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REVIEW ARTICLE

Energetics of fish larvae, the smallest vertebrates

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In this review recent findings on the energetics of fish larvae are presented, highlighting some of the physiological problems linked to small body size. The existence of a mass-independent phase of specific metabolic rate is confirmed but it is pointed out that in young fish ontogenetic transitions of metabolic scaling have so far been documented only for the routine level of activity. Maximum metabolic rate is limited by mitochondrial density in the swimming muscles which scales with a mass exponent of ~ 0.9. Mitochondrial density in the swimming muscles of a species of fish, from larva to adult, covers about the same range as mitochondrial density in the skeletal muscles of mammals. However, the aerobic capacity (power density) of mitochondria is one order of magnitude lower in fish than in mammals. Energy metabolism in embryos and early larvae of fish is almost entirely aerobic. Anaerobic power in the fast muscle fibres is low after hatching but increases during the transition from larva to juvenile with a mass exponent greater than one. In hypoxic water fish larvae swim more economically (i.e. their cost of transport is lower) than in normoxic water. If the rate of growth exceeds a critical threshold (about 10% d^{-1}) fish larvae are capable of increasing the apparent efficiency of growth, probably by reducing the costs of other energy-consuming functions of maintenance.

Keywords: aerobic and anaerobic energy metabolism, compensatory strategies of metabolism, growth, metabolic scaling, mitochondrial density and capacity, muscle development, temperature, oxygen content, oxygen debt.

The larvae of fish are the smallest self-supporting, actively feeding vertebrates. The larvae of turbot (*Scophthalmus maximus*) or northern anchovy (*Engraulis mordax*) hatch at body lengths of 2–3 mm and weigh as little as 0.5 mg wet body mass (wbm). Within a few days, after resorption of their yolk sac, they begin to feed actively on small zooplankton (Blaxter 1988). As these animals represent a miniaturized version of the vertebrate Bauplan it may be asked to what extent miniaturization has affected bodily functions, which so far, have been studied only in much larger representatives of this phylum (Burggren & Pinder 1991).

The following review aims to present and discuss recent findings on the energetics of fish larvae that highlight some of the physiological problems linked to small body size. They also illustrate the importance of the comparative approach in physiology and may allow the perception of old physiological problems in a new light.

METABOLIC SCALING

The relationship between metabolic rate (R) and body mass (M) is of the form $R = aM^b$, 'a' representing the metabolic intensity and 'b' the

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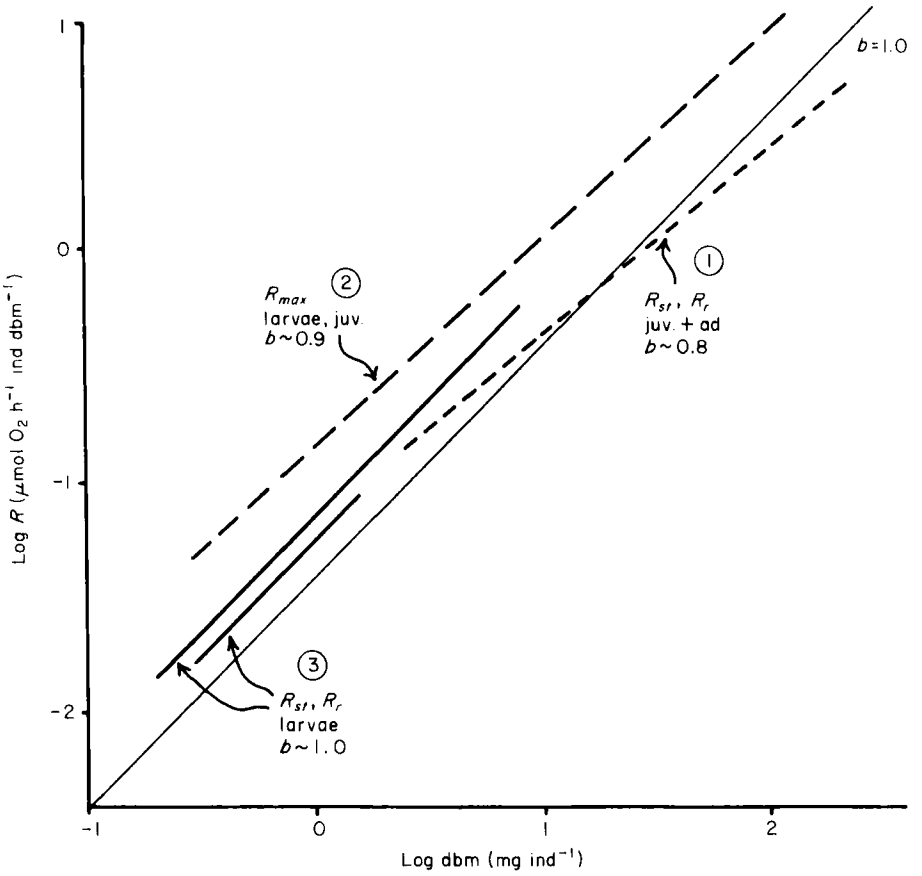

Fig. 1. Relationship between log metabolic rate (R) and log dry body mass (dbm) at different developmental stages (larvae, juveniles, adults) and different levels of activity in fish (R_{st} = standard, R_r = routine, R_{max} = maximum activity). The circled numbers refer to the three types of scaling pattern discussed in the text. The regression lines shown are generalizations based on the data of Table 1 and, for adults, on the data compiled by Winberg (1956) and other authors cited in the text. The isometric line with a mass exponent of $b = 1.0$ is also shown.

mass exponent of the group of animals compared. In interspecific comparisons, the exponent b of adult fish resting or swimming in the routine mode is usually assumed to be close to 0.8 (Winberg 1956), whereas for the basal rates of mammals a value of 0.75 is more often quoted (Kleiber 1961, Wieser 1986). However, the scaling exponent of the relationship between metabolic rate and body mass is not a constant (Wieser 1984, Feldman 1995). For example, in many, and probably in most, animals an ontogenetic sequence can be distinguished, in which early phases of development are characterized by values close to unity and later phases are characterized by values closer to Rubner's surface rule, i.e. 0.67. This is true for mammals (Brody 1945, Wieser 1984, 1986) but has recently also been documented in fish (Giguère *et al.* 1988, Rombough 1988, Kamler 1992, Finn 1994). Why this should be so is not entirely clear but it is reasonable to assume that during the early phase of free-living existence the power requirements for locomotion, growth and other physiological functions, are so high that there has been strong selection pressure for the maximization of mass-specific energy expenditure in growing animals. This implied overriding the constraints of the surface rule by maintaining or even increasing the mass-specific aerobic capacity of metabolically active tissues.

