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THE SCALING OF AEROBIC AND ANAEROBIC MUSCLE POWER IN RAINBOW TROUT (*SALMO GAIRDNERI*)

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Summary

The scaling of anaerobic metabolism and red muscle mass was examined in rainbow trout (*Salmo gairdneri*) ranging in size from 2 to 1200 g. The initial rate of white muscle lactate production during maximal burst activity was significantly higher in large (28·1 cm) than in small (8·0 cm) fish. 'Resting' lactate concentrations in anesthetized trout (approximately 30 s of stress) increased with fish size, also reflecting higher glycolytic potential for larger fish. Maximum muscle lactate concentrations following 6 min of exhaustive exercise increased from approximately 25 to 45 μmol g^{-1} with increased fish size ($= L^{0.36}$, where L is fish length). Total white muscle lactate production, including changes in muscle mass, scaled as $L^{3.52}$. A scaling comparison of total anaerobic capacity with theoretically predicted power requirements indicated decreased burst swimming performance with increased size. Red muscle mass increased from approximately 1 to 3 % of body mass with increased fish size. The positive allometry in red muscle mass ($= L^{3.62}$) is greater than the scaling of power requirements during aerobic swimming predicted from hydrodynamic theory, and may provide compensation for decreased mass-specific power output with increased size.

Introduction

A fundamental issue in the study of vertebrate swimming is the relationship between muscle power production and the power required to achieve a particular level of performance (Gray, 1936; Bainbridge, 1961; Webb, 1978). The scaling of power requirements has been the subject of considerable analysis (Vlymen, 1974; Weihs, 1977; Webb *et al.* 1984) and, in general, displays positive allometry for both sustained and burst swimming. Less attention has been given to the scaling of muscle power output, but it appears that the mechanical limitations for maximum power during a single muscle contraction are not size-dependent (Schmidt-Nielsen, 1977; Webb & Johnsrude, 1988).

The scaling of muscle power output in fish is complicated by its differentiation into aerobic red muscle tissue (used for sustained swimming) and anaerobic white

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muscle tissue (used for high-speed burst or sprint swimming). It has generally been assumed that the scaling of red muscle mass and mass-specific anaerobic metabolism are isometric. Limited data on the scaling of red muscle tissue among specialized scombrids (Graham *et al.* 1983) suggest that red muscle mass may increase more rapidly with size than expected for isometric scaling. The results for endothermic species, however, indicate the opposite relationship and therefore the general situation for fish remains unclear.

Intraspecific studies on the scaling of glycolytic enzyme activity in white muscle tissue suggest that the potential for anaerobic metabolism in fish may also be positively allometric (Somero & Childress, 1980). Expressed as a function of body mass ($y = aM^b$), mean mass-specific lactate dehydrogenase (LDH) and pyruvate kinase (PK) activities increase with $M^{0.35}$ and $M^{0.21}$, respectively. It is not known if this allometric scaling of enzyme activity translates into the rate of anaerobic energy production or total capacity during burst activities.

The main purpose of the present study was to quantify the scaling of red muscle tissue and anaerobic metabolism (lactate production) in the rainbow trout (*Salmo gairdneri*) and compare these results with theoretically predicted power requirements during prolonged and burst swimming, respectively.

Materials and methods

Fish

Rainbow trout were obtained from the Fisheries Laboratory of the Ministry of Agriculture, Fisheries and Food at Lowestoft, England. The fish were fed a commercial trout food and maintained in flowthrough tanks (15 ± 1°C) using dechlorinated fresh water.

Experimental protocol

The rate of white muscle lactate production after 1, 2 and 6 min of maximal burst activity was determined for small ($8{\cdot}0 \pm 0{\cdot}15$ cm; $\bar{x} \pm$ S.E.) and large ($28{\cdot}1 \pm 0{\cdot}55$ cm) fish. Four, five or six fish of each size group were sampled at each time interval. Individual fish were chased by net in a way that produced sequential bursts rather than continuous swimming. Tanks of the same relative size, approximately 3×4 body lengths, were used for each size of fish. As a measure of total anaerobic capacity, 21 additional fish (7·0–40·5 cm; 3·5–1225 g) were exercised for a period of 6 min and analyzed for white muscle lactate production. Most of the fish were physically exhausted after 3 or 4 min of activity, and by the end of 6 min all the fish appeared fatigued.

