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SCALING EFFECTS ON MUSCLE FUNCTION: POWER OUTPUT OF ISOLATED FISH MUSCLE FIBRES PERFORMING OSCILLATORY WORK

BY JOHN D. ALTRINGHAM

Department of Pure and Applied Biology, The University, Leeds LS2 9JT

AND IAN A. JOHNSTON

Gatty Marine Laboratory, Department of Biology and Preclinical Medicine, The University, St Andrews, Fife KY16 8LB

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Summary

Bundles of 3–10 live fast fibres were isolated from the abdominal myotomes of cod (*Gadus morhua* L.) 13–67 cm in length. The preparations performed work under conditions simulating their activity during swimming: sinusoidal length changes were imposed about *in situ* fibre length, and the fibres were stimulated at a selected phase in each cycle. Strain amplitude, and the number and timing of stimuli were chosen to give maximum power output over a wide range of cycle/tailbeat frequencies. For each preparation power output was maximal at a particular frequency, although the peaks were rather broad. As the size of the fish increased the cycle frequency for maximum power output (f_{opt}) decreased, from 12.5 Hz (13 cm fish) to 5 Hz (67 cm fish) ($f_{opt}=1.67\,L^{-0.52}$, where L is body length).

Introduction

The maximum speed (U_{max}) attained by fish declines with increasing duration of activity, and can be divided into three main levels of performance: sustained (>200 min), prolonged (15 s to 200 min) and burst (<15 s) (Beamish, 1978). With increasing speed there is a progressive recruitment of faster-contracting muscle fibre types with higher power outputs (Johnston *et al.* 1977; Bone *et al.* 1978). This reflects the power requirement for swimming which increases as an approximately cubed function of velocity (Webb, 1975). Wardle and He (1988) summarised data on burst swimming from the literature and found that $U_{max} \propto L^{0.85}$ (where L is body length). Thus, 10 cm fish can achieve speeds of $25\,L\,s^{-1}$, whereas 100 cm fish can only swim at around $6\,L\,s^{-1}$ (Wardle, 1975). The maximum frequency (f_{max}) and amplitude (a/L) of tailbeats also decrease with increasing fish length (Bainbridge, 1958; Archer and Johnston, 1989).

Scale-dependent changes in swimming performance and kinematic parameters

Key words: fish, locomotion, oscillatory work, scaling, mechanics, muscle, swimming.

reflect the increased drag on larger bodies and are matched by increased strength of supporting structures and changes in muscle properties (Wardle, 1977; Archer *et al.* 1990). For example, in the cod (*Gadus morhua*), muscle mass, myotome cross-sectional area and fibre length have been shown to scale geometrically (Greer-Walker, 1970; Archer *et al.* 1990), whereas twitch contraction time is proportional to $L^{0.29}$–$L^{0.41}$ (Wardle, 1975; Archer *et al.* 1990). Curtin and Woledge (1988) studied fast muscle fibres from dogfish (*Scyliorhinus canicula*) ranging in length from 15.5 to 64.5 cm. From the force–velocity relationship, they calculated that the velocity of shortening required for maximum power output was essentially independent of fish length. However, isotonic or isometric contractions are not directly relevant to locomotion (for a discussion see Johnston and Altringham, 1988). Josephson (1985) has described a method for measuring the power output of muscle fibres undergoing repeated cycles of shortening and lengthening, conditions which more closely mimic the *in vivo* situation. Using a similar approach, we found that in the sculpin (*Myoxocephalus scorpius*) (23–29 cm length) maximum power output (at 3 °C) was produced at a tailbeat frequency of 5–7 Hz for fast fibres (25–35 W kg^{-1}) and 2 Hz for slow fibres (5–8 W kg^{-1}) (Altringham and Johnston, 1990). In the present study on the Atlantic cod (*Gadus morhua* L.) we have systematically investigated the effects of fish length on the various parameters that determine the power output of fast muscles during oscillatory work.

Materials and methods

Cod, *Gadus morhua*, were caught in the Firth of Forth during May–August, 1989, and kept in the laboratory in flow-through aquaria at 10 °C for up to 2 weeks before use. All experiments were carried out at 4±0.2 °C, on fish ranging from 13.2 to 67 cm in length. Fish were killed by a blow to the head and pithed. After total length and mass had been recorded, the preparation was removed. Fast fibre preparations consisted of parallel bundles of 3–10 fibres, 3.3–16 mm in length. Fibres were dissected from abdominal myotomes as previously described (Altringham and Johnston, 1988) in chilled Ringer (composition in mmol l^{-1}: NaCl, 132.2; sodium pyruvate, 10; KCl, 2.6; $MgCl_2$, 1; $CaCl_2$, 2.7; NaH_2CO_3, 18.5; NaH_2PO_4, 3.2; pH 7.4 at 4 °C).

The preparation was quickly transferred to a flow-through chamber containing the same Ringer's solution, one end was attached to a servo motor, the other to an isometric force transducer (AME 801, SensoNor, Horten, Norway), at *in situ* rest length, as measured in a fish laid flat on the bench prior to dissection. Preliminary experiments established that this corresponded to the length for maximum force generation, and a sarcomere length of 2.4 μm, as measured by laser diffraction. The preparation was then left in the chamber for at least 1 h before experimentation. The fibres were stimulated directly, by means of two parallel platinum wire electrodes, with a 2 ms supramaximal stimulus.

