MECHANICAL PROPERTIES OF THE MYOTOMAL MUSCULO-SKELETAL SYSTEM OF RAINBOW TROUT, *SALMO GAIRDNERI*

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SUMMARY

Net forces and velocities resulting from *in situ* contractions of the myotomal musculature on one side of the body were measured at the hypural bones. Forces, velocities and power were determined with the body bent into a range of postures typical of those observed during fast-start swimming. For trout averaging 0.178 m in length and 0.0605 kg in body mass, the muscle system exerts a maximum normal force of 2.2 N at the base of the caudal fin. This force is equivalent to 11.8 kN m^{-2} based on the mean cross-sectional area of the myotomal muscle. The maximum velocity was 1.11 m s^{-1}, and the maximum mechanical power output, 0.64 W, or 42.4 W kg^{-1} muscle.

Based on estimates of swimming resistance, these results would suggest acceleration rates of 7.5 to 16.5 m s^{-2}, similar to averages observed during fast-starts. Maximum sprint speeds would range from 6.5 to 17.8 body lengths s^{-1}, spanning the range of maximum speeds reported in the literature. It is suggested that maximum speed is limited by interactions between muscle contraction frequency and endurance.

Losses in the mechanical linkages between muscle fibres and propulsive surfaces were estimated at about 50 % for power with possibly greater losses in force transmission.

Maximum force and power did not vary over the range of postures tested, supporting Alexander's (1969) suggestions that white muscle should contract over a small portion of the resting length of the fibres.

INTRODUCTION

Most knowledge of fish locomotion is derived from studies of swimming kinematics and rates of oxygen consumption (Bainbridge, 1958, 1963; Brett, 1964; Brett & Glass, 1973) and is usually interpreted within a framework derived from hydromechanical models (Webb, 1975; Wu, 1977; Wu & Yates, 1978; Webb, Kostecki & Stevens, 1984). Fairly good agreement has been found between power requirements predicted from these models and observed oxygen consumption rates for fish swimming at steady cruising speeds (Webb, 1971, 1975). However, few data exist for power

available and swimming resistance at high swimming speeds and acceleration rates, activities where energy requirements are not immediately met *via* oxygen consumption (Wardle, 1977; Jones, 1982).

High performance activities are powered anaerobically by the myotomal muscles (Hudson, 1973; Blight, 1977; Bone, Kicenuik & Jones, 1978), which comprise up to 55 % of total body mass (Webb, 1978). Therefore, the dynamic properties of the musculo-skeletal system could be measured to determine power input for fish burst swimming performance, which in turn could be used to evaluate performance limits (Gray, 1936; Wardle, 1975).

However, the geometric arrangement of mechanical components within the fish muscle system is extremely complex (Nursall, 1956; Willemse, 1966; Alexander, 1969. Wainwright, 1983). Although the physiology of fish muscle fibres themselves does not differ substantially from that of other vertebrates (Johnston, 1981, 1983), the functional consequences of the complex musculo-skeletal geometry are unknown. Thus, useful forces transmitted through the system cannot be predicted from the muscle properties alone.

The present experiments examine the performance of the myotomal musculo-skeletal system by evaluating net forces and velocities at the body surface resulting from *in situ* contractions of fish axial musculature. The approach treats the myotomal system as a black box whose principal action is to bend the body when its isotonic force-velocity relationships can be quantified for typical swimming postures.

MATERIALS AND METHODS

Fish

Rainbow trout (*Salmo gairdneri* Richardson) were obtained from a local hatchery. Fish were kept in 200-litre oval tanks, and acclimated to 14 °C, the temperature of the preparation used in experiments described below, for at least 3 weeks prior to experiments. Tanks were continuously flushed with water, and a submerged pump generated a current against which fish swam. Air stones were used to maintain dissolved oxygen levels close to air saturation.

Procedure

Individual fish were carefully netted with minimal chasing and quickly (<1 s) immersed in water containing 1:10 000 tricaine methanesulphonate (MS 222). Respiratory movements ceased in approximately 5 min, and fish did not respond to tactile stimuli. Total body mass was then measured to the nearest 0·01 g and fork length to the nearest 0·1 cm.

