

## TEMPERATURE AND THE FORCE-VELOCITY RELATIONSHIP OF LIVE MUSCLE FIBRES FROM THE TELEOST *MYOXOCEPHALUS SCORPIUS*

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*Accepted 21 March 1989*

### Summary

Small bundles of fast fibres were isolated from the myotomal muscle of the teleost *Myoxocephalus scorpius*. The temperature-dependence of isometric contractile properties and the force-velocity (P-V) relationship were studied. Fibres were found to deteriorate above 18°C, and the force plateau during tetanic stimulation was not maintained above 15°C. Twitch and tetanic tension ( $P_0$ ) showed optima at around 8°C. Force-velocity curves were fitted using either Hill's hyperbolic equation or a hyperbolic-linear equation (hyp-lin). The best fit to the data was provided by the hyp-lin equation, which gave consistently higher values for unloaded contraction velocity ( $V_{max}$ ): 4.3, 8.1 and 9.5 muscle lengths  $s^{-1}$  at 1, 8 and 12°C, respectively. The P-V relationship was found to become progressively more curved at higher temperatures. Muscle power output calculated from the hyp-lin equation was 123 W  $kg^{-1}$  at 1°C and 256 W  $kg^{-1}$  at 8°C. Curves normalized for  $P_0$  and  $V_{max}$  at each temperature show that the change in curvature is sufficient to increase the relative power output of the muscle by around 15% on decreasing the temperature from 8 to 1°C.

### Introduction

Studies using skinned (demembranated) fibres have shown that in fish muscle the force-velocity (P-V) relationship becomes less curved as temperature decreases (Johnston & Altringham, 1985). This is reflected in the increase in the value of the constant  $a$  in Hill's (1938) equation. We have suggested that this may provide a mechanism that would partially compensate for the decrease in power output as both force and contraction velocity decline (Johnston & Altringham, 1985; Johnston & Wokoma, 1986). However, skinned fibre preparations differ in their P-V relationships from those of live fibres. Data from skinned fibres are generally well described by Hill's (1938) equation, but data from live fibres deviate from a hyperbola at both high and low loads (e.g. Edman, 1988; Julian *et al.* 1986; Marsh & Bennett, 1986; Altringham & Johnston, 1988). Furthermore, skinned

■ **Key words:** muscle, fast twitch, force-velocity, temperature, teleost.

fibre preparations develop low tensions relative to live preparations from the same muscle (Altringham & Johnston, 1988).

Recently, isolated live (electrically excitable) preparations from myotomal muscle have been developed for elasmobranchs (Curtin & Woledge, 1988) and teleosts (Altringham & Johnston, 1988). The tensions generated by these preparations (when normalized to cross-sectional area) are comparable to those of a wide range of whole vertebrate muscles, suggesting their suitability for quantitative modelling of muscle power output.

The aim of the present study was to investigate the effects of temperature on the P-V curve of live fibre preparations and compare the results with published data from skinned fibres. The data have been used to calculate the degree of compensation of power output achieved by changes in the curvature of the P-V relationship. We have also studied the effects of temperature on isometric contractile properties. All experiments were carried out on fast myotomal muscle of the sculpin *Myoxocephalus scorpius*, a teleost found in the North Sea at 0–60 m which experiences a seasonal temperature range of around 2–17°C.

### Materials and methods

Specimens of the sculpin *Myoxocephalus scorpius* L. were obtained in the Firth of Forth between November 1987 and May 1988. All fish were held in seawater tanks at 5–7°C for 1–14 days prior to use. Fish were killed by a blow to the head, followed by decapitation. The mean length of the fish used was  $21.7 \pm 0.8$  cm, and mean mass was  $282 \pm 16$  g ( $\pm$ s.e.,  $N > 20$ ).