Kinematic analysis of swimming fish (Hess and Videler, 1984) shows that length

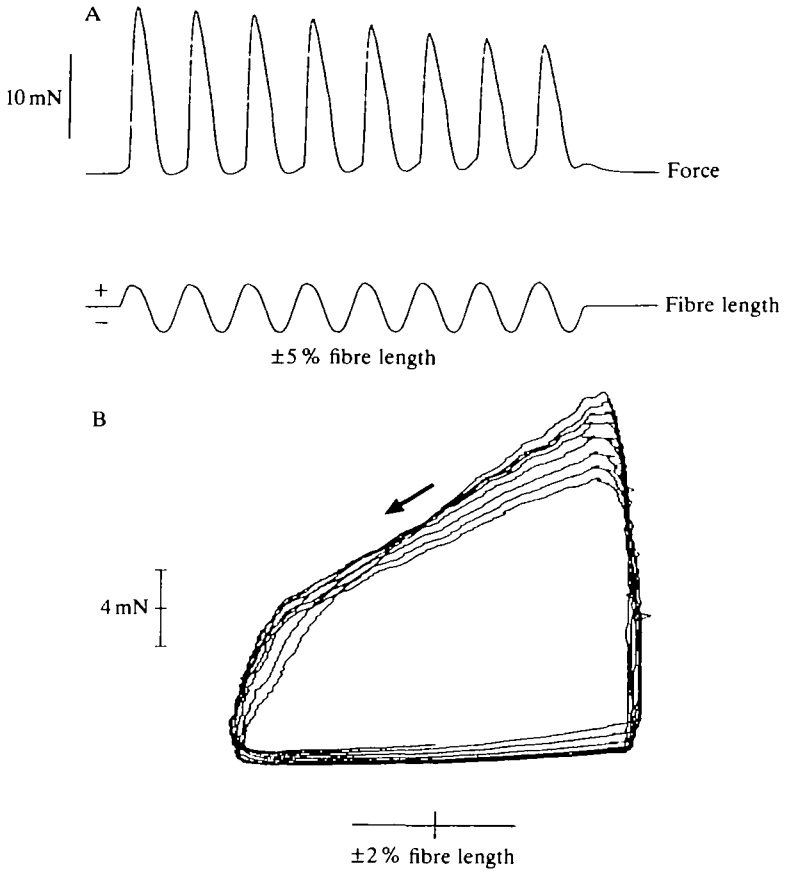

Fig. 1. (A) Force and fibre length records from a preparation performing oscillatory work at 5 Hz. Muscle strain=±5 % resting length. The preparation was stimulated three times every cycle, with a phase shift of 50° (i.e. the first stimulus was delivered 50° after the start of each cycle from rest length, full cycle=360°). Fish length=23.5 cm. (B) Force plotted against muscle length for successive cycles shown in A. Arrow indicates the direction of travel of the 'work loops', which in this case are wholly anti-clockwise, and the muscle fibres are performing positive work.

changes of myotomal fibres during steady swimming describe a nearly perfect sine wave. Preparations were therefore subjected to sinusoidal length changes, symmetrical about *in situ* rest length, and stimulated at a selected phase in each cycle. Eight cycles were performed in each experimental run, with a 10 min rest between runs. A typical experiment is shown in Fig. 1A, in which a preparation is subjected to sinusoidal length changes at an amplitude of ±5 % resting fibre length. By plotting force against muscle length for each cycle a series of loops is generated (Fig. 1B), the areas of which are the work performed during each cycle. Anti-clockwise components indicate positive work, clockwise components negative work (see Josephson, 1985; Altringham and Johnston, 1990). Power output is net work per cycle multiplied by frequency. The amplitude of the length change

(strain), the cycle/tailbeat frequency, the number of stimuli and the phase shift between the start of stimulation and the start of each length change cycle all interact to determine power output. The aim of the present study was to manipulate these parameters to obtain maximum power output at different cycle/tailbeat frequencies for different sizes of fish. Further details can be found in Altringham and Johnston (1990). The experiments were set up and controlled through a microcomputer (IBM 'clone'), and the data collected and analysed on-line, using in-house software.

Results

Records from a representative experiment are shown in Fig. 1. In Fig. 1A, force and length records are shown plotted against time, and in Fig. 1B, force has been plotted against fibre length for successive loops. Both maximum force and net work per cycle decreased over the eight cycles, the magnitude of the decline being largely dependent upon the cycle frequency (see below and Fig. 4). This is in contrast to results obtained from fast and slow fibres from the sculpin, *Myoxocephalus scorpius* (Altringham and Johnston, 1990), and from slow fibres of the cod (J. D. Altringham and I. A. Johnston, unpublished observations), when force and net work remained almost constant. Under optimum conditions, the majority of preparations were able to relax almost completely between cycles, with force returning to less than 1–2 % peak force. In some, relaxation was incomplete and minimum force during cyclical work rose to around 5 % maximum force (Fig. 1B, see also Figs 3–5). Relaxation between cycles may be far from complete under less than optimal conditions. Similar behaviour has been observed in dogfish muscle (Curtin and Woledge, 1989).