Myotomal muscle was removed from one side of the body and an inelastic thread was sewn through the centre of the hypural complex. This 'half-myotomal' preparation was placed on its side on a holding apparatus with the intact muscle upwards (Fig. 1). The head was clamped firmly up to the cleithrum, while the remainder of the body lay freely on a rigid aluminium template, 0·64 cm thick. The template was oriented to apply forces and measure velocities normal to the hypural complex. The thread
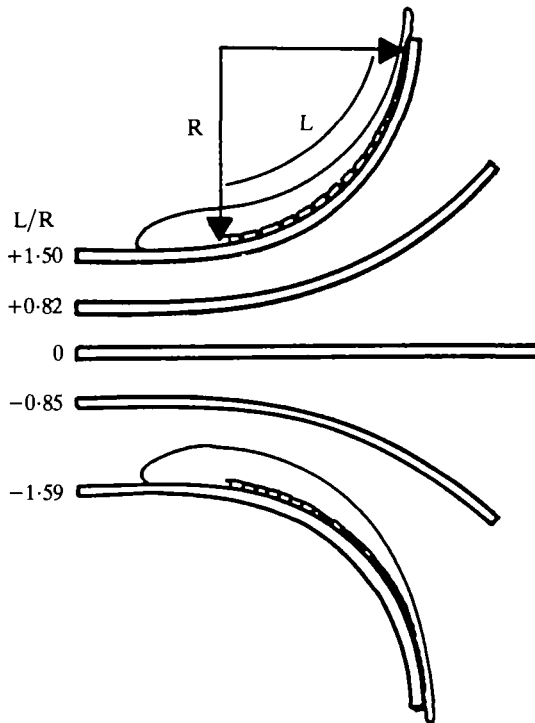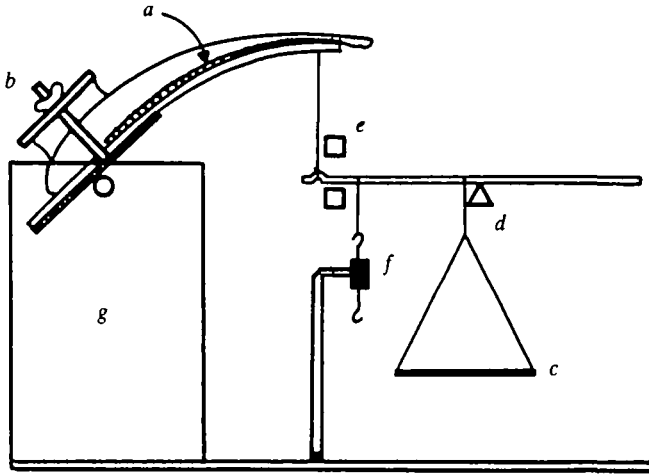
Fig. 1. Holding apparatus used in isotonic experiments showing the half-myotomal preparation on different curved templates. Top: *a*, fish backbone; *b*, head clamp; *c*, pan for applying a range of loads to the preparation; *d*, beam fulcrum; *e*, adjustable stops; *f*, isotonic displacement transducer and *g* rigid Plexiglas base. Bottom: replaceable curved aluminium templates with different curvature radii and mean L/R values for experimental fish.

attached to the hypural complex passed through a slit in the template and was connected to a low-mass beam parallel to the caudal fin. Muscle contractions lifted loads attached to the beam close to a fulcrum. Adjustable stops were used to limit caudal

Table 1. *Morphometric measurements for fish used in isotonic experiments*

Posture L/R	Length (cm)	Body mass (g)	Myotome length, L (cm)	Mean muscle cross-sectional area (cm^2)	Muscle mass (g)	N
-1.59 ± 0.08	18.5 ± 1.1	66.76 ± 13.21	12.4 ± 0.6	2.0 ± 0.2	17.11 ± 3.36	5
-0.85 ± 0.07	18.2 ± 1.7	61.95 ± 17.02	12.3 ± 1.0	1.8 ± 0.3	15.90 ± 4.56	5
0	18.2 ± 1.4	61.38 ± 15.77	12.2 ± 1.0	2.0 ± 0.3	15.50 ± 4.44	5
$+0.82 \pm 0.09$	17.7 ± 4.2	61.64 ± 24.93	11.9 ± 1.3	2.0 ± 0.4	15.45 ± 6.91	4
$+1.50 \pm 0.18$	16.8 ± 1.7	48.63 ± 19.40	11.5 ± 1.1	1.7 ± 0.5	11.13 ± 5.10	4
Grand	17.9 ± 0.8	60.05 ± 7.63	12.1 ± 0.5	1.9 ± 0.2	15.17 ± 2.12	23
P	0.6646	0.7120	0.7822	0.6468	0.5293	