An attempt was made to obtain resting levels of white muscle lactate in fish ranging in size from 7·2 to 37·9 cm (3·8–649 g). Individual fish were isolated in separate tanks for 36–42 h prior to sampling to minimize their level of excitement. The anesthetic 2-phenoxyethanol was introduced into each tank to minimize activity, and then the fish were quickly removed and sampled. Although intended

as a resting sample, these lactate levels unavoidably reflect an approximately 30 s period of stress (i.e. 20 s for anesthesia and 10 s for sampling).

An approximately 500 mg sample of white muscle tissue was excised from each fish below the dorsal fin and immediately immersed in liquid nitrogen. The sample was pressed against the side of the container to facilitate freezing. All tissue samples were homogenized in cold 8 % perchloric acid using a Polytron tissue grinder and centrifuged for 10 min at 1500 *g*. Lactate was quantified spectrophotometrically at 340 nm using lactate dehydrogenase and nicotinamide adenine dinucleotide (Sigma, 1984).

The problems associated with obtaining accurate muscle concentrations of lactate are well documented (Adcock & Dando, 1983; Wieser *et al.* 1986). They are related to the rate of tissue cooling which, even when using liquid nitrogen, may be affected by the size of the tissue sample. As a check on this source of error, and the variability of the procedure used here, a 27 cm fish was exercised to increase its muscle lactate level (6 min) and then sampled in replicate. Six adjacent tissue samples ranging from 0·50 to 2·00 g were excised, frozen and analyzed for lactate. White muscle lactate concentrations following activity have been shown not to vary with location on the body (Wieser *et al.* 1986) or to vary by less than 10 % (Schwalme & Mackay, 1985).

Scaling of red and white muscle mass

Sixteen fish ranging in size from 5·5 to 37·9 cm (2·02–648 g) were used to determine the relationship between red and white muscle mass and body mass. To account for any allometry in growth of the head or caudal fin, measurements were made at regular intervals along the length of the myotome and not the entire fish. Nine equally spaced sections were cut along the entire length of muscle mass (cleithrum to base of hypurals) from each frozen fish. A thin (1–3 mm) slice was taken from each of the eight internal cross-sections and examined with a *camera lucida*. A digitizing pad connected to a BBC Microcomputer System B+ was used to quantify the area of both red and white muscle. Red muscle area at each section was expressed as a percentage of total muscle cross-sectional area. The cross-sectional areas were converted to mass from the known length of muscle tissue and assuming a tissue density of 1·05 g cm^{-3} (Alexander, 1959). The value Q_n, which describes the longitudinal distribution of absolute red muscle area normalized for body length, was also calculated following Aleyev (1977). For each section (n) the area of red muscle (A_n) is expressed as the ratio of the side of a square of equal area, to the fish's effective length (L), i.e.:

$$Q_n = A_n^{0.5} L^{-1.0} . \quad (1)$$

Means and regression coefficients are presented ±1 S.E.; statistical significance was set at $P < 0.05$. Fish size is given as mass (g) and total length (cm); lactate concentration as μmol g^{-1} of white muscle tissue (wet mass).

Results

Lactate production

The values of replicate lactate samples obtained from a single fish were not affected by the size of muscle tissue sampled ($P > 0{\cdot}40$). Tissue samples weighing 0·56, 0·63, 0·72, 1·03, 1·70 and 2·02 g had lactate concentrations of 46·6, 43·9, 44·1, 44·8, 43·1 and 44·5 μmol g^{-1}, respectively.