Effects on power output of strain amplitude and the timing of stimulation

All measurements of power output were based on the fourth cycle of each run. Because work declined in successive cycles, it is arguable which measurement of power output is most relevant. We were concerned that the simple one chosen did not draw a false picture. Power output for a number of preparations was also calculated from the mean work performed in the first four cycles. The latter will clearly give a slightly higher value but, when normalised, curves such as those presented in Figs 5 and 6 superimposed very well. After verifying this result, the first method was retained.

In Fig. 2A power output has been plotted against the amplitude of the sinusoidal strain for a preparation from a 35 cm fish. Power output was optimal at ±5 % fibre length, but declined slowly at larger amplitudes. A similar result was obtained for preparations from a 13.2 cm fish (Fig. 2B). Note that other parameters were changed to optimise power output: the dependence of power output on strain amplitude alone was not studied systematically for different sizes of fish. Optimum amplitude was also independent of cycle frequency (Fig. 2B).

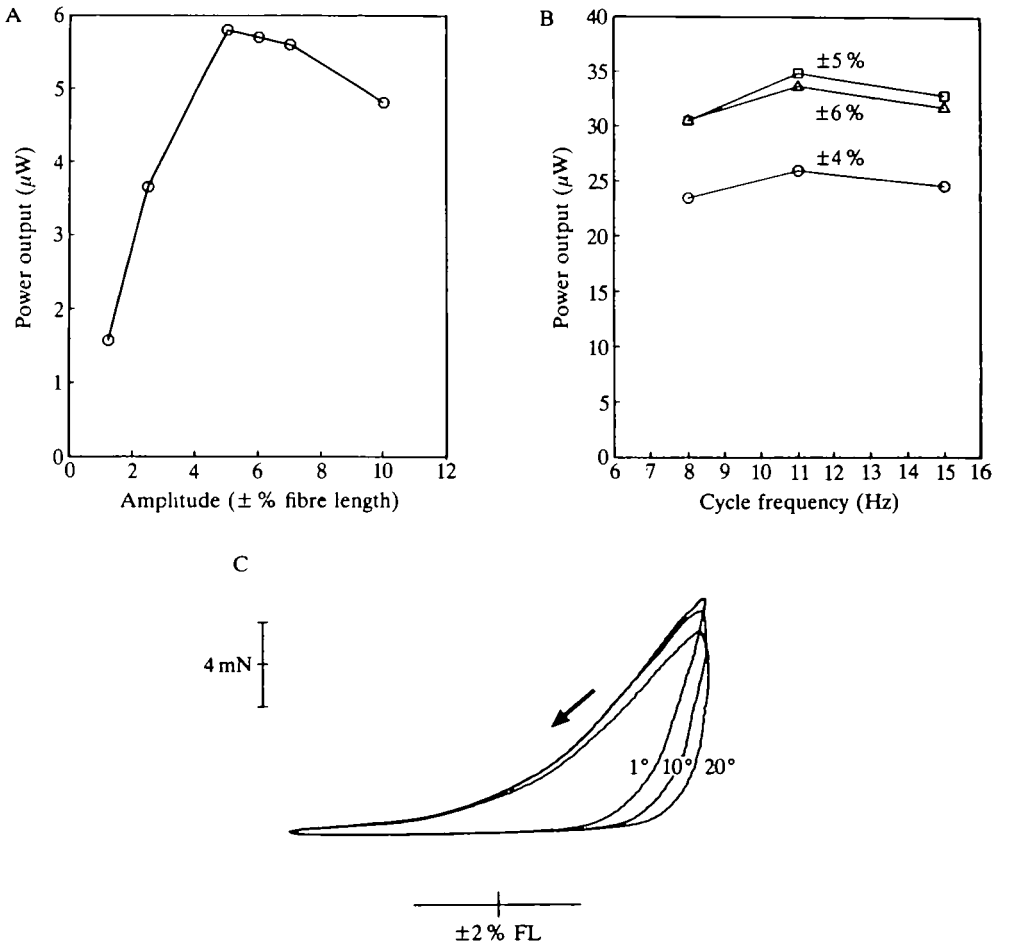

Fig. 2. (A) Power output plotted against strain amplitude for a preparation isolated from a 35 cm cod. Oscillatory work performed at 5 Hz, with three stimuli delivered per cycle; phase shift=30°. (B) Power output plotted against cycle frequency for three different strain amplitudes. Stimulus parameters: 8 Hz, three stimuli, phase shift=35°; 11 Hz, two stimuli, phase shift=15°; 15 Hz, one stimulus, phase shift=5°, Fish length=13.2 cm. (C) Work loops (fourth cycle from each run) performed at 11 Hz, with one stimulus. Stimulus phase shifts (and work in μJ)=1 (16.12), 10 (18.90) and 20° (18.74). Arrow indicates direction of travel around the loop. Fish length=28.5 cm.