A review of the extensive literature on the scaling of metabolic rate in fish leads to a tentative generalization illustrated in Fig. 1 which may be summarized as follows.

Table 1. Examples used for the construction of Fig. 1 illustrating the scaling of *metabolic rate in young fish*. R = rate of oxygen consumption in μmol h^{-1} ind^{-1}; M = dry body mass in g. R_{st} = standard rate, R_r = routine rate; R_{max} = rate at maximum activity. All values have been recalculated for a temperature of 10°C by using a Q_{10}-value of 2.5 (Finn 1994). The data on roach (*Rutilus rutilus*) are from Kaufmann (1990) (A) and Wieser & Medgyesy (1990a) (B), on Danube bleak (*Chalcalburnus chalcoides*) from Kaufmann (1990), and on Atlantic halibut (*Hippoglossus hippoglossus*) from Finn (1994)

Species	Weight range (mg dbm)	Activity level	Scaling relationship
Roach (A)	0.3–1	R_{st}	$49\ M^{0.96}$
	1–56		$18\ M^{0.77}$
	0.1–56	R_{max}	$62\ M^{0.84}$
Roach (B)	1–140	R_r	$17\ M^{0.79}$
Danube bleak	0.3–1.6	R_{st}	$63\ M^{1.05}$
	1.6–114		$17\ M^{0.78}$
		R_{max}	$80\ M^{0.87}$
Atlantic halibut	0.2–8	R_r	$72\ M^{1.08}$

(1) The metabolic rate of standard (R_{st}) and routine (R_r) swimming activity in juveniles and adults appears to scale with an exponent of ~ 0.8 (Winberg 1956, Brett 1964, 1965, Beamish 1978).

(2) There is a tendency for the rate of activity metabolism (R_a or R_{max}) to scale with a higher mass exponent, usually around 0.9 (Brett 1965, Brett & Glass 1973, Brett & Groves 1979).

(3) A scaling exponent of about 1.0, i.e. mass-independence of the specific rate of metabolism, has been documented for the larvae of many – but by no means all – species of fish after hatching.

With respect to the last point the data assembled by Rombough (1988), Giguère *et al.* (1988) and Finn (1994) indicate that so far isometric scaling of metabolic rate has been documented almost exclusively for R_r. With the exception of one single study dealing with two cyprinid species (Kaufmann 1990), R_{st} and R_{max} have not been determined with sufficient precision and reliability in the larvae of any species of fish. The study by Kaufmann together with that by Wieser & Medgyesy (1990a) suggests the following refinement of the concept of metabolic scaling in fish larvae: isometric scaling is characteristic of R_{st} and R_r (No. 3 in Fig. 1) and it is in this respect that the larvae differ most clearly from juveniles and adults in which a scaling exponent of $b \approx 0.8$ appears to be the rule (No.1 in Fig. 1). The metabolic rate of larvae swimming at maximum velocity (R_{Umax}) scales with the same mass exponent as R_{max} of juveniles and adults, i.e. with $b \approx 0.9$ (No. 2 in Fig. 1, based on relationships summarized in Table 1). It should also be noted that the isometric phase may be of different duration in the larvae of different species, up to 8 mg dry body mass (dbm) in the marine species studied by Finn (1994), but only up to a body weight of 1.6 mg dbm in the two species studied by Kaufmann (1990).

Thus species specific differences and the confounding effect of swimming velocity on the mass exponent may be partly responsible for the large variability of the scaling exponent in fish larvae, commented upon by Rombough (1988) and Finn (1994).

COST OF SWIMMING AND EXERCISE: MATCHING SUPPLY AND DEMAND

The development of anaerobic power and aerobic capacity

As a result of their small size the larvae of fish are characterized by a large surface area to volume ratio. This is one of the reasons why after hatching the surface of the body, including yolk sac, serves as the major respiratory organ (Oikawa & Itazawa 1985, Rombough 1988). Before metamorphosis oxygen reaches the swimming muscles entirely by diffusion since neither the gills nor the blood capillaries in the musculature are yet differentiated (Rombough 1988, Wells & Pinder 1995). The absence of gills seems to be because of hydrodynamic constraints preventing effective oxygen diffusion in the buccal cavity of early larvae (Osse 1989). However, diffusion across the skin to the underlying tissues is an efficient process since several lines of evidence support the notion that energy metabolism is almost entirely aerobic both in embryos and in early larvae of fish. The capacity for anaerobic glycolysis develops gradually after termination of the yolk sac stage. For example, very little lactate is produced in embryos and yolk sac

