# Effects of temperature on power output and contraction kinetics in the locomotor muscle of the regionally endothermic common thresher shark (*Alopias vulpinus*)

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**Abstract** The common thresher shark (*Alopias vulpinus*) is a pelagic species with medially positioned red aerobic swimming musculature (RM) and regional RM endothermy. This study tested whether the contractile characteristics of the RM are functionally similar along the length of the body and assessed how the contractile properties of the common thresher shark compare with those of other sharks. Contractile properties of the RM were examined at 8, 16 and 24 °C from anterior and posterior axial positions (0.4 and 0.6 fork length, respectively) using the work loop technique. Experiments were performed to determine whether the contractile properties of the RM are similar along the body of the common thresher shark and to document the effects of temperature on muscle power. Axial differences in contractile properties of RM were found to be small or absent. Isometric twitch kinetics of RM were ~fivefold slower than those of white muscle, with RM twitch durations of about 1 s at 24 °C and exceeding 5 s at 8 °C, a $Q_{10}$ of nearly 2.5. Power increased approximately tenfold with the 16 °C increase in temperature, while the cycle frequency for maximal power only increased from about 0.5–1.0 Hz over this temperature range. These data support the hypothesis that the RM is functionally similar along the body of the common thresher shark and corroborate previous findings from shark species both with and without medial RM. While twitch kinetics suggest the endothermic RM is not unusually temperature sensitive, measures of power suggest that the RM is not well suited to function at cool temperatures. The cycle frequency at which power is maximized appeared relatively insensitive to temperature in RM, which may reflect the relatively cooler temperature of the thresher RM compared to that observed in lamnid sharks as well as the relatively slow RM phenotype in these large fish.

**Keywords** Thresher shark · Red muscle · Contractile kinetics

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## Introduction

The use of aerobic heat production to warm the locomotor muscles has evolved independently in at

least three fish groups: the tunas (Scombridae, tribe Thunnini) (Carey and Teal 1966; Dickson and Graham 2004), the lamnid sharks (Lamnidae) (Carey and Teal 1969; Carey et al. 1985) and the common thresher shark (Alopiidae), *Alopias vulpinus* (Bernal and Sepulveda 2005). These three lineages have remarkably converged upon a similar myotomal framework in which the red oxidative swimming muscle (RM) has shifted to a medial position (i.e., near the vertebral column) and force transmission is uncoupled from local body bending (Shadwick et al. 1999; Donley et al. 2004, 2005; Bernal et al. 2010). Although tunas and lamnids have been the focus of several studies highlighting this convergence, few works have focused on the common thresher shark and information on thresher muscle performance and functional mechanical design are not available for comparison with other regionally endothermic species.

Unlike lamnids and tunas, which possess several adaptations for high-performance locomotion (e.g., fusiform body shape, a lunate, high-aspect-ratio caudal fin; reviewed by Bernal et al. 2001), the common thresher shark lacks significant body streamlining and has an extremely elongate upper caudal lobe, which approaches the length of the body (Compagno 1984). The apparent differences in external morphology exist despite the strikingly similar myotomal framework and supporting vasculature (Bone and Chubb 1983; Sepulveda et al. 2005). This divergence in body shape raises questions about whether the locomotor muscle of the common thresher shares the mechanical or physiological characteristics present in the other regionally endothermic species (Bernal et al. 2005; Donley et al. 2005) or whether its muscle functions more similar to that of ectothermic sharks (Donley and Shadwick 2003).

Previous studies of muscle performance in sharks have highlighted similarities in the contractile properties of locomotor muscle between endothermic and ectothermic species. For example, work examining contractile properties along the body in the ectothermic leopard shark (*Triakis semifasciata*) and the endothermic mako shark (*Isurus oxyrinchus*) has demonstrated a similar pattern in both species in which the stimulus duration, stimulus phase, net work and power output of the locomotor muscles are relatively consistent in both anterior and posterior portions of the body (Donley et al. 2007). This contrasts that described for bony fishes, where

temporal patterns of RM shortening and activation have been shown to differ along the length of the body (Williams et al. 1989; van Leeuwen et al. 1990; Rome et al. 1993; Wardle and Videler 1993; Jayne and Lauder 1995; Gillis 1998; Hammond et al. 1998; Shadwick et al. 1998; Knower et al. 1999; Ellerby and Altringham 2001). In contrast to bony fishes, comparatively few data exist on functional mechanical design in sharks, and no data are available for any species exhibiting an elongate caudal fin, such as the common thresher shark.

Studies have also shown a striking difference in the thermal sensitivity of the RM between endothermic and ectothermic sharks. Specifically, at a given temperature, maximal power output occurs at higher cycle frequencies in the endothermic mako than in the ectothermic leopard shark, and the range of operating temperatures at which peak muscle performance is produced is narrower in the mako shark (Donley et al. 2007). Further, work on the regionally endothermic salmon shark (*Lamna ditropis*) has shown heightened thermal sensitivity, such that the RM fails to produce positive power output if allowed to cool much below 20 °C, a temperature nearly 15 °C above ambient (Bernal et al. 2005).

The present study focused on quantifying the contractile kinetics along the body and thermal sensitivity of the locomotor muscle in the common thresher shark. We tested the following hypotheses: (1) Contractile properties of RM are functionally similar along the body in the common thresher shark and (2) the thermal sensitivity of contraction in the RM of the common thresher is heightened as observed in other large sharks with warm RM. Additionally, we focused on whether the contractile properties of the common thresher shark exhibit convergence with the RM of lamnid sharks, a group with a similar myotomal design despite apparent differences in morphology, swimming mode and phylogeny.