L/R represents posture as relative radius of curvature.
Values are given as mean ± 2 s.e.
P values are given from analysis of variance to test for differences between groups.
N = number of fish in each group.

fin excursions to 1 cm to sample discrete postures when contractions would occur over small changes in fibre length. An isotonic myograph transducer was connected to the lever to measure tail velocities normal to the caudal fin as muscle contractions bent the body, raising the tail. Velocities were displayed on an oscilloscope, and were recorded on tape and a pen recorder.

Several template shapes were used to bend the body into a range of curved postures typical of those seen in burst performances (Fig. 1). These were based on body postures during fast-starts when body bending geometry is most simple and performance is maximal (Weihs, 1973; Eaton, Bombardieri & Meyer, 1977; Webb, 1978). Postures were quantified in terms of relative radius of curvature, L/R, where L is myotome length measured from the posterior edge of the cleithrum to the point of thread attachment to the hypural complex, and R is radius of curvature. This also provides an index of relative muscle length. The ratio L/R is zero when the body is stretched-straight, positive when the contracting muscle is on the concave side of a bend (muscle fibres are shorter than resting length), and negative when on the convex side (fibres stretched relative to resting length).

Intramuscular electrodes were inserted into the myotomal muscle at 1-cm intervals. Muscle contraction was elicited by a d.c. stimulus of 10 V cm^{-1} for 10 ms, determined as the minimum stimulus giving maximum contraction in preliminary experiments. Approximately 20 s was allowed between contractions. Velocities measured for the hypural complex were compared for each stimulus. Velocities for a given load were constant for about 8 min before declining due to fatigue. Data from fatigued muscle were rejected. The long period of constant muscle performance in the repeated contractions suggests that the small but inevitable amount of swimming by the fish at capture did not affect the performance of the preparation.

At the end of an experiment the length of the myotome, L, was measured. Tracings were made of muscle cross-sections at 8 to 11 equal intervals along the myotome length. Muscle cross-sectional areas were determined from these tracings. Myotomal muscle was also separated from the vertebral column, spines, abdominal ribs and skin, and weighed to the nearest 0·01 g. Intramuscular bones were included with the

muscle. There were no significant differences ($a = 0.2$) between classes for morphometric measurements that might influence measured muscle properties (Table 1).

Analysis

Best-fit relationships between force and velocity were calculated for each preparation using linear regression techniques. Maximum force, velocity and power output were calculated from force-velocity equations. These data were normalized to obtain values of specific velocity (lateral velocity of the hypural bones/L), specific power (power output/muscle mass on one side of the body) and specific force (lateral force at the hypural bones/mean cross-sectional area of the muscle). Force is commonly normalized by mean muscle cross-sectional area (McMahon, 1984). This average was used here as a reproducible area probably correlated with true physiological cross-sectional area. The details of the geometry of the myotomal musculo-skeletal system are still unclear (Wainwright, 1983) so that the latter is unknown.

Analysis of variance was used to examine the effect of posture on these variables. Simple pairwise comparisons (Scheffe's confidence interval approach) were used to examine differences between posture classes (Neter & Wasserman, 1974).

RESULTS

The specific force generated by contraction of the myotome, measured at the hypural bones, was inversely related to velocity measured normal to the hypural complex (Fig. 2). This is consistent with expectations from other studies of muscle mechanics (Abbott & Wilkie, 1953; Close, 1965; Lannergren, 1978). The force-velocity relationships were best described by simple linear regressions ($P < 0.006$). Hill's equation, appropriate for single muscle fibres and many muscle preparations, did not describe the force-velocity data well. This departure from Hill's equation is probably related to the complex geometry of muscle, connective tissue and skeleton in fish myotomes.

