

SCALING OF POWER OUTPUT IN FAST MUSCLE FIBRES OF THE ATLANTIC COD DURING CYCLICAL CONTRACTIONS

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Summary

Fast muscle fibres were isolated from abdominal myotomes of Atlantic cod (*Gadus morhua* L.) ranging in size from 10 to 63 cm standard length (L_s). Muscle fibres were subjected to sinusoidal length changes about their resting length (L_f) and stimulated at a selected phase of the strain cycle. The work performed in each oscillatory cycle was calculated from plots of force against muscle length, the area of the resulting loop being net work. Strain and the number and timing of stimuli were adjusted to maximise positive work per cycle over a range of cycle frequencies at 8°C.

Force, and hence power output, declined with increasing cycles of oscillation until reaching a steady state around the ninth cycle. The strain required for maximum power output (\dot{W}_{\max}) was ± 7 –11% of L_f in fish shorter than 18 cm standard length, but decreased to ± 5 % of L_f in larger fish. The cycle frequency required for \dot{W}_{\max} also declined with increasing fish length, scaling to $L_s^{-0.51}$ under steady-state conditions (cycles 9–12). At the optimum cycle frequency and strain the maximum contraction velocity scaled to $L_s^{-0.79}$. The maximum stress (P_{\max}) produced within a cycle was highest in the second cycle, ranging from 51.3 kPa in 10 cm fish to 81.8 kPa in 60 cm fish ($P_{\max} = 28.2 L_s^{0.25}$). Under steady-state conditions the maximum power output per kilogram wet muscle mass was found to range from 27.5 W in a 10 cm L_s cod to 16.4 W in a 60 cm L_s cod, scaling with $L_s^{-0.29}$ and body mass (M_b) $^{-0.10}$.

Introduction

Length is one of the major factors determining maximum swimming speed in fish. Swimming speed is governed by tail-beat frequency and amplitude, which generally decrease with increasing size (Bainbridge, 1958; Webb, 1977; Archer and Johnston, 1989). The distance moved per tail-beat (stride length) is a constant

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fraction of body length at frequencies above 5–6 Hz (Bainbridge, 1958); therefore, the maximum length-specific speed (distance/fish length) decreases with increasing size. There are also size-related changes in muscle mass, twitch kinetics and innervation during growth, which would be expected to influence swimming performance (Archer *et al.* 1990).

Maximum swimming speeds are achieved by recruitment of fast muscle fibres, which constitute the major part of the myotomal mass (Bone, 1966). Curtin and Woledge (1988) examined the effect of body size on isotonic contractions of fast myotomal muscle fibres from the lesser spotted dogfish (*Scyliorhinus canicula* L.). Both the unloaded shortening velocity (V_{\max}) and maximum relative power output of fast fibres were found to be independent of fish length. The maximum power output, calculated from the force–velocity (P–V) relationship at 12°C, was 91 W kg⁻¹ wet mass at a shortening velocity of 1.3 $\mu\text{m s}^{-1}$ half-sarcomere⁻¹.

Subcarangiform swimming in fish involves alternate contractions of the myotomes on either side of the body. The muscle fibres undergo approximately sinusoidal cycles of lengthening and shortening (Hess and Videler, 1984; van Leeuwen *et al.* 1990), and their degree of activation varies throughout the strain cycle. Altringham and Johnston (1990a) used the work loop technique developed by Josephson (1985) to obtain values for the muscle power output of teleost muscle fibres under conditions appropriate to swimming. Isolated myotomal muscle fibres from the short-horned sculpin (*Myoxocephalus scorpius* L.) were subject to imposed sinusoidal length changes, and the strain and stimulation parameters were adjusted to maximize power output over a range of cycle frequencies. Maximum power output was produced at 5–7 Hz (25–35 W kg⁻¹ wet mass) for fast fibres and 2 Hz (5–8 W kg⁻¹ wet mass) for slow fibres in 23–29 cm fish at 4°C.

The effects of body size on relative muscle power output have also been studied in the Atlantic cod (*Gadus morhua* L.), but absolute values were not obtained as the cross-sectional areas of the preparations were not determined (Altringham and Johnston, 1990b). It was found that the cycle frequency required for maximum power decreased with increasing size, scaling with (fish length)^{-0.52} at 4°C. Using a similar rationale, the present study extends the size range of cod used by Altringham and Johnston (1990b) to smaller fish and determines the scaling relationships for absolute power output and the maximum stress reached within each cycle.