The delay between the start of the length change cycle (i.e. the beginning of stretch from resting length) and the first stimulus is defined as the phase shift. This is expressed in degrees (full cycle=360°). Power output is maximal over a narrow range of phase-shift angles. In Fig. 2C, the effect on net work per cycle of progressively retarding the first stimulus in each cycle is illustrated. At a phase shift of 10° the preparation developed more force than at 20°, as it was actively stretched, and this led to an increase in the amount of work performed during the shortening phase of the cycle, which was greater than the extra negative work

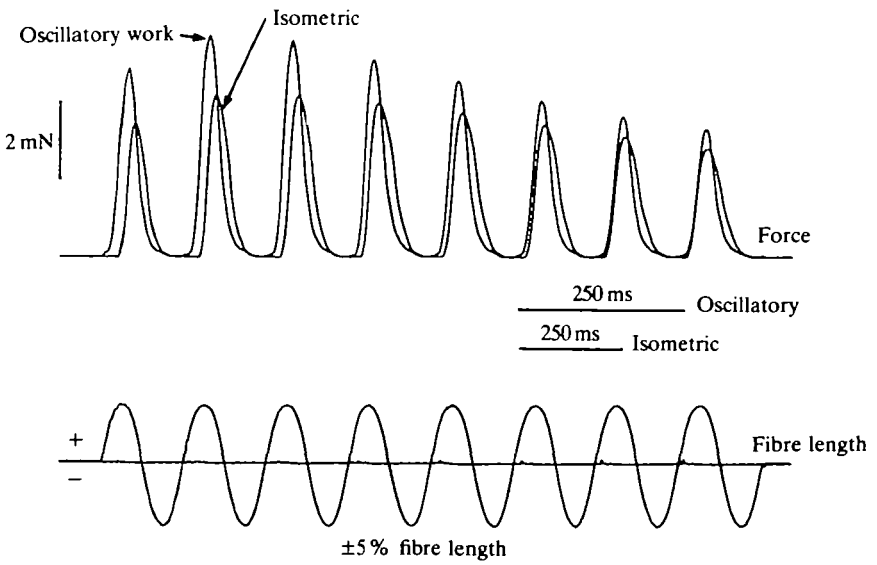

Fig. 3. Force and length records from the same preparation performing isometric twitches and oscillatory work at 8 Hz and ±5% fibre length. In the latter, a single stimulus is given in each cycle, with a phase shift of 20°. Fish length=35 cm.

performed during stretch. When the stimulus was delayed by 1°, the negative work performed during stretch was greater than the positive work gained during shortening, and net work decreased. That the extra force gained at 10° was due to force enhancement by stretch is demonstrated in Fig. 3, which shows isometric twitches superimposed on top of an oscillatory work record for the same preparation, under near optimum conditions for a single stimulus. Considerably higher forces were achieved during oscillatory work. Note that the two records in Fig. 3 are on different timebases. When performing oscillatory work 'twitch' kinetics are significantly faster than under isometric conditions.

The consequences of changing cycle/tailbeat frequency

To maximise net work per cycle, and hence power output, the force·time integral during the shortening phase (minus any negative work) must be maximised. As cycle frequency was decreased more stimuli could be given during each cycle, maintaining high force during shortening. If too many stimuli were given, the preparation was unable to relax before the onset of stretch, increasing the negative work component, and thus decreasing net work. This is illustrated in Fig. 4, which shows force and muscle length records, with associated, superimposed work loops over a range of different cycle frequencies. Conditions are chosen to give optimum power output at each cycle frequency. Optimum power output was obtained with 1, 1, 3 and 7 stimuli at 18, 11, 5 and 3 Hz, respectively (Fig. 4). At a cycle frequency of 18 Hz, twitch kinetics were too slow to enable the preparation to relax fully at the end of each cycle: minimum force increased

