POWER OUTPUT AND FORCE–VELOCITY RELATIONSHIP OF LIVE FIBRES FROM WHITE MYOTOMAL MUSCLE OF THE DOGFISH, *SCYLIORHINUS CANICULA*

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Summary

1. The relationship between force and velocity of shortening and between power and velocity were examined for myotomal muscle fibre bundles from the dogfish.

2. The maximum velocity of shortening, mean value $4 \cdot 8 \pm 0 \cdot 2 \, \mu m \, s^{-1}$ half sarcomere^{-1} ($\pm$S.E.M., $N = 13$), was determined by the 'slack step' method (Edman, 1979) and was found to be independent of fish length.

3. The force–velocity relationship was hyperbolic, except at the high-force end where the observations were below the hyperbola fitted to the rest of the data.

4. The maximum power output was $91 \pm 14 \, W \, kg^{-1}$ wet mass ($\pm$S.E.M., $N = 7$) at a velocity of shortening of $1 \cdot 3 \pm 0 \cdot 13 \, \mu m \, s^{-1}$ half sarcomere^{-1} ($\pm$S.E.M., $N = 7$). This power output is considerably higher than that previously reported for skinned fibres (Bone *et al.* 1986). Correspondingly the force–velocity relationship is less curved for intact fibres than for skinned fibres.

5. The maximum swimming speed (normalized for fish length) predicted from the observed power output of the muscle fibres decreased with increasing fish size; it ranged from $12 \cdot 9$ to $7 \cdot 8$ fish lengths s^{-1} for fish $0 \cdot 155 – 0 \cdot 645 \, m$ in length.

Introduction

There has been much interest in measuring maximum speed at which fish can swim (burst swimming) (reviewed by Beamish, 1978) and in describing the quantitative relationships among the factors that determine the power required to achieve this speed (Lighthill, 1971). The maximum power output of the muscle fibres must, of course, be no less than the power required to move the fish at its maximum swimming speed. The power that the fibres can produce has seldom been measured, and these measurements have been made on fibres from which the surface membrane has been removed and the intracellular solution replaced

('skinned fibres', Altringham & Johnston, 1982; Bone *et al.* 1986). Results from muscle fibres from frog show that, at least in this species, the power output is lower in skinned fibres than in live fibres (Ferenczi *et al.* 1984). It therefore seems desirable to measure power output of live, intact fibres from myotomal muscle of fish.

Fish length is one of the important variables that determines the maximum swimming speed. We have therefore investigated whether the mechanical characteristics of the muscle fibres depend on the length of the fish.

Some of the results have been reported in a preliminary form (Curtin & Woledge, 1987).

Materials and methods

Dogfish, *Scyliorhinus canicula* (L.), of a wide range of sizes were obtained from holding tanks in the Marine Biological Association Laboratory in Plymouth, where they were stored in circulating sea water at about 16°C. Fish were killed by decapitation followed by pithing and thin slices of white muscle were cut from the immediately postanal region of the body. Bundles of 1–10 fibres were dissected under saline solution, taking care to preserve a strong tendon at each end. Aluminium T-clips (Ford *et al.* 1977) were attached to these tendons. The saline solution contained (mmol l^{-1}): NaCl, 292; KCl, 3·2; CaCl$_2$, 1·8; MgCl$_2$, 2·2; Na$_2$SO$_4$, 3·5; NaHCO$_3$, 5·9; urea, 483; and curare, 1·5 mg l^{-1}; it is similar to that used by Stanfield (1972). Preparations were mounted in a bath of saline solution maintained at 12 ± 0·5°C, between a force transducer (Cambridge Technology Inc., model 401) and a combined motor and length transducer (Cambridge Technology Inc., model 300H). Electrical stimuli (2 ms square waves) were delivered *via* bright platinum wire electrodes positioned on either side of the fibre bundle. The sarcomere length of the unstimulated muscle fibres in the bath could be observed by diffraction of light from a He/Ne laser. Length and force records were made on a digital oscilloscope (Nicolet Instrument Corp., model 4094) and stored on floppy disks for later analysis.