The preparation consisted of a bundle of 5–20 fibres, isolated from the fast muscle of the abdominal myotomes, dissected at 5°C as previously described (Altringham & Johnston, 1988). The preparation was bathed in Ringer's solution (in  $\text{mmol l}^{-1}$ : NaCl, 132.2; sodium pyruvate, 10; KCl, 2.6;  $\text{MgCl}_2$ , 1;  $\text{CaCl}_2$ , 2.7;  $\text{NaH}_2\text{CO}_3$ , 18.5;  $\text{NaHPO}_4$ , 3.2; pH 7.4 at 5°C), which was changed frequently. Aluminium foil clips were attached close to the fibre insertions, and these were placed on stainless-steel hooks, one of which was attached to a strain gauge (AE 801, AME Horten, Norway), the other to a servomotor (MFE model R4-077, Emerson Electronics, Bourne End, Bucks), controlled by a unit built in the laboratory. Aerated Ringer circulated constantly through the Perspex chamber in which the preparation was placed, and temperature was controlled to  $\pm 0.1$ °C. The preparation was stimulated *via* two platinum wire electrodes using 1.5 ms pulses at 1.2 times the voltage generating maximum tension. The sarcomere length of the preparation (measured by laser diffraction) was set to  $2.3 \mu\text{m}$  at the beginning of an experiment (this length gave a maximal twitch response). Data were collected and analysed on a Nicolet 3091 digital oscilloscope, stored on a BBC microcomputer and dumped to a printer for hard copy.

The effects of temperature on isometric properties were studied by varying the temperature of the Ringer in the chamber and giving a single twitch and tetanus at 10-min intervals. Over a range of 1–18°C the effects were reversible and so forc

records from each preparation could be obtained over several cycles of heating and cooling.

The force-velocity relationship was determined by means of isovelocity releases (Altringham & Johnston, 1988). Force-velocity curves were obtained at three temperatures, but each preparation was studied only at a single temperature. P-V data for individual fibres were fitted to Hill's (1938) hyperbolic function:

$$V = b(P_0 + a)/(P + a) - b ,$$

where  $V$  is velocity,  $P$  is tension,  $P_0$  is maximum tension and  $a$  and  $b$  are constants. A least-squares regression was iteratively fitted to the data by computer, without constraining the curve to go through  $P_0$ , to obtain the minimum mean-squared differences between observed and predicted data. The curvature of the P-V relationship is inversely related to  $a/P_0$ . In fitting to Hill's equation, data above  $0.8P_0$  were omitted, since it has been shown that they consistently deviate from the curve (Edman *et al.* 1976).

The data were also fitted to a hyperbolic-linear (hyp-lin) curve described by Marsh & Bennett (1986):

$$V = B(1 - P/P_0)/(A + P/P_0) + C(1 - P/P_0) ,$$

where  $A$  is dimensionless and  $B$  and  $C$  have dimensions of velocity. The ratio  $\dot{W}_{\max}/V_{\max}P_0$ , where  $\dot{W}_{\max}$  is maximum power output, is inversely related to the curvature of the P-V relationship, and has been calculated using values derived from both curve-fitting procedures. The methods are detailed in a previous paper (Altringham & Johnston, 1988).

#### Statistical analysis

The standard error of the estimate (S.E.E.) for both curve-fitting procedures was determined for each fibre from the equation:

$$\text{S.E.E.} = \sqrt{\text{RSS}}/(N - 2) ,$$

where RSS is the residual sum of squares and  $N$  is the number of values. The results derived using the two equations were compared with a paired  $t$ -test. Estimates of maximum contraction velocity derived from the two methods were also compared with a paired  $t$ -test. Changes in curvature of the P-V relationship with temperature were tested for with a standard  $t$ -test.

## Results

### Isometric properties

Representative twitch and tetanus records at various temperatures are shown in Fig. 1A. The force plateau was not maintained during tetanus above  $15^\circ\text{C}$ , and preparations deteriorated irreversibly above  $18^\circ\text{C}$ . Fused tetani were obtained at 40-50 Hz at  $1^\circ\text{C}$ , but fusion frequency increased with temperature to 75 Hz at  $8^\circ\text{C}$ . Both maximum tetanic tension and twitch tension increased with tempera-