The concentration of white muscle lactate from anesthetized rainbow trout increased with the size of the fish ($P < 0{\cdot}001$; $r^2 = 0{\cdot}72$). Lactate levels of the largest fish were approximately threefold higher than those of the smallest (Fig. 1). The behavior of the fish during anesthesia suggests that the elevated lactate concentrations were the result of stress and activity, and that they do not accurately reflect the resting values for large fish. The typical response of fish as they lost equilibrium involved slow periodic body/caudal fin movements, and in a few instances the fish first moved to a new location in the tank as the presence of the anesthetic was sensed. Furthermore, if the observed rate of increase in resting lactate concentration were accurate it would indicate the unlikely possibility that large fish have no anaerobic scope. The actual resting white muscle lactate concentration is probably between 0·0 and 7·0 μmol g^{-1} (Black *et al.* 1962; Wieser *et al.* 1986). The lowest concentration observed in the present study was 5·6 μmol g^{-1} (8·2 cm fish), and this value was used to estimate conservatively the lactate production of exercised fish.

The initial rate of muscle lactate production during maximal burst activity was much higher for large fish (28·1 cm) than for small fish (8·0 cm; Fig. 2). Larger fish reached maximum muscle lactate concentrations after approximately 1 min rather

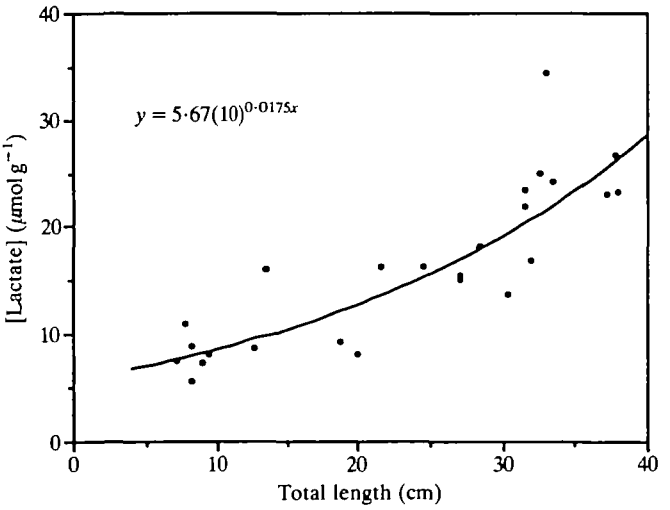

Fig. 1. Effect of fish size on the 'resting' white muscle lactate concentration of anesthetized rainbow trout. The values reflect a period of approximately 30 s of stress.

than 2 min, and also produced twice as much lactate per gram of tissue after 6 min of activity.

The 6-min lactate concentrations from the time series study above are plotted in Fig. 3 together with data for intermediate and larger-sized fish following 6 min of

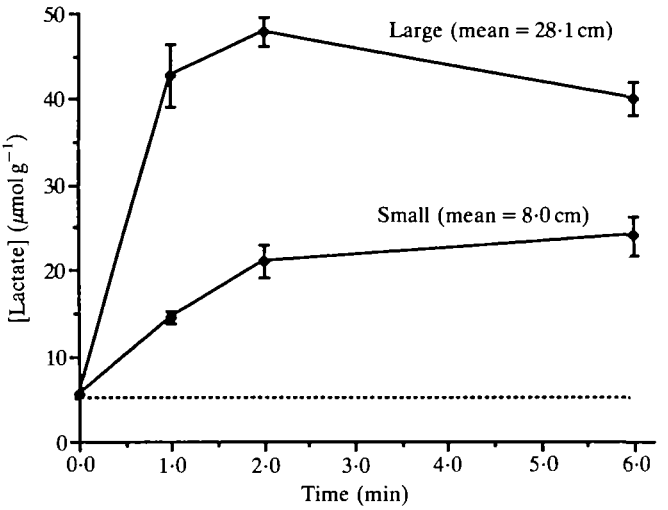

Fig. 2. Rate of white muscle lactate production by large (mean 28·1 cm) and small (mean 8·0 cm) rainbow trout during maximal burst-type activity. The dashed horizontal line indicates the lowest observed resting concentration of lactate. Values are mean ± S.E.

