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CONTRACTILE PROPERTIES OF THE STRIATED ADDUCTOR MUSCLE IN THE BAY SCALLOP *ARGOPECTEN IRRADIANS* AT SEVERAL TEMPERATURES

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Summary

The isometric and isotonic contractile properties of the cross-striated adductor muscle of the bay scallop (*Argopecten irradians*) were measured *in vitro* at 10, 15 and 20˚C. The length at which twitch force was maximal as a function of the closed length *in situ* (L_0/L_{cl}) averaged 1.38±0.01 (mean ± S.E.M.) at 10˚C. This length is very close to the typical length at maximum gape during natural swimming at this temperature. Passive force was very low over the range of lengths measured here; at L_0, passive force averaged approximately 0.08 N cm^{-2}, or only 0.5% of the corresponding peak twitch force. The mean peak isometric twitch force ($P_{tw,max}$) at 10˚C was 21.43±0.68 N cm^{-2} (S.E.M.), and the ratio of peak twitch force to tetanic force ($P_{tw,max}/P_0$) averaged 0.89±0.01. Temperature did not affect either twitch force (P_{tw}), once fatigue was taken into account, or $P_{tw,max}/P_0$. In contrast, the time-related properties of twitch contractions (latent period, t_L; time to peak tension, t_{Ptw}; and time from peak tension to half-relaxation, $t_{50\%R}$) were positively modified by temperature at all temperatures measured (Q_{10}>1.8). All three properties were more temperature-sensitive over the range 10–15˚C than over the range 15–20˚C.

The force–velocity relationships of the striated adductor muscle were fitted to the hyperbolic-linear (HYP-LIN) equation. The force–velocity curves of the striated adductor muscle of the scallop were strongly influenced by temperature. Maximal velocity at zero force (V_{max}), and therefore maximal power output, increased significantly with temperature. The Q_{10} over the temperature range 10–15˚C (1.42) was significantly lower than that over the range 15–20˚C (2.41). The shape of the force–velocity relationship, assessed through comparisons of the power ratio ($\dot{W}_{max}/V_{max}P_0$), was not influenced by temperature.

Introduction

The locomotor performance of animals is determined in part by the characteristics of the skeletal muscles that provide the power for movement. Because temperature has profound effects on the time-dependent contractile properties of striated muscle,

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locomotor performance in ectotherms is dependent upon body temperature (John-Alder and Bennett, 1981; Josephson, 1981; Bennett, 1984, 1990; Marsh and Bennett, 1985, 1986*b*; Else and Bennett, 1987; John-Alder *et al.* 1989). Ascertaining the relationship between the *in vitro* contractile properties of a particular muscle and locomotor performance, however, is often complicated (Marsh and Bennett, 1985, 1986*a*,*b*).

One approach to clarifying these relationships is to choose a simple locomotor system that allows precise correlates to be drawn between *in vitro* and *in vivo* performance. Scallops (Family Pectinidae) swim short distances primarily to escape predators (Stephens and Boyle, 1978; Winter and Hamilton, 1985; Peterson *et al.* 1982). These animals swim by jet propulsion using a succession of claps consisting of alternate adductions (closures) and abductions (openings) of the two valves (see Dakin, 1909; Marsh *et al.* 1992). During adduction, increased pressure in the sealed mantle cavity propels the animal ventral (gape) side first as water escapes through one or two jets near the hinge. Adduction of the valves during swimming is powered solely by the striated ('fast') portion of the single adductor muscle (Lowy, 1954), which is morphologically distinct and much larger than the adjacent smooth portion. The muscle is attached directly to the valves with no intervening tendons. Morphological evidence suggests the cells in this muscle are electrically coupled *via* gap junctions (Nunzi and Franzini-Armstrong, 1981), but this has been not been confirmed by electrical recordings (Mellon, 1968). Moreover, although this muscle has conventional sarcomeres, it is regulated *via* the thick filaments ('myosin activated') rather than the thin ones as in vertebrate striated muscle (Kendrick-Jones *et al.* 1970). Abduction of the valves is powered by energy stored in an elastic hinge ligament, which is compressed during adduction (Trueman, 1953; Alexander, 1966). During a swim, the entire muscle is activated nearly simultaneously with typically one to three nerve impulses (Mellon, 1968, 1969; J. M. Olson and R. L. Marsh, unpublished results). Because the activation of the striated adductor muscle appears to be under reflex (Mellon, 1969) as well as central (Wilkens, 1981) control, normal cyclical contractions of the muscle are dependent upon the re-establishment of the starting muscle length (i.e. the length at maximum gape). Therefore, the thermal effects on both the force and kinetics of contraction in the striated adductor muscle influence the thermal sensitivity of clapping frequency during swimming in the bay scallop (R. L. Marsh, J. M. Olson and S. K. Guzik, unpublished results).

Despite the advantages of the scallop locomotor system for studying muscle performance *in vivo* (Marsh *et al.* 1992), information about the general contractile properties of this muscle is sparse and no study has examined thermal effects systematically. The biochemical characteristics of Ca^{2+} binding in this myosin-regulated muscle have been the subject of numerous investigations (e.g. Kendrick-Jones *et al.* 1970), and skinned fibers from the adductor muscle have been used to study the regulation of contraction (Simmons and Szent-Györgyi, 1985). Only one well-documented study (Rall, 1981) provides information on the isometric contractile properties of intact fibers from the adductor muscle from a scallop (*Placopecten magellanicus*). Unpublished observations of isometric and isotonic contractile properties have been cited several times (e.g. Hanson and Lowy, 1960; Millman, 1967), but it is impossible in these cases to evaluate fully the conditions under which the observations

were made. Indeed, outside the arthropods, very little information exists on the contractile properties of invertebrate striated muscle in general.

We have measured the isometric and isotonic contractile properties of the striated adductor muscle of the bay scallop (*Argopecten irradians*) over the temperature range 10–20˚C. These temperatures are within the range of natural water temperatures (5–24˚C) found between April and September at the sites these animals were collected near Cape Cod, Massachusetts (E. Enos, personal communication). This study was performed in conjunction with a larger study investigating the effects of temperature on the *in vivo* and *in vitro* mechanical performance of the striated adductor muscle in this species.

Materials and methods

Animals

Bay scallops [*Argopecten irradians* (Lamarck)] were collected between April and September off the southern coast of Cape Cod, MA, by the Department of Marine Resources at the Marine Biological Laboratory, Woods Hole, MA. Individuals were intermediate in size for this species. Body mass including the shell averaged 29.45±1.50 g (mean ±1 S.E.M.; N=20), and the shell dimensions were 56.91±0.89mm (anterior–posterior), 53.39±0.84mm (dorsal–ventral) and 23.00±0.51mm (thickness). Animals were kept in aerated artificial salt water (Instant Ocean) maintained at 10˚C until used in the experiments.