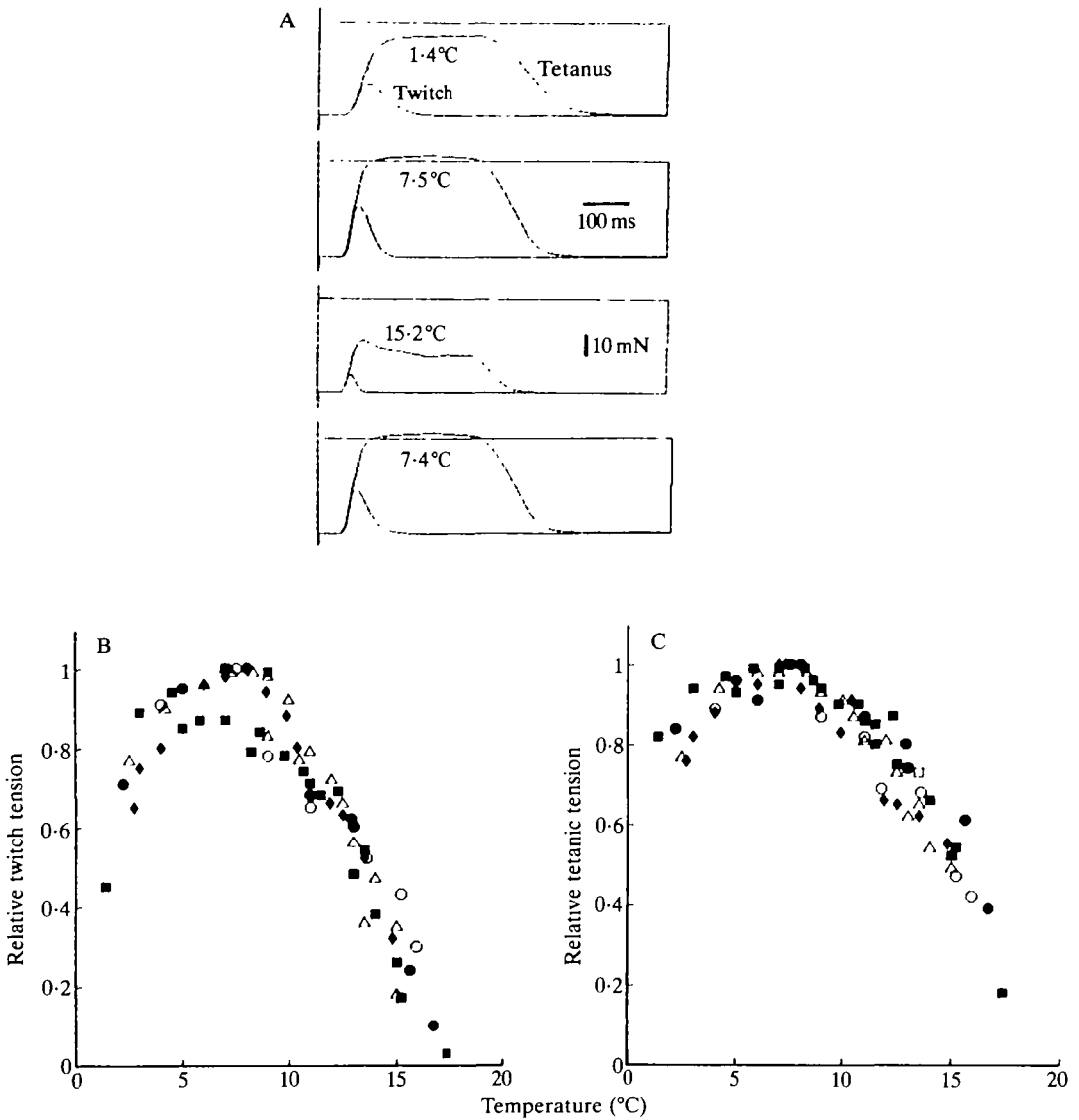


Fig. 1. (A) Isometric force records from a single preparation (12 fibres) at a series of temperatures. Each record shows a single twitch and tetanus. (B) Twitch tension plotted against temperature. Different symbols identify different preparations, data normalized to maximum tension. (C) Effects of temperature on tetanic tension.

ture up to a maximum at around 8°C, then decreased as temperature was increased further (Fig. 1B,C).