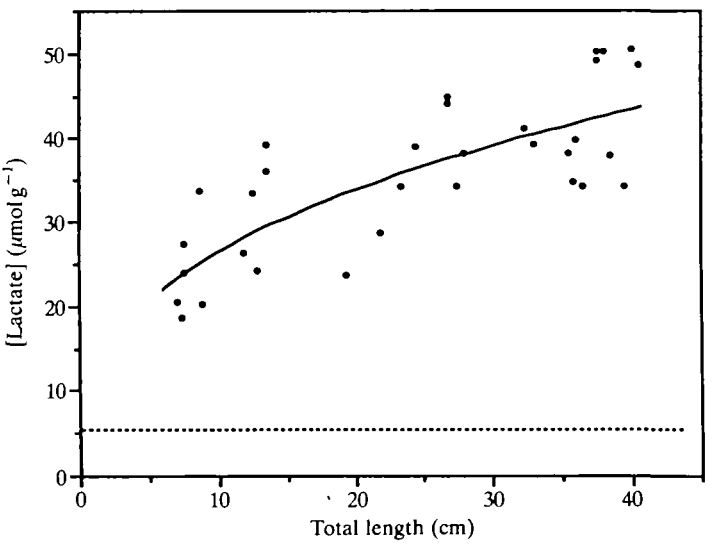

Fig. 3. Relationship between fish size and the white muscle lactate concentration of rainbow trout following 6 min of exhaustive exercise. The dashed horizontal line indicates the lowest observed resting concentration of lactate.

activity ($N = 32$). The overall relationship between fish size in length (cm) and muscle lactate concentration ($\mu mol\,g^{-1}$) after 6 min of activity is significant ($P < 0{\cdot}001$; $r^2 = 0{\cdot}67$) and best described by the equation:

$$\log[\text{lactate}] = (2{\cdot}435 \pm 0{\cdot}158) + (0{\cdot}361 \pm 0{\cdot}051)\log L \ . \quad (2)$$

Scaling of red and white muscle mass

The relationship between fish length (L) and mass (M) was:

$$\log M = (-4{\cdot}695 \pm 0{\cdot}089) + (3{\cdot}047 \pm 0{\cdot}030)\log L \quad r^2 = 0{\cdot}99,\ N = 91 \ . \quad (3)$$

Red muscle tissue, expressed as a percentage of total muscle cross-sectional area, increased towards the caudal peduncle (Fig. 4A). The pattern was similar for all sizes of fish, but larger fish had increasingly higher proportions of red muscle