## Methods

### Experimental animals

Eight common thresher sharks (*Alopias vulpinus*) ranging in size from 155 to 190 cm fork length (*FL*) were examined in this study (Table 1). All specimens were collected off the coast of Southern California

**Table 1** Common thresher shark body size, gender and number of preparations obtained from anterior (40 % FL) and posterior (60 % FL) axial locations from each specimen studied

| FL (cm) | ~ mass (kg)[a] | Sex | A-RM[b] | P-RM[c] | A-WM[d] |
|---|---|---|---|---|---|
| 155 | 61 | M | 1 | 0 | |
| 160 | 67 | M | 1 | 1 | |
| 166 | 73 | F | 2 | 2 | 1 |
| 169 | 77 | F | 2 | 2 | |
| 175 | 84 | F | 2 | 2 | |
| 177 | 86 | M | 2 | 2 | 2 |
| 188 | 100 | F | 1 | 1 | |
| 190 | 103 | F | 1 | 0 | 1 |

Not all preparations were exposed to all temperatures; see "Methods" for details on the number of preparations studied at each experimental temperature

[a] Estimated from Kohler et al. (1995)

[b] Number of anterior RM bundles analyzed

[c] Number of posterior RM bundles analyzed

[d] Number of anterior WM bundles analyzed

using standard hook and line techniques (Bernal and Sepulveda 2005; Aalbers et al. 2010) and were first utilized in sonomicrometric studies of muscle strain during swimming (Bernal et al. 2010). All threshers were subsequently euthanized prior to tissue removal by rapidly severing the central nervous system following procedures approved by the University of Massachusetts Dartmouth animal care protocol #05-06 and University of Calgary animal care committee.

Muscle preparations

Segments of RM ($\sim 1$ cm length) were isolated from two axial positions along the body (40 % FL anterior and 60 % FL posterior), body positions which encompass the majority of RM in the common thresher shark (Sepulveda et al. 2005). Once isolated, the bundles were placed under slight tension in chilled (5–10 °C), oxygenated elasmobranch saline (composition in mmol $l^{-1}$: NaCl, 292; KCl, 3.2; $CaCl_2$, 5.0; $MgSO_4$, 1.0; $Na_2SO_4$, 1.6; $NaHCO_3$, 5.9; TMAO, 150; urea, 300; glucose, 10; pH 7.8 at 20 °C) following the procedures described in Donley et al. (2007) (Fig. 1). These preparations were then returned to the laboratory onshore and dissected further to isolate small bundles of fibers, $\sim 0.5$–1.0 mm in diameter, spanning a single myomere. The final preparations were then

transferred to a temperature-controlled experimentation chamber filled with circulating oxygenated saline following Donley et al. (2007). Braided silk (6-0) surgical suture was used to attach the collagenous myosepta on the ends of each muscle bundle to a force transducer (model 402A, Aurora Scientific Inc., ON Canada) and a servomotor lever arm (model 305B-LC, Aurora Scientific Inc.). RM preparations were tested from both anterior and posterior locations from most of the 8 shark specimens (Table 1), resulting in a total of 14 preparations studied at 8 °C, 12 preparations at 16 °C, and 14 preparations at 24 °C. Preliminary data on two WM bundles from the anterior axial position are also presented for comparison purposes (Table 1).

Work loop experiments

Once in the experimentation chamber, the muscle bundles were prepared as described in Syme and Shadwick (2002). Briefly, a pair of platinum stimulating electrodes was positioned on either side of the muscle bundle, and the minimal stimulus voltage required to produce maximum isometric twitch force was determined. This voltage was then increased by 50 % to ensure full activation of the preparation. Optimal muscle length was determined by stimulating the bundle (using 1-ms stimulus duration) over a series of lengths and recording twitch force (Donley et al. 2007). The bundle length producing maximum isometric twitch force without excessive resting tension was used in the experiments. For tetanic contractions, a stimulus frequency of 100 Hz was found to elicit maximal force across all temperatures studied.