Rates of rise and relaxation of tension were measured as the time taken to rise to half-maximal tension ( $T_{0.5a}$ ) and to relax to half-maximal tension ( $T_{0.5r}$ ).  $T_{0.5a}$  and  $T_{0.5r}$  for twitch and  $T_{0.5r}$  for tetanus decreased with temperature,  $Q_{10}$  (2–12°C) ■

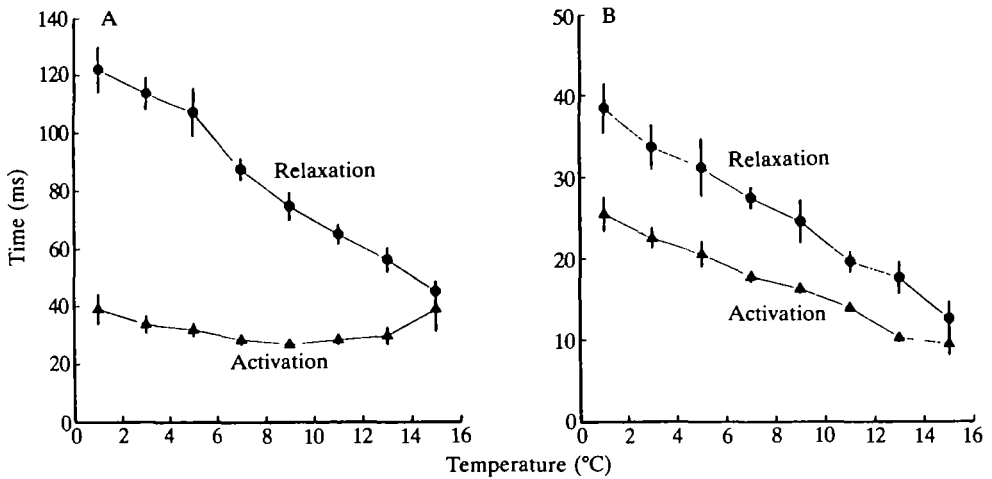


Fig. 2. Half-rise and half-relaxation times plotted against temperature. Data  $\pm$  s.e. and grouped in 2°C intervals. (A) Tetanus; (B) twitch.

Table 1. *Contractile properties of fast myotomal muscle fibres*

	Temperature			
	2°C	8°C	12°C	16°C
Maximum isometric tension (kNm <sup>-2</sup> )	242	315	255	172
Twitch-tetanus ratio	0.55 $\pm$ 0.07	0.66 $\pm$ 0.04	0.55 $\pm$ 0.05	0.32 $\pm$ 0.05
Tetanic fusion	50 Hz	60 Hz	65 Hz	75 Hz
Half twitch rise time (ms)	25.5 $\pm$ 2.1	17.7 $\pm$ 0.7	13.9 $\pm$ 0.47	9.4 $\pm$ 1.4
Half twitch relaxation time (ms)	38.4 $\pm$ 3.0	27.4 $\pm$ 1.3	19.5 $\pm$ 1.3	12.5 $\pm$ 2.1
Half tetanus rise time (ms)	39.0 $\pm$ 5.1	28.3 $\pm$ 1.8	28.2 $\pm$ 1.8	38.7 $\pm$ 7.7
Half tetanus relaxation time (ms)	121.9 $\pm$ 8.1	87.1 $\pm$ 3.7	64.6 $\pm$ 3.4	44.6 $\pm$ 3.6

Values represent mean  $\pm$  s.e.,  $N = 5$ .

Maximum isometric tensions are extrapolated from tension derived at 3°C in a previous study (Altringham & Johnston, 1988).

1.8–2.0. In contrast,  $T_{0.5a}$  for tetanus was relatively independent of temperature (Fig. 2). Isometric properties are summarized in Table 1.

*Force-velocity relationship*

The P-V relationship was studied at 1, 8 (optimum) and 12°C. The results from both curve-fitting procedures, for each temperature, are summarized in Table 2, and representative P-V curves shown in Figs 3 (Hill's) and 4 (hyp-lin). A better fit to the data was achieved using the hyp-lin equation ( $P < 0.01$ , Table 2).

