the different values of b_M . Thus the physiological costs of growth amounted to about one-third of the energy deposited.

To see whether the estimated costs of growth were correlated with rates of growth, M_G/G was plotted against the weekly instantaneous growth rate μ (Fig. 3). There was no obvious effect of growth rate on the energetic costs of growth.

Net metabolic costs of synthesis of macromolecules from monomers

The physiological costs of growth, determined as the difference between total metabolism and maintenance metabolism, include energetic costs of synthesis of macromolecules from monomers derived from the food. These net biochemical costs can be calculated from standard values of energy yields on oxidation of

Table 2. *Conversion factors used in calculation of net metabolic costs of synthesis of macromolecules from monomers*

Monomer	M_r^*	kJ mol^{-1} ATP	ATP per bond	kJ g^{-1} product
Glucose	162	76	2	0.94
Palmitic acid	238	76	2	0.64
Amino acids	approx. 100	97	5†	4.85

* Corrected for water eliminated with the bonds; † including costs of synthesis of DNA/RNA.

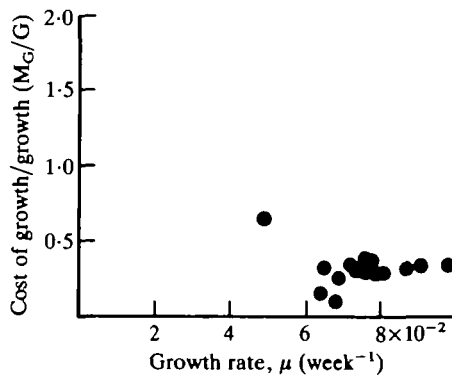


Fig. 3. Relationship between weekly rate of growth calculated as $\ln(W_t/W_0)/16$, and the fraction which the metabolic costs of growth constitutes of growth, M_G/G , in young female toads.

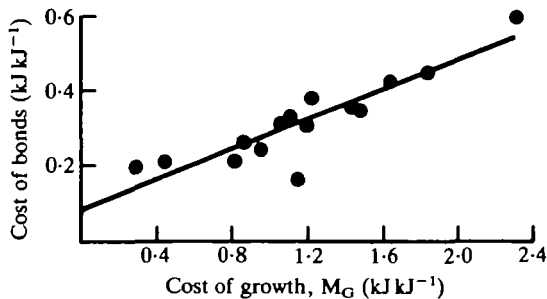


Fig. 4. Relationship between estimated physiological costs of growth and calculated net biochemical costs of synthesis of component macromolecules from monomers in young female toads.

substrates and costs of synthesis of bonds in the macromolecules, as shown in Table 2 (Blaxter, 1971; Atkinson, 1977; Stouthamer, 1979; Lehninger, 1982; Riis, 1983). These conversion factors were applied to the data on deposited protein, lipid and glycogen given in Table 1. Protein accounted for by far the largest proportion of the biochemical costs of synthesis of bonds, accounting for $85.6 \pm 2.1\%$ (s.d.). The figure for fat was 13.0 ± 2.1 , leaving 1–2% for the synthesis of glycogen.

The relationship between the calculated biochemical net costs of synthesis of bonds and the physiological costs of growth is shown in Fig. 4. The relationship could be described by $y = 0.086 + 0.20x$ ($r = 0.888$). The mean value of biochemical costs, expressed as a percentage of M_G , amounted to $30 \pm 12\%$. The calculated net costs of synthesis of macromolecules thus appear to represent 20–30% of the total costs of growth.

Discussion

In investigations aimed at estimating metabolic costs of growth/production, metabolism may be determined in terms of oxygen consumed (when metabolism is aerobic) or as the difference between matter absorbed/assimilated and matter deposited. Continuous measurement of oxygen consumption over long periods in animals feeding and growing at different rates is a theoretically appropriate but technically difficult approach. The accuracy with which metabolism can be determined as the difference between absorption and growth depends upon how precisely absorption and growth can be determined. Absorption can be determined accurately for animals in which rates of feeding and defaecation are monitored. Growth is determined as the increase in total body mass and/or mass of body constituents. The accuracy of estimation therefore depends upon how accurately initial and final masses and changes in body composition are determined. Greatest accuracy is likely to be achieved when growth is fast and/or measured over relatively long periods.