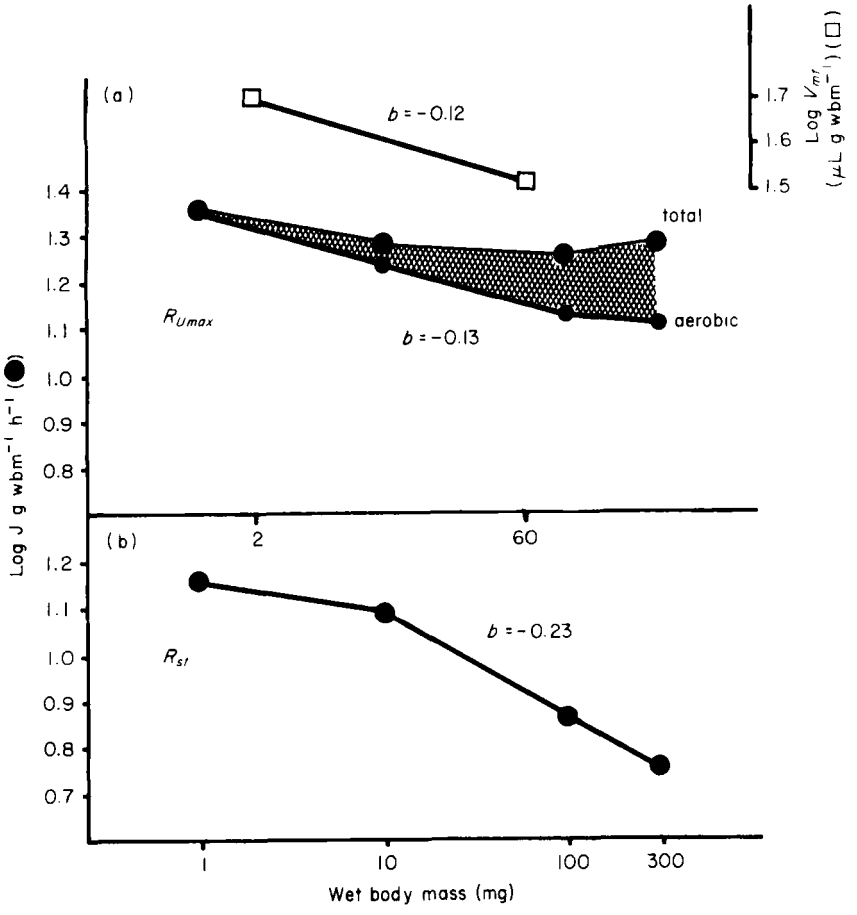

Fig. 2 Relationship between log mass-specific rate of energy expenditure (oxygen equivalent: 0.45 J μmol O_2^{-1}) and log wet body mass in larvae and young juveniles of roach (Rutilus rutilus), based on the data compiled by Kaufmann (1990) (●). (a) R_{st} = standard rate at zero swimming speed. (a) R_{Umax} = metabolic cost of swimming at maximum speed, i.e. $R_{total} - R_{st}$. A distinction is made between aerobic and total energy expenditure, the latter calculated by adding the energy equivalent of the oxygen debt (cross-hatched areas) to the measured rate of oxygen consumption. Also shown is the mass relationship of log mitochondrial density ($V_{(mt)}$:■) in the swimming muscles of larvae weighing 2 and 60 mg, respectively (Stoiber 1991).

larvae of marine fish (Finn 1994), the activities of glycolytic enzymes are very low in early larvae of freshwater fish (El-Fiky *et al.* 1987, Hinterleitner *et al.* 1987), and a very small oxygen debt is incurred even at the highest swimming velocities (Kaufmann 1990). However, a few exceptions have been noted. A peak of lactate production at the beginning of gastrulation was observed in Atlantic cod, but not in turbot and halibut (Finn 1994), and the embryos of rainbow trout and Arctic charr were shown to tolerate periods of anoxia (Devillers & Rosenberg 1953, Gnaiger *et al.* 1981). Thus, we are confronted, not unexpectedly, with species differences which should stimulate the search for comparative patterns and mechanisms. On the other hand, a quantitative estimate of the development of anaerobic power together with that of maximum aerobic capacity in anoxia-intolerant species provides further insight into the ontogeny of energy metabolism in fish larvae (Fig. 2).

As mentioned above, R_{umax}(i.e. the aerobic rate of fish swimming at maximum velocity) scales with an exponent of about 0.9. In the larvae of two cyprinid species, *R. rutilus* and *C. chalcoides*, values for the exponent between 0.84

Table 2. Parameters for the calculation of respiratory capacity of mitochondria (mito) in *Rutilus rutilus* at 20 °C. Mitochondrial density in muscle and R_{max} of fish are referred to g wet body mass (wbm): r = red, w = white muscle. R_{max}fish: μmol O_2 g^{-1} h^{-1}; R_{max}mito: μmol O_2 μL(mito)$^{-1}$ h^{-1}. Data from Koch and Wieser (1983), Kaufmann (1990), Wieser and Medgyesy (1990), Stoiber (1991), Sänger *et al.* (1991)

Age	wbm	Muscle mass % (wbm) r	w	volume (μL) r	w	Mito density (μL g^{-1})	R_{max} fish	R_{max} mito
5 d	2 mg	6	44	0.05	0.05	50	83	1.66
50 d	60 mg	7.5	42	1.35	0.65	33	48.6	1.47
1 yr	10 g	3.5	45	87.5	45.0	15	22	1.47

and 0.87 were found (Table 1), corresponding to values between -0.16 and -0.13 for the mass-specific rate. Since at maximum swimming speed the muscles use about 95% of the total oxygen inspired (Randall & Daxboeck 1982, Videler 1992) R_{max} of the fish reflects the aerobic capacity of the swimming muscles. This relationship is corroborated by the observation that mitochondrial volume density in this tissue also scales with a mass-specific exponent of about -0.1 (Stoiber 1991), supporting the further hypothesis that the flow of oxygen to the muscles is not limited by diffusion resistance. However, this can be true only for fast-swimming fish in which the surface layer is rapidly renewed by turbulent flow. Combining the data of Koch & Wieser (1983), Kaufmann (1990), Sänger *et al.* (1990), and Stoiber (1991), the volume-specific maximum power of the mitochondria of *R. rutilus* can be estimated for larger specimens as well (Table 2). By extrapolating the mass-specific relationship of R_{max} given by Kaufmann, a 10-g fish swimming with maximum velocity at 20 °C would consume oxygen at a rate of 22 μmol g^{-1} h^{-1} which is 3.5 times the routine rate measured by Koch & Wieser (1983), a plausible factorial scope for this size class. As summarized in Table 2 the volume-specific maximum power of the mitochondria of *R. rutilus* decreased slightly as the larvae grew from 2 to 60 mg, but remained constant up to a body weight of at least 10 g. Since above a body weight of about 60 mg the gills are already well developed and have replaced the skin as the major respiratory organ, the high scaling exponent of mass-specific R_{max} and mass-specific $V_{(mt)}$also suggests that oxygen supply to the tissues is limited by mitochondrial capacity rather than by the respiratory area of the gills, as surmised by Pauly (1981) and others.

The careful analysis of Kaufmann (1990) allows consideration of the oxygen debt incurred by the larvae swimming at maximum velocity. Expressing this debt in units of oxygen consumed and adding it to the maximum aerobic rate of metabolism results in a nearly mass-independent rate of total energy expenditure. This indicates that the mass-specific capacity for anaerobic glycolysis in the swimming muscles scales with approximately the same exponent, although positive (i.e. $b \approx +0.13$), as the mass-specific rate of aerobic metabolism ($b \approx -0.13$; see Fig. 2). The near mass-independence of anaerobic power appears to be a characteristic feature of the energy metabolism of vertebrates in general (Somero & Childress 1980, Emmett & Hochachka 1981, Wieser 1986). In the larvae of *R. rutilus* the increase in anaerobic power with age is reflected in the decreasing aerobic capacity of the central muscle mass, which, at later stages of development, consists almost entirely of fast glycolytic fibres. In the youngest (5-d-old) larvae weighing 2 mg this central muscle mass represents 88% of the swimming muscles and has a mitochondrial volume density (μL mito. μL muscle^{-1}) of 5.7% (red muscle fibres: 42%). Sixty days after hatching the volume density of mitochondria in the central muscle mass has dropped to 2.6%, and in a 10-g juvenile it amounts to as little as 1% (Table 2; ratios calculated on the basis of values given in columns 3 and 4).