Materials and methods

Atlantic cod (*Gadus morhua* L.) were caught locally, or obtained from the University Marine Biological Station, Millport, throughout the year. Fish were maintained in seawater aquaria at ambient temperature (6–12°C) until required for experiments. Cod were killed by a blow to the head followed by transection of the spinal cord, and standard length (L_s , distance from the snout to the end of the trunk) and body mass (M_b) were recorded.

Bundles of 10–60 fast muscle fibres were isolated from the superficial hypaxial

region of abdominal myotomes 10–16 (counting from the head) in dishes of chilled aerated Ringer's solution (composition in mmol l^{-1} : NaCl, 132.2; sodium pyruvate, 10; KCl, 2.6; MgCl_2 , 1; CaCl_2 , 2.7; NaHCO_3 , 18.5; NaH_2PO_4 , 3.2; pH 7.4 at 8°C). Foil clips were attached at each end of the preparation to the remains of the myosepta and peritoneum. Preparations were transferred to a flow-through chamber with one end attached to a servo motor and the other to a force transducer (AME801, SensoNor Horten, Norway). Muscle fibres were stimulated directly with single or multiple supramaximal square wave pulses of 2 ms duration at 50 Hz, administered *via* two platinum electrodes lying on either side of the preparation. Circulating Ringer was maintained at 8°C by a cooling unit. The resting muscle fibre length was adjusted to give an optimal twitch, typically corresponding to a sarcomere length of $2.2\ \mu\text{m}$, as measured by laser diffraction. Muscle fibre length was measured with a binocular microscope (magnification $\times 20$).

Muscle fibres were subjected to cycles of lengthening and shortening at preset amplitudes about the *in situ* resting length in order to approximate sarcomere length changes during swimming. Stimulation was timed to commence at selected phases of each oscillatory cycle (the full cycle from the point at which the fibre passes through the resting length is 360°). Muscle fibres were subjected to up to 16 cycles of oscillatory work with a 10–15 min rest between trains of cycles. Cycle frequency, strain and stimulus parameters could all be varied and the data were collected and analysed using a microcomputer and in-house software. The work performed in each cycle was calculated by plotting force against muscle length, the area of the resulting loop being net work (μJ) (Fig. 1). Anticlockwise loops

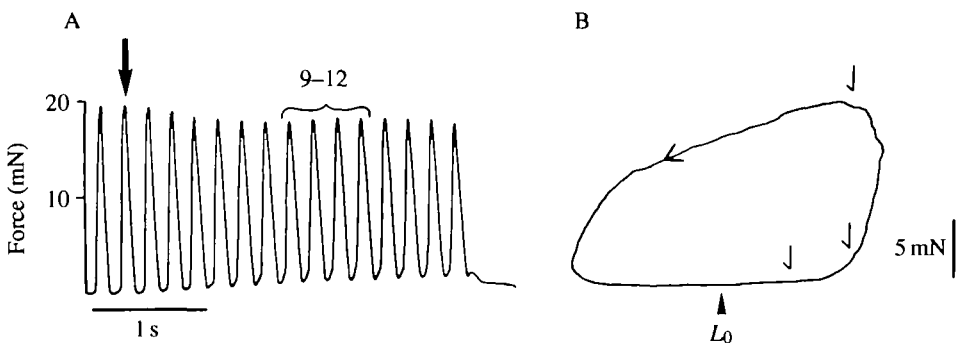


Fig. 1. A typical record illustrating the experimental protocol. (A) Force recording for muscle fibres from a 54.5 cm cod subjected to imposed sinusoidal length changes about the *in situ* resting fibre length (L_0). The strain in this experiment was $\pm 5\% L_0$. Sixteen oscillatory cycles are illustrated with 3 stimuli per cycle at 30° stimulus phase shift at a cycle frequency of 5 Hz. Arrow indicates the second cycle, which was used to calculate maximum power output. Brackets indicate cycles 9–12, which were used to calculate the average power output under steady-state conditions. (B) A work loop plotted for the twelfth cycle; the ticks indicate the timing of stimulation. Note the anticlockwise loop indicating positive work.