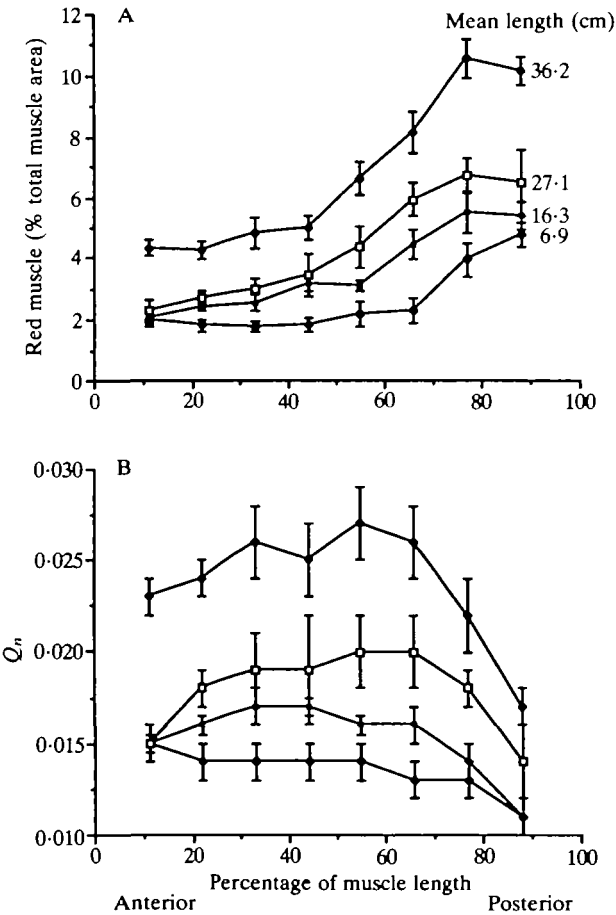

Fig. 4. Effect of fish size on the longitudinal distribution of red muscle mass in rainbow trout expressed (A) as a proportion of total muscle area and (B) as absolute area normalized for body length (Q_n). See text for details. Values are means ± S.E. ($N = 3$–5).

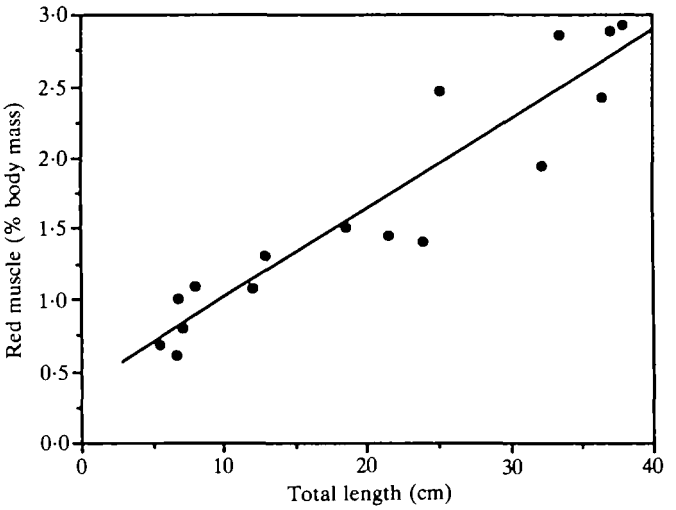

Fig. 5. Relationship between fish size and total red muscle mass (% of body mass) in rainbow trout.

tissue. Maximum percentages at the caudal peduncle increased with fish size from approximately 4 to 11 % of total muscle area.

The cross-sectional area of red muscle normalized for fish length (Q_n) also increased in larger fish (Fig. 4B). These values were not influenced by changes in the quantity of white muscle, and are therefore a measure of the absolute amount of red muscle present at each section of the fish's length.

Expressed in terms of mass, red muscle tissue increased linearly with increased fish length from approximately 1·0 to 3·0 % of total body mass (Fig. 5; $r^2 = 0{\cdot}88$). The relationship between red muscle mass and body mass was described by a power function (Fig. 6; $r^2 = 0{\cdot}98$), and as a function of length red muscle mass increased as:

$$\log(\text{red muscle mass}) = (-10{\cdot}44 \pm 0{\cdot}32) + (3{\cdot}62 \pm 0{\cdot}11)\log L \ . \quad (4)$$

The mass of white muscle tissue was also related to body mass by a power function (Fig. 6; $r^2 = 0{\cdot}99$), and increased with body length according to the equation:

$$\log(\text{white muscle mass}) = (-5{\cdot}54 \pm 0{\cdot}18) + (3{\cdot}07 \pm 0{\cdot}06)\log L \ . \quad (5)$$

Discussion

The results of this study indicate that both the rate and the total capacity of anaerobic metabolism increase with size in rainbow trout. A possible source of error in the estimate of total anaerobic capacity using 6-min muscle lactate production is the loss of lactate into the blood. The data of Turner *et al.* (1983*a*) on rainbow trout permit an evaluation of the magnitude of this error. In that study,