The usual experimental protocol, which was followed with each preparation, was first to observe a stimulus strength–response curve for twitches, from which the number of active fibres could be estimated. The fibre length was then varied to find the length optimum for twitch force development. A series of observations was then made for determining the maximum velocity of shortening by the 'slack step' method (Edman, 1979). This was followed by a series of short tetanic contractions (0·3–0·7s at 30–40 Hz), repeated at regular intervals of 3–5 min, to measure the force–velocity curve. Shortening started after force had developed under isometric conditions and the fibre length was then altered at a constant velocity (see Fig. 2A). The distance shortened was kept constant for each fibre bundle and the range for all bundles was 6–11 % of fibre length.

At the end of the series of observations the sarcomere length was observed over the range of fibre lengths used. The fibre length and widths were measured with an

eyepiece micrometer under the dissecting microscope. We noted that all the fibres within a bundle appeared to have the same diameter, in contrast to preparations from amphibians. For fish lengths between 0·355 and 0·645 m, the range of fibre lengths was 3·3–7·6 mm and fibre diameter was 75–240 μm; correlation among these variables was obvious. In the one smaller fish used (0·155 m length), the fibre length was 1·3 mm and the fibre diameter was too small to be measured in the dissecting microscope. The fibre length and sarcomere length were used to estimate the number of sarcomeres in the fibre, and this number was used to convert the velocity of shortening to units of $\mu m \, s^{-1}$ half sarcomere^{-1}.

Curve fitting

The following equation was fitted to the data for each fibre bundle:

$$P'/P_0^* = (1 - V'/V^*)/(1 + GV'/V^*)$$

where P' is force during shortening at velocity V', P' is expressed as a fraction of the isometric force at the same fibre length (see Fig. 2A), V' is expressed as a fraction of the maximum velocity of shortening determined by the slack step method described above and P_0^*, V^* and G are constants; G is analogous to P_0/a of Hill (1938) (see Woledge *et al.* 1985, p. 49) and indicates the curvature of the force–velocity relationship. In selecting the values for the constants, the fitting procedure minimized the squares of the deviations of predicted force from the observed value; all points were given equal weighting. Fitting was done with the results for each fibre bundle (1) including the isometric value, $P' = 1·0$ and $V' = 0$, and (2) excluding these values (Edman *et al.* 1976; Edman, 1986). Among all the results for shortening, the highest force value was $P' = 0·86$.