Posture had no significant effects on maximum specific force ($P = 0.63$), maximum specific velocity ($P = 0.29$) or maximum specific power output ($P = 0.66$) of the musculo-skeletal preparation (Fig. 3). The maximum specific force was $11.8 \pm 1.02 \, \text{kN m}^{-2}$ ($\bar{X} \pm 2 \, \text{s.e.}$). The muscle had a mean cross-sectional area of $1.9 \times 10^{-4} \, \text{m}^2$, so that the maximum normal force at the hypural complex was $2.2 \, \text{N}$. Maximum specific velocity at the hypural plates was $9.2 \pm 0.08 \, \text{L s}^{-1}$ ($1.11 \, \text{m s}^{-1}$). Maximum specific power output was $42.4 \pm 4.33 \, \text{W kg}^{-1}$ muscle or $0.64 \, \text{W}$ for a half-myotomal muscle mass of $0.0152 \, \text{kg}$.

Although these maxima were independent of posture, some trends in the data occurred (Fig. 3). Maximum specific velocity and specific power were somewhat higher when the body was stretched-straight compared to curved postures. Maximum specific force appeared higher when L/R was negative, decreasing as L/R became positive. However, these trends were not statistically significant ($P < 0.2$).

DISCUSSION

The experiments evaluate the net dynamic properties of the fish myotomal
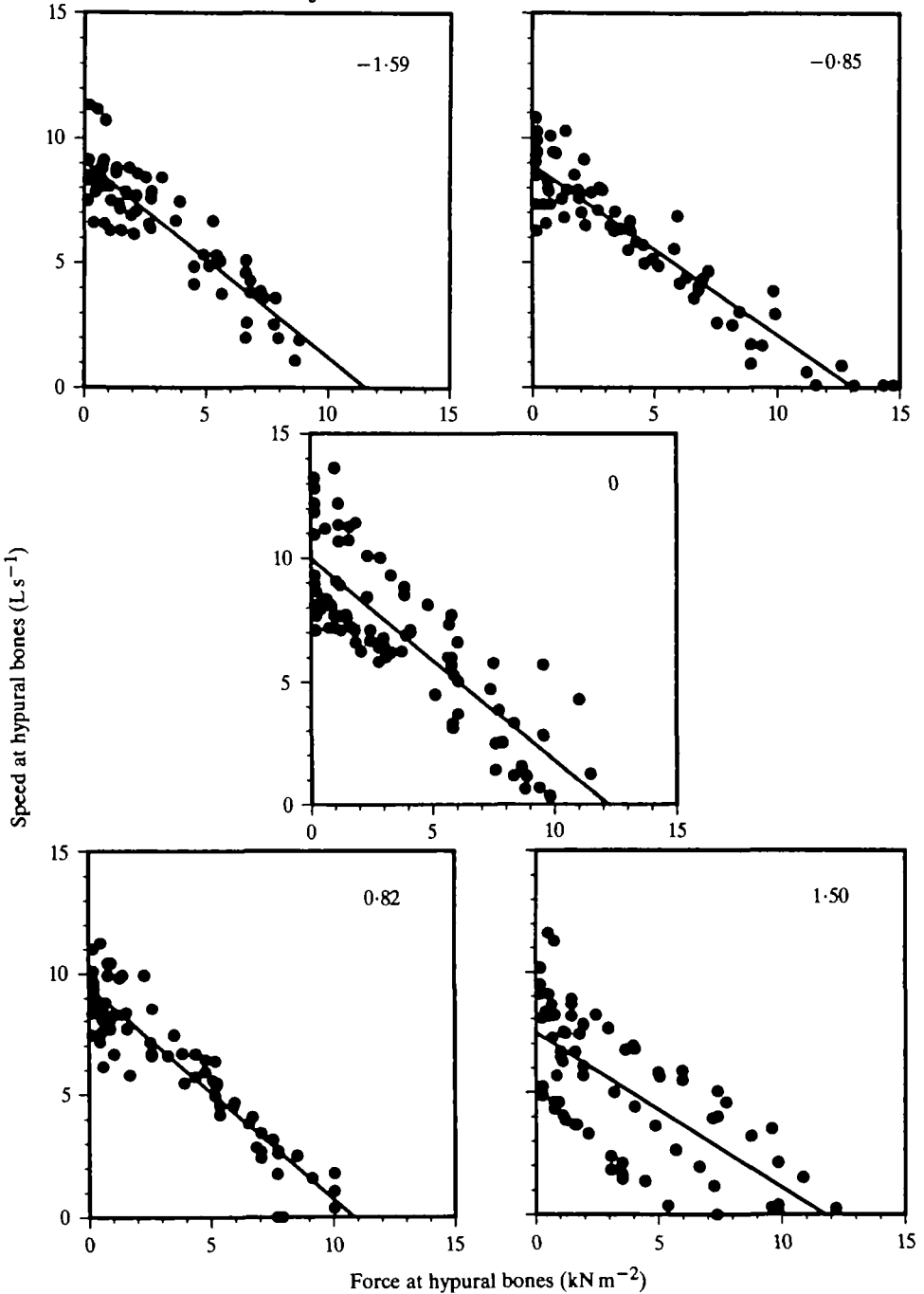
Fig. 2. Relationships between force and speed of the hypural complex for the five posture classes used in isotonic experiments. Regression lines are from data pooled within each class. L/R values are given in the top right-hand corner of each plot.