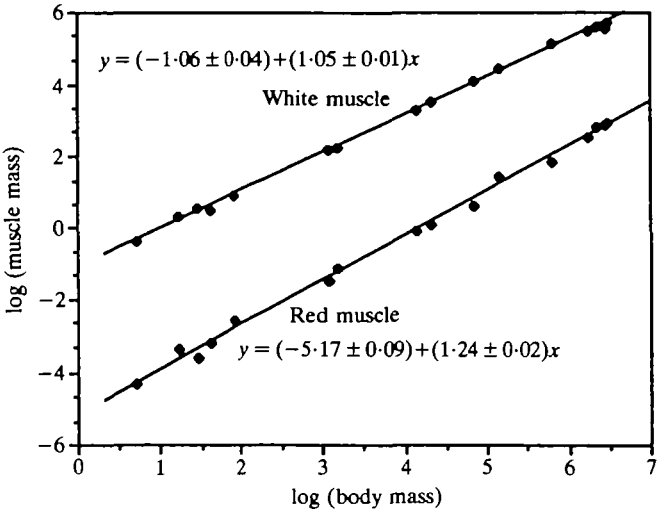

Fig. 6. Scaling relationships between total white and red muscle mass and body mass in rainbow trout.

white muscle lactate concentrations following 6 min of activity reached approximately 43 mequiv kg^{-1} of muscle cells. For a 1-kg fish with approximately 50 % white muscle (Webb & Johnsrude, 1988; the present study), this is equivalent to 21·5 mequiv of muscle lactate production. Blood lactate levels are known to reach maximum levels several hours after exhaustive activity (Wood & Perry, 1985), and after 6 min increased to only 6·5 mequiv l^{-1} in the rainbow trout (Turner *et al.* 1983*a*). With a blood volume of approximately 50 ml kg^{-1} (Smith, 1966; Stevens, 1968), the total blood lactate of a 1-kg fish after 6 min of activity (0·325 mequiv) would be just 1·5 % of muscle lactate production. The 6-min lactate data, therefore, appear to be realistic estimates of total white muscle lactate production.

In the present study a much higher rate of lactate production was observed in larger fish during maximal burst activity (Fig. 2). This increased potential for anaerobic metabolism by larger fish was even apparent in the lactate concentration of anesthetized (resting) fish. These results are consistent with the intraspecific scaling of glycolytic enzyme activity in fish, which is also characterized by positive allometry (Somero & Childress, 1980). The intraspecific scaling of whole-body LDH activity, averaged for several species, increases as $L^{4·6}$ (Somero & Childress, 1980). The several-fold difference in rate of lactate production between 8·0 and 28·1 cm fish is of approximately the same magnitude as that for LDH activity over the same size range. The maximum concentrations of lactate accumulated per gram of white muscle tissue were also higher in larger fish after exhaustive swimming. Interspecific reports on the scaling of anaerobic metabolism (Castellini & Somero, 1981) suggest that the allometry in anaerobic potential seen in the present study may be accompanied by changes in muscle buffering capacity.

know of no studies, however, that have examined the intraspecific scaling of muscle or blood buffering capacity.

The scaling of total anaerobic capacity can be described by combining the mass-specific relationship for lactate production with the observed changes in white muscle mass. Lactate levels after 6 min of activity (equation 2) were used as measures of total lactate production, subtracting $5{\cdot}6\,\mu\text{mol}\,\text{g}^{-1}$ as the resting concentration. Combining these data with white muscle mass (equation 5) gives:

$$\text{Total[lactate]}(\mu\text{mol}) = 0{\cdot}0287L^{3{\cdot}52}\,. \tag{6}$$

How does this scaling of anaerobic capacity compare with the scaling of power requirements during burst swimming? The exact scaling relationship for burst swimming performance remains unclear. In general, length-specific burst performance has been considered to vary little with body size for streamlined fish, with $10\,\text{L}\,\text{s}^{-1}$ ($= L^{1{\cdot}0}$) considered representative for most fish less than 1 m in length (Wu, 1977). However, other authors have reported slight ($L^{0{\cdot}94}$; Blaxter & Dickson, 1959) and even moderate allometry for burst performance in fish (Wardle, 1975).