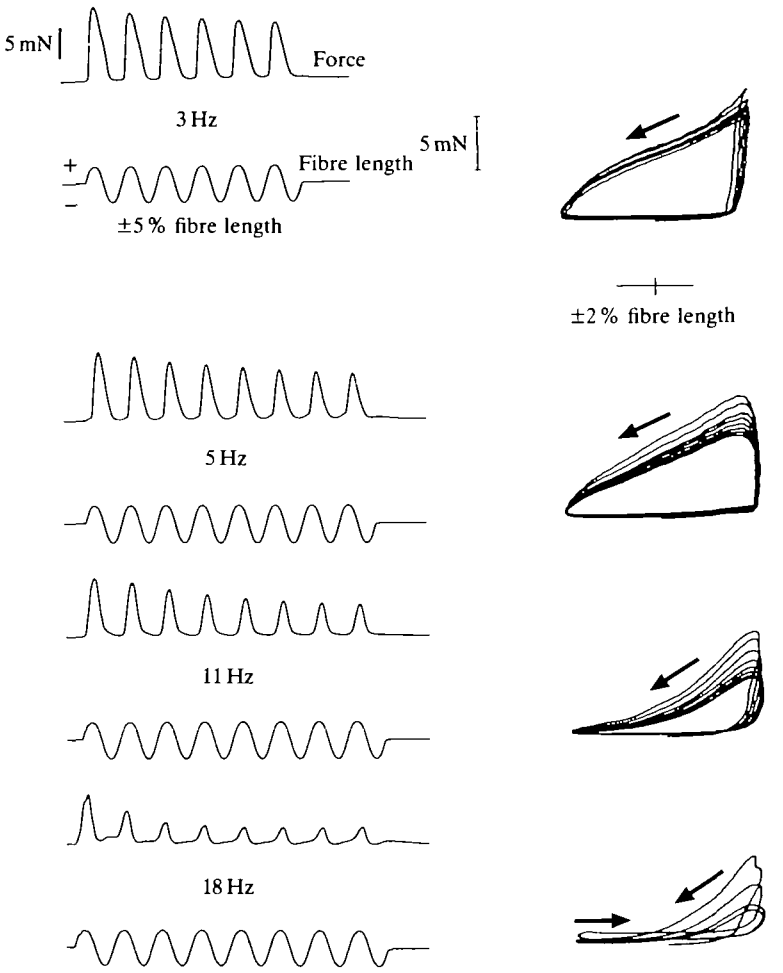

Fig. 4. Force and length records, and superimposed work loops, from a preparation operating under conditions of optimum power output at four different cycle/tailbeat frequencies. Stimulus parameters (number of stimuli/phase shift): 3 Hz=7/50°, 5 Hz=3/50°, 11 Hz=1/0°, 18 Hz=1/0°. At 3 Hz, only six loops were performed to avoid the risk of fatigue. At 18 Hz only the first four loops have been drawn for clarity. Arrows indicate direction of travel. Fish length=28.5 cm.

markedly, maximum force declined, and the work loops described a figure of eight, with anti-clockwise positive and clockwise negative components. At higher frequencies, net work and thus power output would rapidly decline to zero. At frequencies below around 2 Hz, so many stimuli were required that preparations began to show signs of fatigue, and it was often not possible to determine optimum conditions with the same precision as at higher frequencies.

We noted above that force and work declined in successive loops at a given cycle frequency. The rate at which they declined increased as cycle frequency increased.

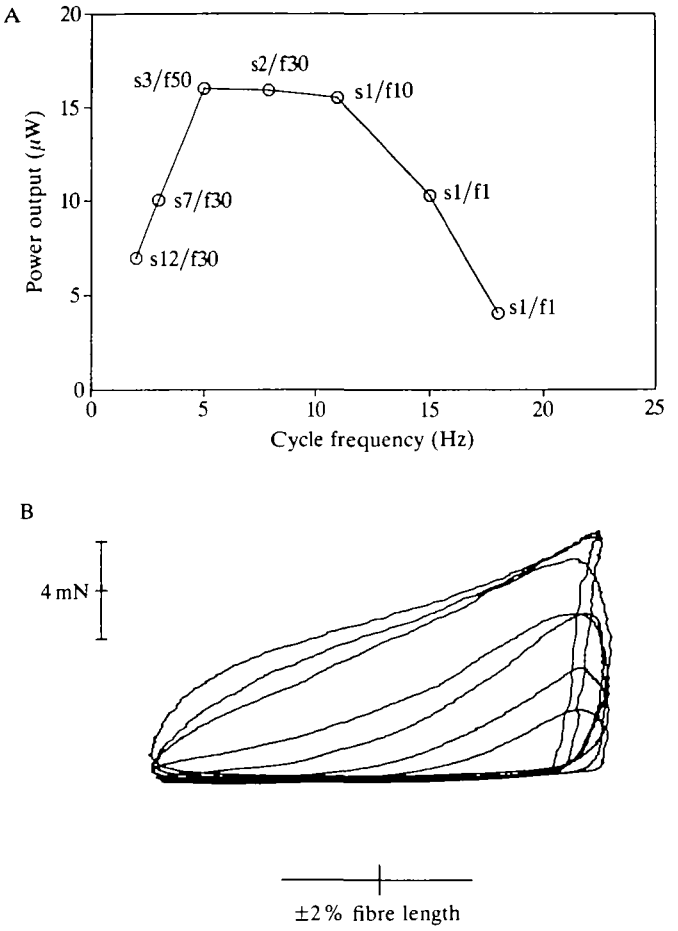

Fig. 5. (A) Optimum power output plotted against cycle frequency for a preparation from a 25.5 cm fish. sx/fy=number of stimuli/phase shift. Muscle length change=±5%. (B) Superimposed work loops used to derive A.

This point is illustrated in Fig. 4. At low frequencies, when the decline was minimal, preparations received more stimuli, and performed more net work, in each cycle. This suggests that the decline in work in successive cycles was not due to fatigue. With a 10 min rest between runs, the force records for a given set of parameters were highly reproducible.