correspond to positive work and clockwise loops to negative work. The net work per cycle is a complex function of strain, cycle frequency, number and timing of stimuli (Altringham and Johnston, 1990a). The rationale behind the initial series of experiments was to maximise work per cycle by varying strain, stimulus phase and the number of stimuli per cycle at a range of frequencies in fibre preparations from fish of different sizes. We also investigated the effects of varying strain on net work per cycle whilst maintaining stimulus phase and stimulation parameters constant. Values for stimulus phase and stimulation parameters were chosen to give the maximum work per cycle at a strain corresponding to $\pm 5\%$ L_f .

At the end of each experiment, preparations were pinned out to their resting length on a strip of silicone elastomer (Sylgard 184, Dow Corning, Seneffe, Belgium) and frozen in isopentane cooled in liquid nitrogen. Transverse frozen sections (10–15 μm thick) of preparations were cut on a cryostat and stained for myosin ATPase (Johnston *et al.* 1974). The cross-sectional area of undamaged muscle fibres was determined using a microscope drawing arm and a digitizing pad interfaced to a microcomputer (Hewlett-Packard 86B) with area measurement software. Scaling relationships were determined from logarithmically transformed data (\log_{10}) fitted by least-squares regression using Minitab statistical software (Minitab Inc., USA), and the slopes were tested for significance against a value of zero (Sokal and Rohlf, 1969). The intercepts and the slopes of the regression equations relating L_s to the maximum stress and power in cycle 2 and in cycles 9–12 of oscillatory work were tested for significant differences by analysis of covariance using Systat (Systat Inc, USA).

Results

Data were collected from muscle fibre preparations of fish measuring 10–63 cm in standard length (L_s). Muscle fibre length was positively correlated with standard length and with body mass as reported by Archer *et al.* (1990) (Table 1). Force declined in all preparations over the series of oscillatory cycles, reaching a steady state around the ninth cycle. In general, the decline in force with successive contractions was greater at higher cycle frequencies, falling by as much as 30% over the first eight cycles at 13 Hz. Since force and work were dependent on the cycle number, scaling relationships have been derived for the second cycle where force was generally maximal, and over the cycles 9–12 where force had attained a steady value (Table 1).

The number of stimuli required to maximize work per cycle was dependent on the cycle frequency and the size of the fish, as reported previously by Altringham and Johnston (1990b). As frequency increased, the number of stimuli required decreased. For example, in fish 20–29 cm in standard length the optimum number of stimuli decreased from 8 at 3 Hz to 1 at 13 Hz. At frequencies of 3–5 Hz, muscle fibres from small fish required more stimuli than those from larger fish. This difference became less apparent as frequency increased, until at 13 Hz a single stimulus was sufficient to obtain maximum work per cycle in all sizes of fish. Signs

Table 1. Scaling relationships for cod fast muscle fibres performing oscillatory work under conditions for maximum power output

Variable	Units	Scaling equation	Statistics		
			<i>N</i>	<i>P</i>	<i>t</i>
Body mass (M_b)	g	$M_b = 131.8L_s^{3.11}$	64	<0.001	
Muscle fibre length (L_f)	cm	$L_f = -33.9L_s^{0.91}$	53	<0.001	
		$L_f = -8.3M_b^{0.29}$	53	<0.001	
Stress (P_{max})	kPa	$P_{max(2C)} = 28.2L_s^{0.25}$	41	0.05	2.13
		$P_{max(2C)} = 42.7M_b^{0.08}$	41	NS	(1.98)
		$P_{max(9C)} = 18.6L_s^{0.29}$	41	<0.05	2.21
		$P_{max(9C)} = 29.5M_b^{0.1}$	41	0.05	2.11
Maximum contraction velocity (V)*	Muscle lengths s^{-1}	$V_{(9C)} = 17.4L_s^{-0.79}$	12	<0.001	7.63
Optimum cycle frequency (F_{opt})†	Hz	$F_{opt(9C)} = 43.7L_s^{-0.51}$	46	<0.001	6.95
		$F_{opt(9C)} = 20.0M_b^{-0.17}$	46	<0.001	7.02
Power (\dot{W}_{max})	W kg^{-1}	$\dot{W}_{max(2C)} = 95.4L_s^{-0.40}$	41	<0.05	2.89
		$\dot{W}_{max(2C)} = 53.7M_b^{-0.13}$	41	<0.005	3.02
		$\dot{W}_{max(9C)} = 53.7L_s^{-0.29}$	41	<0.05	2.18
		$\dot{W}_{max(9C)} = 35.5M_b^{-0.10}$	41	0.05	2.25