Table 2. Summary of force-velocity data of fast myotomal muscle fibres at three temperatures

	1°C	Temperature 8°C	12°C
Hill's equation			
$V_{\max}$ ( $L s^{-1}$ )	$4.08 \pm 0.05$	$7.10 \pm 0.26$	$8.10 \pm 0.20$
$\dot{W}_{\max}$ ( $W kg^{-1}$ )	123	256	223
Load for maximal power output	$0.31P_0$	$0.30P_0^{NS}$	$0.28P_0^*$
$a/P_0$	$0.27 \pm 0.02$	$0.22 \pm 0.02^{NS}$	$0.17 \pm 0.02^{**}$
$b$ ( $L s^{-1}$ )	$0.98 \pm 0.08$	$1.35 \pm 0.12$	$1.17 \pm 0.10$
$\dot{W}_{\max}/V_{\max}P_0$	$0.125 \pm 0.002$	$0.115 \pm 0.003^*$	$0.109 \pm 0.004^{**}$
$r^2$	0.98	0.98	0.96
Hyp-lin equation			
$V_{\max}$ ( $L s^{-1}$ )	$4.27 \pm 0.08$	$8.14 \pm 0.22$	$9.46 \pm 0.16$
$\dot{W}_{\max}$ ( $W kg^{-1}$ )	140	313	292
Load for maximal power output	$0.44P_0$	$0.47P_0^{**}$	$0.50P_0^{**}$
$A$	$0.10 \pm 0.02$	$0.06 \pm 0.01$	$0.04 \pm 0.01$
$B$ ( $L s^{-1}$ )	$0.26 \pm 0.05$	$0.27 \pm 0.02$	$0.21 \pm 0.05$
$C$ ( $L s^{-1}$ )	$1.60 \pm 0.14$	$3.22 \pm 0.13$	$3.90 \pm 0.22$
$\dot{W}_{\max}/V_{\max}P_0$	$0.136 \pm 0.002$	$0.126 \pm 0.002^{**}$	$0.119 \pm 0.002^{**}$
$r^2$	0.99	0.99	0.99
S.E.E.			
Hill's equation	$0.027 \pm 0.004$	$0.041 \pm 0.005$	$0.055 \pm 0.007$
Hyp-lin equation	$0.010 \pm 0.001^{**}$	$0.012 \pm 0.002^{**}$	$0.019 \pm 0.007^{**}$

Data represent mean  $\pm$  s.e.,  $N = 6$ .

$V_{\max}$ , extrapolated maximum contraction velocity;  $\dot{W}_{\max}$ , maximum power output;  $a$  and  $b$  are constants from the Hill equation,  $A$ ,  $B$  and  $C$  constants from the hyp-lin equation.

$L s^{-1}$ , muscle lengths per second.

\*  $P < 0.05$ , \*\*  $P < 0.01$ , NS, not significant.

In the first two sections of the table, values at 8 and 12°C have been compared to those obtained at 1°C. The standard errors of the estimates (s.e.e.) derived from the two curve-fitting procedures are compared at each temperature.

The hyp-lin equation yielded significantly higher  $V_{\max}$  values than Hill's equation at all temperatures (1°C,  $P < 0.05$ ; 8 and 12°C,  $P < 0.01$ ).

$V_{\max}$  was calculated using both Hill's and the hyp-lin equation, values being 4.08, 7.10 and 8.10  $L s^{-1}$  (Hill's) and 4.27, 8.14 and 9.46  $L s^{-1}$  (hyp-lin) at 1, 8 and 12°C, respectively, where  $L$  is muscle length.  $V_{\max}$  values calculated using the hyp-lin equation were significantly higher at all temperatures (Table 2), and exhibited less scatter than values from Hill's equation.  $Q_{10}$  values for  $V_{\max}$  were 1.82 for Hill's and 2.01 for the hyp-lin equation.