Muscle preparation

Contractile properties were measured on bundles of fibers obtained from the middle of the anterior side of the striated adductor muscle. Portions of the valves near the anterior edge of the muscle were cut away with a cutting wheel connected to a Dremel Moto-tool *via* a flexible shaft. Most of the soft parts of the animal were then dissected away leaving the striated adductor muscle attached to the valves. With the valves held closed, the length of the muscle at its anterior edge (L_{cl}) was measured with dial calipers to the nearest 0.1mm. The dorsal and ventral sections of the muscle were then dissected away leaving a small bundle attached to the valves. Subsequently, the valves were cut around the bundles leaving small (approximately 11mm×15mm) pieces attached at each end of the muscle. The scallop was kept submerged in sea water chilled to approximately 5˚C throughout the dissection. The resulting preparation was arranged in a thermostatted bath of scallop Ringer (440mmol l^{-1} NaCl, 10mmol l^{-1} KCl, 14mmol l^{-1} $MgSO_4$, 30mmol l^{-1} $MgCl_2$, 10mmol l^{-1} $CaCl_2$, 20mmol l^{-1} imidazole, pH7.9; modified from Simmons and Szent-Györgyi, 1985) saturated with 100% oxygen.

Measurement of contractile properties

The contractile properties of the muscle preparation were measured at three experimental temperatures using an apparatus similar to that used by Marsh and Bennett (1985, 1986*a*). The section of right (bottom) shell at one end of the muscle preparation was clamped securely to the bottom of the chamber and the section of left shell was

attached *via* a light silver chain harness to the transducer arm of a Cambridge Technology model 305 servo-controlled ergometer. In all cases, muscles were initially placed in a bath maintained at 10˚C and at a length equal to $1.3L_{cl}$. Muscles were stimulated *via* parallel platinum plate electrodes with 0.5ms pulses from a Grass S48 stimulator amplified by a d.c.-coupled power amplifier. After initially determining stimulus strength, the muscle was allowed to rest for 1h. Force increased significantly following this rest period, an observation similar to those on other preparations (e.g. Marsh and Bennett, 1985, 1986*a*) and presumably as a result of the recovery of the muscle from the dissection. Maximal stimulus voltage was rechecked and length adjusted to achieve maximal force during isometric twitch contractions. These twitches and all subsequent twitches and tetani were separated by approximately 4min (4.1±0.22 S.E.M.) intervals. The muscle was subsequently set at $1.4L_{cl}$, a muscle length close (within 1%) to the mean length for maximal force (see below) and typical of that at maximal gape during swimming *in vivo* at 10˚C (Marsh *et al.* 1992). One to three pairs of isometric twitches and tetani were elicited to determine twitch–tetanus ratios. For tetani, stimuli were given for 300ms at 30Hz (10˚C), 40Hz (15˚C) or 50Hz (20˚C). After a final isometric twitch, the temperature of the muscle chamber was either left at 10˚C or changed to 15 or 20˚C. In the transfers to a new experimental temperature, temperature stabilized after 17±1.4min (mean ± 1 S.E.M.; N=19). Two isometric twitches were given to determine accurately the effect of temperature on peak twitch force. Muscles were then subjected to one of two protocols. In the first, muscles were used to measure power output in cyclical contractions (data not reported here) at one or more temperatures in addition to measurements of isometric and isotonic properties. The second protocol was designed to follow carefully the effects of temperature on isometric twitch dynamics and tetanic force. The details of this procedure and of the investigation of isotonic properties on all muscles are as follows. After the initial twitches at the new temperature, one to two pairs of isometric tetani and twitches were measured, as above. The muscle was then transferred to the third temperature (20 or 15˚C), and the above series of isometric measurements was repeated. For all muscle preparations, a set of 8–12 after-loaded isotonic tetanic contractions was obtained, using a stimulus frequency of 30Hz for measurements at 10˚C, 40Hz at 40˚C and 50Hz at 20˚C. An isometric tetanus was measured before, in the middle of and after each set of isotonic contractions as references for peak isometric tetanic force (P_0) during the isotonic experiment. In many cases, chamber temperature was reduced to 10˚C after the isotonic measurements and an additional two isometric twitches were elicited as a reference to evaluate further fatigue and the existence of any changes in the time-dependent properties of the isometric twitch. Temperature was monitored continuously throughout the experiment with a Keithley thermocouple thermometer.

Force and position outputs from the ergometer and the output from the stimulator were collected at 4 or 8kHz (isotonic measurements at 15 and 20˚C) using a MacAdios II 12-bit A/D converter and GW Instruments Superscope software running in a Macintosh II computer. Peak twitch force (P_{tw}), latency period (t_L), time to peak force (t_{Ptw}) and time to 50% relaxation ($t_{50\%R}$) were recorded for each isometric twitch. Peak isometric tetanic force and latency period were recorded for each isometric tetanus.

Following the contractile measurements, muscle length was measured precisely *in situ.* The muscle was then removed from the chamber, the two pieces of shell and any damaged fibers were dissected away, and the remaining intact muscle bundle was blotted and weighed to the nearest 0.1mg on a Mettler AE 163 balance. The bundles had a mean mass of 0.237±0.012g (mean ± 1 S.E.M.) and a mean cross-sectional area of 0.084±0.004cm^2 (N=18). The cross-sectional area of each bundle was calculated by dividing the mass of the muscle by the corresponding length.

Statistical analysis

Parametric and, where appropriate, non-parametric statistics were used to test for differences among groups. Analyses were performed using the programs Statview II and SuperAnova running on a Macintosh II computer. Statistical significance was accepted at the 0.05 level. Values reported are means ± 1 S.E.M., unless otherwise noted.

The force–velocity data were described by fitting both Hill's characteristic equation:

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

and the three-parameter hyperbolic–linear equation (HYP-LIN) of Marsh and Bennett (1986*a*):

$$V = [B(1 - P/P_0)/(A + P/P_0)] + C(1 - P/P_0).$$

In both equations, V is the velocity of shortening in lengths per second ($L_0\,s^{-1}$) and P/P_0 is force as a fraction of the maximum isometric tetanic force. B and C have the dimension of velocity and A is dimensionless. These curves were fitted using the Levenberg–Marquardt algorithm implemented in the program Igor (WaveMetrics) running on a Macintosh II computer. The average variables for the force–velocity relationship at each of the three temperatures (see Table 2) were calculated by fitting the data for each muscle individually (with very little error; e.g. see Fig. 6) and then computing the mean values for each of the three variables. This procedure is appropriate because it correctly reflects the degree of variability among muscles from different animals (Marsh and Bennett, 1986*a*).