Allometric equations of the general form $y = aM_b^b$, where b is the mass exponent and a is the proportionality constant (intercept at unity), are shown for parameters scaled to standard fish length (L_s) and body mass (M_b) calculated for the second (2C) and the ninth to twelfth (9C) cycles of oscillatory work.

N values refer to the number of fish studied.

*Note that only the 12 experiments in which all the parameters including strain had been systematically optimised are included.

† Includes five additional experiments in which measurements of muscle fibre cross-sectional areas were not obtained.

P, significance of correlation coefficient; *t* values represent deviations of regression slope b from a value of 0. Values greater than the critical value of 1.65 are significantly different from 0 with a probability $P=0.05$; $P=0.01$, critical value=2.33. NS, not significant.

of fatigue were evident in some muscle fibre preparations from small fish where a large number of stimuli were required to maximize work at low cycle frequencies. Maximum work was obtained by giving the muscle fibres a small stretch prior to the start of stimulation, but there was no clear relationship between body size and the stimulus phase required to maximize work at the optimum strain and number of stimuli per cycle. However, with increasing cycle frequency, optimum work was generally produced by stimulating nearer the start of each oscillatory cycle in fish of all sizes.

The effect of varying strain on the work performed per cycle was also investigated whilst maintaining all other parameters constant at the optimal values for a 10% strain (Fig. 2). The extension of the size range of cod to fish

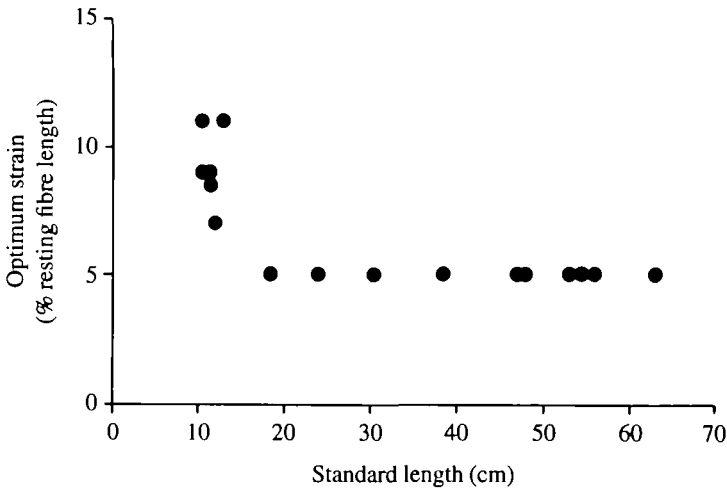


Fig. 2. Strain required for optimum oscillatory power output in relation to standard length of fish.

shorter than 13 cm revealed a change in the strain required for maximum power not noticed in our previous study (Altringham and Johnston, 1990b). The optimal strain decreased from ± 7 –11 % of resting fibre length in fish smaller than 18 cm in L_s to ± 5 % of resting fibre length in larger fish (Fig. 2). The curves of power output against strain were much broader in muscle fibres from small than from large fish. Thus, the power output of muscle fibres from large fish declined sharply at strains above and below the optimum of ± 5 % of resting fibre length. In contrast, the power output of muscle fibres from small fish was within 75 % of the maximum over a range of strains from ± 5 to ± 15 % of resting muscle fibre length (Fig. 3). Unstimulated fibres produced negligible force even at the highest values of strain studied.