Mechanical work and power output were measured using the work loop technique (Josephson 1985, 1993; Johnson and Johnston 1991; Syme and Shadwick 2002; Donley and Shadwick 2003; Donley et al. 2005; Shadwick and Syme 2008). Muscle bundles were subjected to a series of cycles of sinusoidal strain centered about the optimal length. Strain amplitude was ±5.0 %, similar to that recorded in swimming thresher sharks in vivo (Bernal et al. 2010). Experiments were performed at three temperatures (8, 16 and 24 °C) encompassing those recorded in the muscle of the fish as well as ambient conditions in which this species commonly inhabits (Bernal and Sepulveda 2005). Cycle frequencies, defined as the number of length change cycles per second, ranged from 0.5 to
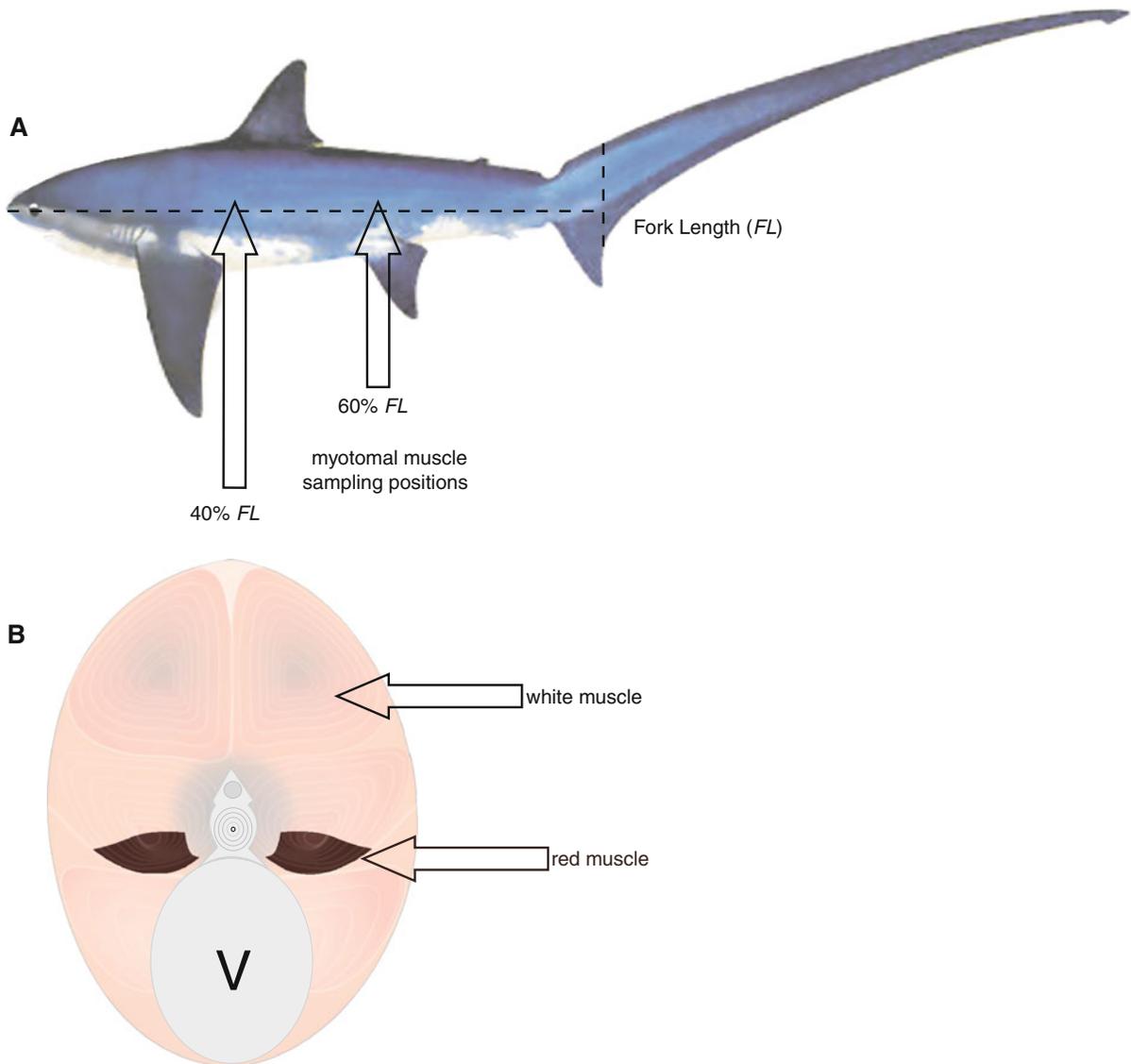
**Fig. 1 a** Common thresher shark showing the two axial positions (i.e., 40 and 60 % fork length, *FL*, *dashed line*) where the myotomal muscle samples were collected. **b** Transverse section of a thresher shark at 40 % *FL* showing the position of red and white muscle (*v* viscera)

2.0 Hz for RM bundles and from 0.5 to 4.0 Hz for the preliminary WM preparations. The range of cycle frequencies was determined based upon the ability of the preparations to produce net positive work as well as from tailbeat frequencies observed in free-swimming threshers (Aalbers et al. 2010). Stimulus phase was defined as the point in the strain cycle when the stimulus begins and is expressed as a percent of the sinusoidal length change cycle ranging from 0 to 100, where 0 is mean muscle length during the lengthening

portion of the cycle. Phase and stimulus duration (defined as the period of muscle activation) were systematically adjusted in increments of 10 ms to maximize net work for each bundle at each cycle frequency and temperature. All parameters were controlled using custom software written in Labview (National Instruments, Austin, TX, USA). Net work of each complete strain cycle was calculated as the integral of force with respect to length change. Power output was calculated as the product of work per cycle

and cycle frequency. Isometric tetanic force was recorded routinely throughout the experiments to monitor stability of the preparation. When tetanic force declined by 10 % from the initial value, the experiment was concluded.

Net work and power output for each preparation were standardized to values obtained at 16 °C and 1 Hz for that preparation (Syme and Shadwick 2002). This allows for direct comparisons of the relative effects of temperature and cycle frequency on work and power. Maximum tetanic stress and mass-specific work were not calculated because of the uncertainty of the amount of tissue in a bundle that was intact, excitable and contributing to the contractile performance. Further, we did not want to introduce an additional source of experimental error when only relative comparisons of performance across temperature and cycle frequency were of interest. Statistical analyses were performed based upon previous muscle performance studies (Rome and Swank 1992; Syme and Shadwick 2002; Donley et al. 2007). A paired $t$ test ($\alpha = 0.05$) was conducted to determine temperature and position effects on twitch kinetics and optimal cycle frequencies for net work and power as well as to test for differences in these parameters between RM and WM. Values presented are mean ± standard error (SE).

## Results

### Isometric twitch kinetics

Comparisons of time to peak force of RM showed no significant differences between axial locations at 8 and 16 °C, ($p > 0.27$), but at 24 °C, the anterior RM was significantly faster (A 0.35 ± 0.1 s; P 0.55 ± 0.14 s; $p < 0.002$). In addition, there were no differences between anterior and posterior locations in relaxation rates ($p > 0.15$). Time from the stimulus to peak force and time from peak force to 50 % relaxation both decreased with increasing temperature in both RM and WM (Fig. 2). The $Q_{10}$ values for both the twitch contraction and relaxation rates were greater in the RM than in WM (∼2.5 RM vs. 1.9 WM) over the temperature range studied (8–24 °C). The twitch kinetics for the RM were five- to sixfold slower than those of the preliminary findings for the WM ($p < 0.001$ paired $t$ test within fish). RM bundles

exhibited isometric twitches that were extremely slow at 8 °C, lasting up to 7 s.

### Stimulus duration and phase

There were no significant differences between anterior and posterior RM in the stimulus duration resulting in maximal net work at any given temperature ($p = 0.85$ at 24 °C, $p = 0.085$ at 16 °C, $p = 0.67$ at 8 °C), so these data were pooled. Pooled averages for optimal stimulus duration in RM were 157 ms at 24 °C, 259 ms at 16 °C, and 100 ms at 8 °C, all significantly different from one another ($p < 0.05$). In contrast, within the WM, there was no significant effect of temperature on optimal duration ($p > 0.2$); however, this observation is based on a limited number of preparations.