Results

Length–tension relationship

The relationship between muscle length and twitch tension was determined for all muscle preparations. Twitch contractions were used in these experiments for several reasons. First, adductions in the bay scallop during swimming *in vivo* appear to be the result of twitch contractions by the adductor muscle (J. M. Olson and R. L. Marsh, unpublished electromyographical data). Second, similar to the observations of Rall (1981) in *Placopecten magellanicus*, the adductor muscle from *Argopecten irradians* became increasingly susceptible to ripping during contractions at longer lengths, particularly during tetani. Moreover, results of preliminary experiments indicated that the optimal lengths determined for twitch contractions were probably not very different from those for tetanic contractions. Twitch–tetanus ratios measured at 1.3L_{cl} in two muscle

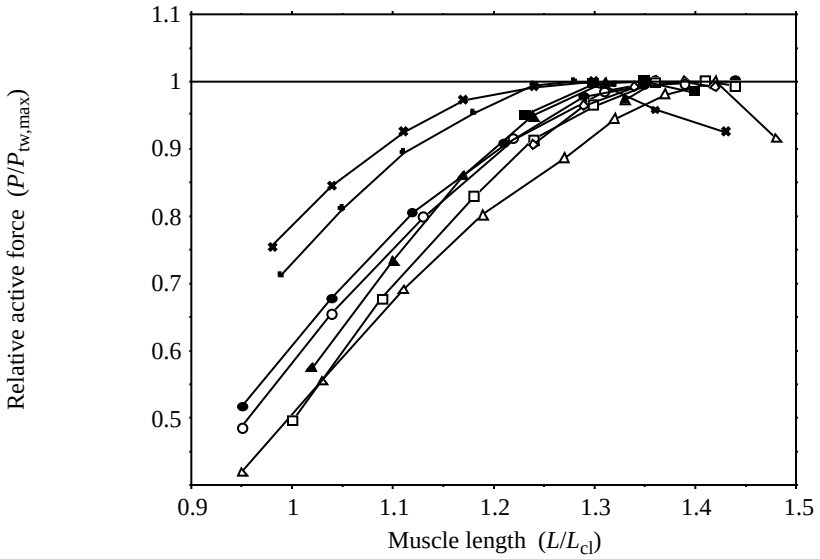

Fig. 1. Isometric twitch tension of the striated adductor muscle of the bay scallop (*Argopecten irradians*) as a function of muscle length. Each set of symbols represents measurements obtained on a single bundle of muscle fibers during twitch contractions at 10˚C. For each bundle (N=9), force was measured and normalized to the maximum twitch force measured during the length–tension measurements ($P_{tw,max}$). Muscle length is expressed as a multiple of the *in situ* muscle length measured on the anterior side with the valves closed (L_{cl}).

preparations were very similar to the corresponding ratios measured at the length where twitch force was maximal (0.87 and 0.89, respectively). In addition, twitch contraction times (the sum of t_L, t_{Ptw} and $t_{50\%R}$) were independent of muscle length down to 1.25L_{cl}, and only decreased by approximately 10% from these values down to the L_{cl}.

The overall shape of the ascending limb of the length–tension curve for scallop muscle was similar to that of other striated muscles (Fig. 1). The length at which twitch force was maximal as a fraction of closed length (L_0/L_{cl}) averaged 1.38±0.010 (N=19 muscles) at 10˚C. This length is very close to the muscle length at maximal gape during swimming *in vivo* at 10˚C (Marsh *et al.* 1992). Because of the susceptibility of the muscle to ripping at long lengths, the shape of the descending limb was not determined for the adductor muscle. Passive force in the striated adductor muscle was very low over the range of lengths used (Fig. 2), averaging approximately 0.08 N cm^{-2} at L_0 (N=7). This force was only 0.5% of the active force at this length.

Isometric contractile properties

The striated adductor muscle of the bay scallop responded to a single stimulus with a twitch contraction and was capable of temporal summation during repeated stimuli (Fig. 3). The force generated during a twitch was very close to that during tetanus at all three temperatures (see below). The striated adductor muscle was unable to sustain tetanic force during prolonged stimulation (data not shown), a situation similar to that in muscle from the scallop *Placopecten magellanicus* (Rall, 1981).

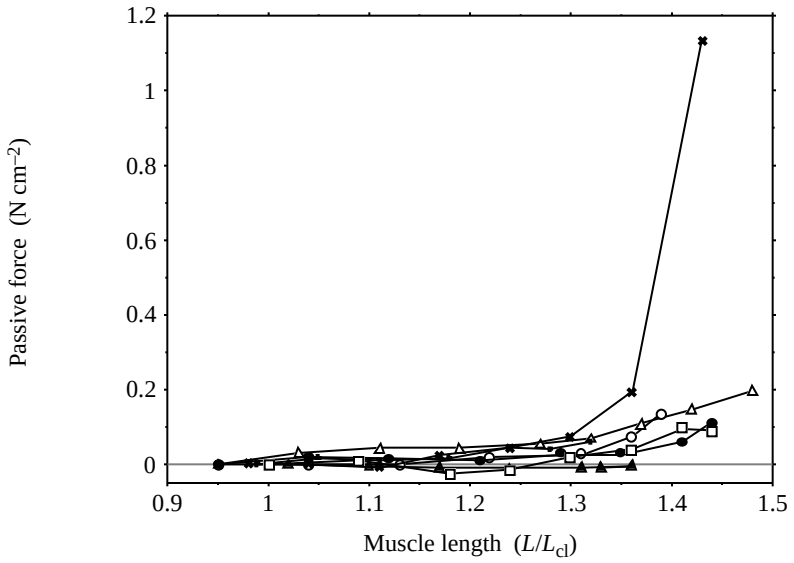

Fig. 2. Passive force of the striated adductor muscle of the bay scallop (*Argopecten irradians*) as a function of muscle length. Each set of symbols represents a single muscle (N=9). Passive force is expressed in absolute units (Ncm^{-2}) and length is expressed as a multiple of L_{cl} on the anterior side of the muscle.

The isometric twitch force of the striated adductor muscle decreased nonlinearly throughout the experiment (Fig. 4). The rates of this decrease were independent of experimental temperature and were unaffected by any of the temperature transitions (P>0.20 for comparisons among four transitions, 10 to 15˚C, 15 to 20˚C, 10 to 20˚C and 20 to 15˚C; ANOVA), but were strongly dependent upon the number of stimuli, suggesting that the decline was due to fatigue induced by contractile activity. Relative P_{tw}, the twitch force at a given time as a proportion of the initial P_{tw} measured immediately after the 1h rest period, decreased fastest early in the experiment, but stabilized at approximately 65% of the initial P_{tw} after approximately 60 stimuli (Fig. 4).

