

DEVELOPMENTAL AND METABOLIC CONSTRAINTS OF THE SCOPE FOR ACTIVITY IN YOUNG RAINBOW TROUT (*SALMO GAIRDNERI*)

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Accepted 18 March 1985

SUMMARY

1. The relationship between routine or 'steady' rate ($\dot{V}_{O_2s.r.}$) and maximum rate of metabolism after forced bursts of activity (\dot{V}_{O_2max}) was studied in the fry and young (weight range 0.08–7 g) of *Salmo gairdneri* at 4 and 12°C.

2. The relationship between metabolic rate (y) and body weight (x) can be described by the function $y = ax^b$. The mass exponent b equals 0.96 and 0.93 for the routine rate, and 1.11 and 1.14 for the maximum rate of metabolism at 4 and 12°C respectively, the two sets of b -values differing significantly from each other.

3. The difference between the routine and the active rate of metabolism is called the *relative scope for activity*. Expressed as a percentage of the routine rate it increases from 85–166% in the sac fry, to approximately 400% in fish weighing 10 g.

4. Within each of four size classes there is a linear relationship between $\dot{V}_{O_2s.r.}$ and \dot{V}_{O_2max} , the slope of the relationship always being greater than one and increasing with the weight of the fish from 1.1 in the sac fry to 5.3 in the 3–7 g size class. That is, in the larger size class each increase in the steady rate of oxygen consumption by one unit adds 5.3 units to the aerobic scope for activity.

5. It is speculated that routine and active rate of metabolism are related by a constant factor of expansion so that, up to a limiting value, an increase of the former will lead to an increase of the amount of oxygen available to each fish for additional locomotor activity.

INTRODUCTION

The relationship between activity and resting metabolism in fish has most often been studied in terms of the 'scope for activity' as introduced by Fry (1947). That is, fish are forced to swim against currents of different velocities in a respirometer until a 'critical swimming speed' (Brett, 1964) is reached. The difference between the rate of oxygen consumption at this stage of maximum (aerobic) activity and the resting state is called the *aerobic scope for activity* and indicates the maximum

amount of oxygen available to a fish at a particular temperature for covering the energy costs of all sorts of biological activity. The resting state is seldom observed in a respirometer but can be derived by extrapolation from measurements of swimming metabolism (Brett, 1964).

In nature most fish, except the truly benthic forms, are usually not at rest nor do they swim at their critical speed for long periods. Rather, their activity fluctuates around an average level, called *routine* activity, from which they are stimulated by endogenous or exogenous factors to brief bouts of activity fuelled by both aerobic and anaerobic energy. It follows that if predictions are to be made about the transformation and the partitioning of energy in fish under natural conditions then more information about routine metabolism and its relationship to maximum effort is needed. This applies particularly to very young fish in which the pattern and intensity of swimming activity depend to a large extent on the developmental state of the swimming muscles, which in most species are not fully differentiated until many weeks after hatching (Wieser, Platzer & Hinterleitner, 1985).

The objective of this investigation was to study the effects of size and temperature on the relationship between routine and maximum rate of oxygen consumption in young fish. The method chosen was to follow the routine rate of oxygen consumption in alevins, fry and juveniles of rainbow trout (*Salmo gairdneri*) at two temperatures, before and after stimulating the fish to brief bursts of activity by means of weak electrical pulses. The difference between the maximum and the routine level of aerobic metabolism is considered to represent a measure of the amount of aerobic energy available to the fish under more or less natural conditions. Since this difference will always be a fraction of the scope for activity as defined by Fry (1947, 1971) and Brett (1964), the term *relative* scope for activity will be used for it.

MATERIAL AND METHODS

The fish studied were alevins, fry and juveniles of *Salmo gairdneri*, ranging in weight from 80 mg to approximately 7 g. Hatched from eggs, they were shipped from a fish farm in Italy (Preore) to Innsbruck and maintained in running water at $8 \pm 2^\circ\text{C}$. Food (Trouvit) was accepted by the fry for the first time about 20 days after hatching. Oxygen consumption was measured in flow-through respirometers as described previously (Forstner, 1983; Wieser *et al.* 1985). From one to five specimens were put into chambers varying in volume so that the relationship between total fish weight and water volume remained approximately constant at 300 ml g^{-1} fresh weight of fish. Each fish, or group of fish, was measured only once; that is, all the differences observed are those between individuals and not between different states of the same individual.