Similar to stimulus duration, there were no significant differences between anterior and posterior RM in the stimulus phase resulting in maximal net work at any given temperature ($p = 0.052$ at 24 °C, $p = 0.38$ at 16 °C, $p = 0.052$ at 8 °C). Averages pooled across anterior and posterior RM for stimulus phase were 13 % at 24 and 16 °C, and 14 % at 24 °C, with no significant differences among the groups ($p > 0.18$). Similarly, there were no significant temperature effects on optimal phase in WM ($p > 0.11$), but again this is based on a limited sample size.

### Effects of temperature on net work and power output

A comparison of results between anterior and posterior RM within sharks revealed no significant differences in the cycle frequencies producing maximal power output (optimal cycle frequencies) at any given temperature ($p > 0.33$; paired $t$ test), so anterior and posterior data were pooled. Maximal power of RM declined substantially with cooling (Fig. 3, lowest panel). Relative to 24 °C, power declined about 40 % at 16 °C and by about 95 % at 8 °C. The cycle frequency resulting in maximal power output was much less sensitive to temperature than power itself, with no difference between 8 and 16 °C ($p > 0.33$) and a ∼0.5 Hz increase at 24 °C ($p < 0.001$) (Fig. 3).

Both decreasing temperature and increasing cycle frequency resulted in a decline in net work output per cycle (Fig. 4), largely through an inability of the muscle to sustain force production while shortening,

**Fig. 2** Isometric twitches in red and white myotomal muscle bundles of common thresher sharks ($n = 18$ at 8 °C, 16 at 16 °C, 20 at 24 °C; see Table 1). *Circles* and *solid lines* show the time from stimulus to peak force, and *squares* and *dashed lines* show the time from peak force to half relaxation. The thermal rate coefficients ($Q_{10}$) for twitch duration are shown at each temperature interval. Values at 40 and 60 % fork length were not statistically different ($p > 0.08$) except at 24 °C in RM for contraction time, so data were pooled. *Insets* show representative twitches of red muscle at 8, 16 and 24 °C. Values are mean ± SE
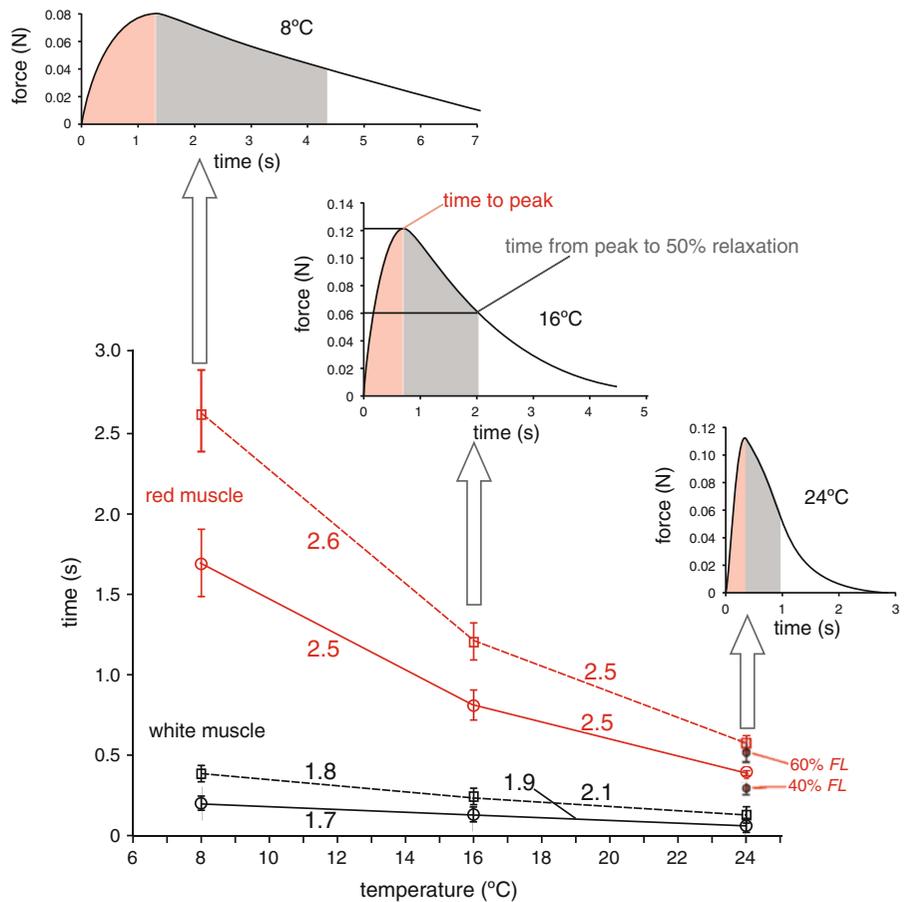


but also through a reduced ability to relax before lengthening (Fig. 4). As such, at 8 °C, RM could only sustain net positive work output at a relatively slow cycle frequency of 0.5 Hz, while at the relatively warm temperature of 24 °C, the preparation sustained net positive work up to a cycle frequency of 2.0 Hz.

## Discussion

The objectives of this study were to determine whether the contractile characteristics of the RM in the common thresher shark are functionally similar along the length of the body and to establish how the contractile properties of RM compare with those of other sharks. Additionally, this work focused on understanding the functional consequences of temperature elevation in the RM of the common thresher shark and whether the contractile properties of the RM display convergence with those observed in lamnid

sharks, the only other group of sharks known to possess a similar RM morphology (Carey et al. 1985).