Table 1 summarizes the thermal dependence of the contractile properties of the striated adductor muscle. All preparations were initially equilibrated at 10˚C. At this temperature, maximal P_{tw} ($P_{tw,max}$) was 21.43±0.68 N cm^{-2} (range 15.77–27.56 N cm^{-2}) (N=18). To evaluate the effect of temperature on P_{tw} statistically, the observed difference in force between twitches before and after the transition was compared with that predicted given the rate of fatigue, which in turn was calculated from the average change in force per stimulus (dP stim^{-1}) over all stimuli at the temperature before the transition. Two comparisons were made for each individual muscle preparation: (1) the difference between P_{tw} before the transition and the first twitch afterwards was compared with dP stim^{-1} and (2) the difference between P_{tw} before the transition and the second twitch after it (4min after the first twitch) was compared with 2×dP stim^{-1}. Each of the four temperature transition groups was considered separately. The force of isometric contractions was independent of temperature over the range 10–20˚C. Both P_{tw} and P_0, once adjusted to account for fatigue, were not significantly different from the values at

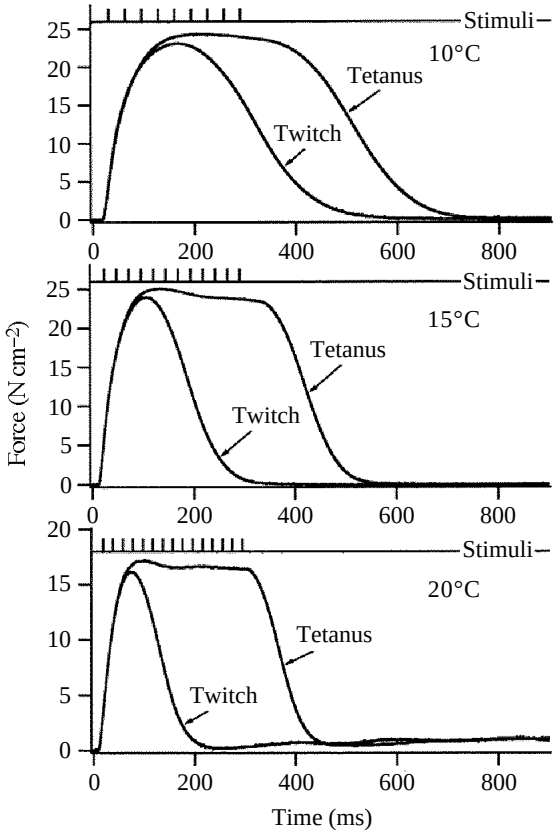

Fig. 3. Representative isometric twitch and tetanic contractions of the same fiber bundle from the striated adductor muscle of the bay scallop (*Argopecten irradians*) at 10, 15 and 20˚C. Stimuli were given at supramaximal voltage at time 0 (twitch) or for the first 300ms (tetanus). Stimulus frequencies (traces marked 'stimuli') varied with temperature, and were 30Hz (10˚C), 40Hz (15˚C) and 50Hz (20˚C). The lower absolute force at 20˚C was due to the effects of fatigue on the preparation (see text).

10˚C measured at the beginning of the experiment. The first twitch after the transition was higher than predicted, regardless of the direction of the temperature change ($P<0.05$; paired *t*-test; $N=5$ in each comparison), suggesting that the muscle recovered somewhat during the rest period of approximately 17min necessary for the transition to the new temperature. However, P_{tw} of the second twitch after the transition to the new temperature did not differ significantly from that predicted ($P>0.05$, paired *t*-test).

Twitch–tetanus ratios (calculated using values collected within about 4min) averaged 0.89±0.01 (range 0.81–0.95) for all preparations used (Table 1). To examine the effects of temperature on twitch–tetanus ratios, we measured twitch and tetanic force at all three temperatures in six muscle preparations. These ratios were not significantly different among the three temperatures ($P>0.6$; Kruskall–Wallis; $H=0.433$; Table 1), averaging 0.92±0.01, 0.91±0.01 and 0.92±0.01 at 10, 15 and 20˚C, respectively.

The time-related properties of isometric twitches were strongly affected by

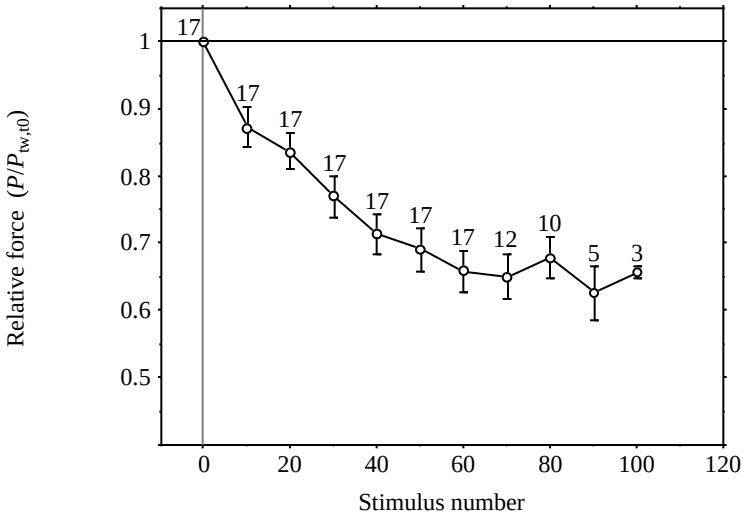

Fig. 4. Fatigue of striated adductor muscle of the scallop *Argopecten irradians* as a function of total number of stimuli. Fatigue was assessed by first determining the effect of number of stimuli on the relative twitch force for each individual preparation. Relative force was calculated as the twitch force at a given point in time normalized to the corresponding twitch force at time 0 ($P_{tw,t0}$) for the individual. Next the relative force was calculated at intervals of ten stimuli for each preparation and then averaged over all scallops. Each point is a mean ± 1 S.E.M. Sample sizes are indicated above each point.

temperature (P<0.0001; ANOVA; F=516.1, 79.12 and 183.4 for t_L, t_{Ptw} and $t_{50\%R}$, respectively; Table 1; Figs 3 and 5). The average Q_{10} values for $1/t_L$, $1/t_{Ptw}$ and $1/t_{50\%R}$ (calculated for each individual animal, N=13) over the entire range of temperatures studied (10–20°C) were 1.98±0.032, 2.28±0.040 and 2.77±0.042, respectively. In addition, the pattern of thermal dependence of all three properties was similar (Fig. 5); the average Q_{10} values for $1/t_L$, $1/t_{Ptw}$ and $1/t_{50\%R}$ over the temperature range 10–15°C (2.18±0.06, 2.46±0.07 and 3.27±0.11, respectively) were higher than the corresponding values over the range 15–20°C (1.81±0.07, 2.12±0.06 and 2.37±0.08, respectively; N=13 for each). These differences were significant for each time-related property (P<0.001; t=3.97, 3.74 and 6.58, respectively).