The respirometer chambers were equipped with two metal grids connected to electrical contacts which permitted the fish to be stimulated by weak electrical impulses (0–25 V, pulse widths 5 ms, 2 Hz). The electrical fields thus created did

not interfere with the measurement of oxygen consumption by means of oxygen-sensitive electrodes. Stimulation for 60 s elicited bursts of swimming activity driven by both anaerobic and aerobic energy (Wieser *et al.* 1985). During and after the end of the 1-min stimulus oxygen consumption rose to a peak value ($\dot{V}_{O_2\max}$) which was always much higher than the highest spontaneous (i.e. non-enforced) rate measured in the course of the experiments. With the system used it was not possible to resolve the exact onset of $\dot{V}_{O_2\max}$ but it began either within or immediately after the stimulus period and always lasted longer than the duration of the stimulus. Thus it may be considered as part exercise, part recovery, being identical with, or close to, maximum aerobic capacity of these fish (see below). Water flow through the respirometer system was maintained at approximately 250 ml min^{-1} . This was sufficient to induce apparently normal, slow swimming activity in the fish. In preliminary tests, oxygen-free water was injected into the system in order to establish the extent of distortion of the signal after stimulation between respirometer chamber and electrode. No detailed analysis of lag effects was attempted but distortion was slight and identical at the two experimental temperatures. Since the relationship between maximum and routine rates of metabolism proved to be size-dependent, the following weight classes have been distinguished: I, yolk sac stage (80–120 mg); II, 120–200 mg; III, 200–1000 mg; and IV, 3–7 g. The fish were taken from the holding tanks and acclimated to the experimental temperatures (4 and 12°C in this study) for 24 h without food. When the rate of oxygen consumption showed no obvious upward or downward trend but fluctuated by not more than about 20% around a stable average, the latter was considered a *steady rate* ($\dot{V}_{O_2\text{s.r.}}$). Usually the fish were put into the respirometers in the afternoon and left there until the next morning. When a steady rate had been achieved for several hours the fish were stimulated for exactly 60 s. In response to stimulation the rate of oxygen consumption rose to the level of $\dot{V}_{O_2\max}$ and decreased again to a steady level within a certain interval which has been called 'recovery time'. The post-stimulus rate of oxygen consumption was either identical with or higher than the pre-stimulus level (Wieser *et al.* 1985).

At the end of each experiment the fish were removed from the respirometers and weighed. Bacterial oxygen consumption was measured at the beginning and at the end of each experiment. A correction was applied to fish respiration assuming a linear increase of bacterial oxygen consumption. All rates of oxygen consumption will be expressed in $\mu\text{mol g}^{-1}$ fresh weight h^{-1} .

RESULTS

Effects of size and temperature on the relative scope for activity

In Fig. 1 the individual data of steady and maximum rates of oxygen consumption at 4 and 12°C are plotted against fresh body weight. The smallest specimens (approximately 80 mg) still possessed small yolk sacs but were already swimming