To arrive at correct estimates of metabolic costs of growth, growth should be continuous and approximately exponential within the period considered. Variation in growth rates during an experiment will tend to result in underestimates of the metabolic costs of maintenance and thus in overestimates of the costs of growth. If metabolic cost of growth is dM/dG and growth is restricted to a fraction f of unit time, the cost of growth will be overestimated by $(1-f)dM$. This fact has so far been ignored, presumably because growth appears continuous and even exponential when measured over periods of days, weeks or months. However, instantaneous growth, in terms of net synthesis of macromolecules, varies with the availability of monomers, particularly amino acids, required for the synthesis of body constituents. The availability of monomers, in turn, depends upon the pattern of feeding, digestion and absorption, and in animals that feed discontinuously and perhaps at long and irregular intervals, growth may show corresponding variations.

In toads, feeding, absorption and deposition can be accurately determined, and instantaneous rates of growth may remain constant and independent of body mass over a large range of growth rates and body masses. The indirect approach is, therefore, appropriate for estimating metabolic costs of growth in toads. This approach was adopted in a previous paper, but the costs of maintaining body mass added with growth were disregarded (Jørgensen & Wind-Larsen, 1987). The costs of growth were therefore overestimated and the degree of error thereby introduced in calculated costs of growth can be estimated from the two relationships: total metabolic rate *vs* growth rate and metabolic costs of growth *vs* growth rate, as shown in Fig. 2. The fractional costs of growth are given by the ratio of the slopes of the two equations, or $0.35/0.44 = 0.80$. This leaves 20% of the increase to costs of maintenance of the increased body mass. At the extreme situation of proportionality between maintenance metabolism and body mass, that is $b_M = 1$, the slope of the regression of M_G on G would have been 0.28, which would reduce the fractional costs of growth to $0.28/0.44 = 0.64$ and thus increase the fractional costs of maintenance of the increased body mass to 36%.

Thus, even after correction for metabolic costs of maintenance the costs of growth contribute substantially to the total metabolic rate of the growing organism. The costs of growth M_G at maximum growth rate amounted to about 60% of the total metabolism M , with total metabolic rate being 2.5 times the rate at zero growth (Fig. 2). This is comparable to the increase in metabolic rate during activity in amphibians (Bennett & Licht, 1973).

The metabolic costs of growth include energy expended in eating, digesting and absorbing food in excess of that needed for maintenance. These costs are presumably small compared with the costs of synthesis of macromolecules (Kjørboe *et al.* 1985). The estimated costs of synthesis were small compared with the physiological costs, defined as the difference between food energy absorbed in excess of maintenance and energy deposited as growth/production. This discrepancy between biochemically calculated and physiologically estimated costs of growth may arise from the dominant role of protein synthesis in growth. The accuracy of the calculated biochemical net costs of growth depends primarily upon the correctness of the factor adopted for converting peptide bonds into ATP equivalents. The factor of 5 adopted in the current study is based on stoichiometrical knowledge about the intermediary metabolism of biosynthesis. Recent studies of the relationship between protein synthesis and heat production in chickens indicate that the costs may be higher, about 6 ATP per peptide bond in starving chickens and 13 in fed chickens, the discrepancy between costs of protein synthesis in the starving and fed state remaining unexplained (Muramatsu *et al.* 1987).