The frequency required to produce optimum power (F_{opt}) was calculated by plotting power output against cycle frequency for individual preparations after optimising all other parameters. In order to reduce the number of experiments required, a strain of ± 5 % of L_f was assumed to be optimal for the majority of fish over 18 cm in L_s . F_{opt} was taken from the midpoint of the frequency range where power output reached 95 % of the maximum value under steady-state conditions at the optimum strain for individual preparations. Muscle fibres from small fish had broad power–frequency curves, whereas fibres from large fish had relatively narrow frequency optima (Fig. 4A). F_{opt} was highly dependent on length (L_s) (Fig. 4B) and body mass (Table 1). The maximum shortening speed of the muscle at F_{opt} was significantly correlated with fish length and body mass (Fig. 5, Table 1); decreasing from 2.82 muscle lengths s^{-1} in 10 cm L_s fish to 0.66 muscle lengths s^{-1} in 60 cm L_s fish.

The maximum force per cross-sectional area (stress) (P_{max}) reached within a cycle was measured in fibres under conditions for optimum oscillatory work and

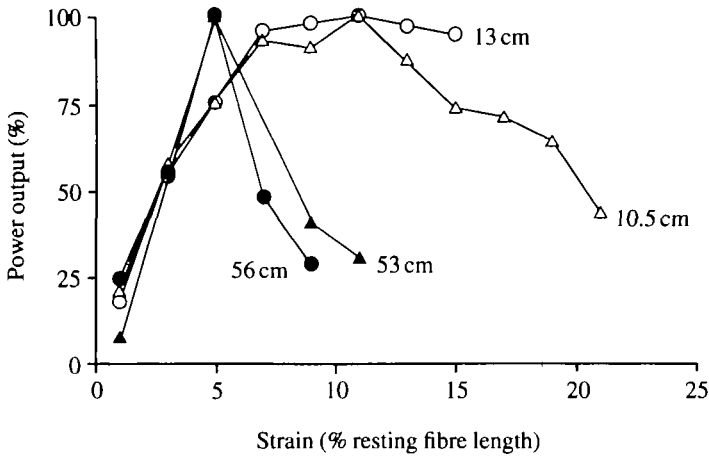


Fig. 3. Power output of muscle fibres from small and large fish in relation to strain. Power output was expressed as a percentage of the maximum obtained under conditions for optimum oscillatory work measured over cycles 9–12.

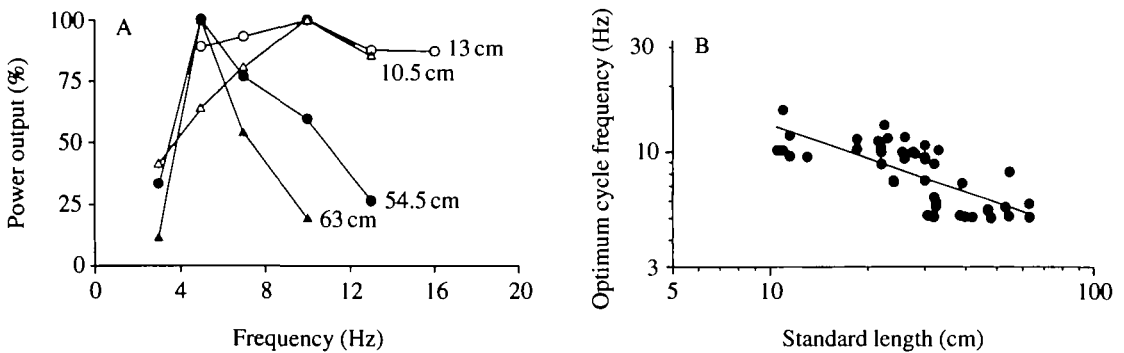


Fig. 4. (A) Power output of muscle fibres from small and large fish in relation to cycle frequency. Power output was expressed as a percentage of the maximum obtained under conditions for optimum oscillatory work averaged over cycles 9–12. (B) Relationship between cycle frequency for optimum power output of muscle fibres and standard length of fish. Optimum cycle frequency was determined from the mid-point of the frequency range where power output was 95% of the maximum obtained by optimising all other parameters.

scaling relationships were calculated (Fig. 6). The proportionality constant a was significantly higher for the second cycle (28.2 ± 1.5) than for cycles 9–12 (18.6 ± 1.6) of work (mean \pm s.d., $P < 0.02$). There was, however, no significant difference in the slopes of the equations relating P_{\max} to L_s ($P = 0.8$, Table 1). Thus, in the second cycle of oscillatory work P_{\max} ranged from 51.3 kPa in fish of 10 cm L_s to 81.8 kPa in fish of 60 cm L_s . Measured over cycles 9–12, the maximum stress varied from an average of 36.3 kPa in 10 cm fish to 61.0 kPa in 60 cm fish, scaling to $L_s^{0.29}$.