Mitochondrial capacity: a comparative point of view

The maximum rate of oxygen consumption of an organism is determined by the maximum rate at which oxygen can be reduced in the mitochondria. Differences in maximum aerobic rate may occur as a result of: (1) differences in mitochondrial density in the major ATP-consuming tissues, or (2) differences in the capacity (power density) of individual mitochondria. In mammals it has been shown that mitochondrial capacity, expressed as μmol O_2 μL(mito)$^{-1}$ h^{-1}, remains more or less constant so that differences

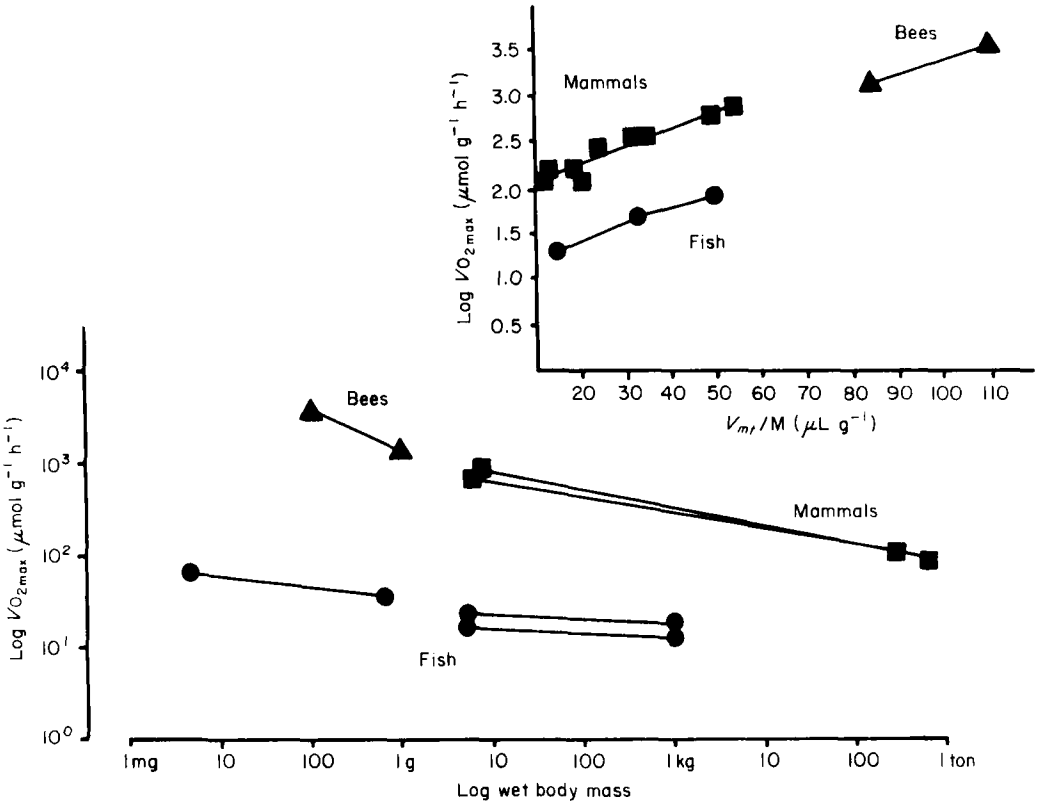

Fig. 3 Comparison of whole body mass-specific rate of oxygen consumption at maximum activity and of mitochondrial aerobic capacity in the locomotor muscles of three groups of animals. Two sets of experiments are presented for $\dot{V}o_{2max}$of mammals, three sets for $\dot{V}o_{2max}$ of fish. Mitochondrial aerobic capacity (equal to power density) as presented in the inset is the ratio of $\dot{V}o_{2max}$ over volume density, with the dimension μmol O_2 μL(mito)$^{-1}$ h^{-1}. Data on mammals from Hoppeler (1990) and Hoppeler & Turner (1989); data on bees from Casey & Ellington (1989); data on fish from Tables 1 and 2.

in R_{max} must result almost entirely from differences in mitochondrial density (Schwerzmann *et al.* 1989, Hoppeler 1990). In the muscles of the species investigated by Hoppeler & Turner (1989), from woodmouse to cattle, mitochondrial density ranged from about 10–50 μL g(wbm)$^{-1}$.

How do representatives of other taxa compare with this relationship? In addition to mammals reliable data on $V_{(mt)}$ and R_{max} are available for bumble-bees (Casey & Ellington 1989) and fish (Table 2). The information summarized in Fig. 3 allows the following conclusions.

(1) The volume density of mitochondria in the swimming muscles of *R. rutilus* during development covers about the same range as the volume density of mitochondria in the skeletal muscles of the mammalian species listed by Hoppeler & Turner (1989). $V_{(mt)}$ of the smallest larvae weighing 2 mg corresponds to that of the smallest mammals weighing 10 g (about 50 μL g^{-1}), whereas adult *R. rutilus* have the same mitochondrial density as horse and steer, the largest mammals investigated (about 10 μL g^{-1}). However, since mass-independent R_{max} of the fish is approximately one order of magnitude lower than that of the mammals, mitochondrial aerobic capacity is also lower by about this factor, i.e. 1.5–1.7 as against 9.3–13.3 μmol O_2 μL^{-1} h^{-1}. (In Fig. 3 the $\dot{V}o_{2max}$ data were transformed logarithmically so as to allow a better comparison between the three groups of animals with their wide range of metabolic intensities. However, in the nine species of mammals a linear regression model describes the relationship between $\dot{V}o_{2max}$ and

$V_{(mt)}$ just as well as the semilogarithmic model used here. Thus, as already pointed out by Hoppeler & Turner (1989), a truly proportional relationship exists between the two variables of interest.