### Axial variation in contractile properties

Although axial variation in RM contractile kinetics and presumably function are common among teleosts (for reviews, see Altringham and Ellerby 1999; Coughlin 2002; Syme 2006), studies investigating the contractile properties of RM in sharks have not shown a pattern of axial variation. In a diversity of sharks, including both regionally endothermic and ectothermic species, work loop experiments have demonstrated a lack of variability in RM contractile properties along the length of the body (Donley and Shadwick 2003; Donley et al. 2007). Specifically, these studies have not identified significant differences in optimal stimulus duration or phase for work output, net work or power output, or twitch kinetics in RM from anterior versus posterior body positions.
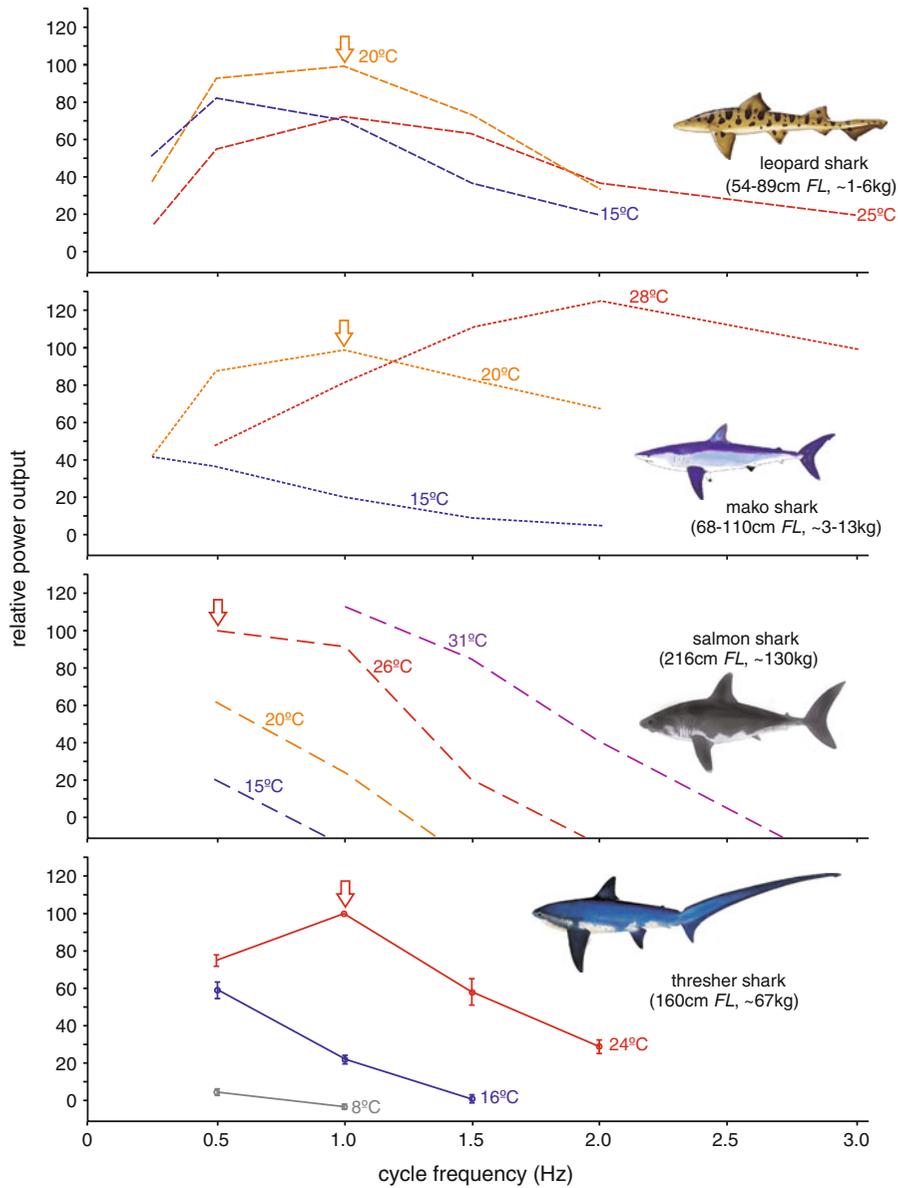
**Fig. 3** Relative power output in the red muscle of sharks as a function of temperature. *Arrows* indicate the parameters (i.e., cycle frequency and temperature) used to establish relative power output (i.e., 100 %) for each species. Values for the common thresher shark are mean ± SE (*n* = 22, see Table 1). Species are leopard shark, mako shark, salmon shark and common thresher shark (*lowest panel*, this study). *Sources* Bernal et al. (2005) and Donley et al. (2007). Note the relatively small variability in maximal power output across temperature in the ectothermic leopard shark compared with the regionally endothermic mako, salmon and common thresher sharks. Also note the relatively large variability in the range of cycle frequencies over which power is maximized at different temperatures in the relatively small and endothermic specimens of mako shark (i.e., a very high optimal cycle frequency for power at warm temperatures) compared with the ectothermic leopard shark and relatively large specimens of endothermic salmon and common thresher shark (i.e., a slow optimal cycle frequency for power even at warm temperatures)

Similarly, in the present study, the RM of the common thresher sharks showed no significant differences in twitch kinetics between anterior and posterior locations (Fig. 2) except for the time to peak force at 24 °C. At this temperature, the anterior RM was faster than posterior. Furthermore, no significant axial