musculo-skeletal system that drives axial propulsion, and hence could be used to examine limits on burst swimming performance.

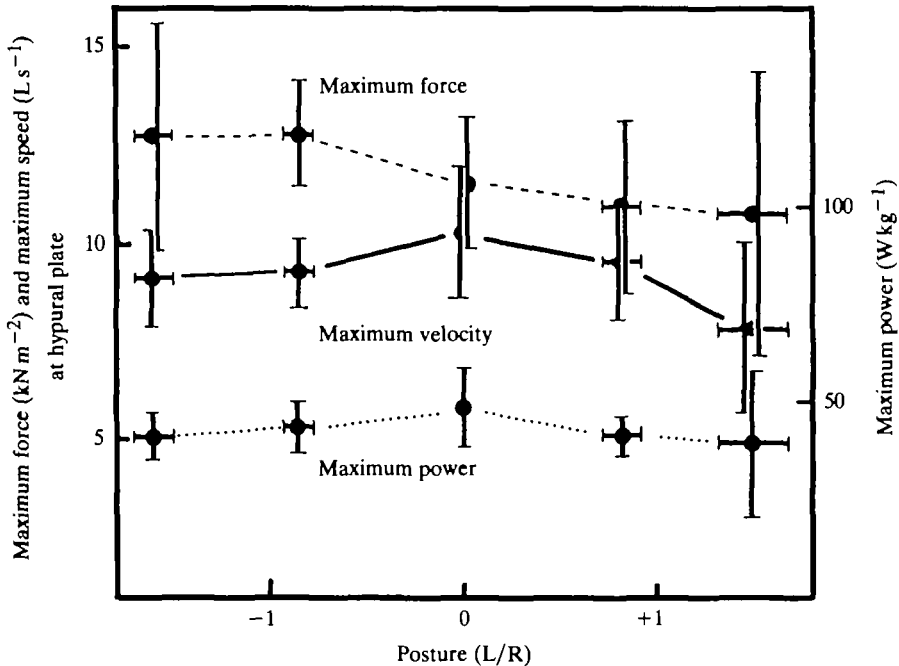However, before doing this, the validity of using the myotomal preparation must

Fig. 3. Relationships between posture and maximum force, maximum velocity and maximum specific power output calculated using individual force-velocity equations of the hypural complex and morphometric data from 23 fish. Values were pooled within each posture class, and are given as mean ± 2 s.ᴇ.

be considered. The shapes of the preparations modelled the body in fast-starts when C-postures are typical (Weihs, 1973; Eaton *et al.* 1977; Webb, 1978) and the whole myotome contracts together to maximize performance (Kashin, Feldman & Orlovsky, 1979; Johnsrude, 1984). However, during steady swimming the body is usually bent into S-shaped postures (Bainbridge, 1958, 1963). At low to moderate swimming speeds, waves of contraction pass caudally along the myotomal muscles as these muscles contract in sequence (Grillner & Kashin, 1976; Blight, 1977). No systematic investigation of myotomal muscle activity during sprints has yet been reported. However, it appears from available electromyographs for fish moving rapidly (Grillner & Kashin, 1976; Blight, 1977; Kashin *et al.* 1979) that the contraction wave pattern characteristic of slow, steady speeds converges on one where contractions of homolateral muscles are more nearly simultaneous at very high speeds. This is further supported by Hess & Videler (1984). Therefore, the maximum performance of the half-myotomal preparation undoubtedly reflects maximum net forces and power available for sprint speeds.

