

ENERGY ALLOCATION AND YIELD AND COST OF GROWTH IN YOUNG *ESOX LUCIUS* AND *COREGONUS LAVARETUS* (TELEOSTEI): INFLUENCE OF SPECIES, PREY TYPE AND BODY SIZE

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Summary

Energy partitioning was studied in the larvae and early juveniles of two species of freshwater fish with different life styles, *Coregonus lavaretus* and *Esox lucius*, by measuring simultaneously the rates of feeding, oxygen consumption and growth in long-term experiments. Comparison between the two species is based on measurements at 15°C, but a group of *C. lavaretus* was also monitored at 10°C.

The intensity of routine oxygen consumption was mass-independent in the smallest larvae, but above about 10 mg wet body mass (m) it scaled with an allometry of $m^{-0.103}$ in *C. lavaretus* and $m^{-0.154}$ in *E. lucius*. Routine, minimum and maximum rates of metabolism were higher in *C. lavaretus* than in *E. lucius*, whereas the mass-specific rate induced by feeding showed a quite different and more complex relationship to species.

The mass-specific rate of growth scaled with $m^{-0.133}$ ($r=0.54$) in *C. lavaretus* but with $m^{-0.24}$ ($r=0.90$) in *E. lucius*.

Comparison of five experimental groups, differing from each other with respect to species, type of prey (*Artemia* nauplii or *Rutilus rutilus* larvae), experimental temperature and body size, suggested a general pattern of energy partitioning, with $62\pm 3.7\%$ of metabolizable food energy being allocated to growth, and $38\pm 3.7\%$ to metabolic expenditures.

The relationship between metabolic rate and growth rate, expressed as the 'yield ratio', mg dry body mass $\mu\text{mol}^{-1}\text{O}_2$, the inverse of the net cost of growth, proved to be nearly invariant in all experimental groups, namely $0.043\text{ mg } \mu\text{mol}^{-1}$. However, two experiments with the smallest pike larvae led to higher growth rates per metabolic expenditure, suggesting that in *E. lucius* oxygen consumption may reach an aerobic maximum for growth at a routine rate of about $200\text{--}220\text{ } \mu\text{mol O}_2\text{ g}^{-1}\text{ dry body mass h}^{-1}$.

Gross costs of growth include mass-dependent maintenance expenditures. Expressed in mass-independent units, *E. lucius* was more efficient in converting

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food energy into growth than was *C. lavaretus*; its superiority in this respect ranged from 7 to 17% depending on body mass and diet.

The results are discussed with regard to the question of whether in small poikilothermic metazoans the allocation of metabolic energy follows the rules of *addition* or *compensation*. Furthermore, growth performance of the fish larvae is compared with that of microorganisms on the basis of the 'yield ATP' concept.

Introduction

We are still quite ignorant about the rules by which metabolic energy is allocated to different physiological functions in small animals. Small body size implies a high rate of maintenance metabolism with little scope for additional physiological functions such as locomotion, stress responses, defence, repair and growth (Wieser, 1991). In consequence, the energy metabolism of small animals must respond sensitively to changes in internal or external conditions, so that metabolic energy can be allocated to different functions according to priority of demand. The rules by which priority is established are unknown, but the rapidity with which switching is likely to proceed makes it mandatory to measure simultaneously energy consumption (usually as oxygen consumption) and the intensity of the function to be investigated.

By means of a 'feeding respirometer' we have been able to identify some of the rules governing the conversion of food energy into body substance in small fish (Wieser and Medgyesy, 1990*a,b*, 1991). Since in these (and probably other) small metazoans the energy expenditures for the sum of all physiological functions may exceed the aerobic maximum, individual functions are believed to substitute for each other when metabolic energy becomes limiting. Thus, uncertainty exists as to the true costs of growth, particularly during periods of embryogenesis and larval development (Rombough, 1992). In such animals a precise accounting of energy fluxes will probably never be possible since this would require the simultaneous measurement of all energy-consuming functions. However, our knowledge of the rules of energy allocation could be furthered by comparing species with different life styles and by studying the responses of organisms to changes in external and internal factors, such as food, temperature, stress, body size, etc.

The present investigation extends previous analyses of flux and allocation of metabolic energy in fish larvae (Wieser and Medgyesy, 1990*a,b*, 1991). Specifically, we asked to what extent the rules of energy partitioning may be influenced by (1) the life style of the fish species, and (2) the type of food offered. In order to answer the first question we compared the larvae of the white fish *Coregonus lavaretus* (L.), a fast-swimming predator, with those of the pike, *Esox lucius* (L.), a sit-and-wait predator, feeding on the nauplii of *Artemia* sp. To answer the second question we compared the larvae of pike feeding on *Artemia* with juveniles of the same species feeding on the larvae of a cyprinid species, *Rutilus rutilus*. An additional aim of the present investigation was to compare the two forms, or subspecies, of *C. lavaretus*, i.e. *C. l. wartmanni* (Gangfisch) and *C. l. macrophthalmus* (Blaufelchen), which spawn at different depths in Lake Constance and are

believed by aquaculturists and fishermen to differ in their rates of growth (Ruhlé, 1986; Roesch, 1987). In a feeding experiment with dry food, Roesch and Dabrowski (1986) observed *Gangfisch* to grow faster than *Blaufelchen*, but this difference may have been due to the latter hatching from smaller eggs. At any rate, we found no differences between the two forms and shall, for the purposes of this investigation, consider them as representing a single taxon.