Isotonic contractile properties

In all cases (N=18), the HYP-LIN equation was superior to Hill's characteristic equation for fitting the isotonic force–velocity data collected in this study (P<0.0002; Wilcoxon signed-rank test comparing χ^2 goodness-of-fit statistics; Fig. 6). The Hill equation underestimated velocities at either or both of the extremes of the range of relative force (P/P_0) values. Maximum velocity was underestimated by 5–13 % (P<0.0005; Wilcoxon signed-rank test), and therefore the Hill equation typically overestimated the power ratio, $\dot{W}_{max}/V_{max}P_0$ (P<0.0005; Wilcoxon signed-rank test). Similar deficiencies of the empirical fit of the Hill equation have been noted in several other studies (Ritchie and Wilkie, 1958; Cecchi *et al.* 1978; Edman *et al.* 1976;

Lännergren, 1978; Rome, 1983; Marsh and Bennett, 1985, 1986*a*; Altringham and Johnston, 1988). Accordingly, all further analyses of the isotonic contractile properties in this report are based on the HYP-LIN equation.

Table 1. *Isometric contractile properties of the striated adductor muscle of the bay scallop* Argopecten irradians

T_m (°C)	$P_{tw,max}$ (Ncm^{-2})	P_0 (Ncm^{-2})	t_L (ms)	t_{Ptw} (ms)	$t_{50\%R}$ (ms)
10	21.43±0.68 (18)	24.17±0.87† (18)	20.42±0.22 (18)	135.20±5.24 (18)	160.41±5.12 (18)
15	‡	‡	13.95±0.24 (13)	90.71±3.28 (13)	94.21±2.16 (13)
20	‡	‡	10.42±0.23 (13)	62.35±2.19 (13)	61.36±1.00 (13)

†Tetanic forces were corrected based on fatigue as measured in twitch contractions (see text).

‡Absolute force at the other two temperatures was lower than the values at 10°C, but was not statistically different from value at 10°C when fatigue was taken into account (see text).

T_m, muscle temperature.

$P_{tw,max}$, maximal isometric twitch force, measured at 10°C.

P_0, maximal isometric tetanic force, calculated from $P_{tw,max}$ at 10°C and twitch–tetanus ratios. All ratios were calculated from twitch and tetanic measurements separated by 4min.

t_L, latency period, time from stimulus to first change in tension during twitch contraction.

t_{Ptw}, time from onset to peak tension during twitch.

$t_{50\%R}$, time from peak tension during twitch to 50% relaxation.

Numbers of muscle preparations are given in parentheses.

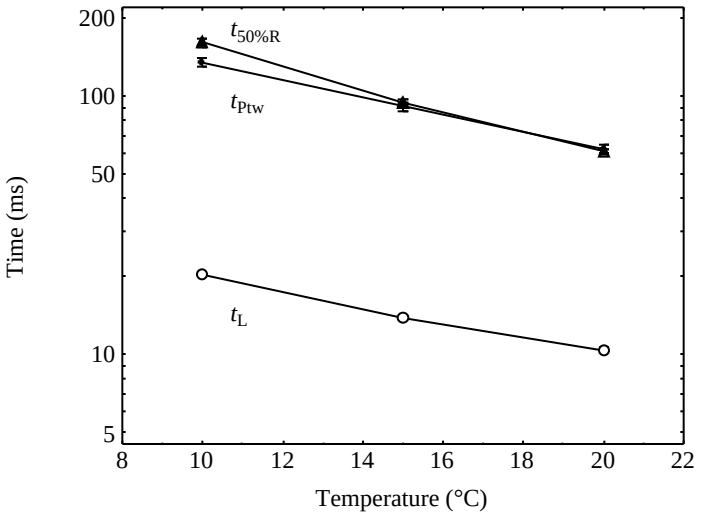

Fig. 5. Relationship between the time-dependent properties of twitch contractions and temperature in the striated adductor muscle of the scallop *Argopecten irradians*. t_L, time from stimulus to onset of twitch tension (○); t_{Ptw}, time from onset to peak twitch tension ( ); $t_{50\%R}$, time from peak twitch tension to half relaxation (▲). Vertical scale is logarithmic. Each point is a mean ± 1 S.E.M.; values are taken from Table 1.

The force–velocity curves of the striated adductor muscle of the scallop were strongly influenced by temperature (Fig. 7; Table 2). Not surprisingly, the predicted maximal velocity at zero force (V_{max}) increased significantly with temperature (Q_{10}=1.85 between 10 and 20˚C), with the magnitude of the increase being higher over the temperature range

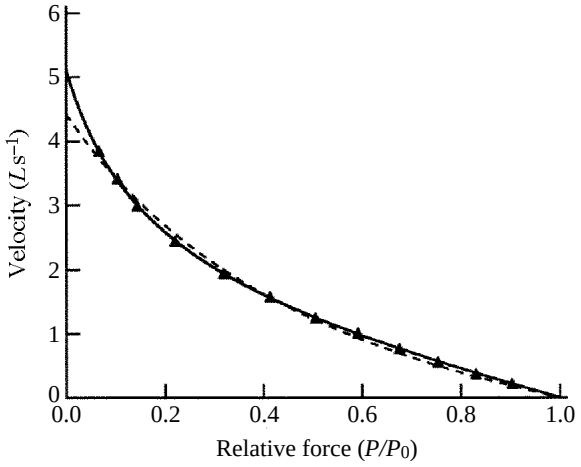

Fig. 6. Representative force–velocity relationship obtained from after-loaded isotonic measurements from the striated adductor muscle of the scallop *Argopecten irradians*. Individual data points (▲) were obtained from one preparation at 10˚C and fitted to the Hill equation (- - -) and the HYP-LIN equation (—) for comparison. The same procedure (Levenberg–Marquardt algorithm; see Materials and methods) was used for fitting both equations.