The preparation also differs from real swimming in that forces and velocities were measured at one point, whereas hydrodynamic forces would be distributed along the body length. However, contractions of homolateral myomeres would be expected to summate along the length of the myotome in the absence of water. Furthermore, most work is done caudally against the water. During locomotion, lateral velocity, W, of the body increases caudally, especially in fast-starts (Hertel, 1966; Weihs, 1973; Webb, 1982). The force at any point on the propulsive surface is proportional to the square

of this velocity and to the local added mass, the latter a function of the square of body depth, D (see Lighthill, 1975). The caudal fin, supported by the hypural complex, has a large added mass, associated with the largest lateral velocities. Therefore, the force exerted at the hypural complex measurement position is expected to represent most of the total muscle force exerted during swimming. The product of W^2 times D^2 was calculated from data available for sprinting fish in Bainbridge (1963) and for fast starts in Weihs (1973) and Webb (1982). It was found that the caudal fin contributed at least 75 % of the total thrust.

The use of the half-myotomal preparation could yield larger forces than are actually exerted against water. This is because viscoelastic effects of contralateral tissue (removed in the preparation) would dissipate some energy. In practice the effect of removing one side of the myotome is probably negligible.

Overall, the preparation should provide good estimates of the maximum dynamic performance of the musculo-skeletal system.

Performance

Estimates of muscle performance have been traditionally important in attempts to deduce the limits of swimming performance. Earlier attempts assumed that the mechanical properties of the fish axial muscle system were the same as for muscle from tetrapod limbs (see Bainbridge, 1961), implicitly regarding the complex muscle-skeleton geometry as unimportant. The present experiments attempt to address this assumption, so that the measured forces and power outputs should be more appropriate to calculate maximum swimming performance.

Fast-starts

The forces measured for the half-myotomal preparation can be used to estimate performance in fast-starts. Then, acceleration resistance, F, is (Webb, 1982):

$$F = (M_b + M_a)A, \qquad (1)$$

where M_b = total body mass, M_a = added mass contributing to net resistance and A = acceleration rate. The sum of $(M_b + M_a)$ is the 'apparent mass'. For 0·27-kg trout used by Webb (1982), this was $1·2(M_b)$. It is assumed that the same relationship applies to the 0·060-kg trout used in the present experiments, so that the inertia of the system to be accelerated would be 0·071 kg. The force at the hypural complex was 1·1 N at maximum power output, but if the contraction were initially close to isometric, the musculo-skeletal system could deliver about 2·2 N. Based on illustrated fast-start sequences for trout (see Weihs, 1973; Webb, 1976), the thrust component averages about 50 % of the normal force exerted at the caudal fin base. Then trout would accelerate at rates of $7·5-16·5 \, m \, s^{-2}$. These values are similar to average acceleration rates observed in fast-starts (Weihs, 1973; Webb, 1976, 1978).

Maximum swimming speed

Maximum swimming speed could be limited by one or more of: (a) force generated by the musculo-skeletal system; (b) muscle power output (Bainbridge, 1961); (c) maximum tail-beat frequency and stride length (Wardle, 1975). Speeds calculated by
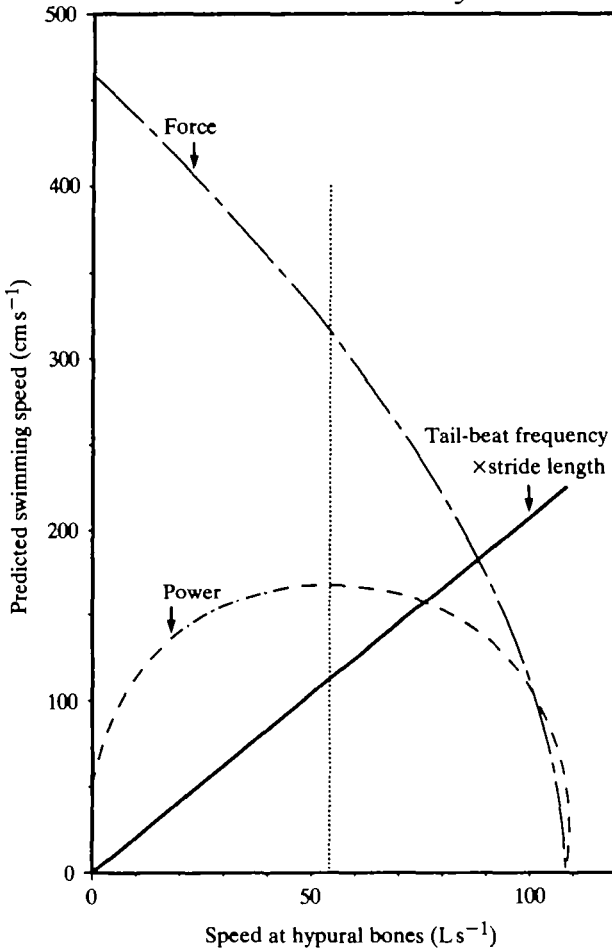
Fig. 4. Relationships between predicted swimming speeds and the dynamics of the myotomal musculo-skeletal system based on regression of pooled data for all experiments. Swimming speeds were calculated for the force, power and maximum tail-beat frequencies calculated for each speed of the tail.