In conjunction with the results of previous reports, the present investigation permits the formulation of some general rules of energy allocation and growth efficiency in small fish.

Materials and methods

Fish

Larvae and juveniles of *Coregonus lavaretus* (L.) and pike, *Esox lucius* (L.), were raised from eggs fertilized in the laboratory, the parent fish originating from Bodensee (Lake Constance; Vorarlberg) and Mondsee (Upper Austria), respectively. After hatching, the fish were maintained in running water at 15°C and fed *Artemia* nauplii. When the pike had reached a wet body mass of about 200 mg, they were fed larvae of the cyprinid species *Rutilus rutilus* (L.). A group of *C. lavaretus* was also raised at 10°C.

Respirometry

Oxygen consumption was determined on groups of fish by means of the automatic feeding respirometer described previously (Wieser and Medgyesy, 1990a,b; Medgyesy and Wieser, 1991). The experiments comparing the two fish species were performed at 15°C, but a group of *C. lavaretus* was also studied at 10°C. The experiments consisted of four feeding periods in the light, each lasting 15 h, interrupted and terminated by four non-feeding periods in the dark, each lasting 7 h. Between these periods, the fish were removed from the respirometer for 1 h, and the bacterial oxygen consumption of the system was determined. When *Artemia* nauplii were used as food, each feeding period was again subdivided into eight 1-h periods of actual feeding, and seven 1-h periods when the nauplii were flushed out of the system, the unconsumed prey being retained by a plankton net for later counting. The approximate number of prey presented to the fish was known from the concentration of *Artemia* in the holding cylinder and the volume of the solution passing through the magnetic valve into the experimental chamber (which had a volume of about 0.5 dm³). At the end of a feeding period the live nauplii retained by the faeces sampler were counted and added to the number remaining in the holding cylinder. Subtracting this figure from the initial number of nauplii in the holding cylinder yielded an estimate of the number of prey consumed by the fish.

A different approach had to be used when juvenile pike were fed larvae of *R. rutilus*. During each of the four 15-h feeding periods, two groups of 15–20 prey larvae were introduced into the respirometer chamber, one at 1 and one at 6 h

after the beginning of the feeding period. The pike preyed upon the larvae rapidly and efficiently. After about 15 min they seemed to be satiated and stopped feeding, at which time the respirometer chamber was opened, the remaining prey were removed by suction and the chamber was closed again. In this way, a nearly uninterrupted record of oxygen consumption of the pike was obtained prior to, during and after consumption of two meals of *R. rutilus* larvae during four feeding periods of 15 h each. The mass of the prey eaten was estimated by weighing samples of *R. rutilus* from the same group as those used in the experiments.

Protocol

The fish fed *ad libitum* were deprived of food for about 12 h and were then introduced into the respirometer chamber, where they were left for another 6 h without food to ensure that the lowest rate of oxygen consumption measured during this period represented what, in the usual terminology, has been called the 'basal', 'standard' or 'resting' rate of metabolism (Brett, 1972). The fish were then removed, bacterial oxygen consumption was determined and the fish were returned to the experimental chamber.

To monitor growth, wet body mass, dry body mass and protein concentrations (measured by the method of Lowry) were determined at the beginning and at the end of each experiment. The initial values were determined on samples of fish from the same group from which the experimental animals had been taken. There was no significant difference in body water and protein concentration between fish at the beginning and at the end of the experiments (Wieser and Medgyesy, 1990b). The method of sample weighing was employed for fish up to a wet body mass of about 70 mg, which were too sensitive to be subjected to the stress of weighing. In larger fish, the initial wet body mass was determined on the experimental animals themselves by lightly anaesthetising them with benzocaine (stock solution: 1 g dm⁻³ 70% ethanol, 4 ml added to 150 ml tap water) before weighing.

Assimilation efficiency was expressed as $(P+R)/C \times 100$; P , R , and C being the energy equivalents of growth, total oxygen consumption and food consumption, respectively, during a 4-day experiment. The following energy equivalents were used for the construction of energy budgets: 1 $\mu\text{mol O}_2 = 0.45 \text{ J}$; 1 mg dry body mass fish = 22.7 J; 1 mg dry body mass *Artemia* nauplii = 20 J; 1000 nauplii = 42 J (Wieser and Medgyesy, 1990a).