(2) The rate of oxygen consumption of the larger of the two bumble-bee species investigated by Casey & Ellington (1989) was only slightly higher than that of a mammal of the same mass (1 g) would be, whereas the metabolic intensity of the smaller bee species (0.1 g) was higher than that of a hypothetical mammalian equivalent by about 80%. Since the flight muscles of bees occupy a smaller volume of the body than the active swimming muscles of fish or the active running muscles of mammals at maximum effort, a higher mitochondrial volume density is required to meet the extraordinary demand on active metabolism in flying as compared with running or swimming animals. In a bee weighing 100 mg, mitochondrial density in the flight muscles was about twice the highest density observed in the skeletal muscles of small mammals or fish larvae (inset Fig. 3).

The high metabolic intensity of the smaller of the two bumble-bee species studied by Casey & Ellington (1989) indicates that the principle of mass-independent mitochondrial capacity which Hoppeler and coworkers have shown to hold for mammals does not necessarily apply to other taxa. The structural features responsible for the extraordinarily high power density of mitochondria in the flight muscles of small bumblebees (about four times the power density of the smallest mammals studied) are unknown.

Ecological constraints and phenotypic flexibility

All components of energy budgets and metabolism are influenced by environmental factors. One would expect this to be particularly true for small animals with their high basal energy expenditures and, in consequence, low metabolic scopes (Wieser 1991). On the one hand, environmental factors may constrain the responses of animals, on the other hand, these constraints may activate defence mechanisms designed to preserve certain phenotypic properties of the animals in question (Hochachka 1988).

It would be of interest to learn the extent to which small animals and early ontogenetic stages differ in their phenotypic responses to environmental disturbance from large animals and late ontogenetic stages. Because of the paucity of relevant information available I have to restrict myself to a few comments on the effects of water temperature and oxygen content on the energetics and performance of fish larvae.

Table 3. Swimming performance of larvae of *Chalcalburnus chalcoides* reared at 20°C after acute exposure to 15°C. Values shown indicate relative change of performance at 15°C as compared to performance at the acclimation temperature of 20°C. Data from Kaufmann & Wieser (1992)

Performance function	Lower by (%)	Higher by (%)
Critical speed	30	–
Scope for activity	20	–
Speed exponent (b)	–	22
Oxygen debt	–	30
Cost of transport	–	32

Temperature. Temperature is an environmental factor which interacts with most structural and functional components of an organism, and this is the reason why responses of the whole system are complex and difficult to analyse (Koch *et al.* 1992). For example, the critical levels of swimming velocity display a bell-shaped relationship to temperature although viscosity and oxygen content, two important temperature-related factors in the aquatic environment, decrease proportionally with increasing temperature (Randall & Brauner 1991). An enquiry into the relationship between temperature and the energetics of swimming in the larvae of the cyprinid species, *Chalcalburnus chalcoides* (Danube bleak) by Kaufmann & Wieser (1992) revealed that the performance of larvae reared at 20°C was seriously impaired by acute exposure to 15°C. The functional relationship between rate of oxygen consumption (R) and swimming speed (u) can be described by the equation:

$$R_{(u)} = R_{st} + a\ u^b, \qquad (1)$$

where R_{st} is the standard rate, a and b the coefficient and exponent, respectively, of the power relationship between the active rate of metabolism (R_a) and swimming speed. Some features and parameter values of this relationship at 15°C differed from those at 20°C as summarized in Table 3.

The magnitude of these responses far exceeds

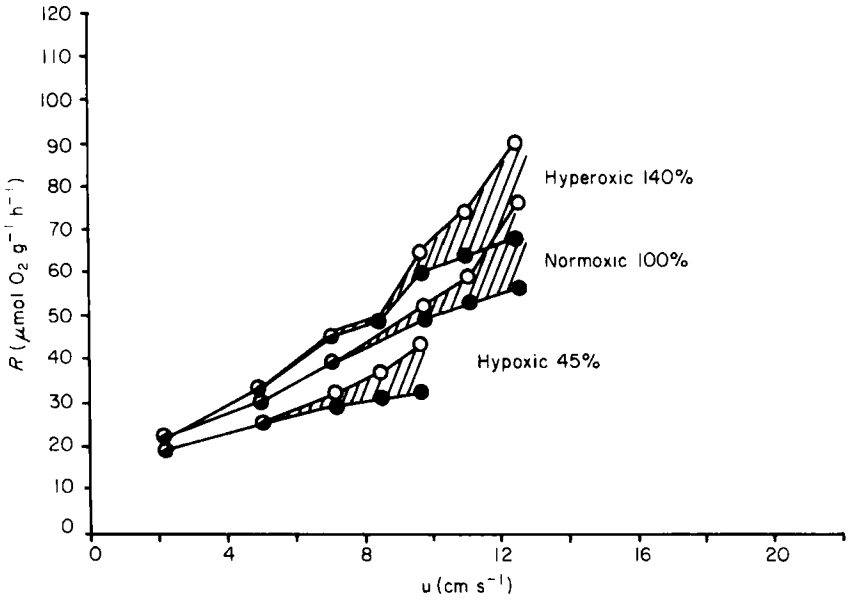

Fig. 4 Effects of oxygen content of water on the relationship between rate of oxygen consumption (R) and swimming speed (u) in larvae and young juveniles of the Danube bleak (*Chalcalburnus chalcoides*) at 20 °C. Rate of oxygen consumption denoted by ●. Total energy expenditure (○) calculated by adding the equivalent of the oxygen debt (hatched areas) to the measured aerobic rate. Unpublished data from the investigation by Kaufmann & Wieser (1992).

the possible effects of the higher viscosity of water at 15 °C and most probablyis a result of the effects of low temperature on structural and metabolic properties of the swimming muscles (Rome *et al.* 1985, 1990). This view is supported by the large effects of rearing temperature on fibre structure, distribution of fibre types, and protein polymorphism observed in the swimming muscles of fish larvae (Calvo & Johnston 1992, Vieira & Johnston 1992, Usher *et al.*1994).