the three methods are shown in Fig. 4 as a function of the velocity measured at the hypural complex for the half-myotomal preparation.

Sprint speeds associated with the force generated for the range of muscle contraction velocities were calculated by equating force to drag, where drag is given by:

$$\text{drag} = \text{muscle force} = \tfrac{1}{2}\rho S U^2 C_D K \ (\cos \theta), \tag{2}$$

where ρ = density of water, S = wetted surface area ($0 \cdot 0108 \, \text{m}^2$ from Webb, 1976), U = swimming speed, C_D = drag coefficient for an equivalent flat plate, K = modifier for drag increments of a self-propelling flexing body. K was taken as 4 (Alexander, 1967; Webb, 1975) and θ = angle subtended by the tail to the direction of motion, which takes values of about 18° (Wu, 1971; Webb, 1975, 1977).

The boundary layer is assumed turbulent. Then,

$$C_D = 0 \cdot 016 U^{-0 \cdot 2}. \tag{3}$$

Sprint speeds expected for the muscle power output were calculated by equating power at various contraction velocities to the power required to overcome drag. The power required to overcome drag was obtained from equation 2, with both sides multiplied by U and replacing $\cos\theta$ with Froude efficiency, assumed to be 0·95 (Wu, 1971).

The third method of estimating speed derives from ideas developed by Wardle (1975). He argued that the limit of fish swimming speed is determined by the minimum twitch time of the myotomal muscle. He calculated maximum tail-beat frequency from the twitch time, which gives swimming speed when multiplied by stride length (the distance travelled per beat, independent of swimming speed). Bainbridge (1958) found the stride length of rainbow trout was about 70% of total length.

Twitch times were not recorded here. Instead maximum tail-beat frequencies were calculated from maximum speeds of the hypural bones of the musculo-skeletal preparation and the expected tail-beat amplitude. The latter data were obtained from Bainbridge (1958) when the amplitude would be 0·03 m for fish of the size used here. This gives a value of tail-beat frequency of 9·3 Hz at maximum power output. In contrast, the minimum twitch time measured by Wardle (1975) for fish of the size used here and at the same temperature was 27 ms, giving a maximum tail-beat frequency of 18·5 Hz. These two methods would be expected to give comparable values for maximum tail-beat frequency. The difference suggests that contractions may be prolonged beyond the duration of a single twitch in order to complete a tail beat at maximum sprint speeds. Webb (1980) also found times required to complete tail beats in fast-starts were longer than the minimum twitch times measured by Wardle. This implies that the attractively simple method of calculating maximum sprint speeds as described by Wardle is inadequate.

The three approaches to estimating speed limits do not give a common intersection (Fig. 4) and predicted maximum speeds were quite variable, ranging from 6·5 to 17·8 L s^{-1} (body lengths per second). Thus the maximum power output of the muscle (0·64 W) could support a maximum speed of 1·65 m s^{-1} (9·3 L s^{-1}), while the thrust at maximum power (1·1 N) is sufficient to propel the fish at 3·17 m s^{-1} (17·8 L s^{-1}). However, at maximum muscle power, the tail-beat frequency would be 9·3 Hz, sufficient to propel the fish at only 1·15 m s^{-1} (6·5 L s^{-1}). These speeds are in the published range of 2 to 17 L s^{-1}, but sprint speeds for salmonids of the size used in the present experiments typically fall around 11 L s^{-1} (Bainbridge, 1958; Blaxter, 1969; Beamish, 1978). Then the maximum speed of 17·8 L s^{-1}, predicted from forces, seems much too high, while that of 6·5 L s^{-1}, obtained from the tail-beat frequency at maximum power, is too low. Therefore, maximum speeds are presumably determined by some combination of muscle force, power and contraction speed. Reconciling sprint speed and the musculo-skeletal system properties is most easily considered at the intersection points of the various curves shown in Fig. 4.