In each experiment the following rates were distinguished: R_{\min} , the average of the three lowest preprandial rates of oxygen consumption; R_{\max} , the average of the three highest postprandial rates of oxygen consumption; R_{rout} , the average rate of oxygen consumption during an experiment, determined by dividing the total amount of oxygen consumed by the number of experimental hours; and R_f (called FIT in previous publications), the rate of oxygen consumption connected with feeding, i.e. $R_{\text{rout}} - R_{\min}$. This definition assumes that all oxygen consumed above the preprandial minimum is connected with the uptake and conversion of food energy. In agreement with Jobling (1981, 1983, 1985), we assume that most of

R_f has to do with fuelling growth but, as will be shown below, this is not the whole story.

All metabolic rates are given in $\mu\text{mol O}_2 \text{g}^{-1} \text{h}^{-1}$, based on either wet or dry body mass.

We also determined g , the relative or specific rate of growth, calculated from $(\ln \text{dbm}_{\text{end}} - \ln \text{dbm}_{\text{begin}}) / \Delta t$ (where dbm is dry body mass), and expressed as either % per day or $\text{mg dry body mass g}^{-1} \text{h}^{-1}$, where t is time.

Statistics

Simple regressions were calculated for the relationship between metabolic or growth rate and body mass. The relationship between metabolic rate and growth rate, which are both subject to error, was defined by calculating Bartlett's best fitting lines. Differences in physiological variables between groups were estimated by means of Student's t -test.

Results

Body composition and levels of metabolic rate

In Table 1 the results of the present investigation are summarized and compared with relevant data from previous investigations. Although the pike larvae

Table 1. Basic variables (means \pm s.d.) for the construction of energy budgets in two species of freshwater fish *Coregonus lavaretus* and *Esox lucius*

| | <i>Coregonus lavaretus</i> | | <i>Esox lucius</i> | | |
|---|----------------------------|-----------------|--------------------|-----------------|----------------|
| | A | B | C | D | E |
| T ($^{\circ}\text{C}$) | 15 | 10 | 15 | 15 | 20 |
| Range of wet body mass (mg) | 7–70 | 19–83 | 8–50 | 200–1600 | 2200–3600 |
| Food | <i>Artemia</i> | <i>Artemia</i> | <i>Artemia</i> | <i>Rutilus</i> | <i>Rutilus</i> |
| N | 18 | 10 | 11 | 11 | 5 |
| Percentage water | 83.9 \pm 0.90 | 84.2 \pm 0.4 | 87.2 \pm 0.6 | 84.5 \pm 0.6 | 76.0 |
| Relative rate of growth (% per day) | 12.8 \pm 2.8 | 7.9 \pm 2.5 | 14.0 \pm 4.8 | 7.1 \pm 2.4 | 4.4 \pm 1.1 |
| Food consumption ($\text{J g}^{-1} \text{h}^{-1}$) | 74.0 \pm 11.7 | 52.1 \pm 8.4 | 66.7 \pm 12.2 | 22.1 \pm 6.4 | 22.0 \pm 3.7 |
| Rate of oxygen consumption ($\mu\text{mol g}^{-1} \text{h}^{-1}$) | | | | | |
| R_{rout} | 29.7 \pm 2.9 | 19.9 \pm 1.4 | 22.5 \pm 1.5 | 14.2 \pm 2.6 | 11.4 \pm 0.8 |
| R_{min} | 19.2 \pm 3.9 | 11.6 \pm 1.1 | 11.0 \pm 2.0 | 7.8 \pm 1.4 | 5.2 \pm 0.1 |
| R_{max} | 36.2 \pm 3.6 | 25.0 \pm 2.5 | 26.0 \pm 1.4 | 20.9 \pm 3.4 | 16.3 \pm 2.1 |
| R_f | 10.8 \pm 1.7 | 8.6 \pm 1.1 | 12.3 \pm 1.7 | 6.5 \pm 1.5 | 6.3 \pm 0.9 |
| Assimilation efficiency | 42.3 \pm 6.3 | 40.3 \pm 10.3 | 40.7 \pm 10.8 | 80.0 \pm 15.7 | 69.6 \pm 4.5 |

For explanation of symbols see Materials and methods. Data in columns A–D are from this investigation, those in column E from Wieser and Medgyesy (1991).

contained significantly more body water than the white fish larvae (columns A,C; $P < 0.001$), the water content of the two species was fairly similar up to a wet body mass of about 1.5 g (mean $85 \pm 1.5\%$). However, the water content of the larger juvenile pike described in Wieser and Medgyesy (1991) was very much lower (76%) than that of smaller fish. Protein content was significantly higher in pike than in white fish larvae and early juveniles ($60 \pm 5.5\%$ as against $44.4 \pm 2.2\%$ of dry body mass).