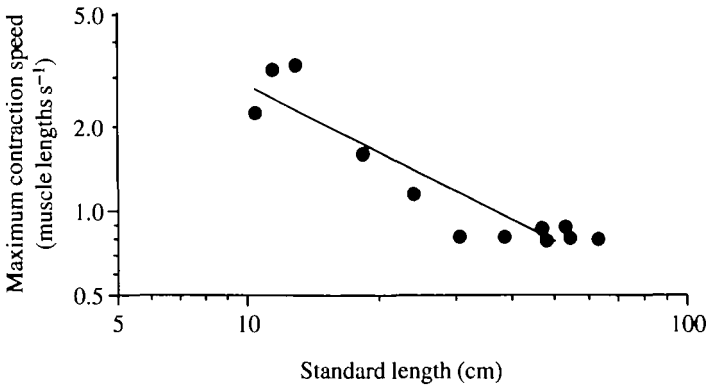


Fig. 5. The relationship between maximum fibre contraction speed at the optimal cycle frequency for maximum power output and fish standard length. Note that, in optimising power output, stimulus parameters and strain were systematically varied at a range of frequencies.

Sea temperatures fluctuate throughout the year and in order to test for acclimation effects fish were divided into two groups corresponding to those caught at water temperatures above and below 10°C. The mean power output (\pm s.d.) of muscle fibres from winter-caught fish was $21.5 \pm 11.2 \text{ W kg}^{-1}$ wet mass ($N=21$), whereas the mean power output from summer-caught fish was $23.4 \pm 8.4 \text{ W kg}^{-1}$ wet mass ($N=20$). As there was no significant difference in the mean power output of muscle fibres from summer- and winter-caught fish at 8°C, all the data were pooled (Student's t -test, $t=-0.61$, $P>0.1$).

Power output (\dot{W}_{\max}) was significantly correlated with standard length (Fig. 6), and the following scaling relationships were calculated for the second cycle and cycles 9–12 (mean \pm s.d.):

$$\dot{W}_{\max} = (95.4 \pm 1.6)L_s^{-0.40 \pm 0.20} \quad (\text{second cycle}),$$

$$\dot{W}_{\max} = (53.7 \pm 1.5)L_s^{-0.29 \pm 0.13} \quad (\text{cycles 9–12}).$$

The intercepts, but not the slopes, of these equations were significantly different ($P<0.02$). For the second cycle of work the \dot{W}_{\max} per kilogram wet muscle mass decreased from 38.0 W in 10 cm fish to 18.6 W in 60 cm L_s fish. Under steady-state conditions, the maximum power was 27.5 W kg^{-1} wet muscle mass in a 10 cm L_s fish and 16.4 W kg^{-1} wet muscle mass in a 60 cm L_s fish.

Discussion

Modelling studies using information on *in vivo* stimulation patterns and sarcomere length fluctuations suggest that muscle fibres in anterior myotomes produce net positive work over almost the entire tail-beat cycle (Hess and Videler, 1984; van Leeuwen *et al.* 1990). Thus, in our experiments with isolated muscle fibre bundles we varied strain and stimulation parameters in order to maximise net