The intersection point of the swimming speed curves based on power and tail sweep speeds would represent the most obvious combination limiting speed as this is the only point where speeds possible on the basis of the third factor, force, exceed that expected of the intersection. Here, the maximum speed would be about 8·5 L s^{-1} at a tail-beat frequency of 12 Hz. However, Bainbridge (1958) showed that

trout of the size used should swim at about 11 L s^{-1} with a tail-beat frequency of about 17 Hz. Therefore, maximum performance is not predicted by an interaction between power and speed of contraction of the muscle.

The intersection between the swimming speed curves based on thrust and tail sweep speeds occurs at 10·3 L s^{-1} and a tail-beat frequency of 15 Hz, which is close to expectations (Bainbridge, 1958). However, the measured power appears inadequate to support such speeds. In practice, higher power outputs might be possible in swimming fish if the muscle were rapidly stretched prior to contraction (Abbott & Aubert, 1952; Cavagna, Komarek & Mazzoleni, 1971; Cavagna, Citterio & Jacini, 1980). Alternatively, power output may be an inappropriate measure of the way energy is used. Instead, there could be a finite energy reserve available which can be used over a variable period of time. For example, the muscles of a fish swimming at 1·65 m s^{-1} do 0·64 J of work every second. A speed of 1·84 m s^{-1} (10·3 L s^{-1}) corresponds to the same amount of work done in 0·8 s, at an average muscle power output of 0·8 W. Higher swimming speeds are sustained for shorter periods (Bainbridge, 1958; Beamish, 1978), but there are no observations of both speed and endurance for speeds maintained for very short periods.

Therefore we suggest that speed limits of fish depend on the interplay of muscle contraction speeds, muscle force, and power and endurance, and that no single factor can be used to predict maximum speed.

Muscle losses in musculo-skeletal connections

The observations on the myotomal musculo-skeletal system can be used to obtain crude estimates of the effectiveness of transmission of muscle force and power to propulsive surfaces by comparing the performance of the preparation with that of excised muscles. Myotomal muscle forces are transmitted through mechanical linkages of myosepta, horizontal septa, dermis and vertebrae, all of which could modify the useful muscle force converted into thrust, and waste energy (Wainwright, 1983). Maximum isometric tensions developed by teleost fast fibres range from 40 to 186 kN m^{-2}, and maximum power is about 80 W kg^{-1} (Bainbridge, 1961; Flitney & Johnston, 1979; Altringham & Johnston, 1982; Johnston & Salamonski, 1984). These compare to maximum forces of the preparation of 12 kN m^{-2} and maximum power of 42 W kg^{-1}, suggesting 70–94 % the muscle force is lost in transmission and 47 % of the power dissipated. These values are probably somewhat high especially for force transmission because appropriate cross-sectional areas for the myotomal preparation are unknown. For example, specific forces based on maximum cross-sectional area instead of the mean would reduce the force transmission losses by half. Nevertheless, it is apparent that substantial losses in muscle performance occur in the mechanical linkages between the fibres and the propulsive surfaces.

Muscle dynamics and fibre length

The experiments showed that posture has no significant effect on the dynamics of the whole myotomal system (Fig. 3). Experimental studies on excised vertebrate muscle have shown an inverted U-shaped curve relating muscle stress and fibre length (Gordon, Huxley & Julian, 1966; McMahon, 1984). Since muscle length should be related to posture, a similar curve might be expected for the fish myotomal preparation.

The absence of an inverted U-shape relationship between maximum force and power with posture probably relates to the organization of muscle fibres in the myotome. In his mathematical analysis of myotomal muscle fibre trajectories, Alexander (1969) predicted that teleost fibres should only shorten by a small proportion of their resting length over the range of postures seen in steadily swimming and accelerating fish. He also suggested that the white muscle should maximize power output. Under these conditions, the myotomal muscle should not only work on the plateau region of the force-length relationship, but changes in length over the normal physiological range should not substantially change force and power output. The independence of maximum force and power with posture of the myotomal preparation confirms Alexander's suggestions. In addition this indicates that the myotome can sustain delivery of large forces to the caudal fin over the whole range of the amplitude swept by the tail during normal fish locomotion.

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