In fish of identical size, the routine, minimum and maximum rates of oxygen consumption were 1.3–1.7 times higher in *C. lavaretus* than in *E. lucius*. However, R_f was higher in the latter species by a factor of 1.15 (12.3 ± 1.7 as against $10.8 \pm 1.7 \mu\text{mol g}^{-1} \text{h}^{-1}$; $P = 0.0166$) (Table 1, columns A and C). The ratio of the highest to the lowest metabolic rates measured ($R_{\text{max}}/R_{\text{min}}$) ranged from 1.9 to 2.1 in *C. lavaretus* but from 2.4 to 3.1 in *E. lucius*, which may reflect the characteristic 'sit-and-wait' life style of the pike, already fully developed in the larvae.

Scaling of physiological rates

As has been pointed out before (Giguere *et al.* 1988; Rombough, 1988; Wieser, 1991), the mass-specific rates of metabolism of fish pass through a short mass-independent phase after hatching. In *C. lavaretus* and *E. lucius* this phase lasted until the larvae had reached a wet body mass of about 10 mg (from a hatching mass of 1.5–2 mg). Above 10 mg, R_{rout} at 15°C is defined by the following scaling relationships (m in mg wet body mass; R_{rout} in $\mu\text{mol O}_2 \text{g}^{-1} \text{wet body mass h}^{-1}$; Fig. 1):

$$C. \textit{lavaretus} \quad R_{\text{rout}} = 42.6(\pm 1.1)m^{-0.103(\pm 0.022)} \quad (N=16; r=0.80), \quad (1)$$

$$E. \textit{lucius} \quad R_{\text{rout}} = 38.0(\pm 1.0)m^{-0.154(\pm 0.014)} \quad (N=22; r=0.93). \quad (2)$$

Whereas R_{rout} was distinctly higher in *C. lavaretus* than in *E. lucius* over the whole size range tested, this was not true for R_f (Fig. 2). Up to a wet body mass of about 100 mg the mass-specific metabolic rate of *C. lavaretus* induced by feeding is represented by a mass-independent rate of $10.8 \pm 1.7 \mu\text{mol O}_2 \text{g}^{-1} \text{h}^{-1}$. In *E. lucius*, however, R_f decreased with body mass (m in mg wet body mass) according to:

$$R_f = 22.9(\pm 1.04)m^{-0.197(\pm 0.013)} \quad (N=22; r=0.96). \quad (3)$$

Thus, R_f was about 50% higher in a 10 mg pike larva than in a white fish larva of the same mass.

The specific rates of growth also scaled negatively with body mass (Ursin, 1979; Reiss, 1989), the inter-specific pattern resembling that of R_f (g in $\text{mg g}^{-1} \text{h}^{-1}$; m in mg):

$$C. \textit{lavaretus} \quad g = 8.02(\pm 1.22)m^{-0.133(\pm 0.05)} \quad (N=18; r=0.54), \quad (4)$$

$$E. \textit{lucius} \quad g = 12.0(\pm 1.23)m^{-0.24(\pm 0.03)} \quad (N=22; r=0.90). \quad (5)$$

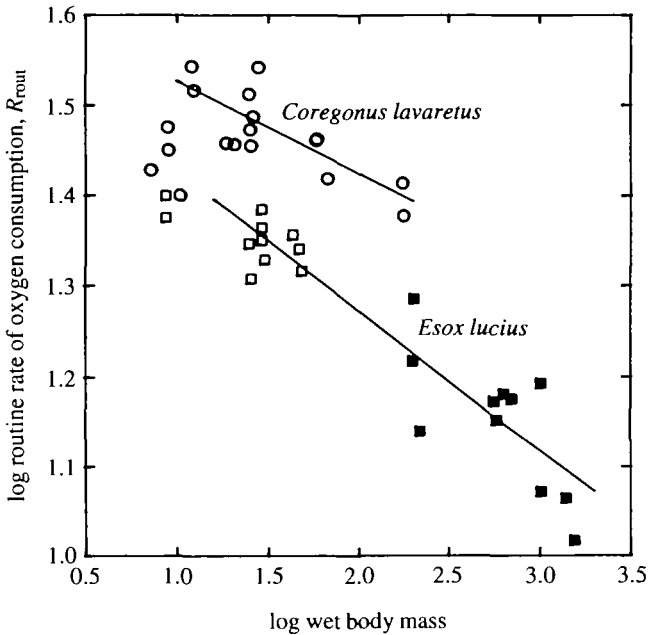


Fig. 1. Scaling of R_{rou} ($\mu\text{mol O}_2 \text{g}^{-1} \text{wet body mass h}^{-1}$) against wet body mass (mg) in *C. lavaretus* (circles) and *E. lucius* (squares). Open squares, pike fed *Artemia* nauplii; filled squares, pike fed *Rutilus rutilus* larvae. Each symbol represents one feeding experiment of 4 days duration. The values representing larvae below 10 mg wet body mass ($\log 1.0$) were not included in the calculation of the regression lines (see text).