The data obtained in the present study on the scaling of total anaerobic capacity can be used to evaluate the interactions between size and burst swimming performance by comparison with the rates of working estimated from hydrodynamic theory (Bainbridge, 1961). If predictions of burst performance are to be meaningful, however, the duration of activity must also be specified. The power required to overcome drag (P_t) is given by

$$P_t = 0{\cdot}5\rho SV^3C_D \tag{7}$$

where ρ is the density of water, S is the wetted surface area of the fish, and V is swimming velocity. The drag coefficient used ($C_D = 0{\cdot}074Re^{-0{\cdot}2}$) assumes turbulent flow over the fish's body, which is the most likely condition during burst speeds (Webb, 1978). The Reynolds number, Re, is $(LV)\nu^{-1}$, where ν is the kinematic viscosity of water.

The scaling of anaerobic energy availability is estimated from the total anaerobic capacity of each size of fish (equation 6). A conversion value of $558\,\text{J}\,\text{g}^{-1}$ of glycogen metabolized is used (Wardle, 1975), which assumes an ATP energy equivalence of $12{\cdot}0\,\text{kcal}\,\text{mol}^{-1}$. The burst speeds that are possible from the energy available to fish of a certain size will, of course, depend on the rate at which energy is used. Rates of power output were calculated for each size of fish as the ratio of total anaerobic energy available to the duration of activity for periods ranging from 0·5 to 6·0 min. These rates of power output were entered into equation 7 for each size of fish and the equation was solved for velocity.

If the same stamina is assumed for fish of all sizes, these calculations indicate that a large decrease in length-specific burst performance should occur with increased size, and that this decrease in performance should be most severe during short swimming episodes (Fig. 7). However, the time series data for lactate production (Fig. 2) suggest that the rate of depletion of anaerobic reserves is faster

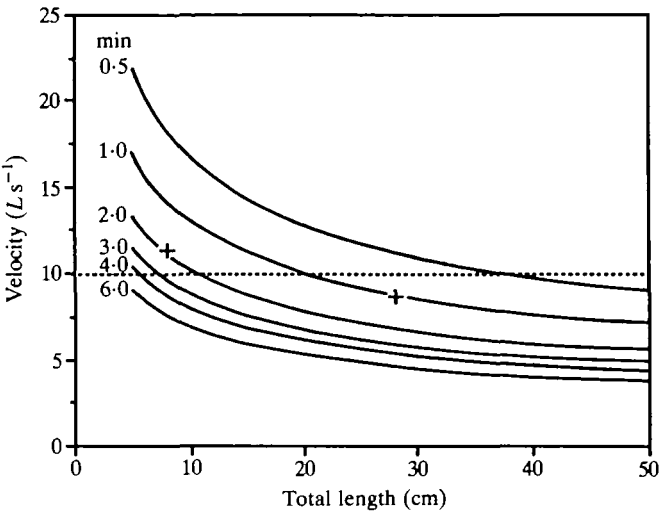

Fig. 7. Effect of fish size on estimated burst swimming velocities of rainbow trout based on the scaling of total anaerobic capacity and predicted power requirements from hydrodynamic theory. Velocities are presented for swimming durations ranging from 0·5 to 6·0 min. The two crosses represent approximate observed stamina for fish of 8·0 and 28·1 cm.

for larger fish and, hence, they would exhibit less stamina at higher sprint speeds. In fact, if the commonly accepted velocity of $10\,L\,s^{-1}$ is considered, stamina is predicted to fall from 4 min to 30 s for fish of 5 and 40 cm, respectively. When the observed staminas of large and small fish (approximately 1 and 2 min, respectively) are plotted onto Fig. 7, their location suggests that, in addition to decreased stamina, burst swimming velocities also fall from near 12 to $9\,L\,s^{-1}$ with an increase in size from 8·0 to 28·1 cm.