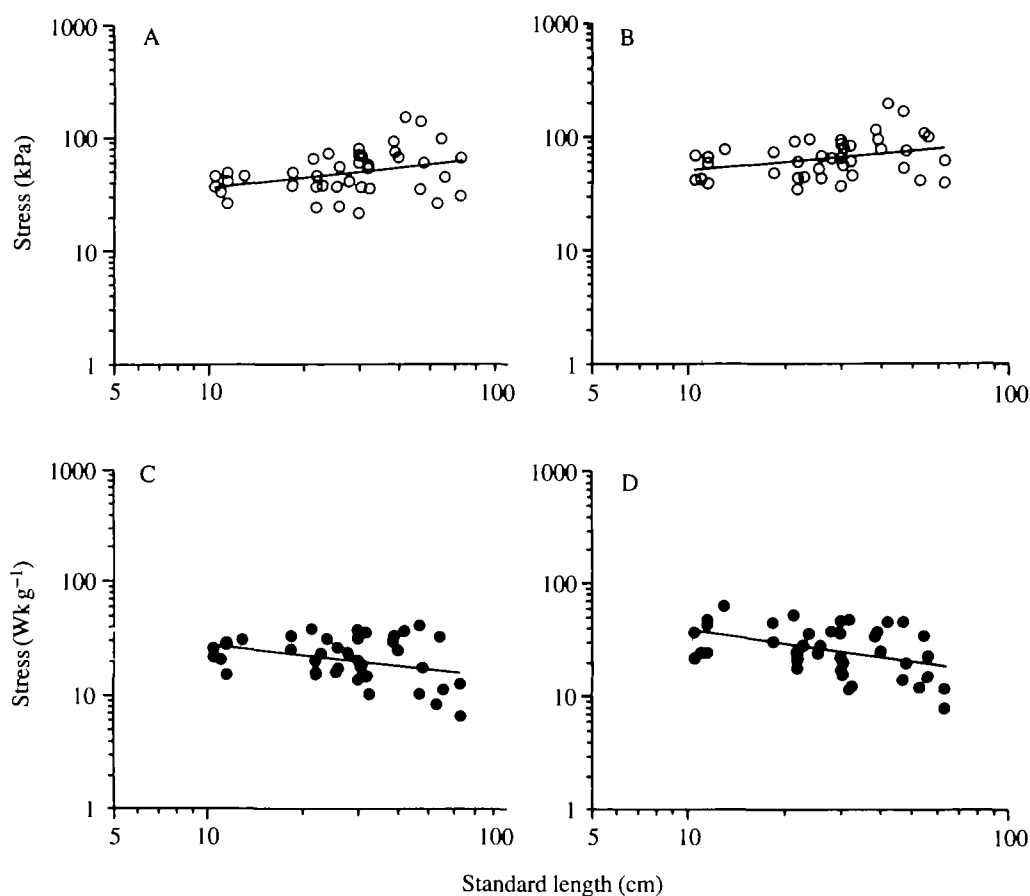


Fig. 6. Scaling relationship of stress and power output in muscle fibres under conditions of maximum power output at 8°C. (A) Stress measured over cycles 9–12 of oscillatory work. (B) Stress measured in the second cycle of oscillatory work. (C) Power output measured over cycles 9–12 of oscillatory work. (D) Power output measured in the second cycle of oscillatory work.

positive work. We found that maximum work output declined with the number of oscillatory cycles and that the intercepts, but not the slopes, of scaling equations varied with cycle number (Table 1). The decline in work performed with increasing numbers of cycles was more pronounced at higher frequencies where fewer stimuli per cycle were necessary, indicating that the phenomenon was not due to fatigue. It may represent a particular property of cod muscle fibres since a similar frequency-dependent decline in work with cycle number was not evident in fast fibres from the short-horned sculpin, *Myoxocephalus scorpius* (Altringham and Johnston, 1990a; Johnson and Johnston, 1991).

Tail-beat frequency declines with increasing body size (Bainbridge, 1958). In the present study, cycle frequencies of 3–19 Hz were examined encompassing the range of maximum tail-beat frequencies expected for other fish of this size

(Videler and Wardle, 1991). The cycle frequency required for maximum power output (F_{opt}) increases with the temperature (Johnson and Johnston, 1991). For example, fast muscle fibres from the short-horned sculpin produce maximum power at 5–7 Hz at 4°C rising to 9–13 Hz at 15°C (Johnson and Johnston, 1991). F_{opt} for cod muscle fibres has a scaling exponent of -0.51 at 8°C (Table 1), giving a value of 6.5 Hz for maximum power production in muscle fibres of a fish of 42 cm L_s . This may be compared with a maximum tail-beat frequency of 6.7 Hz recorded for a 42 cm cod at the same temperature (Videler and Wardle, 1991). Few authors have studied scaling relationships for the maximum tail-beat frequencies (F_{max}) of fish *in vivo*. Webb (1977) calculated from the literature that F_{max} was proportional to length $^{-0.44}$ for laminar boundary flow and proportional to length $^{-0.61}$ for turbulent boundary flow. Thus, the scaling exponent of -0.51 for F_{opt} found in our study is broadly similar to that for F_{max} . It has been suggested that isotonic twitch contraction times of myotomal muscle blocks can be used to predict maximum tail-beat frequency. Wardle (1975) found that $F_{\text{max}}=1/2t$, where t was the time from the stimulating pulse to peak force in seconds. Using Wardle's equation, the F_{max} for a 10 cm fish would be 19.8 Hz and that for a 60 cm fish would be 11.8 Hz. These figures are much higher than the cycle frequencies we found for maximum power output (\dot{W}_{max}) in isolated muscle fibres, though it should be noted that \dot{W}_{max} -frequency curves are quite broad, particularly for small fish (Fig. 4A).