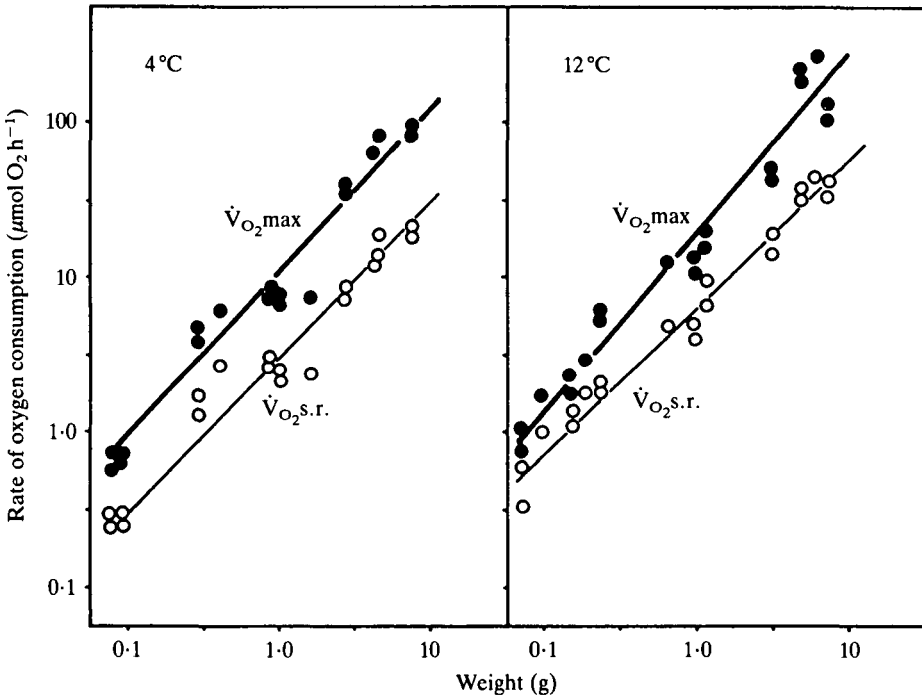


Fig. 1. Log rates of oxygen consumption ($\mu\text{mol h}^{-1}$) of young rainbow trout plotted against log body mass (g) at two experimental temperatures. The rates distinguished are a 'steady rate' ($\dot{V}_{\text{O}_2\text{s.r.}}$, open symbols), which may be considered an average routine rate maintained in respirometer chambers for several hours, and a maximum rate ($\dot{V}_{\text{O}_2\text{max}}$, closed symbols) maintained for a few minutes when the fish are forced to maximum locomotor activity by electrical stimulation.

freely and had just begun to accept dry food. The relationship between metabolic rate and body weight can be described by the function $y = ax^b$: the mass exponent b is close to unity in all four cases, but the slope of $\dot{V}_{\text{O}_2\text{max}}$ is significantly steeper than the slope of $\dot{V}_{\text{O}_2\text{s.r.}}$ (Table 1). What these data imply is an increase of the relative aerobic scope for activity with body mass – an implication that will be put

Table 1. Relationship between metabolic rate and body weight for juvenile *Salmo gairdneri* (range of weight 80 mg to 7 g) at two temperatures

	4°C	12°C
	$y = ax^b$	$y = ax^b$
	Difference between slopes	Difference between slopes
Routine rate ($\dot{V}_{\text{O}_2\text{s.r.}}$)	$y = 3.1x^{0.96}$	$y = 6.76x^{0.93}$
	$F_{(1,36)} = 4.97$ $P \sim 0.025$	$F_{(1,36)} = 5.28$ $P \sim 0.025$
Maximum rate ($\dot{V}_{\text{O}_2\text{max}}$)	$y = 11.0x^{1.11}$	$y = 19.9x^{1.14}$
$y = \dot{V}_{\text{O}_2}$ in $\mu\text{mol h}^{-1}$; $x = \text{body weight in g}$. The terms 'routine rate' and 'maximum rate' are explained in the text.		

into better perspective by comparing it with the results of an older investigation by Brett & Glass (1973), in which standard and maximum metabolic rates of larger representatives of a related species of salmonid were estimated (see below).

The relationship between steady and maximum rate of metabolism

Over long periods the routine metabolic rate of fish varies by a factor of at least two (Dolinin, 1973). The long-term *routine* rate may be composed of different 'steady rates', maintained for shorter periods of time, as described in this and in a previous paper (Wieser *et al.* 1985). Starting from the level of an average routine rate, fish may display spontaneous bursts of activity, or they may be forced to enter such activities. The question of interest here is whether the maximum metabolic rate that can be achieved at a given moment is related to the metabolic state of the animal before it entered the period of activity. It is often assumed that the maximum rate of metabolism represents a kind of 'ceiling': if the starting rate is higher, less 'scope for activity' remains than if the starting rate is lower.