**Fig. 4** Representative red muscle work loops of a common thresher shark (160 cm *FL*, ∼67 kg, male) at different temperatures and cycle frequencies. Muscle preparations were sampled from 40 % *FL*. Stimulus phase and duration were adjusted to maximize net work. Strain was 10 %, based on previous in vivo studies (Bernal et al. 2010)
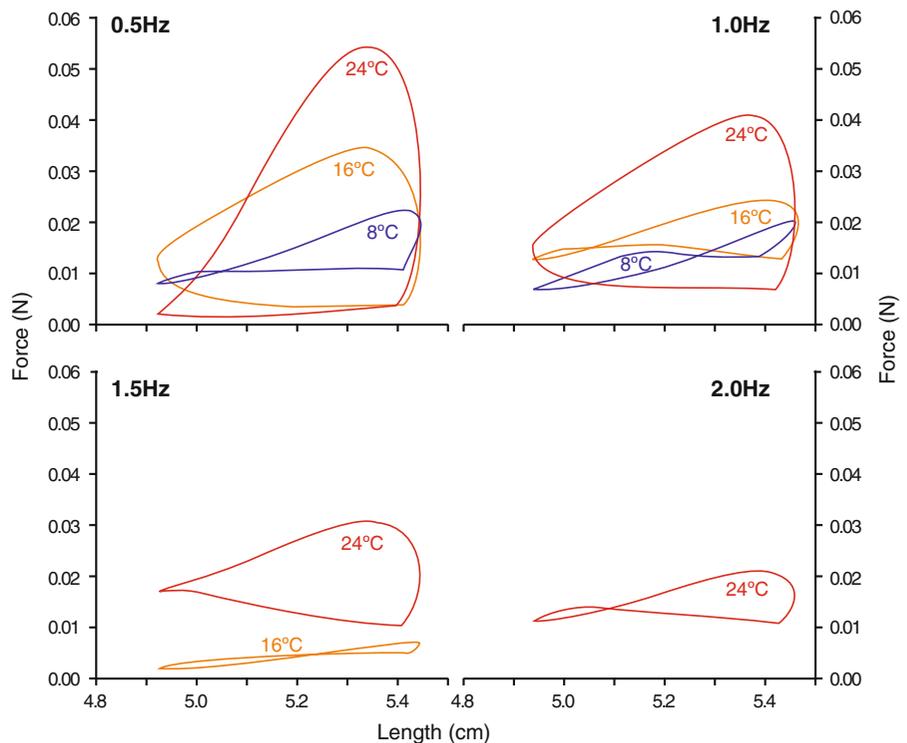


variation was observed at any temperature in the cycle frequency for maximal power, optimal stimulus phase or optimal stimulus duration.

It is noteworthy that this apparent lack of axial specialization in contractile properties of RM in sharks has now been observed in species with a number of functional designs. These include mako sharks, which have medial RM and RM endothermy and exhibit a relatively thunniform swimming mode (reviewed by Bernal et al. 2001); common threshers, which have medial RM and RM endothermy but appear to exhibit a large degree of lateral undulation while swimming (Aalbers et al. 2010; Bernal et al. 2010); and leopard sharks, which have superficial (i.e., subcutaneous) RM, lack RM endothermy and have a carangiform swimming mode (Donley et al. 2007).

Even within the tunas (Scombridae), a group that shares several lamnid attributes (i.e., medial RM, RM endothermy, and thunniform swimming), there exists some evidence of anterior–posterior variability in RM contractile properties (Syme and Shadwick 2002; Shadwick and Syme 2008). Thus, while the sharks studied to date are not unique among fishes in their lack of axial variation in contractile kinetics of RM (Syme 2006), they are notable in that no shark species

has shown such variation to any considerable extent, even across a range of species with varied swimming modes and RM architecture where such variability might be anticipated. The functional basis for the lack of variability in sharks is unclear. Rome et al. (1993) proposed that faster contraction kinetics in anterior muscle may serve to compensate for the relatively small muscle strain near the head which tends to impair relaxation, while Syme et al. (2008) suggested faster contraction kinetics in anterior musculature may improve maneuverability. Donley et al. (2007) proposed that the lack of axial variability in twitch kinetics in sharks observed to date may reflect a limited range of swimming behaviors compared with teleosts. Currently, we know little about RM function in sharks, and it may be that a greater emphasis is placed on power output from RM in sharks than is apparently the case in most teleosts (Syme 2006; Syme et al. 2008) and that more power can be produced through muscle whose contractile properties remain constant axially. It is noteworthy that the size of the sharks studied to date is considerably larger than the size of most teleosts in which axial variability in twitch kinetics is observed; perhaps axial variability in twitch kinetics is less productive in large fishes, or

perhaps it is a synapomorphy in sharks with implications that are not yet understood.

Thermal sensitivity

Contraction kinetics tend to slow with decreasing temperature, and in turn the work and power output, optimal cycling frequency (tail-beat frequency), and optimal stimulus phase and duration tend to decrease as well. These relationships are well established in both the RM and WM of bony fishes (reviewed by Syme 2006) and sharks (Donley and Shadwick 2003; Bernal et al. 2005; Donley et al. 2007). The RM and preliminary findings for the WM of common thresher sharks also followed these patterns, although there appear to be differences between RM and WM in their sensitivity to temperature, as well as interspecific differences when compared to other sharks (Donley et al. 2005, 2007).

Twitch kinetics became slower with decreasing temperature in both RM and WM, with $Q_{10}$ values for contraction and relaxation rates approximately 30 % greater in RM than WM (Fig. 2). The higher thermal sensitivity of RM compared with WM suggests the RM is less able to maintain twitch speeds at cool temperatures, perhaps a product of the thermal stability afforded by the elevated temperatures of the RM of common threshers (Bernal and Sepulveda 2005). However, the $Q_{10}$ of twitch speed in RM of common threshers is still considerably less than that recorded for the highly endothermic salmon shark over a similar range of temperatures ($Q_{10}$ over 3; Bernal et al. 2005). This may be attributed to species-specific differences in thermal stability and capacity for temperature elevation, as the salmon shark has been shown to maintain elevated RM temperatures even under extreme environmental conditions (Anderson and Goldman 2001). Along with the higher thermal sensitivity of twitch speed, the RM in the common thresher had much longer twitch durations than WM, being about 2 s at 24 °C and upwards of 7 s at 8 °C (Fig. 2). The slowing of twitch speed at cool temperatures was so marked that it resulted in a substantial decrease in the stimulus duration (from 260 to 100 ms) required for maximal power output of RM when cooling from 16 to 8 °C. This prolonged relaxation will clearly limit the ability of RM to power swimming at cool temperatures.