The  $P$ - $V$  relationship becomes significantly more curved with increasing temperature (see Table 2).  $a/P_0$  is inversely related to the degree of curvature and

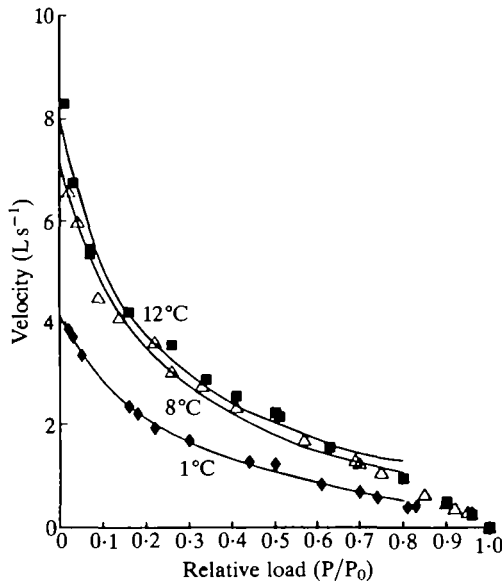


Fig. 3. Force-velocity data from single, representative preparations fitted to Hill's equation. Data above  $0.8P_0$  were omitted and the curve was not constrained to pass through  $P_0$ .  $a/P_0 = 0.27$  at  $12^\circ\text{C}$ ,  $0.22$  at  $8^\circ\text{C}$  and  $0.17$  at  $1^\circ\text{C}$ .

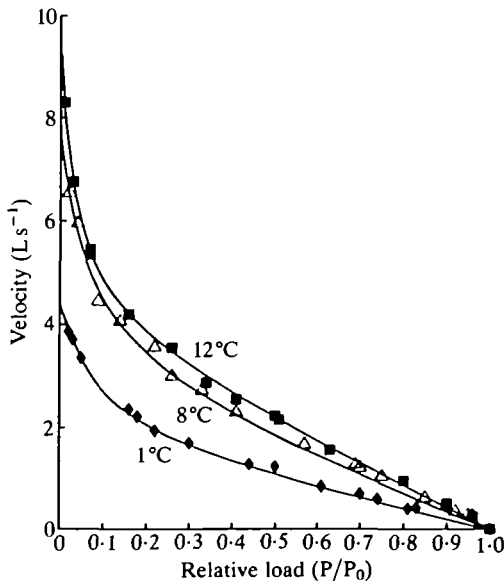


Fig. 4. Data from preparations used for Fig. 3 fitted to the hyp-lin equation. The entire data sets were fitted.  $\dot{W}_{\max}/V_{\max}P_0 = 0.136$  at  $12^\circ\text{C}$ ,  $0.126$  at  $8^\circ\text{C}$  and  $0.119$  at  $1^\circ\text{C}$ .