However, this assumption cannot be generally true because $\dot{V}_{O_2,max}$ increases with temperature. In fact, in all cases so far studied (Brett, 1964; Beamish, 1978) the maximum rate of aerobic energy metabolism in fish increases more steeply with temperature than the standard rate, causing the scope for activity to increase with temperature to a maximum which is reached at approximately the preferred temperature of the species, or population, in question. I found in *S. gairdneri* a similar relationship between the peak rate of metabolism after short-term stimulation and the steady rate of metabolism prior to stimulation. If one rate is plotted against the other (Fig. 2) a highly significant relationship emerges within each of the four weight classes distinguished. The relationship between $\dot{V}_{O_2,max}$ and $\dot{V}_{O_2,s.r.}$ at a given temperature can be fitted by the same function that describes the relationship *between* experimental temperatures. Moreover, the slope of the linear function connecting the two metabolic rates increases in proportion with the weight of the fish. This conclusion is strengthened by including the data of Brett & Glass (1973) on larger specimens of another salmonid, *Oncorhynchus nerka*, although in that case the source of variability is restricted to experimental temperature. The functions describing the relationship between maximum and routine (or standard) rate of metabolism in the two salmonid species studied are listed in Table 2. There is a surprising constancy of the intercept value in all but one size class; on the other hand, the slope increases with the weight of the fish in a regular manner. The physiological meaning of parameter 'a' remains unclear, but the fact that the slope parameter 'b' is always greater than 1.0 implies that an increase in routine metabolism might be a means of expanding the scope for activity. Moreover, the degree of expansion depends on body mass. For example, in the smallest size class of *S. gairdneri*, each increase in the *steady* rate of oxygen consumption by one unit adds 1.1 units to the *maximum* rate of oxygen consumption: in the largest size class of *S. gairdneri* the coefficient of expansion is 5.3, and in the largest members of *O. nerka*, shown in Fig. 2, it is 8.1.