A notable effect of temperature on the stimulus phase for maximal work output for the common thresher was not observed. While this appears to counter reports from many other studies of fish muscle (reviewed by Syme 2006), it is consistent with reports from both leopard and mako shark RM (Donley et al. 2007). Although an effect of temperature on optimal stimulus phase was not observed, it may also be a result of the relatively slow contractile kinetics, as might be expected in a large fish, where the variability in optimal durations and phases at slow-operating frequencies may mask any changes that occur with temperature. It was not an initial objective of the study to determine precisely the optimal stimulus phases, only those that resulted in maximal power, and as such it is possible that differences do exist but they were small and not detected.

Net power output and the optimal cycle frequency for power tended to decrease with decreasing temperature in the common thresher shark preparations (Figs. 3,5), with the optimal cycle frequency being two- to threefold faster in WM than in RM. Similar findings have been reported from muscle studies on other fishes, including sharks (Bernal et al. 2005; Syme 2006; Donley et al. 2007). However, the relative thermal sensitivity of optimal cycle frequency in RM
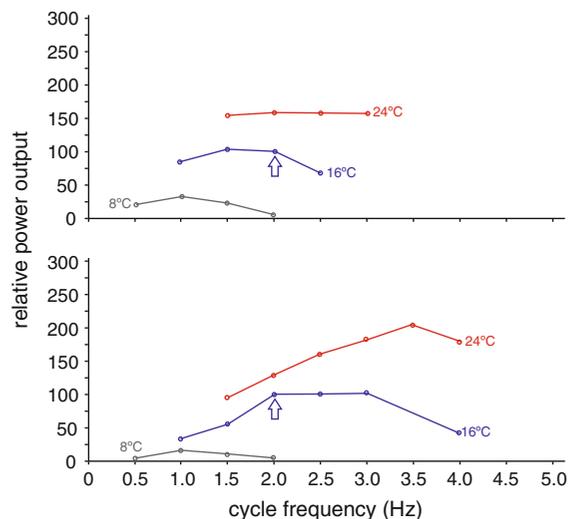


**Fig. 5** Relative power output from white muscle of two common thresher sharks (upper panel 190 cm *FL*, ∼103 kg, female, *lower panel* 177 cm *FL*, ∼86 kg, male) as a function of temperature. *Arrows* indicate the parameters (i.e., cycle frequency and temperature) to which values of power output have been standardized

appeared to be much less than that observed in the preliminary WM preparations. For example, the optimal cycle frequency for power output of RM only changed from about 0.5 to 1.0 Hz between 8 and 24 °C (Fig. 3), while in WM, it changed from about 1 to 3 Hz over the same temperature range (Fig. 5). While this does represent an approximate doubling of the optimal cycle frequency for power in RM, the absolute change in cycle frequency (0.5 Hz) is quite small. In contrast to the relative temperature insensitivity of optimal cycle frequency in RM, RM twitch duration changed about three- to fourfold across this same temperature range (Fig. 2) and RM power increased by 95 % (Fig. 3). Comparatively, the cycle frequency for maximal power output is relatively insensitive to temperature in the common thresher despite the clear evidence that other aspects of contraction remain quite temperature sensitive. The large size of the specimens studied may be responsible for this apparent contradiction. The impacts of slow contraction kinetics, in part associated with large fish size, will have a considerable influence on the cycle frequency for maximal power output. Of particular note is the near-complete failure of RM to produce substantial power at temperatures much below 16 °C (Fig. 3), likely a combined effect of the thermal sensitivity of power in the RM and the slow contraction kinetics in these large fish. Because the common thresher is capable of RM endothermy (Bernal and Sepulveda 2005), it may be that in situ temperatures do not regularly fall below this threshold. However, additional in situ thermal data from common thresher sharks at the northern extent of their range (where water temperatures are <16 °C) as well as data from free-swimming individuals are needed to fully understand the ecological significance of the inability of RM to sustain positive net power output below 16 °C.

Comparisons with other sharks

Comparison of the thermal sensitivities of power output, optimal cycle (tail-beat) frequency and twitch kinetics between the various shark species studied to date reveals patterns associated with endothermy and fish size (Figs. 3,6). Thus far, the twitch durations of RM from the relatively large ($\sim$200 cm *FL*, >100 kg) salmon sharks and common thresher sharks are substantially longer than those from the smaller ($\sim$100 cm *FL*, $\sim$3–10 kg) mako sharks and leopard

sharks (Fig. 6; Bernal et al. 2005; Donley et al. 2005, 2007). This difference is maintained across a wide range of temperatures and across both regionally endothermic (salmon shark, thresher shark, mako shark) as well as ectothermic (leopard shark) species. Likely, the large size of the salmon and thresher sharks contributes to the possession of a slower RM phenotype, as noted in many other animals including fish (Syme 2006).

The $Q_{10}$ of twitch duration in RM of large salmon sharks, which maintain a very large thermal gradient between their RM and ambient water temperatures (Bernal et al. 2005), exceeds 3 at most temperatures and is suggestive of a muscle best suited to operate in a warm and relatively stable thermal environment. Likewise, the RM of the smaller mako sharks studied to date, which also demonstrate pronounced RM endothermy, also exhibits a $Q_{10}$ of about 3 for twitch duration (Donley et al. 2007). The thermal sensitivity of twitch duration in RM of the common thresher shark is somewhat less than that described for the lamnids ($Q_{10}$ of 2.5; Fig. 2) and is consistent with the common thresher's modest ability to elevate RM temperature above ambient. Thus, it may be that the common thresher benefits from having a lower thermal sensitivity, as in situ temperatures likely fluctuate more when compared to lamnid sharks during exposure to varying conditions. While RM of the ectothermic leopard shark also shows a thermal sensitivity of twitches with a $Q_{10}$ near 3, the twitches are considerably faster in an absolute sense (Donley et al. 2007), perhaps allowing these sharks to maintain adequate tail-beat frequencies with cooler muscle temperatures. Similarly, the WM data collected thus far for common thresher sharks displayed a modest $Q_{10}$ ($\sim$1.7) for twitch duration but faster kinetics than RM (Fig. 2).