Results

Maximum velocity of shortening

The slack step method (Edman, 1979) was used to determine the maximum velocity of shortening, V_0. The graphs of distance shortened *vs* duration of shortening were linear for distances between 6·1 ± 0·6 % and 12·9 ± 0·8 % (±S.E.M., $N = 13$) of the fibre length; this indicates that the maximum velocity of shortening is constant over this range. The fibres may have been able to shorten at V_0 over longer distances; we did not test this. Fish of widely different sizes were used (range of fish length 0·155–0·645 m, mass 10–860 g). The smallest was a newly hatched specimen, and the largest was close to the maximum length to which this species grows. Fish length and fibre length were clearly correlated. To determine whether the maximum velocity of shortening at the level of the sarcomere depended on fish size, the values of V_0 were expressed in units of $\mu m \, s^{-1}$ half sarcomere^{-1} (see Materials and methods). The values in Fig. 1A show that the maximum velocity of filament sliding does not change as the dogfish grows.
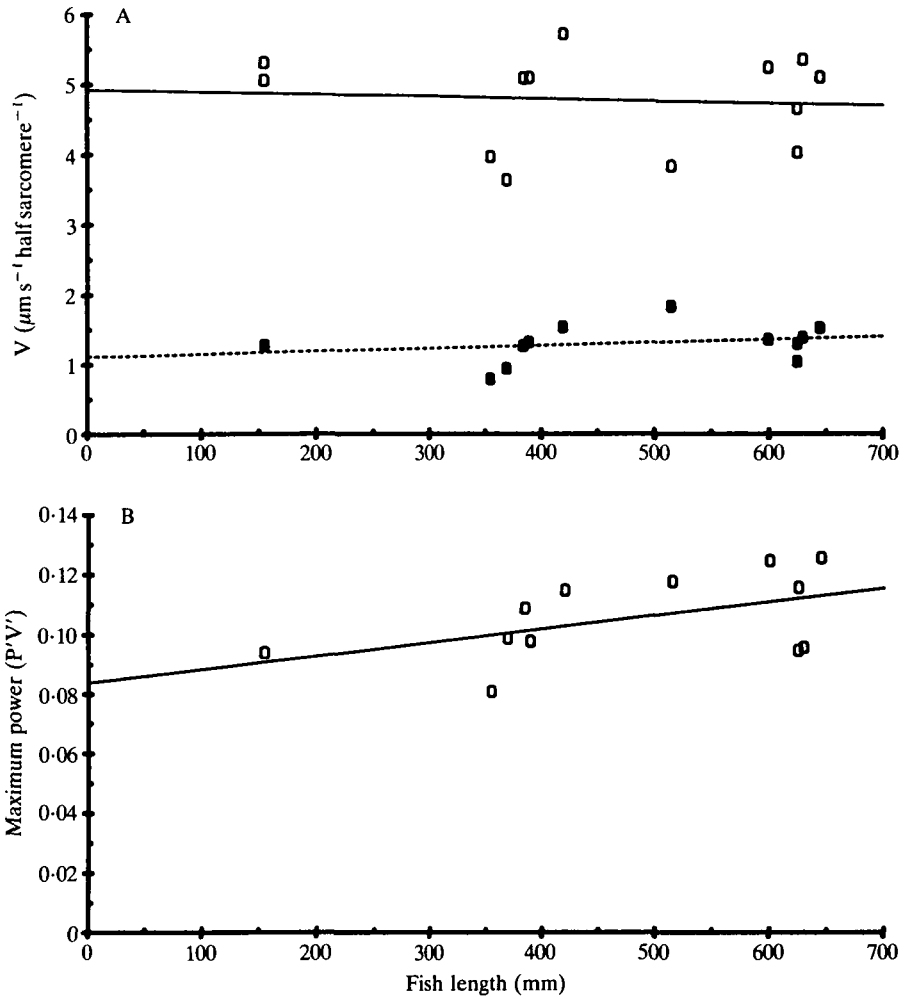
Fig. 1. (A) Relationship between (□) the maximum velocity of shortening (V_0, determined by the slack step method) and (■) the velocity at which the maximum power was produced by fibres from fish of different length. The velocity is expressed in units of $\mu m\ s^{-1}$ half sarcomere^{-1} to take account of the larger number of sarcomeres in the longer fibres from larger fish. The lines are the least squares regression (all error in velocity); the correlation with fish length is not statistically significant in either case. (B) Relationship between the maximum observed power output and fish length. Power is product of P', force expressed relative to the isometric force at the same fibre length, and V', velocity expressed relative to the maximum velocity measured by the slack step method. The line is the least squares regression (all error in power); the correlation with fish length was not statistically significant.

Relationship between force and velocity of shortening

The relationship between length and force in isometric tetani was established for each fibre bundle, and striation spacing under resting conditions at each length was determined by laser diffraction. The striation spacing at which maximum force was

developed varied among fibre bundles within the rather large range $2 \cdot 3 - 2 \cdot 8 \mu m$. This information was used in choosing lengths used in the study of the force–velocity relationship; the final length to which the fibre bundle shortened was set to be near the length optimum for active force development, and the initial length was about 10 % longer. Fig. 2A shows superimposed records of force and length during tetani, including a period of shortening at three different velocities and during an isometric tetanus at the final length reached in the tetani with shortening. As shown in Fig. 2A, force was measured at the end of the period of shortening, that is, just as the final length was reached.

In many fibre bundles, the force record did not reach a plateau during rapid shortening, but continued to fall (see record with lowest force in Fig. 2A). In an experiment where the effect was prominent, the possibility that the effect was an artefact due to series elasticity was tested by giving various sizes of step releases at the start of shortening. This had no effect on the rate of fall of force during shortening even when the step was sufficient to drop the force below the level during subsequent shortening. From this we conclude that the decline of force is not an effect of series elasticity. Another possible cause of the decline of force is 'deactivation' due to shortening, which has been observed in frog fibres (Edman, 1975). This possibility is supported by results with two bundles in which the effects of different frequencies of stimulation were tried; at higher frequency the force was maintained better, in agreement with Edman's (1980) observation on deactivation in frog fibres. Thus, at high velocities of shortening, our measurement of force may, in some cases, be lower than that characteristic of fully activated (not deactivated) fibres. The continued decline of force during shortening occurs only at velocities greater than that optimal for power output. Four bundles in which force decline was most marked had the same maximum power output ($P'V' = 0 \cdot 106 \pm 0 \cdot 005$, S.E.M.) as three bundles in which force did not decline during shortening at high velocity ($0 \cdot 102 \pm 0 \cdot 003$, S.E.M.).