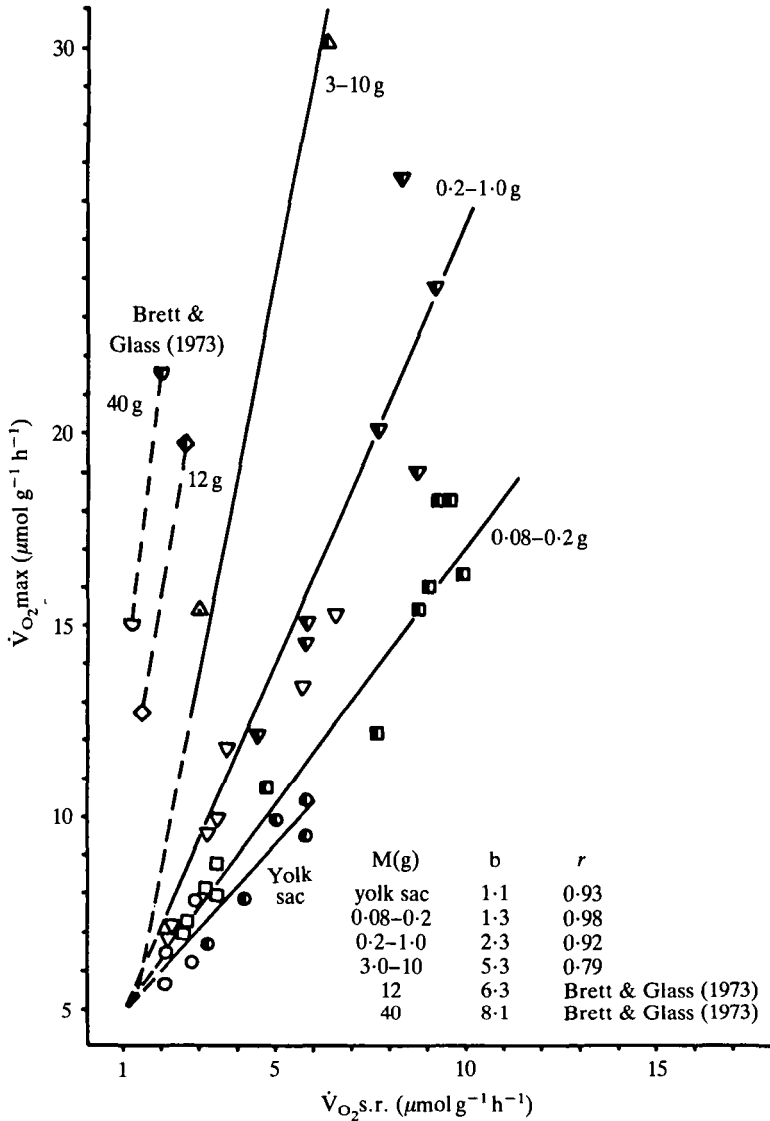


Fig. 2. Maximum rate of oxygen consumption ($\dot{V}_{O_2\max}$) plotted against steady rate of oxygen consumption ($\dot{V}_{O_2s.r.}$) in four size classes of rainbow trout measured at 4°C (open symbols) and 12°C (half-filled symbols). Also shown are data taken from Brett & Glass (1973) referring to *Onchorhynchus nerka* for which the experimental temperatures had been 5.3°C (open symbols) and 15°C (half-filled symbols). The *Salmo gairdneri* data are fitted by least square regression lines through the individual values except that, for clarity's sake, in the largest size class (3-10 g) only mean values are shown. Dashed lines are extrapolations beyond the ranges actually measured. The *O. nerka* data are represented by two dashed lines which connect the mean values at the two experimental temperatures. Inset gives ranges of body mass (M in g), slopes of the regression lines (b) and coefficients of correlation (r).

DISCUSSION

This study reveals two major sources of intraspecific variability of the scope for activity in fish: body size and metabolic state. As far as body size is concerned it

Table 2. *Functional relationship of the form $y = a + bx$ between standard or routine rate (x) and maximum rate (y) of aerobic metabolism in different weight classes of two salmonid species*

Species and experimental temperatures	Weight class (g)	Function	Correlation (r)
<i>Salmo gairdneri</i> (4 and 12°C)	0.08–0.12	$y = 3.8 + 1.1x$	0.93
	0.12–0.20	$y = 3.8 + 1.3x$	0.98
	0.20–1.0	$y = 2.5 + 2.3x$	0.92
	1.0–7.0	$y = -1.9 + 5.3x$	0.79
<i>Onchorhynchus nerka</i> (5.3 and 15°C)	12	$y = 3.2 + 6.3x$	—
	40	$y = 5.3 + 8.1x$	—

The data for *Onchorhynchus nerka* are based on mean values taken from Brett & Glass (1973), so no measure for the degree of correlation is possible.

has been claimed that the mass exponent of activity metabolism is higher than (Brett, 1965) or equal to (Ivlev, 1960) the mass exponent of standard metabolism. Which of these two possibilities applies may depend on a number of factors, the most important probably being whether the metabolic rates have been determined over a sufficiently wide range of body sizes. In the present investigation the range covered two orders of magnitude, beginning with the sac fry. It may be extended by another two orders of magnitude by linking it to an investigation by Brett & Glass (1973), who measured oxygen consumption at critical swimming speed and calculated oxygen consumption at rest in *Onchorhynchus nerka*, ranging in size from approximately 10 to 2000 g, at 5.3, 15 and 20°C. If the low and medium temperature data of Brett & Glass are converted to the same units and plotted on the same scale as my own data (Fig. 3) the conclusions drawn from the latter are strengthened. An extrapolation of the regression lines through the *S. gairdneri* data nearly coincides with the regression lines through the *O. nerka* data, although the causes of maximum activity were quite different in the two species: electrical stimulation in *S. gairdneri* and critical swimming speed in *O. nerka*. This is a strong indication that the rate of oxygen consumption of the electrically stimulated fish is identical with, or close to, maximum oxygen consumption during swimming at critical speed. Thus the difference between $\dot{V}_{O_2\max}$ and $\dot{V}_{O_2\text{s.r.}}$ measures a true – albeit relative – scope for activity in the sense of Fry (1947, 1971).

The standard rates as given by Brett & Glass (1973) for *O. nerka* are lower than the 'steady rates' as measured by myself in *S. gairdneri*. This is not surprising since my data refer to *routine* rates, whereas Brett & Glass calculated *resting* rates by extrapolating to zero velocity the oxygen consumption values measured at a range of swimming speeds. Since Brett & Glass also report a significantly higher mass exponent for activity metabolism than for standard metabolism, it may be concluded that in salmonids the intraspecific scope for activity increases with body mass, at least at low and medium temperatures, from the sac fry to the adult stage.