Of particular value in understanding the impacts of fish size and thermal sensitivity on RM performance is a comparison of thermal sensitivity of power output and optimal cycle frequency (tail-beat frequency) for maximal power across species (Fig. 3). While the ectothermic leopard shark has thermal sensitivities of RM twitch duration that appear similar to its endothermic relatives (discussed above), RM power is notably insensitive to temperature (Fig. 3, upper panel). We might attribute this to a system well suited to function across a wide range of thermal environments. In contrast, RM from all three regionally

**Fig. 6** Isometric twitch kinetics of red myotomal muscle of different shark species ($n = 18$ at 8 °C, 16 at 16 °C, 20 at 24 °C for common thresher sharks; see Table 1). *Upper panel* shows the time from stimulus to peak force, and lower panel shows the time from peak force to half relaxation. Values for the common thresher shark are mean ± SE ($n = x$, see Table 1). Species are leopard shark, mako shark, salmon shark and common thresher shark. *Sources* Bernal et al. (2005) and Donley et al. (2007)
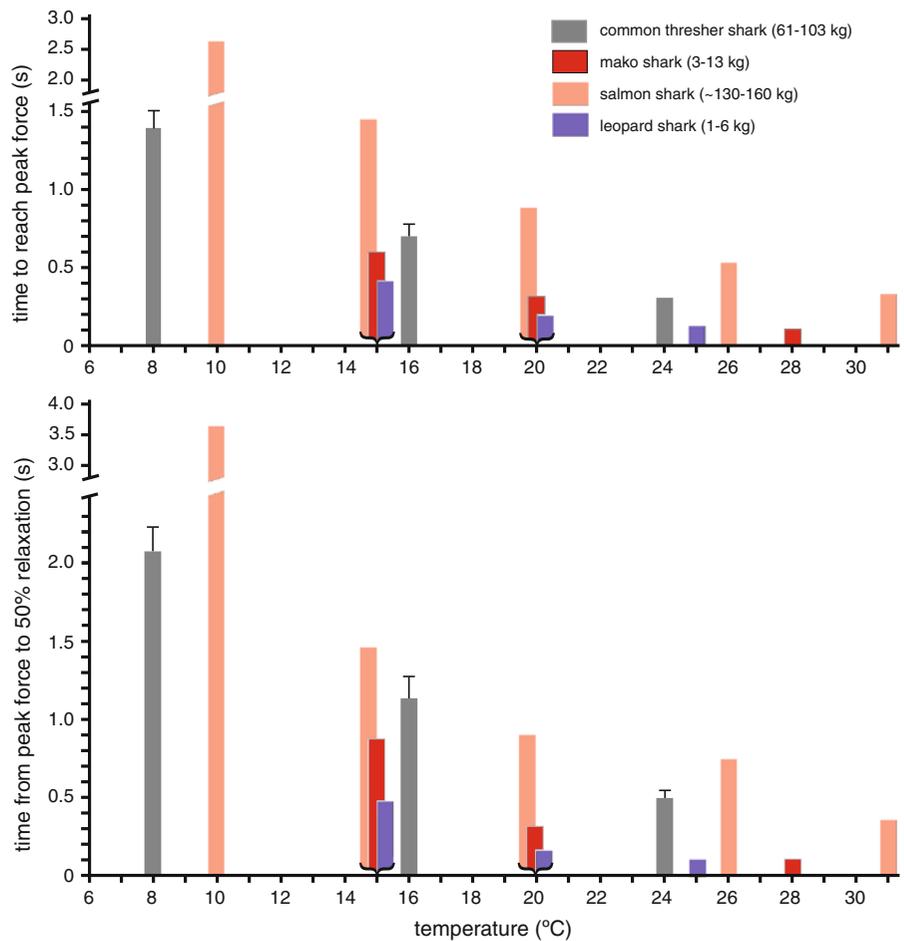


endothermic species (mako, salmon shark, common thresher) show a pronounced thermal sensitivity of power over a similar temperature range (Fig. 3, lower three panels), but with common thresher sharks being the least endothermic and showing the least sensitivity, except at very cool temperatures. Perhaps the RM of regional endotherms is optimally designed to perform in relatively warm in situ environments but not in the cold.

In contrast to thermal sensitivity of power, thermal sensitivity of the cycle (tail-beat) frequency at which power is maximized appears to be influenced considerably by both regional endothermy and fish size (Fig. 3). As for the thermal sensitivity of power itself, studies based on ectothermic RM from relatively small leopard sharks (Donley et al. 2007) reveal a limited thermal sensitivity of optimal cycle frequency for power, perhaps for reasons similar to why power is also not highly sensitive to temperature in muscles that

encounter a wide range of temperatures. Conversely, optimal cycle frequency in relatively small mako sharks has been shown to be highly temperature sensitive, perhaps reflecting the normally warm and stable operating conditions of this muscle and the faster muscle phenotype in smaller fish which have the capacity to work at high speeds (Donley et al. 2007). In contrast to results published for relatively small mako sharks, endothermic RM from the large salmon sharks and common thresher sharks, whose power output is very sensitive to temperature, show little influence of temperature on optimal cycle frequency for power. Perhaps the large size of these fish and their relatively slow RM phenotype biases them to function at only slow speeds regardless of temperature and hence show only a limited response of optimal cycle frequency to temperature. While their contraction kinetics are no doubt temperature sensitive, this sensitivity is overshadowed by the slow contractile kinetics and

resulting slow mechanics of swimming in very large fish at all temperatures.

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