Oxygen content. Experiments with adult fish have shown that swimming performance does not improve in hyperoxic water (Davis *et al.* 1963), but that exposure to hypoxic conditions leads to a reduction of u_{crit} (Jones 1971). Additional information on the relationship between energy metabolism and oxygen content of the water is provided by our work on the energetics of the larvae of *C. chalcoides* (Kaufmann & Wieser 1992). On the one hand, Fig. 4 corroborates the findings of Jones (1971) in that critical swimming speed remained unaffected by hyperoxia but was severely depressed by hypoxia as compared with normoxic conditions. On the other hand, the measurement of oxygen consumption over a range of swimming speeds revealed that the larvae of Danube bleak were capable of adjusting the metabolic costs of swimming to the oxygen content of the water. For example, at a given speed the larvae used 30% less aerobic and 17% less total metabolic energy in 45% saturated than in normoxic water (total metabolic energy = oxygen consumption plus oxygen debt indicated by shaded parts in Fig. 4).

It thus appears that when energy supply is limited, fish larvae swim more economically. Whether this is because of an increase in hydrodynamic efficiency or, as suggested by Wieser (1989, 1994), by suppressing other energy-consuming functions of maintenance remains to be seen. At any rate, macroscopically we were unable to detect any difference in the mode of swimming of the larvae of *C. chalcoides* under the three oxygen regimes.

COST OF GROWTH

Growth rate under the pressure of selection

The size range of fish hatchlings is such that they represent optimal food objects for large aquatic predators, among them adult fish. In fact, cannibalism is a wide-spread mode of feeding

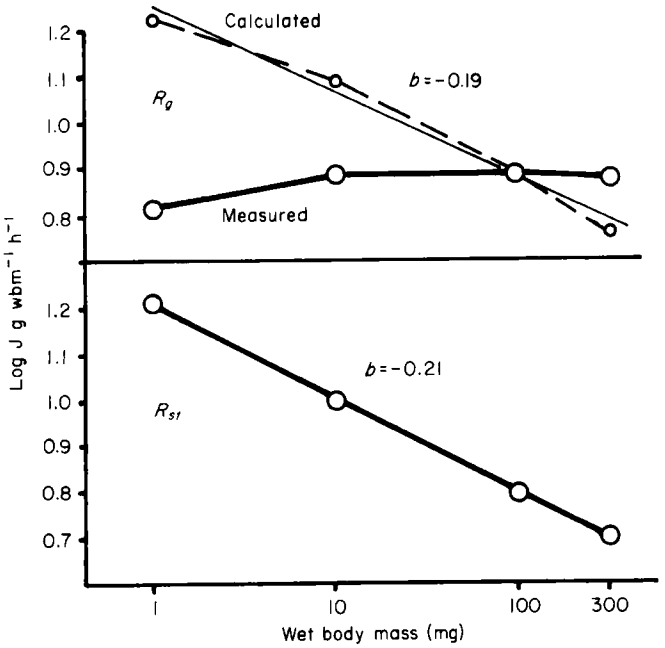

Fig. 5 Relationship between log mass-specific rate of energy expenditure (see Fig. 2) and log wet body mass in larvae and young juveniles of roach (*Rutilus rutilus*), based on the data of Wieser & Medgyesy (1990a,b). (Upper panel) Thick full line: food induced rate of oxygen consumption above R_{st} (= R_g); dashed line: calculated R_g based on calibration curve in Wieser (1994); thin line: regression through calculated data points, with slope indicated. (Lower panel) R_{st} = standard rate, corresponding to minimum prefeeding rate

behaviour in this group of animals, and Nellen (1986) has developed a theory based on the idea that the high fecundity of fish may have evolved as a strategy for bridging the prey size gap existing for adult fish in the pelagic environment between zooplankton on the one hand, and juvenile fish and a few large-bodied invertebrates on the other. The evolutionary consequence of this size relationship is that in fish the selection pressure for the maximization of growth during early development must have been extremely strong. This is reflected in fish larvae growing at rates of up to 30% d^{-1} in the wild (Wieser *et al.* 1988) and even faster under semi-controlled conditions (Kamler 1992).

Fast growth depends on high rates of food uptake. Since about 50% of the dry body mass of a fish consists of protein, the additional requirement is that the externally feeding larvae and early juveniles of all species of fish have to be carnivorous (White 1985). Consequently, with the initiation of external feeding, fish larvae must be capable of successfully preying on zooplankton, which requires the differentiation of locomotor and sense organs, and of the digestive apparatus, to be sufficiently advanced before the end of the yolk sac stage. It is possible to discern the roots of ontogenetic conflicts between differentiation and growth because of this requirement. Trade-offs between these two major developmental processes are likely to occur, with priorities being influenced by the abundance and composition of the food available in the environment at critical stages of development (Mark *et al.* 1989).

Compensatory metabolic strategies

One of the central axioms of nutrition physiology states that in animals the rate of growth is directly proportional to the growth-related increment of the rate of oxygen consumption above maintenance. Thus, if oxygen consumption above maintenance (here termed R_g) is plotted against rate of growth (g) a straight line results, the slope of which represents the cost of growth (Brody 1945, Jobling 1985, Wieser 1994).

It has recently been shown that this re-

lationship does not hold above a critical level of g in fast growing fish larvae (Wieser & Medgyesy 1990a,b, Wieser 1991, 1994, Rombough 1994). In a series of long-term experiments, in which larvae and small juveniles were allowed to feed and to grow inside a respirometer, it proved possible to define a pre-feeding rate of oxygen consumption considered close to the maintenance or standard rate (R_{st}), and to measure fairly precisely the food-induced increment of oxygen consumption above maintenance (R_g). The rate of growth of the fish was determined by the change in body weight during the experimental period. When R_{st} and R_g of *R. rutilus* are plotted against body mass (Fig. 5) results show that mass-specific R_{st} scaled with nearly the same exponent ($b = -0.21$) as mass-specific R_{st} of the fish in the swimming experiments (Fig. 2). On the other hand, R_g proved nearly mass-independent at about 7.6 J = 17 μmol O_2 g wbm^{-1} h^{-1}. Thus, the apparent *scope* for growth, i.e. the difference $R_{tot} - R_{st} = R_g$ (Brett 1976), *increased* with body mass, whereas at the same time the *rate* of growth *decreased*. Thus, the axiom of nutrition physiology mentioned above does not apply in this case. The same conclusion has been drawn by Rombough (1994) for the apparent cost of embryonal and larval growth in chinook salmon, *Oncorhynchus tshawytscha*.