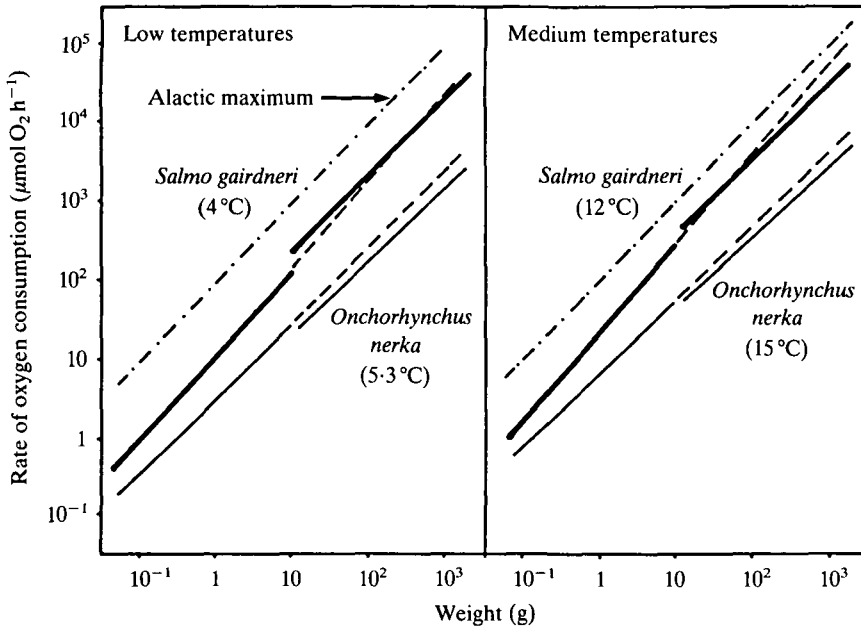


Fig. 3. Log rates of oxygen consumption ($\mu\text{mol h}^{-1}$) plotted against log body mass (g). Shown are the regression lines calculated for two species of salmonids, each measured at two levels of activity and at two experimental temperatures. *Salmo gairdneri* (this paper): routine or 'steady' rate of metabolism (light lines), and maximum rate of metabolism during and after forced bursts of activity (heavy lines), at 4 and 12°C *Onchorhynchus nerka* (Brett & Glass, 1973): resting rates determined by extrapolating to zero velocity the rates of oxygen consumption at various swimming speeds (light lines) and rate at critical swimming speed (heavy lines), at 5.3 and 15°C. The regression lines through the *S. gairdneri* data have been extrapolated into the higher weight range (dashed lines). Also shown is the rate of maximum alactic energy production in rainbow trout, expressed in the form of oxygen equivalents of the rates of phosphocreatine and ATP hydrolysis during 30 s of burst activity (dotted and dashed line) (based on Wieser, Platzer & Hinterleitner, 1985).

In order to meet the demands of locomotor activity, fish weighing 100 mg are capable of expanding their routine rate by not more than 85–166%, fish weighing 1 kg, however, are capable of expanding their routine rate by 900–1155%.

One more feature should be added to this comparison. It has been shown previously (Wieser *et al.* 1985) that the maximum specific rate of anaerobic (alactic) energy production during 30 s of stimulation is independent of body size (between 0.08 and 7 g) and temperature (between 4 and 20°C), amounting to approximately $10 \mu\text{mol ATP g}^{-1} \text{ min}^{-1}$. The equivalent rate of oxygen consumption (assuming $1 \mu\text{mol O}_2 = 6 \mu\text{mol ATP}$) would be $100 \mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$, which in the youngest fry at 4°C is about one order of magnitude greater than the highest rate of oxygen consumption measured. If independence of body size and temperature is assumed to hold beyond the range over which it was actually established, in the largest fish at 15°C the rate of maximum anaerobic energy production would be about three times greater than the rate of maximum aerobic energy production (Fig. 3, dotted and dashed line). This is approximately the