Energy budgets

The results of the present investigation can be fitted into the balanced energy equation (Winberg, 1956):

$$CA = P + R, \quad (6)$$

where C is consumption, A is assimilation efficiency, P is growth and R is respiration.

A comparison of these results with those of previous studies (Wieser and Medgyesy, 1990b, 1991) revealed some general rules of energy partitioning in small fish. From the basic data summarized in Table 1, we extracted the values for C , P and R and converted them to the common unit, $\text{J g}^{-1} \text{dry body mass h}^{-1}$. Table 2 suggests a general pattern of energy partitioning for a wide range of experimental conditions, such as species used (*C. lavaretus* and *E. lucius*), prey (*Artemia* and *R. rutilus*), experimental temperature (10–20°C) and body size (7–3600 mg). Although *E. lucius* allocated a larger proportion of energy to somatic production than did *C. lavaretus*, the difference was small. Across all experimental groups $62 \pm 3.7\%$ of energy was allocated to P and $38 \pm 3.7\%$ to R .

Table 1 (columns D,E) also shows that the reduced consumption rates of the larger pike feeding on *R. rutilus* were partly offset by high assimilation efficiencies

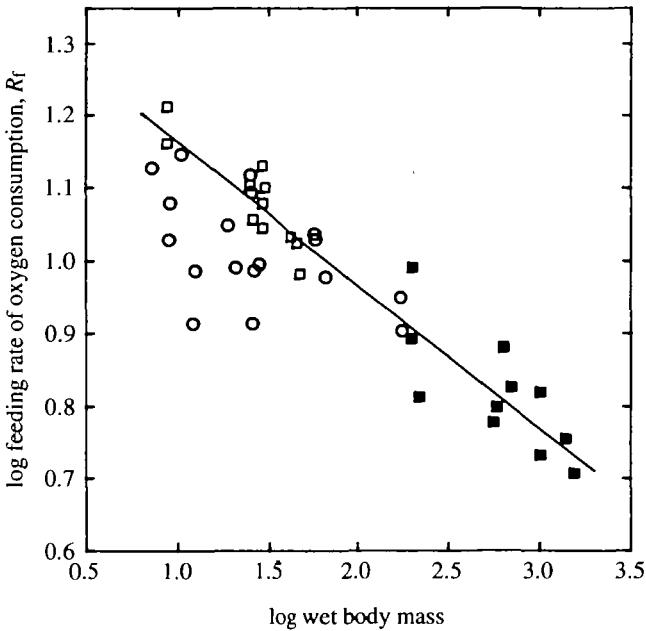


Fig. 2. Scaling of R_f in *C. lavaretus* and *E. lucius*. Symbols as in Fig. 1. A regression line was calculated through all the data for *E. lucius*, but the scatter of the values representing *C. lavaretus* prevented such a calculation (see text).

and that the Q_{10} values of physiological variables in the larvae of *C. lavaretus* feeding on *Artemia* (columns A,B) ranged from 1.6 to 2.7.

Yield and cost of growth

Instead of plotting R_f (=FIT) against relative growth rate as in our previous publications (Wieser and Medgyesy, 1990a,b, 1991) we have chosen this time to plot g (mg dry body mass $g^{-1} h^{-1}$) against the total energy consumed during the feeding experiments, represented by R_{rout} ($\mu\text{mol O}_2 g^{-1} \text{dry body mass h}^{-1}$). This is the inverse of the procedure advocated by Smith (1957), who considered the intensity of R_{rout} to be determined by specific growth rate (g) and maintenance rate, according to

$$R_{rout} = a + bg, \quad (7)$$

where a and b are constants. Our approach results in a 'yield ratio' with the dimension $\text{mg dry body mass } \mu\text{mol}^{-1} \text{O}_2$, the inverse of the net cost of growth, but comparable to the yield ratios customarily employed by microbiologists. The usefulness of this ratio will become apparent in the Discussion.

Fig. 3 combines the data of the present investigation with previous data on *C. lavaretus* (*C. wartmanni* in Wieser and Medgyesy, 1990b), thus including an experiment with reduced rations. By distinguishing between two sets of experiments according to the type of prey used it can be shown that the relationship

Table 2. Allocation of ingested (C) and metabolizable (P+R) food energy to growth and respiration in five experimental groups of freshwater fish

| | <i>Coregonus lavaretus</i> | | <i>Esox lucius</i> | | |
|--|----------------------------|----------------|--------------------|----------------|----------------|
| | A | B | C | D | E |
| T (°C) | 15 | 10 | 15 | 15 | 20 |
| Range of wet body mass (mg) | 7-70 | 19-83 | 8-50 | 200-1600 | 2200-3600 |
| Food | <i>Artemia</i> | <i>Artemia</i> | <i>Artemia</i> | <i>Rutilus</i> | <i>Rutilus</i> |
| N | 18 | 10 | 11 | 11 | 5 |
| Energy flux (J g ⁻¹ dry body mass h ⁻¹) | | | | | |
| C | 462±77 | 330±53 | 521±95 | 143±41 | 92±15 |
| P | 123±27 | 76±24 | 134±46 | 68±23 | 42±10 |
| R | 83±8.0 | 57±4.0 | 79±5.2 | 41±7.5 | 21±1.5 |
| Allocation (%) | | | | | |
| P | 60 | 57 | 63 | 62 | 67 |
| R | 40 | 43 | 37 | 38 | 33 |