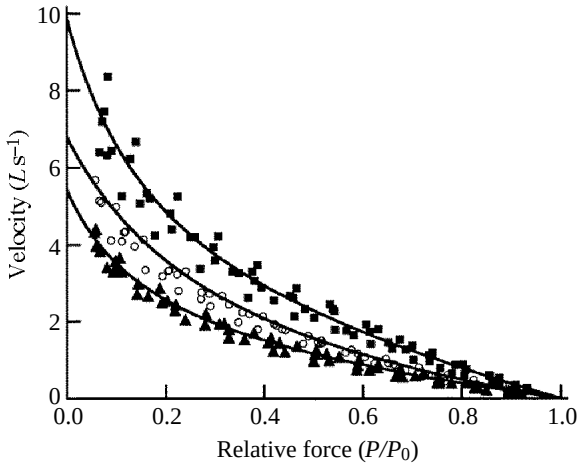

Fig. 7. All force–velocity data collected from the striated adductor muscle of *Argopecten irradians* at 10 (▲), 15 (○) and 20˚C (■). Data obtained from each muscle preparation were fitted using the HYP-LIN equation, and then the three variables (*A*, *B* and *C*) were averaged across preparations (*N*=6) at each temperature (see Table 2), giving the solid curves.

15–20˚C (Q_{10}=2.41) than over the range 10–15˚C (Q_{10}=1.42). Similar trends were evident when comparing velocities at a reference point near that at which maximal power is produced by the muscle (0.4P_0; see Fig. 8A). Consequently, the maximal power output of the muscle also increased with temperature (Table 2). In contrast, the power ratio ($\dot{W}_{max}/V_{max}P_0$) did not change with temperature (Fig. 8B; Table 2), indicating that the shape of the force–velocity relationship was temperature-independent between 10 and 20˚C.

Table 2. *Force–velocity relationships of the striated adductor muscle of the bay scallop* Argopecten irradians

T_m (°C)	N	A	B ($L_0\,s^{-1}$)	C ($L_0\,s^{-1}$)	V_{max} ($L_0\,s^{-1}$)	Power ratio	Force at $\dot{W}_{max}$ (P/P_0)	Velocity at $\dot{W}_{max}$ ($L_0\,s^{-1}$)
10	6	0.18±0.02	0.76±0.12	1.20±0.21	5.35±0.13	0.112±0.003	0.39±0.01	1.53±0.05
15	6	0.34±0.07	2.07±0.57	0.64±0.44	6.45±0.26	0.122±0.004	0.37±0.01	2.10±0.09
20	6	0.18±0.03	1.33±0.24	2.62±0.33	9.89±0.64	0.119±0.005	0.41±0.01	2.87±0.14

Force–velocity data were fitted using the HYP-LIN equation (Marsh and Bennett, 1986*a*):

$$V = \{B[1-(P/P_0)]/[A+(P/P_0)]\} + C(1-P/P_0),$$

where V is velocity in $L_0\,s^{-1}$ and P/P_0 is force expressed as a fraction of the maximum isometric tetanic force.

V_{max} is the maximum shortening velocity at zero force. The power ratio was computed as $\dot{W}_{max}/V_{max}P_0$ and was calculated from the properties of the fitted curves. This ratio was used as a measure of the degree of curvature of the force–velocity relationship (see text).

Values listed for each of the three variables of the equations (A, B and C) and the derived variables (V_{max}, $\dot{W}_{max}/V_{max}P_0$ and force and velocity at $\dot{W}_{max}$) are means ± 1 S.E.M.; constants were determined for each individual data set and then averaged across animals at a given temperature.

T_m, muscle temperature; L_0, muscle length; $\dot{W}_{max}$, maximum power.

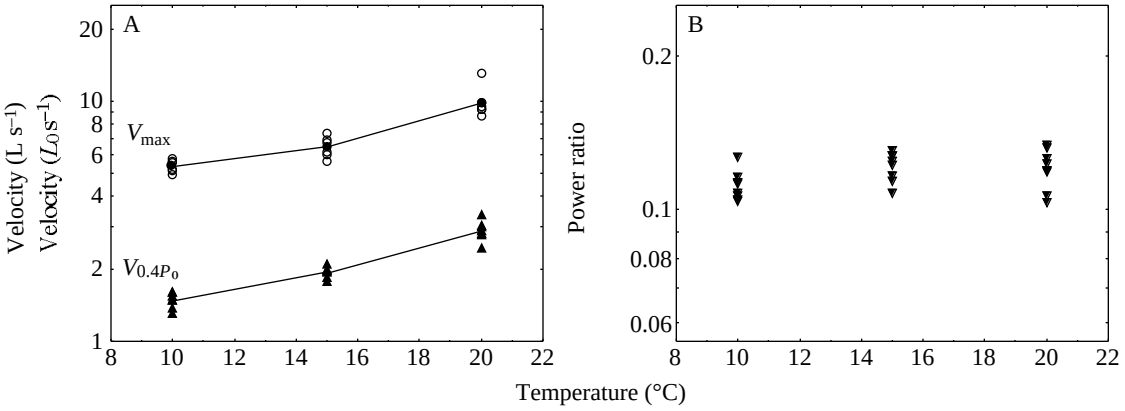

Fig. 8. (A) The predicted velocity of shortening at zero force (V_{max}) and at a reference force that approximates the point at which maximal power is measured ($V_{0.4P_o}$) as a function of temperature (see text). (B) Power ratio ($\dot{W}_{max}/V_{max}P_0$) calculated from the force–velocity relationship as a function of temperature. Each point represents an individual preparation (N=6 at each temperature). Note that vertical scales are logarithmic.

Discussion

Interspecific comparisons

Little is known about the contractile properties of striated muscle from other species of pectinids. The only well-documented study is Rall's (1981) investigation of the isometric contractile properties of intact fibers from the adductor muscle from the scallop *Placopecten magellanicus*. The magnitude of several properties differs substantially between *Argopecten* and the larger *Placopecten.* First, the $P_{tw,max}$ and P_0 of the striated adductor of *Argopecten* are considerably higher (2.8-fold and 1.8-fold, respectively) than those reported for this muscle from *Placopecten* at 10˚C (Rall, 1981), and the twitch–tetanus ratio for *Argopecten* (average over all preparations, 0.89±0.01, N=18; Table 1) was significantly higher than that reported for *Placopecten* (0.58). Second, the time course of isometric contractions in the adductor muscle of *Argopecten* is slow relative to that described for *Placopecten*. Time to peak force and relaxation time at 10˚C in *Argopecten* (135 and 160ms, respectively) are over 50% longer than the corresponding values in *Placopecten* at this temperature (87 and 104ms; Rall, 1981). Whether the interspecific differences in the isometric contractile properties reflect divergent fundamental properties between the muscles of *Argopecten* and *Placopecten* or are due to methodological differences is unclear. For instance, Rall (1981) apparently made measurements at the L_{cl} for his specimens and therefore used shorter relative muscle lengths. In addition, the *Placopecten* used (shell length approximately 94mm) were significantly larger than those considered to be of optimal size for swimming in this species (55mm; Dadswell and Weihs, 1990). However, the slow twitches in *Argopecten* measured here indicate a slower deactivation of contraction (Marsh, 1990) and probably contribute to the high twitch–tetanus ratios in this species. Furthermore, the striated muscle of *Argopecten* probably produces near-maximal force during swimming even when stimulated only once each cycle.