In Fig. 2B the results for one fibre bundle are shown with values (P') of force expressed as a fraction of the force produced in a purely isometric tetanus (not including a period of shortening) at the final length (see legend of Fig. 2A). Hyperbolic functions were fitted to the results for each fibre preparation. When the isometric values, $P' = 1 \cdot 0$, $V' = 0$, were included, the experimental points for high force and low velocity were systematically above the fitted curve (see Fig. 2B, dotted line). For the 12 fibre bundles for which a full set of force–velocity data was obtained, there were 37 points for V' less than $0 \cdot 2$, and 33 of these were above the fitted line. A much better fit was achieved when the values $P' = 1 \cdot 0$, $V' = 0$ were not included (Fig. 2B, solid line). The mean values, for all the fibre bundles, of the parameters of the curves fitted in this way are listed in Table 1. In agreement with previous findings (Edman *et al.* 1976; Edman, 1986), the calculated intercept, $P_0^* = 1 \cdot 19 \pm 0 \cdot 04$ (S.E.M., $N = 12$), was significantly greater than $1 \cdot 0$ (the observed isometric values). The intercept of the fitted curve on the velocity axis, $V^* = 0 \cdot 999 \pm 0 \cdot 020$ (S.E.M., $N = 12$), was close to the value, V_0, that we found by the slack step method.

Relationship between power and velocity of shortening

The mechanical power output (product of relative force and relative velocity) was calculated from the data points on the force–velocity curve (see Fig. 2B,C). The results for all fibre bundles (Fig. 3) show that maximum power output ($P'V'$) varied among fibre bundles from 0·081 to 0·126 (mean ± S.E.M., 0·106 ± 0·004, $N = 12$). In most cases maximum power was produced during shortening at about a quarter of the maximum velocity of shortening ($V' = 0·28 ± 0·019$, mean ± S.E.M., $N = 12$). As shown in Fig. 1B maximum power did not appear to be strongly dependent on fish length.

Maximum isometric force

In the one case where a single fibre was used, an absolute value for isometric force per unit cross-sectional area of fibre was obtained. The area was calculated
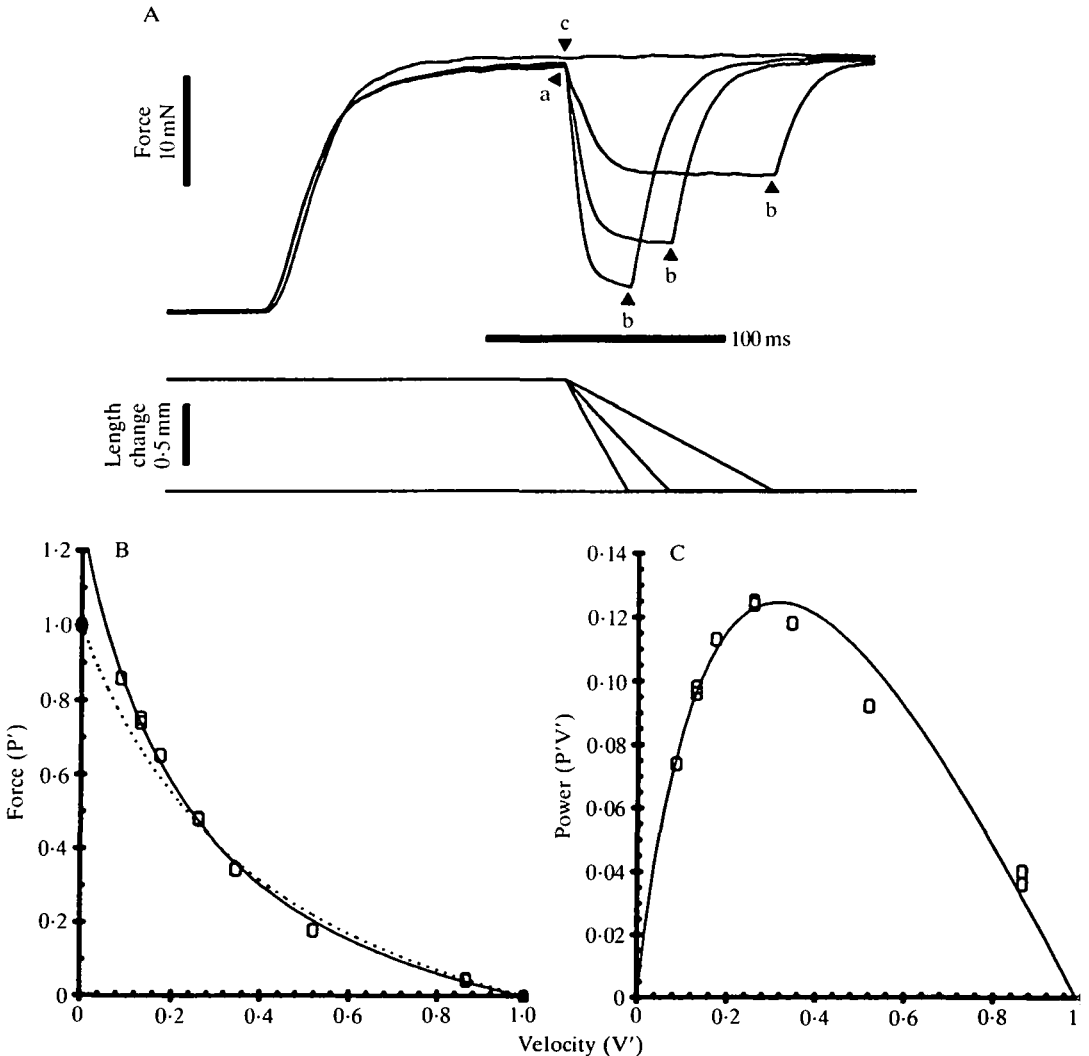