A solution to this problem of physiological energetics is indicated by constructing a calibration curve for the cost of growth in slowly growing animals and to use this curve for the calculation of the cost of growth in the fast-growing larvae. The calibration curve constructed (Wieser 1994) yielded an average cost of growth of 15 μmol O_2 for the deposition of 1 g dbm, applying to aquatic poikilotherms with a caloric density of about 22 J g^{-1} dry body mass. Extrapolating this relationship to include the rates of growth observed in the larvae of *R. rutilus* resulted in the calculated curve shown in Fig. 5 with a slope of $b = -0.19$, very close to the measured slope of R_{st}. This similarity of slope supports the extrapolation procedure used. Below a body weight of about 100 mg the measured and the calculated R_g diverge, the difference increasing with decreasing body mass and increasing growth rate (for data see Wieser & Medgyesy 1990b).

Since the speeding up of growth requires the investment of additional metabolic power it has to be assumed that larvae growing faster than the critical rate of about 10% d^{-1} employ a combination of two strategies; either increasing the true efficiency of growth, or suppressing other energy-consuming functions of maintenance. The former strategy may involve an increase in the efficiency of protein deposition, analogous to the decrease in the ATP cost of protein synthesis observed in trout hepatocytes at different temperatures (Pannevis & Houlihan 1992, see Wieser 1994 for further discussion).

REFERENCES

Beamish, F.W.H. 1978. Swimming capacity. In: *Fish Physiology*. Vol. VII (eds W.S. Hoar & D.J. Randall), pp. 101–187. Academic Press, New York.

Blaxter, J.H.S. 1988. Pattern and variety in development. In: W.S. Hoar & D.J. Randall (eds) *Fish Physiology*. Vol. XI, part A, pp. 1–58. Academic Press, New York.

Brett, J.R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *J Fish Res Bd Canada* **21**, 1183–1226.

Brett, J.R. 1965. The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). *J Fish Res Board Can* **22**, 1491–1501.

Brett, J.R. 1976. Scope for metabolism and growth of sockeye salmon, *Oncorhynchus nerka*, and some related energetics. *J Fish Res Bd Canada* **33**, 307–313.

Brett, J.R. & Glass, N.R. 1973. Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. *J Fish Res Board Can* **30**, 379–387.

Brett, J.R. & Groves, T.D.D. 1979. Physiological energetics. In: W.S. Hoar, D.J. Randall & J.R. Brett (eds) *Fish Physiology* Vol. VIII, pp. 279–352. Academic Press, New York.

Brody, S. 1945. *Bioenergetics and Growth*. Reinhold Publishing. Co., New York.

Burggren, W.W. & Pinder, A.W. 1991. Ontogeny of cardiovascular and respiratory physiology in lower vertebrates. *Ann Rev Physiol* **53**, 107–135.

Calvo, J. & Johnston, I.A. 1992. Influence of rearing temperature on the distribution of muscle fibre types in the turbot (*Scophthalmus maximus*) at metamorphosis. *J Exp Mar Biol Ecol* **161**, 45–55.

Casey, T.M. & Ellington, C.P. 1989. Energetics of insect flight. In: W. Wieser & E. Gnaiger (eds) *Energy Transformations in Cells and Organisms*, pp. 200–210. Georg Thieme Verlag, Stuttgart.

Davis, G.E., Foster, J., Warren, C.E. & Doudoroff, P. 1963. The influence of oxygen concentration on the swimming performance of juvenile pacific salmon at various temperatures. *Trans Amer Fish Soc* **92**, 111–124.

DEVILLERS, C. & ROSENBERG, J. 1953. Les premières phases du développement de l'oeuf de *Salmo irideus* en anérobiose. *Compt Rend Acad Sci* **237**, 1561–1562.

EL-FIKY, N., HINTERLEITNER, S. & WIESER, W. 1987. Differentiation of swimming muscles and gills, and development of anaerobic power in the larvae of cyprinid fish (*Pisces, Teleostei*). *Zoomorphology* **107**, 126–132. *Suppl* **391**, R57 (abstract).

EMMETT, B. & HOCHACHKAI, P.W. 1981. Scaling of oxidative and glycolyric enzymes in mammals

FELDMAN, H.A. (1995) On the allometric mass exponent, when it exists. *J Theor Biol* (in press).

FINN, R.N. (1994) Physiological energetics of developing marine fish embryos and larvae. thesis, University of Bergen, Norway.

GIGUÈRE, L.A., CÔTÉ, B. & ST-PIERRE. J.-F. (1988) Metabolic rates scale isometrically in larval fishes. *Mar Ecol Prog Ser* **50**, 13–19.

GNAIGER, E., LACKNER, R., ORTNER, M., PUTZER, V. & KAUFMANN, R. (1981) Physiological and biochemical parameters in anoxic and aerobic metabolism of embryonic salmonids, *Salvelinus alpinus*. *Eur J Appl Physiol Suppl* **391, R57 (abstract).**

HINTERLEITNER., S., PLATZER, U. & WIESER, W. 1987. Development of the activities of oxidative, glycolytic and muscle enzymes during early larval life in three families of freshwater fish. *J Fish Biol* **30**, 315–326.

HOCHACHKA, P.W. 1988. The nature of evolution and adaptation: resolving the unity – diversity paradox. *Can J Zool* **66**, 1146–1152.

HOPPELER, H. 1990. The different relationship of $\dot{V}o_{2max}$ to muscle mitochondria in humans and quadrupedal animals. *Resp Physiol* **80**, 137–146.

HOPPELER, H. & TURNER, D.L. 1989. Plasticity of aerobic scope: adaptations of the respiratory system in animals, organs and cells. In: W. Wieser & E. Gnaiger (eds) *Energy Transformations in Cells and Organisms*, pp. 116–122. Georg Thieme Verlag, Stuttgart.

JOBLING, M. 1985. Growth. In: P. Tytler & P. Calow (eds) *Fish Energetics New Perspectives*, pp. 213–2. Croom Helm, London.

JONES, J. 1971. The effect of hypoxia and anaemia on the swimming performance of rainbow trout (*Salmo gairdneri*). *J Exp Biol* **55**, 541–551.

KAMLER, E. 1992. *Early Life History of Fish*. An energetics approach. Chapman & Hall, London.

KAUFMANN, R. 1990. Respiratory cost of swimming in larval and juvenile cyprinids. *J Exp Biol* **150**, 343–366.

KAUFMANN, R. & WIESER, W. 1992. Influence of temperature ambient oxygen on the swimming energetics of cyprinid larvae and juveniles. *Env Biol Fish* **33**, 87–95.

KLEIBER, M. 1961. *The Fire of Life*. Wiley, New York.