No other fully documented studies of the isotonic contractile properties of scallop adductor muscles exist. Values for V_{max} of $3L_0\,s^{-1}$ at 14˚C and $5L_0\,s^{-1}$ at 20˚C have been reported for *Pecten* sp. based on unpublished results (Hanson and Lowy, 1960; Millman, 1967). These values are considerably lower than those we measured for *Argopecten irradians* at 15˚C ($6.5L_0\,s^{-1}$) and 20˚C ($9.9L_0\,s^{-1}$). Without knowing the species used or the details of the methods for the measurements, we cannot evaluate this comparison further.

Isometric twitches of *Argopecten* muscle are slow compared to those of fast-twitch muscles in many, though not all, small ectothermic vertebrates. For instance, the t_{Ptw} in *Argopecten* at 20˚C (62ms) is at least 25% longer than the corresponding values of fast-glycolytic leg muscles measured at the same temperature in two species of lizards (21.5–50ms; Putnam and Bennett, 1982; Marsh and Bennett, 1985, 1986*a*) and frogs (48ms; Osgood and Brewster, 1963), but is similar to that of the salamander *Ambystoma tigrinum nebulosum* (approximately 61ms; Else and Bennett, 1987). In addition, the t_{Ptw} values measured in the striated adductor muscle are slower than those predicted given the intrinsic speeds of shortening (V_{max}) in this muscle (see Close, 1965).

In contrast to the difference in contraction times, however, the isometric forces and

isotonic force–velocity properties of the striated adductor muscle of *Argopecten* are remarkably similar to those of the fast muscles of vertebrates. The tetanic force developed by the scallop striated muscle (range 17.5–29.9 N cm^{-2}) is very similar to that observed between 10° and 20°C in the semitendinosus (16–29 N cm^{-2}; Hohmsher and Kean, 1978) and sartorius (approximately 25 N cm^{-2}; Renaud and Stevens, 1981) muscles of frogs, an animal with a comparable physiological range of temperatures. In addition, the shortening velocities measured over the range of temperatures here (Table 2) are similar to values reported for vertebrate muscle (see Bennett, 1984; Marsh and Bennett, 1985, 1986*a*), and the power ratios derived from the isotonic measurements are within the range measured for fast-twitch muscle in several vertebrates (e.g. *Sceloporus occidentalis*, Marsh and Bennett, 1986*a*).

The similarities between *Argopecten* muscle and vertebrate fast muscle are intriguing, given the many structural and biochemical differences between scallop and vertebrate muscles. Although scallop muscles have conventional sarcomeres, they differ from their vertebrate counterparts in possessing (1) cells that are ribbon-shaped (1 μm by 10 μm), uninucleate, and that typically contain only one myofibril (Kawaguti and Ikemoto, 1958; Morrison and Odense, 1968; Sanger, 1971; Sanger and Sanger, 1985; Nunzi and Franzini-Armstrong, 1981); (2) fibers that extend only 3% of the total muscle length (Nunzi and Franzini-Armstrong, 1981); (3) electrical coupling between cells *via* gap junctions (Nunzi and Franzini-Armstrong, 1981); (4) longer sarcomeres (3.1 μm at L_0 [1.38L_{cl}]; J. M. Olson and R. L. Marsh, unpublished data); (5) larger myosin filaments that contain paramyosin (Szent-Györgyi *et al.* 1973); (6) a sarcoplasmic reticulum (SR) that lacks a transverse (T-) tubule system (Sanger, 1971); (7) a higher actin:myosin ratio (6:1; Millman and Bennett, 1976) and a higher density of myosin heads (Vibert and Craig, 1983; Squire *et al.* 1990); (8) Ca^{2+}-activation *via* thick filaments rather than *via* thin ones (Kendrick-Jones *et al.* 1970); and (9) use of octopine (de Zwaan *et al.* 1980) as an anaerobic end product. The functional significance of these differences in scallop muscle is not always clear. However, the longer sarcomeres, higher actin:myosin ratio and higher density of heads on the myosin filaments may increase the force production of each myofibril. This facilitation of force may be especially important in some seasons, because it could compensate for the lower density of fibrils resulting from the seasonally large stores of glycogen in scallop muscle (Morrison and Odense, 1968). The lack of information on the area of myofibrils in this and other muscles precludes the full evaluation of this possibility. In addition, the time course of isometric twitches is generally related to the amount of SR in the muscle but, unfortunately, neither quantitative estimates of the extent of the SR nor the kinetics of Ca^{2+} release are known for scallop muscle. Scallop muscle lacks T-tubules, though the need for such a system is apparently obviated by the small size and dimensions (i.e. ribbon shape) of the cells and the fact that each cell typically contains only one myofibril (Kawaguti and Ikemoto, 1958; Morrison and Odense, 1968; Sanger, 1971; Sanger and Sanger, 1985; Nunzi and Franzini-Armstrong, 1981).

Thermal effects

The overall pattern of thermal dependence observed in the striated adductor muscle of

the bay scallop (*Argopecten irradians*) is similar to those observed in insects (see Josephson, 1981, for a review) and vertebrates (see Bennett, 1984, for a review). The time-dependent isometric contractile properties (t_L, t_{Ptw} and $t_{50\%R}$) are markedly temperature-dependent (Figs 3 and 5; Table 1). The latency period at 10˚C is twice as long as that at 20˚C. The t_{Ptw} and $t_{50\%R}$ are even more temperature-sensitive than t_L over the range 10–20˚C, with Q_{10} values for $1/t_{Ptw}$ and $1/t_{50\%R}$ of 2.2 and 2.8 respectively. All three temporal properties were more temperature-sensitive over the range 10–15˚C (Q_{10}=2.2, 2.5 and 3.3, respectively) than over the range 15–20˚C (Q_{10}=1.8, 2.1 and 2.4, respectively). A similar decrease in thermal sensitivity of twitch kinetics with increasing temperature has been observed in the fast glycolytic portion of the iliofibrilaris muscle of the lizards *Dipsosaurus dorsalis* and *Sceloporus occidentalis* (Marsh and Bennett, 1985, 1986*a*).