In addition to a change in the number of stimuli, there was a systematic change in the stimulus phase shift for optimum power output. This is shown in Fig. 5A, where optimum power output is plotted against cycle frequency for a 25.5 cm fish, and the number of stimuli and the phase shift for optimum power output are given beside each value. Optimum phase shift was greatest at those cycle frequencies giving optimum power output, and declined at higher and lower frequencies. In Fig. 5B the work loops used to derive Fig. 5A are superimposed.

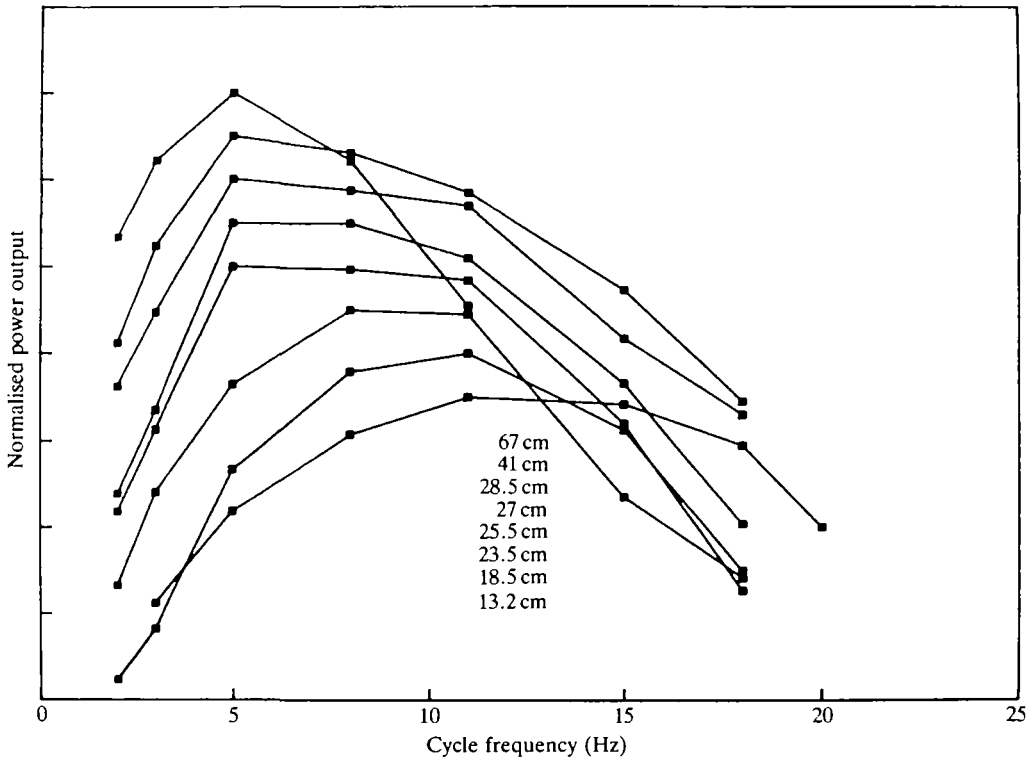

Fig. 6. Relative power output, normalised to the maximum at any frequency, plotted against cycle frequency for fish ranging in length from 13.2 to 67 cm. For clarity, each curve has been displaced on the vertical axis by 0.2 maximum power output. *y*-axis tics represent 0.2 maximum power. The order in which the fish lengths are placed on the graph corresponds to the order of the eight power output curves at 5 Hz.

The effects of fish size on power output–cycle frequency relationships

In Fig. 6 optimum power output has been plotted against cycle frequency for preparations isolated from fish ranging in size from 13 to 67 cm. All values have been normalised to maximum power output obtained at any frequency and, for clarity, the curves have been displaced vertically by equal increments (*y*-axis increments=0.2 maximum power). The cycle frequency for optimum power output increased as the size of the fish decreased. The individual curves are very broad, with high power outputs being maintained over a wide range of frequencies. This is shown in Fig. 7, where the vertical bars indicate the frequency range over which more than 90 % of maximum power output was produced. The data are plotted on a log/log graph, and the mid-points of the bars can be described by the equation:

$$f_{opt} = 1.67L^{-0.52},$$

where f_{opt} is the cycle frequency at the mid-point of the 90 % optimum power output bars of Fig. 7, and L is fish length.