Fig. 2

Table 1. *Mean values of mechanical characteristics of fibre bundles*

Parameter	Mean	±S.E.M.	N
A Maximum velocity of shortening, V_0			
($\mu m\,s^{-1}$ half sarcomere^{-1})	4·8	0·2	13
(fibre length s^{-1})	3·8	0·2	13
Maximum isometric force, P_0			
(mN mm^{-2})	241	22	7
Maximum power			
P'V'	0·106	0·004	12
(W kg^{-1} wet mass)	91	14	7
Velocity for maximum power			
($\mu m\,s^{-1}$ half sarcomere^{-1})	1·3	0·13	7
B P$_0^*$	1·19	0·04	
1/G	0·236	0·022	
a/P_0	0·274	0·020	
V*	0·999	0·020	

(A) V_0, maximum velocity of shortening determined by the slack step method; P_0, maximum isometric force (produced at the fibre length before shortening) per unit cross-sectional area of active fibres (the number of active fibres could be determined for seven of the fibre bundles); maximum observed power (=P'V', where P' is force during shortening expressed relative to P_0 at the same fibre length, V' is velocity relative to V_0), and velocity at which power output was maximum.

N is the number of values used to calculate the mean ± S.E.M.

(B) Mean values (±S.E.M.) for 12 fibre bundles of the parameters, P$_0^*$, 1/G, a/P_0 and V*, of hyperbolae fitted to force–velocity results.

P$_0^*$ and V* are the intercepts on the force and velocity axis, respectively, in the relative units defined above.

Data points at P' = 1·0, V' = 0·0 were not included during fitting (see text).