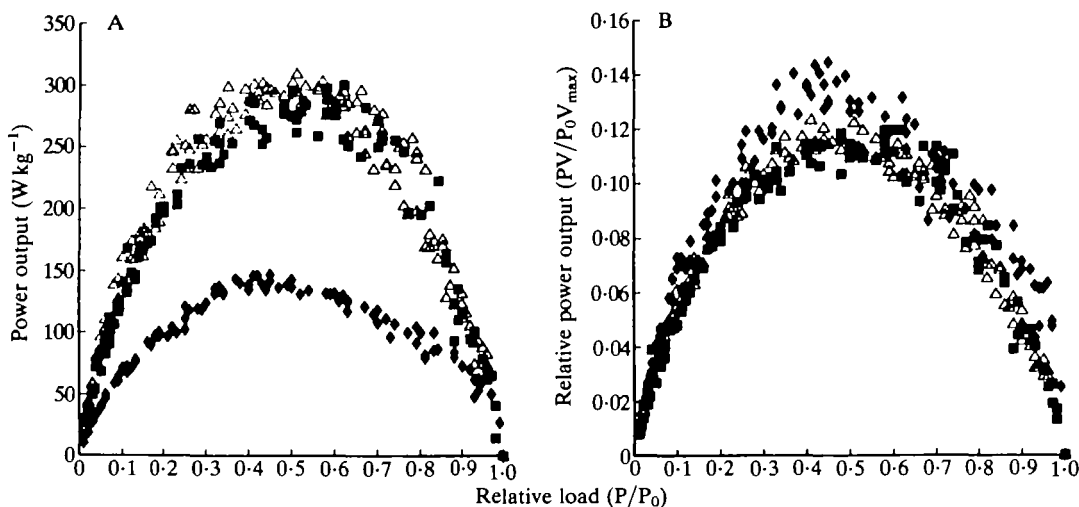


Fig. 5. (A) Power output calculated using parameters derived from fitting the hyp–lin equation plotted against relative load at three temperatures.  $\blacklozenge$  = 1°C,  $\triangle$  = 8°C,  $\blacksquare$  = 12°C. (B) Power output normalized for temperature-induced changes in force and velocity plotted against relative load,  $(PV/P_0V_{\max})$  vs  $(P/P_0)$ .

decreased from 0.27 at 1°C, to 0.24 at 8°C and 0.17 at 12°C. Similarly, the value for  $\dot{W}_{\max}/V_{\max}P_0$  derived from the hyp–lin plot decreased with increasing temperature, from 0.136 at 1°C, to 0.126 at 8°C and 0.119 at 12°C.  $\dot{W}_{\max}/V_{\max}P_0$  values from Hill's equation also decreased between 1 and 12°C (Table 2).

#### Power output

P–V data were used to plot power output (PV) against load for all temperatures for all fibres. In Fig. 5, absolute power output (A) has been plotted alongside curves normalized for temperature-induced changes in both force and velocity (B). Power output was calculated using the hyp–lin equation and a mean value for absolute tension (normalized to cross-sectional area) derived in a previous study on this species (Altringham & Johnston, 1988). In this way, differences between preparations were normalized so that data from all fibres could be plotted on the same graph. Fig. 5B shows the change in power output due only to changes in the curvature of the P–V relationship. The curvature change between 8 and 1°C increased the relative power output at 1°C by around 15%. The load at which maximum power was obtained, calculated using the hyp–lin equation, increased with increasing temperature, from 0.44 $P_0$  at 1°C to 0.50 $P_0$  at 12°C ( $P < 0.01$ , Table 2). This trend is readily apparent in the raw data, shown in Fig. 5A. In contrast, the load for maximum power output calculated using Hill's equation decreased slightly, but significantly, with increasing temperature.



## Discussion

### *Maximum isometric tension*

In sculpin live fibre preparations both twitch and tetanic tensions show a clear optimum at around 8–10°C, the midpoint of the normal environmental temperature range (ET). This is in marked contrast to results from skinned fibre preparations from fish (including the sculpin) where maximum tension increases with increasing temperature, or is largely temperature-independent, over the ET of each species (Johnston & Sidell, 1984; Johnston & Altringham, 1985, 1988; Altringham & Johnston, 1986). The experiments on skinned fibres indicate that the force-generating mechanism itself is largely independent of temperature. The decline in tension observed at high temperatures in intact preparations suggests a marked temperature-dependence, or failure, of excitation–contraction coupling.

The temperature range over which isolated live fibres remain viable is correlated with body temperature. Fibres from the antarctic icefish (ET –1.9 to 2°C) deteriorate rapidly above 10°C (Johnston, 1987). In contrast, fibres from the desert iguana (preferred body temperature, PBT, 40°C) give stable contractions at 22–44°C, but tension declines with time below 15°C (Marsh & Bennett, 1986). Phylogenetic dissimilarities complicate the interpretation of interspecific adaptations in contractile properties. To overcome these problems, John-Alder & Bennett (1987) investigated muscle contractile properties in three genera of Australian skinks. The result indicated that even relatively small differences in average body temperature are sufficient to produce resistance adaptations in muscle contractility. Translational capacity adaptations are also evident in maximum tetanic tension (Precht, 1958). They can be seen both within classes, e.g. in reptiles (Bennett, 1985; John-Alder & Bennett, 1987), and between classes. As an example of the latter, maximum tetanic tension for fast muscle fibres occurs at 5°C in the icefish (ET –1.9 to 2°C) (Johnston, 1987), at 20°C in the tiger salamander (ET 5–25°C) (Else & Bennett, 1987) and at 30°C in the western sand lizard (PBT 35°C) (Marsh & Bennett, 1986). With an optimum tension at 8°C (ET 2–17°C), the sculpin fits appropriately into this sequence.