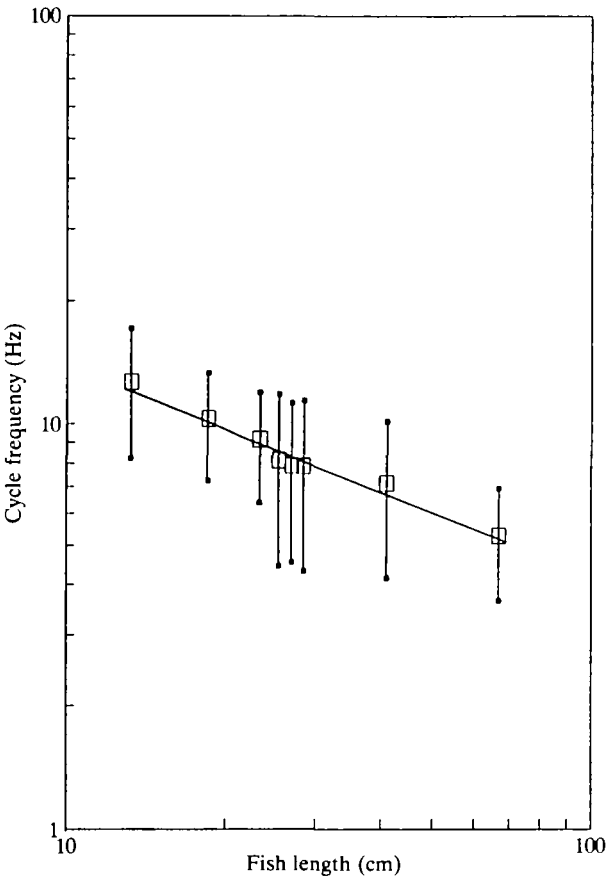

Fig. 7. The vertical bars indicate the cycle frequency range over which each preparation generates more than 90 % of its maximum power output. This has been plotted on a log/log graph against fish length. The midpoints of each bar (f_{opt}) can be fitted to the equation:

$$f_{opt} = 1.67L^{-0.52},\ r^2 = 0.97,\ L = \text{body length}.$$

A marked correlation between fish size and the stimulus parameters (under optimum conditions) at a given cycle frequency was also noted. This was evident at all cycle/tailbeat frequencies. For example, at 8 Hz, phase shift declined from 35° to 20°, and the number of stimuli from 3 to 1, as fish length increased over the range studied. This presumably reflects changes in the twitch kinetics of the muscle fibres with increasing fish size. In Fig. 8, the half-times for activation and relaxation during isometric twitches and tetani have been plotted for four fish of different sizes. There was little change in the time taken to rise to half maximum force but, as fish length decreased below 30 cm, relaxation rate increased dramatically in both twitches and tetani. During oscillatory work experiments, when more than one stimulus was required per cycle, they were given at a frequency which just produced a fused isometric contraction. This has been shown

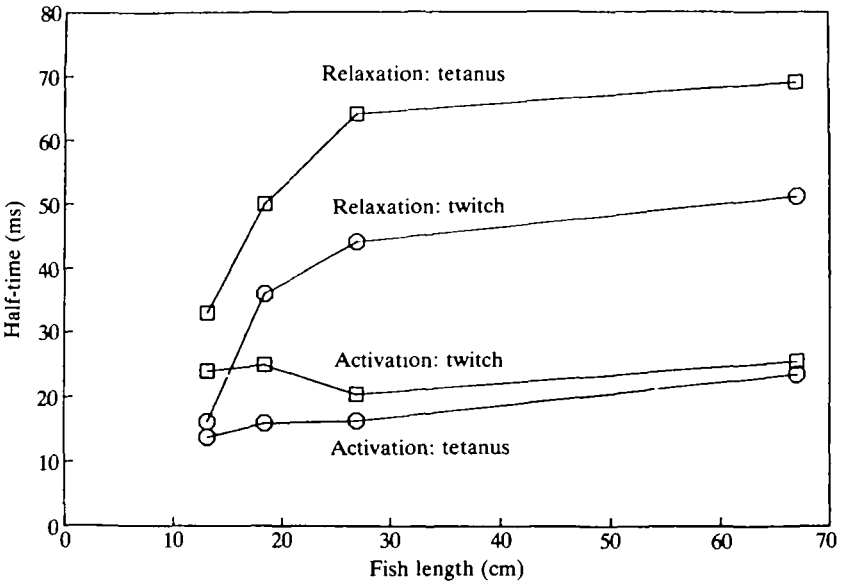

Fig. 8. Half-times of activation and relaxation for isometric twitches and tetani, plotted against fish length. Half-time is defined as the time taken to rise to 50 % maximum force, or to fall from peak to 50 % force.

to maximise power output (Altringham and Johnston, 1990). Stimulation frequency increased from 50 to 70 Hz from the largest to the smallest fish.

Discussion

The power output of myotomal muscles during oscillatory work is a complex function of strain amplitude, cycle frequency and the number and timing of electrical stimuli (Altringham and Johnston, 1990). Swimming is brought about by the sequential stimulation of the muscle fibres on alternate sides of the body. A wave of stimulation travels from anterior to posterior, and the duration of stimulation in each cycle decreases from head to tail (Grillner and Kashin, 1976; Williams *et al.* 1989). The mechanical wave travels more slowly along the body than does the electromyographical wave. Kinematic and electromyographical analyses suggest that, although the wave of body deformation runs from head to tail, the bending moment will be a standing wave, resulting in a systematic phase difference between force and length cycles along the length of the body (Hess and Videler, 1984). Williams *et al.* (1989) suggest that although the activation of muscle is a travelling wave, its high velocity, and long burst duration rostrally, produce some of the features of a standing wave. Broadly speaking, these studies indicate that, for myotomes behind the head, force is maximal during shortening

and hence power output is positive through most of the cycle (Hess and Videler, 1984; Williams *et al.* 1989; van Leeuwen *et al.* 1990). Below we describe how we have modelled this situation for cod, ranging in length from 13 to 67 cm, by selecting parameters that give optimum power output.