Fig. 2. (A) *Sample records of an isometric tetanus and tetani including isovelocity shortening of a bundle of four fibres at 12°C. The fibre length after shortening and in the isometric example was 5·83 mm. The force was measured at the end of the shortening (at b), and P' was expressed as (b/a)×(d/c) to take account of differences in isometric force at the long and short length and changes in force in successive tetani which have been assumed to have proportionally the same effect on isometric force and force during shortening. a is the isometric force at the long muscle length just before shortening, (b defined above); a and b were measured in the same tetanus. From separate tetani, c is the isometric force at the short muscle length, and d is the isometric force at the long muscle length (not shown). In most cases the c and d values were determined both before and after the series of isovelocity shortening. The ratio d/c differed from unity by 3·5 ± 0·7% (±S.E.M., N = 13). (B) The force–velocity results for a bundle of eight fibres. Force, P', is expressed relative to the isometric value at the same fibre length, and velocity of shortening, V', relative to the maximum velocity measured in the slack step method. The lines are hyperbolae fitted to the data points either including (dotted line) the values P' = 1·0 and V' = 0·0, or excluding (solid line) these values (see text). (C) Corresponding relationship between power (P'V') and velocity of shortening. The line was calculated from the solid line in Fig. 2B.*
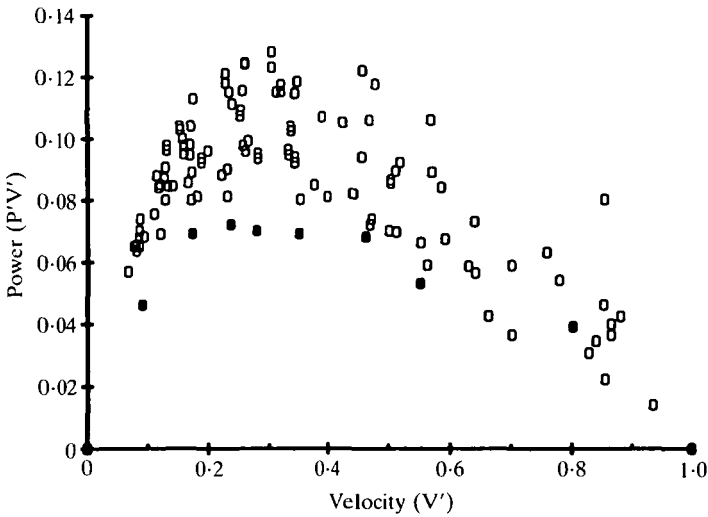
Fig. 3. Summary of measurements of power (P'V', see text and Fig. 2C) as a function of velocity (V') for 12 bundles of intact fibres (□). Results for skinned fibres (■) from Bone *et al.* (1986) are also included.

from the fibre width (assuming a circular cross-section). The ratio of measured force to area was $272 \, mN \, mm^{-2}$. In six other cases the number of active fibres could be estimated from the number of steps (1–6) in the stimulus strength–response curve. Using the number of active fibres and the measured diameters, we calculated the force per area of active fibres. The mean value for all seven preparations was $P_0 = 241 \pm 22 \, mN \, mm^{-2}$ (±S.E.M.).

Discussion

Fish size and maximum power

A muscle fibre can produce its maximum power output only when shortening at one particular velocity. This velocity does not depend on dogfish length (Fig. 1A); we have found a mean value of $1.3 \pm 0.08 \, \mu m \, s^{-1}$ half sarcomere^{-1} (±S.E.M., $N = 12$) (about 1.0 fibre length s^{-1}). The fish will attain its maximum swimming speed if all the muscle fibres are shortening at this velocity during the appropriate phase of the swimming movements. Bainbridge (1958) showed in a study of three different teleost species that tail beat frequency decreases with increasing fish size (within the same species), and that the amplitude of the tail beat remains a constant fraction of fish length. From this result, it follows that the velocity of muscle fibre shortening (relative to fibre length) is lower in the larger fish, provided that the arrangement of the fibres within the fish (Alexander, 1969) is independent of body size. Thus our result that maximum power is produced at the same velocity suggests that not all sizes of fish swim at the speed which makes use of the maximum power their muscle fibres can produce. This seems surprising

because it means that some fish could swim faster if they used a different tail beat frequency. There are, however, at least two other possibilities. First, it could be that the angles the muscle fibres make with the long axis of the fish actually decrease as the fish grows so that their maximum power is always exerted at the actual tail beat frequency used. Alternatively, it could be that the maximum swimming speed of fish of particular sizes is dictated by factors other than maximum power output of the muscle fibres.