Means±s.d. shown.
Relative allocation to P and R is based on P+R=100%.
For more data on groups see Table 1.
C, consumption; P, growth; R, respiration.

between g and R_{rout} (x) is defined by the following equations (based on Bartlett's best fitting lines):

Artemia as prey

$$g = 0.045(\pm 0.005)x - 2.83(\pm 0.94) \quad (N=42; r=0.82), \quad (8)$$

Rutilus as prey

$$g = 0.041(\pm 0.012)x - 0.82(\pm 0.72) \quad (N=11; r=0.74). \quad (9)$$

The *Artemia* experiments were carried out with larvae of *E. lucius* and *C. lavaretus*, ranging in size from 7 to 83 mg wet body mass, whereas the *Rutilus* experiments were with *E. lucius* only, ranging from 200 to 1600 mg wet body mass (Table 1). The slopes of the two lines are identical but the coefficients are significantly different ($P < 0.001$). This means that, irrespective of the experimental conditions (i.e. species, prey type and temperature) the yield ratio amounted to approximately 0.043 mg dry body mass $\mu\text{mol}^{-1} \text{O}_2$. By extrapolating the best fitting lines to $g=0$, a value of R_{rout} is obtained that corresponds to the maintenance level of classic nutrition physiology. These levels were 62.9 and 20 $\mu\text{mol g}^{-1}$ dry body mass h^{-1} for the *Artemia* and *Rutilus* experiments, respectively, which, on the basis of the average water content of 85% (Table 1), convert to 9.5 and 3 $\mu\text{mol g}^{-1}$ wet body mass h^{-1} .

However, this generalisation has to be qualified in one important respect: in calculating the best fitting lines through the data of the *Artemia* experiments, the

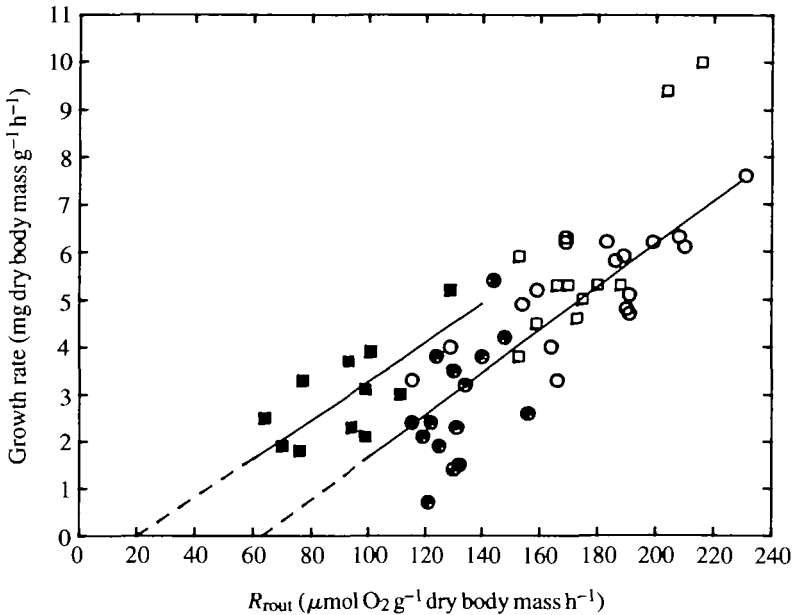


Fig. 3. Growth rate plotted against R_{rouit} in *C. lavaretus* (circles) and *E. lucius* (squares). Different experimental groups are represented by different symbols. Filled squares, pike fed *R. rutilus* larvae; open symbols, *C. lavaretus* and *E. lucius* fed *Artemia* nauplii; dotted circles, *C. lavaretus* at 10°C (all other experiments at 15°C); crossed circles, *C. lavaretus* on reduced rations. See Tables 1 and 3 for more details. Bartlett's best fitting lines were calculated for the experiments with *R. rutilus* larvae and for the experiments with *Artemia* nauplii as prey. However, the two experiments with the highest growth rates (open squares) were not included in the calculation (see text).

two experiments with the smallest pike larvae (1.01 mg) were excluded. The specific growth rates of these fish were nearly twice as high (9.4 and $10 \text{ mg g}^{-1} \text{ h}^{-1}$) as those of the next largest fish, whereas R_{rouit} was in the range of the highest values recorded in other experiments (Fig. 3). Since two samples are not sufficient to determine the shape of the curve in the upper range, we take these samples as merely suggesting that in *E. lucius* R_{rouit} may reach an aerobic maximum at about $200\text{--}220 \mu\text{mol O}_2 \text{ g}^{-1} \text{ dry body mass h}^{-1}$. In our previous investigations, an aerobic maximum for growth has been defined with regard to R_f only (Wieser and Medgyesy, 1990a,b).