Previous studies of red muscle tissue in fish have typically expressed its mass as a percentage of total muscle or fish cross-sectional area (Greer-Walker & Pull, 1975; Graham *et al.* 1983). The occurrence of maximum values near the caudal peduncle has usually been explained by the observation that this is the point of highest flexion (maximum amplitude and lateral velocity). Because of the small total muscle area at the caudal peduncle, however, the absolute forces and red muscle mass required at this point would be relatively small. A more accurate measure of the longitudinal distribution of red muscle power development would be the absolute area (per unit length) of red muscle tissue (Q_n). Considering all sizes of fish, this value is highest at about 50 % along the length of the muscle mass. At this point along the fish the lateral velocity would be intermediate in magnitude but the total muscle area would still be large. There is a general tendency, with increased fish size, for the section where Q_n is at a maximum to move posteriorly. This may reflect the scaling of length-specific body wavelength (flexibility) which has been reported for rainbow trout (Webb *et al.* 1984).

The magnitude of allometric scaling for red muscle mass ($L^{3.62}$) is greater than the scaling of power requirements during sustained aerobic swimming predicted from hydrodynamic theory. Scaling functions predicted from the drag model (Bainbridge, 1961) for the rate of work during aerobic swimming are $L^{2.75}$ and $L^{3.2}$, assuming laminar and turbulent flow, respectively. These relationships are based on sustained swimming performance ($L\,s^{-1}$) increasing as $L^{0.5}$ (Wu, 1977; Beamish, 1978). The bulk momentum model of Lighthill (1970) predicts a scaling function of $L^{3.52}$ for the same level of performance (Webb, 1977).

These direct comparisons of the scaling function for red muscle mass and the power requirements during aerobic swimming assume that the mass-specific power output of red muscle tissue is not influenced by size. Because we are considering sustainable swimming speeds, however, it must be that the continuous aerobic production of energy by red muscle tissue decreases with increased size. This type of scaling relationship is true for both whole-body metabolic rate and, based on enzymatic data, locomotor muscle tissue (Somero & Childress, 1980). The sustainable mass-specific power output of larger fish, therefore, is likely to be lower according to the scaling of aerobic respiration (i.e. $M^{0.81}$; Winberg, 1960). In addition, the average mass-specific power output of red muscle will be proportional to its frequency of contraction. Although no information appears to be available on the scaling of contraction time for fish red muscle, data for white muscle contraction time (Wardle, 1975) and tail-beat frequency during aerobic swimming (Webb *et al.* 1984) suggest that mass-specific power output for red muscle should be greater for small fish. The observed allometry in red muscle growth would provide some compensation for a decrease in mass-specific power output with increased size.

Interspecific studies of anaerobic potential in fish suggest that some relationship exists between anaerobic and aerobic metabolism. Extremely high LDH activities (Guppy & Hochachka, 1978) and lactate production (Pritchard *et al.* 1971) are seen among the scombrids; fish with very high aerobic scope. In contrast, sluggish species, such as the flathead sole, appear to show much lower anaerobic capacity (Turner *et al.* 1983*b*). This relationship could exist because fish which generate high levels of lactate must also have high aerobic capacity to metabolize the lactate and resynthesize glycogen. Alternatively, it may not be whole-body aerobic capacity *per se* but rather the amount of red muscle present that is important; red muscle tissue is believed to be involved in the metabolism of anaerobic endproducts (Wittenberger *et al.* 1975). These two possibilities cannot be resolved in interspecific comparisons since aerobic capacity and red muscle mass are usually correlated. However, in the present (intraspecific) study, increased mass-specific anaerobic potential was observed in large fish in spite of the decrease in aerobic metabolism which occurs with increased size. The similar pattern of scaling for anaerobic metabolism and red muscle mass in the present study suggests, therefore, that the general association between aerobic and anaerobic metabolism may be related more to increased red muscle metabolism than to overall aerobic capacity.

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