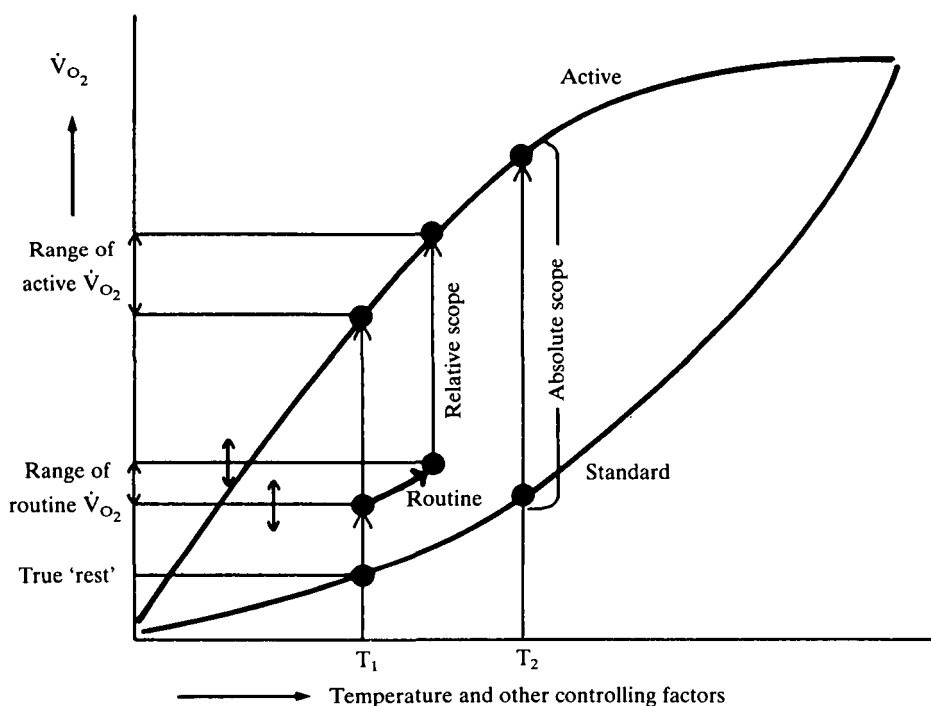


Fig. 4. A model illustrating the possible effects of controlling factors (in the sense of Fry, 1971) on standard, routine and active rate of metabolism in fish. It is assumed that the major controlling factor is temperature, two examples being shown (T_1 and T_2), and that up to a critical value the difference between active and standard rate of metabolism (the *absolute scope* for activity) increases with temperature. On the other hand, the *routine* rate of metabolism is assumed to be influenced not only by temperature but also by some other controlling factor which simulates the effect of temperature. Since the active rate is a more or less constant multiple of the routine rate, the *relative scope* for activity increases with the latter. Arrows indicate that the routine rate may not only occupy different average levels but also fluctuate around these levels, whereas standard and active rates of metabolism are constant for a given combination of controlling factors.

ratio between maximum alactic and maximum aerobic energy production in untrained human adults (di Prampero, 1981).

What is the relationship between *individual* levels of routine and active metabolism – a problem that has recently been studied in lizards by Pough & Andrews (1984)? If for a given size and temperature active metabolism constituted a more or less fixed value, an *indirect* relationship between routine rate and scope for activity would be expected. However, the scatter of individual points around the regression line of Fig. 1 suggests that this is not the case: in each individual fish a high routine rate of oxygen consumption is always correlated with a high active rate, and a low routine rate with a low active rate. This conclusion is more clearly brought home by Fig. 2, in which $\dot{V}O_{2\max}$ values are plotted against $\dot{V}O_{2\text{s.r.}}$ values. In each size class of trout the two rates are positively correlated, irrespective of whether the variability of metabolic rates is due to temperature or to some other, unknown, factor.

My interpretation of this relationship is presented in the form of a model in Fig. 4. It is assumed that the routine rate of metabolism can be influenced by a number of 'controlling factors' in the sense of Fry (1971). Temperature is by far the best known factor of this kind and the only one that Fry considered in his splendid review. But there is no reason to believe that it is the *only* controlling factor.

Over a range of temperatures the standard, or resting, rate of metabolism represents a more or less fixed fraction of the active rate of metabolism (Brett, 1964; Fry, 1971). If, *at a given temperature*, the routine rate of metabolism were influenced in the same way by a second controlling factor, a positive relationship between routine and maximum rate would emerge. As documented in Fig. 2 this is precisely the result of my experiments. One would therefore have to postulate that the metabolism of young rainbow trout at a given temperature is influenced by a factor (perhaps *via* hormonal effects on heart rate or blood flow) which determines the average level of the routine rate of oxygen consumption. Since in each size class the ratio $\dot{V}_{O_2\max}/\dot{V}_{O_2s.r.}$ is constant, it follows that the higher the $\dot{V}_{O_2s.r.}$ value the greater is the amount of oxygen available to each fish for additional locomotor activity, or, expressed the other way round, an individual that achieves a higher $\dot{V}_{O_2\max}$ must be more highly 'geared' and thus consume more oxygen even during routine swimming activity.

This research was supported by project no. 4674 of the 'Fonds zur Förderung der wissenschaftlichen Forschung in Österreich'.

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