Altringham and Johnston (1990*b*) reported that power output was maximal at a strain of $\pm 5\%$ of resting fibre length in cod of about 35 cm total length. A new finding in the present study was that larger strains of ± 7 – 11% of L_f are required to maximize power in fibres from fish less than about 18 cm in L_s (Figs 2 and 3). This finding parallels changes in tail-beat amplitude, which is proportionately larger in small than in large fish (Bainbridge, 1958; Webb, 1977; Archer and Johnston, 1989). Size-dependent changes in the strain required for maximum power output may also reflect morphometric changes in the myotomes during growth. The latter may affect the angles of insertion of fibres with respect to the myosepta and, hence, the mechanical advantage or gearing of the muscle fibres. The values for optimal strain we obtained for isolated muscle fibres are within the range calculated for sarcomere length changes during swimming in other fish species (Hess and Videler, 1984; Rome and Sosnicki, 1991).

Rome *et al.* (1988) have suggested that muscle fibres operate over a restricted range of contraction velocities (V) *in vivo* such that power output is maximal during the shortening phase of the locomotory cycle ($V/V_{\text{max}}=0.17$ – 0.36). In the present study, the maximum shortening speed (V) of fast muscle fibres at the optimum cycle frequency decreased with increasing fish length, from around 2.8 muscle lengths s^{-1} in 10 cm L_s fish to about 0.7 muscle lengths s^{-1} in 60 cm L_s fish. There was some indication that maximum shortening speed reached a plateau in fish around 30 cm in length (Fig. 5), although our data are limited in number. Curtin and Woledge (1988) found that, for dogfish fast muscle fibres, unloaded shortening speed (V_{max}) and the curvature of the force-velocity relationship were essentially independent of fish length. Therefore, it would seem that the

contraction velocity for maximum power output (V) is much more scale-dependent than is V_{\max} , which implies that muscle fibres operate at different values of V/V_{\max} in small and in large animals. However, it is worth pointing out again that the power *versus* cycle frequency curves for oscillatory work are relatively broad (Fig. 4A).

We found that peak stress during oscillatory work cycles scaled to $L_s^{0.25-0.29}$ (Table 1). The increase in stress with increasing body size probably reflects changes in the relative proportions of muscle fibre organelles. Mitochondria constitute up to 20% of the volume of fast fibres in small fish (<1 cm L_s) (Vieira and Johnston, 1992), decreasing to 1–2% in large fish (>30 cm L_s) (Johnston, 1981). Thus, the fraction of muscle cross-sectional area available for myofibrils increases with body size.

The power output of the muscle fibres must exceed that required to overcome drag on the body. Estimates for the total power required to swim at maximum speed can be derived from hydrodynamic theory. However, the scaling relationships for maximum power are uncertain but have been estimated to fall within the range (total length)^{2.5} to (total length)^{4.0} (Goolish, 1991). Data on the power output of muscle fibres *in vivo* is, therefore, required for the hydrodynamic and energetic analysis of fish swimming. In the present study involving imposed sinusoidal length changes the various parameters influencing work have been optimized to achieve maximum power output. We found that the maximum power output per unit mass of muscle scaled to $L_s^{-0.29}$ under steady-state conditions (Table 1; Fig. 6). From our results, we would therefore expect the scaling coefficient for total muscle power to be similar to, or somewhat less than, that for muscle mass, which in cod scales to $L_s^{3.1}$ (Archer *et al.* 1990; Table 1).

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