As in the muscles from many other species of ectotherms, the peak isometric tetanic force (P_0) in the striated adductor muscle is independent of temperature over most of the range of temperatures normally encountered by active animals in nature. In contrast to the results obtained with most vertebrate muscles, however, P_{tw} and therefore the twitch–tetanus ratios in this muscle were also independent of temperature over the range of temperatures studied here (10–20˚C). The scarcity of data on the temperature-dependence of twitch force in the adductor muscle of other scallop species precludes extensive comparisons. However, preliminary experiments by Rall (1981) indicated that the P_{tw} produced by the striated adductor muscle of *Placopecten magellanicus* is similarly independent of temperature over the temperature range 0–10˚C.

Furthermore, as shown in several other studies, the shortening velocities of the adductor muscle during isotonic contractions at both the reference point among temperatures (V at $0.4P_0$) and that predicted at zero force (V_{max}) were also affected by temperature over the range 10–20˚C (Q_{10}=1.85; Figs 7 and 8). Unlike the case with t_{Ptw} and $t_{50\%R}$, however, the largest effect was observed over the temperature range 15–20˚C (Table 2; Fig. 7). Because of the increase in intrinsic shortening velocity, the maximal isotonic power produced by the striated muscle increases with temperature as well. The shape of the force–velocity curve is independent of temperature, a result common to many (e.g. Marsh and Bennett, 1985, 1986*a*; Langfeld *et al.* 1991) but not all (e.g. Langfeld *et al.* 1989) striated muscles.

Relationship between in vitro *properties and* in vivo *performance*

Knowledge of the effect of temperature on the contractile properties of a locomotor muscle may provide some insight into the basis for the thermal dependency of the associated movement *in vivo*. Such a link between the *in vitro* contractile properties of a muscle and the *in vivo* performance has been invoked in studies of lizard and amphibian locomotion (Marsh and Bennett, 1985, 1986*b*; Else and Bennett, 1987; John-Alder *et al.* 1989). Because the frequency of successive valve claps during swimming in scallops is dependent upon the re-establishment of the starting muscle length (i.e. the length at maximum gape; Mellon, 1969), both the force and the time-dependent contractile properties of the single striated adductor muscle (especially the time required for the deactivation of cross-bridge cycling; Marsh, 1990) may be important determinants of

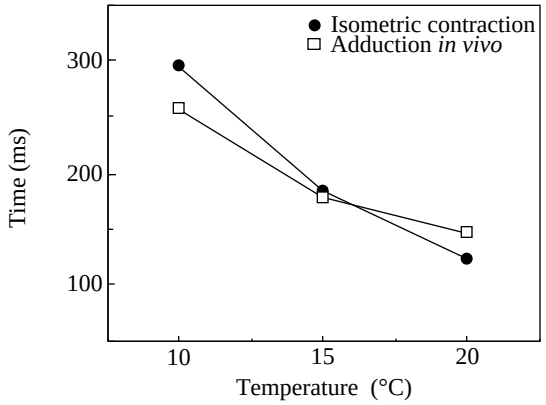

Fig. 9. Mean isometric contraction time of the striated adductor muscle (calculated as $t_{Ptw}+t_{50\%R}$; Table 1) and the time required for adduction *in vivo* in the bay scallop *Argopecten irradians* as a function of temperature. The time for 'adduction *in vivo*' was calculated from the first four claps of a representative swim at each temperature (R. L. Marsh and J. M. Olson, in preparation).

performance. This potential limit may be especially important in the case of the scallop, which lacks an antagonistic muscle to the adductor and instead relies on the elastic properties of the hinge ligament for re-extension.

Temperature has a marked positive effect on the clapping frequency during swimming in scallops (Manuel and Dadswell, 1991), including *Argopecten* (R. L. Marsh, J. M. Olson and S. K. Guzik, unpublished results). Scallops in the same size range as those measured here swam at an average frequency of 2.0Hz at 10˚C and increased their frequency approximately 1.8-fold to 3.6Hz at 20˚C. Adduction accounts for approximately 51% of the total cycle time at all three temperatures (R. L. Marsh and J. M. Olson, unpublished results). The force on the muscle at the end of adduction (shortening) must be low enough to allow re-extension of the muscle with as little resistance as possible for the next locomotor cycle. The overall pattern of thermal sensitivity of time for adduction is similar to that of the isometric contraction time (total of t_{Ptw} and $t_{50\%R}$; Fig. 9). Both properties were especially temperature-sensitive at lower temperatures; Q_{10} values for time for adduction *in vivo* and isometric contraction times *in vitro* over the temperature range 10–15˚C (2.1 and 2.6, respectively) were higher than the corresponding values (1.5 and 2.2) over the range 15–20˚C. In contrast, temperature-induced changes in shortening velocity (Fig. 7) do not correlate well with those of swimming performance *in vivo*, a situation similar to that observed in lizards (Marsh and Bennett, 1986*b*). These results are consistent with the hypothesis that the thermal sensitivity of contraction time (including the rate of deactivation of cross bridges) is an important determinant of the thermal dependence of locomotor performance in scallops.

Evaluating the precise relationship between the *in vitro* contractile properties and *in vivo* performance, however, is difficult given the available data. First, the effects of temperature on the hinge ligament in scallops (Trueman, 1953; Alexander, 1966) have not been fully evaluated. Second, the dynamics of contraction *in vivo* will be influenced

by changes in muscle length during swimming. Isometric twitch kinetics (Fig. 9) would suggest that the muscle was only about 50% relaxed at the end of adduction. However, the hinge ligament could not produce enough force to begin re-extension given this residual force. This discrepancy implies considerable shortening-dependent deactivation of the cross bridges in this muscle, as has been observed in many muscles (Jewell and Wilkie, 1960; Edman, 1980). Indeed, we have observed such shortening-dependent deactivation in scallop muscle during cyclical contractions (R. L. Marsh and J. M. Olson, unpublished data). Such an observation in scallop muscle, which is regulated by Ca^{2+} binding to myosin, is especially intriguing, for length-induced decreases in the binding constant for Ca^{2+} to thin filaments has been implicated as the mechanism for this phenomenon in vertebrate muscle (Edman, 1980; Housmans *et al.* 1983). Length–tension effects are also important, but do not account fully for the required relaxation at the beginning of abduction. During swimming, the adductor muscle in *Argopecten* operates predominantly on the ascending limb of the length–tension curve determined for twitches, shortening from approximately L_0 (approximately $1.4L_{cl}$) to about $1.1L_{cl}$ at 10˚C. Although this represents a rather substantial strain (22.5% of $L_{0;}$ Marsh *et al.* 1992), the change in length would reduce force at the end of shortening by only approximately 25% (Fig. 1). Given the uncertain extrapolations from simple isometric and isotonic measurements, more complex cyclic shortening experiments are required to understand fully the relationships between muscle properties and locomotion (Marsh *et al.* 1992).

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