In all cases, maximum power output was obtained by giving a small pre-stretch in the active state, prior to shortening. We have shown that this increases force above isometric levels, increasing the work performed during shortening. The optimum phase shift required varied with cycle frequency (Fig. 5A) and decreased with increasing fish length. Precise information on the timing of stimulation *in vivo* is unavailable, and it is not known whether the motor system of the fish is able to make the small adjustments necessary to optimise power output. A similar pre-stretch was also required for optimum power output in isolated fast and slow muscle fibres from the sculpin (Altringham and Johnston, 1990), but not, as far as can be ascertained from the published results, in synchronous insect flight muscle (Josephson, 1985) or frog sartorius muscle (Stevens, 1988). An optimum strain for work output during cyclical contractions has been found for a range of invertebrate (Josephson, 1985; Josephson and Stokes, 1989) and vertebrate muscles (Stevens, 1988; Altringham and Johnston, 1990). Factors which determine the relationship between strain and work output include: passive compliance, the length–tension curve, the force–velocity relationship, shortening deactivation and length-dependent changes in twitch duration (Josephson and Stokes, 1989). We found that when phase and the number of stimuli were optimised, the amplitude of the length change needed for maximum power output was essentially independent of fish length at around ±5–6 % fibre length (Fig. 2A,B). This optimum strain falls within the range of muscle length changes predicted in a swimming fish on theoretical grounds (Alexander, 1969) and from kinematic studies (Hess and Videler, 1984; Rome *et al.* 1988).

Grillner and Kashin (1976) found that the duration of electromyographical activity remains a nearly constant proportion of the tailbeat cycle as swimming speed increases. The number of stimuli delivered to a fibre in each cycle is therefore likely to decrease with increasing tailbeat frequency and swimming speed. In our experiments, the number of stimuli required to produce the maximum net work decreased with increasing cycle frequency, consistent with the *in vivo* studies (see also Altringham and Johnston, 1990). Since the twitch duration is significantly shorter in small than in large fish, the number of stimuli needed at a given cycle frequency decreases with increasing fish length. For example, in order to maximise net work and power output at 8 Hz, 3 stimuli cycle^{-1} are required in 13 cm fish, compared with only 1 stimulus cycle^{-1} in 41 cm fish. Under conditions of optimum power output, many preparations did not relax completely between work cycles, with minimum forces rising up to around 5 % maximum force.

Isometric twitch duration in cod fibres is significantly shorter in small than in large fish, largely due to differences in relaxation rate (Fig. 8). This results in a clear shift in the frequency for optimum power output towards lower frequencies in larger fish: $f_{opt} \propto L^{-0.52}$. It should be noted that relative to isometric conditions,

force, and the rates of rise and fall of force, are increased, and the duration of the contractile event is decreased. Positive oscillatory work can therefore be performed at somewhat higher frequencies than might be predicted from the time course of isometric contractions alone. More net work is also performed at lower frequencies, since rapid de-activation results in less negative work being performed during the lengthening phase. As stated above, Curtin and Woledge (1988), using dogfish, found no correlation between fish length and the shortening velocity for maximum power output, determined from force–velocity curves. This is perhaps not suprising, given the lack of correlation between twitch time and maximum shortening velocity reported by Wilson and Woledge (1985) for frog muscle fibres. Since several interacting factors determine power output during oscillatory work, we need not expect all of them to show a significant correlation with fish length.

An interesting observation was that force and net work declined over the initial work cycles in cod fast fibres (Fig. 4). If the decline was due to fatigue, we would predict a greater effect at low frequencies, when the preparations were performing more work in each cycle, yet the reverse was the case. The magnitude of the deactivation effect appears to be positively related to the cycle frequency. This decline is presumably a mechanical deactivation induced by shortening. Because our protocol is so different from that used by other workers, comparison is difficult, but Colomo *et al.* (1986) have also described velocity-dependent shortening deactivation in frog muscle fibres. They observed the effect in the early stages of tetanic force development, a situation comparable to our own, when the shortening phase of the sine wave commences shortly after stimulation. Interestingly, this progressive decline in force and work appears to be variable between fibre types and species. For example, in fast and slow muscle fibres from *Myoxocephalus scorpius*, work per cycle changed very little over the first 2–3 cycles (either increasing or decreasing), and then remained constant over cycles 4–8 (Altringham and Johnston, 1990). There was a rapid recovery of force and work after a brief (4 s) interruption to the work cycles in cod fibres, and a subsequent rapid decline to pre-interruption levels (T. W. Moon, J. D. Altringham and I. A. Johnston, in preparation). These observations also suggest a mechanical rather than a metabolic mechanism. It should also be noted that after 10–12 cycles (at a frequency of 5 Hz) work per cycle reaches a steady state in cod fast fibres, after declining by 20–40 %, and may remain constant for up to a further 50 cycles (T. W. Moon, J. D. Altringham and I. A. Johnston, in preparation). If found *in vivo*, this initial decrease in net work with successive contraction cycles may contribute to the nearly exponential decline in swimming performance observed with increasing duration of burst swimming activity (Bainbridge, 1960).

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