### *Maximum contraction velocity*

$V_{\max}$  values for live preparations from the sculpin were higher than those calculated for skinned fibres by Johnston & Sidell (1984).  $Q_{10}$  values of around 2 are similar to those for other live fibre preparations from *Rana* (Edman *et al.* 1976) and *Xenopus* (Lannergren *et al.* 1982).  $V_{\max}$  was found to be more temperature-dependent at the lower end of the studied temperature range, as reported in amphibians (Lannergren *et al.* 1982) and reptiles (e.g. John-Alder & Bennett, 1987).

### *Force–velocity relationship*

The hyp–lin equation provides a better description of the P–V data for intact fibres than Hill's equation, in agreement with previous results on intact myotomal

fibres (Altringham & Johnston, 1988) and on reptilian muscles (Marsh & Bennett, 1986). The extrapolated value of  $V_{\max}$  from the hyp–lin equation was significantly higher than that from Hill's equation. The fitted line for Hill's equation consistently fell below the data at very low loads, underestimating  $V_{\max}$ . Deviation of the data from the fitted line at high loads, first noted by Edman *et al.* (1976), was also evident. This has been seen in a previous study of sculpin fast muscle (Altringham & Johnston, 1988) and in other vertebrate muscle, e.g. *Xenopus laevis* (Lannergren *et al.* 1982). Edman (1988) has recently studied this part of the P–V curve in detail in the frog *Rana temporaria*. He demonstrated that the P–V relationship undergoes a clear inflection around  $0.8P_0$ . The data above and below this load were fitted to two separate hyperbolic curves. Edman suggests that cross-bridge kinetics change at this point, and proposes that either their rate of attachment decreases, as a consequence of the high density of attached bridges, or a high proportion of bridges enter a low force state. P–V data from sculpin live fibres also show an inflection above  $0.8P_0$ , but undergo a reversal of curvature at high loads (Altringham & Johnston, 1988). The P–V relationship of live fibres became more curved with increasing temperature, a characteristic also observed in fish skinned fibres (Johnston & Altringham, 1985; Johnston & Wokoma, 1986). In contrast, curvature has been shown to be independent of temperature in all other ectotherms studied, e.g. in amphibians (Lannergren, 1978; Edman, 1988) and reptiles (Marsh & Bennett, 1985, 1986; Else & Bennett, 1987; John-Alder & Bennett, 1987; Mutungi & Johnston, 1987), with the exception of *Xenopus* type 1 fibres (Lannergren *et al.* 1982).

#### *Muscle power output*

A less curved force–velocity relationship (i.e. higher  $a/P_0$  or  $\dot{W}_{\max}/V_{\max}P_0$ ) yields a higher velocity, and thus a greater power output, for a given load. When calculated from Hill's equation, maximum power is produced at lower force as curvature increases (Woledge *et al.* 1985). In contrast, the power curves obtained using the hyp–lin equation show maximum power to be produced at lower forces as curvature decreases (Table 2, Fig. 5).

The change in curvature of the P–V relationship in intact fish fibres may be a mechanism for offsetting the decrease in power output induced by decreasing temperature. The observed change in curvature between 8 and 1°C increased the relative maximum power output by about 15% (Fig. 5B). When compared at their normal environmental temperatures, muscle fibres from fish adapted to cold environments have a less curved P–V relationship than those from warm-water species (Johnston & Altringham, 1985). Thus, although  $V_{\max}$  shows no systematic capacity adaptation between fish from different thermal environments (Johnston & Altringham, 1985), changes in the curvature of the P–V relationship may contribute to capacity adaptations in muscle power output and efficiency. However, this mechanism must be of secondary importance to the complete capacity adaptation of maximum isometric tension observed in fibres of fish from

different thermal environments (Johnston & Altringham, 1985, 1988; Altringham & Johnston, 1986).

This work was supported by grants from the SERC, NERC and the Wellcome Trust. KSL was in receipt of an NERC studentship.

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