By using the scaling exponents given in equations 1–5 as well as that of a low-ration group of *C. lavaretus* studied previously (Wieser and Medgyesy, 1990b), we have also calculated R_{rouit} , g and the cost of growth, for two standard fish weighing 10 and 100 mg dry body mass. The values summarized in Table 3 allow the following conclusions. (1) When comparing groups of similar ranges of body mass subjected to identical experimental conditions (groups A and D), the cost of growth was found to be lower in *E. lucius* than in *C. lavaretus*, savings ranging

Table 3. Gross cost of growth based on energy allocation to metabolic expenditures (R_{rout}) and growth (g) in five experimental groups of two species of freshwater fish

| | <i>Coregonus lavaretus</i> | | <i>Esox lucius</i> | | |
|--|----------------------------|----------------------|----------------------|----------------------|----------------|
| | A | B | C | D | E |
| T ($^{\circ}\text{C}$) | 15 | 10 | 15 | 15 | 15 |
| Range of dry body mass (mg) | 1.13–11.3 | 3.0–13 | 7.7–20 | 1.0–6.4 | 31–248 |
| Food | <i>Artemia</i> (sat) | <i>Artemia</i> (sat) | <i>Artemia</i> (low) | <i>Artemia</i> (sat) | <i>Rutilus</i> |
| N | 18 | 10 | 5 | 11 | 11 |
| R_{rout} ($\mu\text{mol h}^{-1}$) | | | | | |
| 10 mg | 2.13 | 1.48 | 1.64 | 2.08 | 1.72 |
| 100 mg | 16.18 | 12.20 | 12.70 | 14.60 | 12.00 |
| g (mg h^{-1}) | | | | | |
| 10 mg | 0.059 | 0.033 | 0.016 | 0.069 | 0.069 |
| 100 mg | 0.43 | 0.33 | 0.16 | 0.40 | 0.40 |
| Cost ($\mu\text{mol mg}^{-1}$) | | | | | |
| 10 mg | 36.1 | 34.4 | 71.0 | 30.1 | 24.9 |
| 100 mg | 39.1 | 47.0 | 85.4 | 36.5 | 30.0 |

Column C contains data from a group of *C. lavaretus* fed reduced rations (low) of *Artemia* nauplii (Wieser and Medgyesy, 1990b). Rations of all other groups were *ad libitum* (sat).

The listed values are based on the scaling relationships for R_{rout} and g given in the text and have been calculated for two standard fish weighing 10 and 100 mg dry body mass, respectively. All values refer to dry body mass of fish.

from 17 to 7% in standard fish weighing 10 and 100 mg, respectively. (2) The cost of growth was lower by 17–18% in the larger fish-fed pike than in the smaller *Artemia*-fed pike. (3) Between 10 and 15°C the cost of growth was more or less independent of experimental temperature in *C. lavaretus*. (4) In the experiments with reduced rations the lower growth rate was not accompanied by an equivalent reduction in total oxygen consumption, leading to exaggerated gross costs of growth. This is due to the increased swimming activity of small fish maintained on low rations, a phenomenon observed previously (Wieser *et al.* 1988). According to the rules of classic nutrition physiology, a proportional decrease in growth rate and metabolic rate would have been expected under these circumstances (Wieser, 1991).

Discussion

A recent subject of discussion has been whether in small poikilothermic animals the allocation of metabolic energy follows the rules of *addition* or of *compensation* (Wieser, 1989, 1991; Rombough, 1992). As far as the metabolic costs of growth

and production are concerned, the classic approach consists of determining the relationship between growth and oxygen consumption following ingestion of food in excess of the maintenance ration (Brody, 1945; Jobling, 1985). The amount of oxygen consumed after ingestion of a meal has been called the specific dynamic action (SDH: Rubner, 1902), diet-induced thermogenesis (DIT: Rothwell and Stock, 1989), feeding-induced thermogenesis (FIT: Wieser and Medgyesy, 1990a) or simply – as in the present paper – oxygen uptake rates associated with feeding (R_f : Jobling, 1985). Despite the difficulty of defining a maintenance level in most poikilothermic animals, a proportional relationship between metabolic intensity above maintenance (R_f) and growth rate (g) has been reported in several studies with fish (Hogendoorn, 1983; Jobling, 1981, 1985). However, in the larvae and small juveniles of several species of freshwater fish R_f was found to become independent of g above a critical threshold (Wieser and Medgyesy, 1990a,b).