Biochemically calculated costs of net protein synthesis should be lower than physiologically determined costs, because protein molecules are also degraded, resulting in turnover of proteins (Waterlow, 1984). In the present experiment, the ratio of physiological costs of growth to biochemical net costs was compatible with protein synthesis, in excess of the basal rate of maintenance, amounting to 3–4 times the amount of protein deposited as growth. Protein synthesis was up to three

Table 3. Relationships between growth and metabolism in the African catfish *Clarias lazera* (data from Hogendoorn, 1983)

Initial body mass		Duration of experiment (days)	Metabolism at zero growth $G = m$		n_M	n_{M_G}	M_G/M
(g)	(kJ)		kJ	kJ day ⁻¹			
1.6	6.6	21	3.59	0.17	0.45	0.39	0.87
7.3	37	28	23.5	0.84	0.28	0.21	0.75
44	256	28	83.4	2.98	0.31	0.26	0.84
92	572	42	198	4.71	0.35	0.27	0.77

n_M is the slope in the regression for total metabolism $M(\text{kJ}) = m + n_{M_G}(\text{kJ})$; n_{M_G} is the slope in the regression of metabolism corrected for maintenance costs ensuing from growth G .

times higher in growing than in non-growing pigs (Reeds *et al.* 1980). In rats at weaning muscle protein synthesized amounted to five times that deposited (Millward *et al.* 1975).

Costs of growth in young toads may be compared with costs of growth in teleosts. Jobling (1985) analysed the relationship between growth and metabolism in the African catfish *Clarias lazera*, based on data from Hogendoorn (1983) on growth and oxygen consumption in fish of different sizes fed at different levels. Jobling calculated the regression of oxygen consumption (in ml) on growth (in mg dry matter deposited). In the regression equation $M = m + nG$, n varied from 0.39 to 0.55, and was not dependent on the initial body mass, which ranged from about 1.6 to 92 g. Jobling interpreted the slopes of the regression lines in terms of metabolic costs of growth and, because the slopes were independent of body mass, he concluded that these costs were constant during growth.

I have recalculated Hogendoorn's data, correcting for costs of maintenance of increased body mass arising during the experiment. Hogendoorn determined the caloric values of the fish, and these values were used to express growth in terms of energy equivalents. Hogendoorn converted metabolic rates into energy equivalents using the conversion factor $11\text{O}_2 = 20.4\text{ kJ}$. The results are shown in Table 3.

m is metabolism at the feeding levels corresponding to zero growth during the experimental period. The relationship between metabolic rate at zero growth and body mass could be expressed by the equations $M(\text{kJ day}^{-1}) = 0.134W(\text{g})^{0.81}$ ($r = 0.994$) and $M(\text{kJ day}^{-1}) = 0.048W(\text{kJ})^{0.74}$ ($r = 0.995$). As mentioned before, the lower value of the exponent when body mass is expressed in energy equivalents reflects the increase in caloric value of the body mass with increasing size.

The metabolic costs of growth, as expressed by $n_{M_G} = M_G/G$, varied from 0.21 to 0.39 kJ kJ⁻¹ body mass deposited (mean value \pm s.d. = 0.28 ± 0.066).

The slope n_{M_G} varied among the groups of fish of different body size, but the variation was not correlated with body mass, confirming that the energetic costs of growth do not vary with body size. However, the large variation from 0.21 to 0.39 kJ kJ⁻¹ stresses the methodological difficulties in assessing the physiological

costs of growth. It remains to be settled whether these costs are well defined or whether they can vary with unnoticed variables in the experimental conditions.

Data on the relationship between growth and metabolism have also been published for the rainbow trout, *Salmo gairdneri* (From & Rasmussen, 1984). A recalculation of these data made by Kiørboe *et al.* (1987) showed that the increase in metabolism over the increase in growth varied between 0.19 and 0.27.

The relatively high physiological costs of growth in young toads and teleosts suggest that protein deposition is accompanied by considerable protein turnover. In contrast, results obtained in embryos and larvae of the herring *Clupea harengus* indicated that physiological costs, with a M_G/G value of 0.10, correspond to the theoretical biochemical net costs, dominated by the metabolic costs of peptide bond formation (Kiørboe & Møhlenberg, 1987; Kiørboe *et al.* 1987). This indication of a lower turnover of protein in the embryonic and larval stages than in juvenile and older stages is unexpected, because physiological costs of growth were found not to vary with body mass either in the toad or in the catfish.

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