Maximum swimming speed predicted from maximum muscle power

The maximum power output of the muscle fibres was observed to be $91 \pm 14 \, \text{W kg}^{-1}$ wet fibre mass (mean $\pm$ S.E.M., $N = 7$). Hydrodynamic equations relate the power required to move the dogfish through the water to the swimming speed. The following equation is based on equation 9.6 of Alexander (1977): power $= (0.5 dS_w u^3 C_D)/(0.75M)$, where d is the density of sea water $(1027 \, \text{kg m}^{-3})$; S_w is the wetted surface area ($0.260 \times$ fish length^2; in m^2) the constant, 0.260, was measured on dogfish by Q. Bone & J. V. Howarth, personal communication); u is the swimming speed (in m s^{-1}); and C_D is the drag coefficient. For a rigid, streamlined body, $C_D = 1.3(Re^{-1/2})$, where Re is (the Reynold's number. We have used the higher value of $4 \times 1.3(Re^{-1/2})$ for an oscillating fish body (Lighthill, 1971). M is the mass of active muscle, taken as 35 % of the fish mass. We estimate that the total mass of muscle is about 70 % of the fish mass, but only half is active at one time. 0.75 is the Froude efficiency (see Alexander, 1977, for example).

To estimate the maximum swimming speed that can be achieved with the muscle power output we have measured, the equation was solved for u. For a fish of length 0.51 m and 0.4 kg wet mass (median values for the seven fish used to obtain the absolute power output by muscle fibres, $91 \, \text{W kg}^{-1}$ wet mass), the calculated swimming speed is $4.2 \, \text{m s}^{-1}$ (8.4 fish lengths s^{-1}). This is similar to the speeds that can be reached by many species (Beamish, 1978), although we know of no published observations for dogfish.

Using this equation it is also possible to predict how swimming speed (u/FL, in fish lengths s^{-1}) varies with fish length (FL) for a constant power output. The value of u/FL is proportional to FL$^{-0.4}$. It should be noted that although the velocity of fibre shortening at which the muscle fibres produce their maximum power is independent of fish length (see Fig. 1A), maximum swimming speed (u/FL) decreases as fish length increases. For our smallest fish (FL = 0.155 m) the maximum swimming speed would be 12.9 FL s^{-1}, and for our largest (FL = 0.645 m) the speed would be 7.8 FL s^{-1}. Wardle (1975, 1977) has predicted a similar decrease in swimming speed (u/FL) with increased fish length; his prediction is based on observations of the duration of twitches (with shortening) of blocks of muscle from teleosts of different lengths. Observations of the maximum swimming speed (over a distance of 1 m) of different sizes of fish show a decrease in swimming speed (u/FL) with increasing FL (Bainbridge, 1958), similar to our prediction and to that of Wardle (1975, 1977). This suggests that both the

maximum power output of the muscle, and its twitch contraction time, are important factors whose values have been adapted for maximum swimming speed.

Comparison of the maximum power output of intact and skinned fibres

The mean value of the maximum power output of intact fibres, 91 W kg^{-1} wet fibre mass, was 1.65 times that of skinned fibres from dogfish, 55 W kg^{-1} wet mass (same fibre type, white, and at the same temperature, Bone *et al.* 1986). This may be partly due to factors relating to the ability of intact fibres to produce higher force under isometric conditions, as suggested by Altringham & Johnston (1982). Another important point is that the force–velocity curve, and thus the power–velocity curve, is different for intact and skinned fibres from dogfish. As shown in Fig. 3 at each velocity of shortening, the power output by the intact fibres is higher. This is a direct consequence of the fact that the force–velocity curve is less curved for the intact fibres, as indicated by the higher values of the constant a/P_0 from the hyperbolic fits to the data. For intact fibres we found a mean value of $a/P_0 = 0.274 \pm 0.020$ ($\pm$ S.E.M., $N = 12$, at $12\,^{\circ}\text{C}$, Table 1B), whereas values of 0.17 (at $12\,^{\circ}\text{C}$, Bone *et al.* 1986) and 0.06 (at $8\,^{\circ}\text{C}$, Altringham & Johnston, 1982) have been reported for skinned white fibres of the dogfish. It seems therefore that, at least in dogfish, the skinned fibre is not an adequate model of the living fibre in that it has lost a large part of its ability to produce mechanical power. This difference between skinned and intact fibres is most obvious when the mechanical energy output is high, suggesting that it may be due to limitation of metabolic energy supply in the skinned fibres. It could be that the conditions for ATP synthesis (for example, the activity of creatine kinase or the level of phosphocreatine) are less favourable in skinned than live fibres. Alternatively, the swelling of the filament lattice that occurs upon skinning may reduce power output.

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