If the metabolic potential above what in this investigation has been called R_{\min} (the lowest preprandial rate) is not sufficient to fuel the rates of growth observed, the most likely explanation is that R_{\min} contains components of energy expenditure that can be replaced by some of the costs of fast growth. This is supported by the finding that extrapolation of the best fitting lines for *Artemia*-fed fish to zero growth resulted in a metabolic rate of $9.5 \mu\text{mol O}_2 \text{g}^{-1} \text{wet body mass h}^{-1}$, which is only half the minimum metabolic rate actually measured in *C. lavaretus* (Table 1). In *E. lucius* the difference between the extrapolated and the empirical maintenance level is much smaller (9.5 as against $11.0 \mu\text{mol g}^{-1} \text{h}^{-1}$), underscoring the conclusion that, in this species, as a result of its larger scope for growth, compensatory measures of energy allocation may have come into play only at the highest growth rates. Growth rates as high as 22–24 % per day were measured in the two experiments with the smallest pike larvae (8.7 mg wet body mass), practically the same relative growth rates as those observed in pike larvae growing in small ponds at 15°C (Bry *et al.* 1991).

Whilst there can be no doubt that compensatory strategies of energy allocation do occur in the larvae of fish, the question remains whether these strategies affect only a fraction or all of the energy budget. Total lack of correlation between growth rate and oxygen consumption has recently been described in the embryos and yolk larvae of chinook salmon, *Oncorhynchus tshawytscha*, by Rombough (1992). This has also been claimed for the nematode species *Caenorhabditis briggsae* and for the feeding larvae of *Rutilus rutilus* by Wieser (1989). However, in the latter species oxygen consumption and growth were not measured simultaneously. The results of the present investigation in combination with those of a previous study (Wieser and Medgyesy, 1990b) provide only marginal support for the occurrence of compensatory strategies in the larvae and young juveniles of *C. lavaretus* and *E. lucius* if the total metabolic rate, R_{total} , is taken into account. There is a hint that in *E. lucius* a metabolic ceiling is reached at growth rates of $6\text{--}7 \text{ mg dry body mass g}^{-1} \text{h}^{-1}$ (=14–17 % per day), but this suggestion is based on two 4-day experiments only (Fig. 3).

The net yield ratio of about $43 \mu\text{g dry body mass } \mu\text{mol}^{-1} \text{O}_2$ was calculated on the

basis of best fitting lines through 43 samples, each representing a 4-day experiment. This figure is, therefore, a fairly robust statement about the efficiency or net cost of somatic production in these small metazoans, usually defined by:

$$R_f = rP, \quad (11)$$

where r is the energy cost per unit growth (Jobling, 1985).

Another way of comparing the use of metabolic energy is by calculating partitioning into somatic production (P) and metabolic expenditure (R). As summarized in Table 2, *E. lucius* allocated slightly more energy into P than did *C. lavaretus* (62–67 % as against 57–60 %) but across all the experimental groups studied about 62 % of metabolizable energy was allocated to P and 38 % to R . This may be compared with the generalized energy budget for larger fish constructed by Brett and Groves (1979), in which the allocation of metabolizable energy to growth and respiration was almost exactly the opposite of our results for the larvae and young juveniles, about 40 % being allocated to P and about 60 % to R (see also Brafield, 1985).

The metabolic cost of production has been intensively studied in microorganisms and is usually expressed as the yield per ATP (Y_{ATP}), i.e. grams dry microbial mass per mole of ATP. According to Stouthamer (1973) the theoretical $Y_{\text{ATP,max}}$ is about 32 g dry body mass mol^{-1} ATP, provided that all the monomers for the synthesis of macromolecules are supplied externally. However, the yield found empirically is only about one-third of the theoretical maximum, and this discrepancy has been the subject of numerous investigations by microbiologists (Stouthamer, 1979; Tempest and Neijssel, 1984).

Since protein synthesis accounts for about 75 % of the total cost of synthesis in microbial cells, and since the protein content of these cells is, on average, 50–60 % of the dry mass, the values for microorganisms can be directly compared with those for the fish larvae in which the average protein content was 55 % of dry body mass.

A net yield of 43 μg dry body mass μmol^{-1} O_2 calculated for the data assembled in Fig. 3 converts to about 7 g dry body mass mol^{-1} ATP (assuming 1 mol $\text{O}_2 = 6$ mol ATP), which is approximately 70 % of the average empirical yield in microorganisms (Stouthamer and Bettenhausen, 1973). The similarity of these values is, perhaps, not particularly surprising since it has been shown on several occasions that the cost of producing 1 g of organism is the same irrespective of the latter's systematic position (Wieser, 1985). However, the fact that the *empirical* cost of growth is 3–4 times higher than the *theoretical* cost, in microorganisms as well as in metazoans, should puzzle zoologists as much as it has been puzzling microbiologists for some time (Stouthamer 1973, 1979).

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Note added in proof

In a recent publication Kamler *et al.* (1992) reported net conversion efficiencies (K_2) of 55–80 % in carp larvae fed zooplankton and different types of formulated diets.

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