KOCH, F. & WIESER, W. 1983. Partitioning of energy in fish: can reduction of swimming activity compensate for the cost of production? *J Exp Biol* **107**, 141–146.

KOCH, F., WIESER, W. & NIEDERSTÄTTER, H. 1992. Interactive effects of season and temperature on enzyme activities, tissue and whole animal respiration in roach, *Rutilus rutilus*. *Env Biol Fish* **33**, 73–85.

MARK, W., WIESER, W. & HOHENAUER, C. 1989. Interactions between developmental processes, growth, and food selection in the larvae and juveniles of *Rutilus rutilus* (L.) (Cyprinidae). *Oecologia* **78**, 330–337.

NELLEN, W. 1986. A hypothesis on the fecundity of bony fish. *Meeresforschung* **31**, 75–89.

OIKAWA, S. & ITAZAWA, Y. 1985. Gill and body surface areas of the carp in relation to body mass, with special reference to the metabolism-size relationship. *J Exp Biol* **117**, 1–14.

OSSE, J.W.M. 1989. A functional explanation for a sequence of developmental events in the carp. The absence of gills in early larvae. *A Morphol Neerl Scand* **27**, 111–118.

PANNEVIS, M.C. & HOULIHAN, D.F. 1992. The energetic cost of protein synthesis in isolated hepatocytes of rainbow trout (*Oncorhynchus mykiss*). *J Comp Physiol* **162B**, 393–400.

PAULY, D. 1981. The relationship between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. *Meeresforschung* **28**, 251–282.

RANDALL, D.J. & DAXBOECK, C. 1982. Cardiovascular changes in the rainbow trout (*Salmo gairdneri* Richardson) during exercise. *Can J Zool* **60**, 1135–1140.

RANDALL, D.J. & BRAUNER, C. 1991. Effects of environmental factors on exercise in fish. *J Exp Biol* **160**, 113–126.

ROMBOUGH, P.J. 1988. Respiratory gas exchange, aerobic metabolism, and effects of hypoxia during early life. In: W.S. Hoar & D.J. Randall (eds) *Fish Physiology* Vol. XI, part A, pp. 59–161. Academic Press, New York.

ROMBOUGH, P.J. 1994. Energy partitioning during fish development: additive or compensatory allocation of energy to support growth? *Funct Ecol* **8**, 178–186.

ROME, L.C., LOUGHNA, P.T. & GOLDSPINK, G. 1985. Temperature acclimation: improved sustained swimming performance in carp at low temperatures. *Science* **228**, 194–196.

ROME, L.C., FUNKE, R.P. & ALEXANDER, R.MCN. 1990. The influence of temperature on muscle velocity and sustained performance in swimming carp. *J Exp Biol* **154**, 163–178.

SÄNGER, A.M., KIM, Z.S. & ADAM, H. 1990. The fine structure of muscle fibres of roach, *Rutilus rutilus* (L.), and chub, *Leuciscus cephalus* (L.), Cyprinidae, Teleostei: interspecific differences and effects of habitat and season. *J Fish Biol* **36**, 205–213.

SCHWERZMANN, K., HOPPELER, H., KAYAR, S.R. & WEIBEL, E. 1989. Oxidative capacity of muscle mitochondria: correlation of physiological, biochemical, and morphometric characteristics. *Proc Natl Acad Sci USA* **86**, 1583–1587.

SOMERO, G.N. & CHILDRESS, J.J. 1980. A violation of the metabolism-scaling paradigm: activities of glycolytic enzymes in muscle increase in larger-size fish. *Physiol Zool* **53**, 322–337.

STOIBER, W. 1991. Differenzierung der Rumpfmuskulatur larvaler Cypriniden: Feinstruktur und Morphometrie. thesis, University of Salzburg, Austria.

USHER, M.L. STICKLAND, N.C. & THORPE, J.E. 1994. Muscle development in Atlantic salmon (*Salmo salar*) embryos and the effect of temperature on muscle cellularity. *J Fish Biol* **44**, 953–964.

VIDELER, J.J. 1993. *Fish Swimming*. Chapman & Hall, London.

VIEIRA, V.L.A. & JOHNSTON, I.A. 1992. Influence of temperature on muscle-fibre development in larvae of the herring *Clupea harengus*. *Mar Biol* **112**, 333–341.

WELLS, P.R. & PINDER, A.W. 1995. The respiratory development of Atlantic salmon II: partitioning of oxygen uptake among gills, yolk sac and body surfaces. *J Exp Biol* (in press).

WHITE, T.C.R. 1985. When is a herbivor not a herbivor? *Oecologia* **67**, 596–597.

WIESER, W. 1984. A distinction must be made between the ontogeny and the phylogeny of metabolism in order to understand the mass exponent of energy metabolism. *Resp Physiol* **55**, 1–9.

WIESER, W. 1986. *Bioenergetik*, 245 pp. Georg Thieme Verlag, Stuttgart.

WIESER, W. 1989. Energy allocation by addition and by compensation: An old principle revisited. In: W. Wieser & E. Gnaiger (eds) *Energy Transformations in Cells and Organisms*, pp. 98–105. Georg Thieme Verlag, Stuttgart.

WIESER, W. 1991. Limitations of energy acquisition and energy use in small poikilotherms: evolutionary implications. *Funct Ecol* **5**, 234–240.

WIESER, W. 1994. Cost of growth in cells and organisms: general rules and comparative aspects. *Biol Rev* **68**, 1–33.

WIESER, W., FORSTNER, H., SCHIEMER, F. & MARK, W, 1988. Growth rates and growth efficiencies in larvae and juveniles of *Rutilus rutilus* and other cyprinid species: effects of temperature and food in the laboratory and in the field. *Can J Fish Aquat Sci* **45**, 943–950.

WIESER, W. & MEDGYESY, N. 1990a. Aerobic maximum for growth in the larvae and juveniles of a cyprinid fish, *Rutilus rutilus* (L.): implications for energy budgeting in small poikilotherms. *Funct Ecol* **4**, 233–242.

WIESER, W. & MEDGYESY, N. 1990b. Cost and efficiency of growth in the larvae of two species of fish with widely differing metabolic rates. *Proc R Soc Lond B* **242**, 51–56.

WINBERG, G.C. 1956. Rate of metabolism and food requirements in fishes (Russian). BeloRussian State University Minsk. (*Transl Ser Fish Res Bd Canada* **194**).