

POWER PRODUCTION DURING STEADY SWIMMING IN LARGEMOUTH BASS AND RAINBOW TROUT

DAVID J. COUGHLIN*

Department of Biology, Widener University, Chester, PA 19013, USA

*e-mail: coughlin@pop1.science.widener.edu

Accepted 17 November 1999; published on WWW 17 January 2000

Summary

Steady swimming in fishes is powered by the aerobic or red muscle, but there are conflicting theories on the relative roles of the anterior and posterior red muscle in powering steady swimming. To examine how red muscle is used to power steady swimming in rainbow trout (*Oncorhynchus mykiss*), electromyographic (EMG) and sonomicrometry recordings were made of muscle activity *in vivo*. These data were used in *in vitro* work-loop studies of muscle power production. Data on *in vitro* power production were also collected for largemouth bass (*Micropterus salmoides*) red muscle from previously published data on *in vivo* muscle activity. The *in vivo* data collected from swimming trout were similar to those for other species. The anterior red

muscle of these fish has the longest duty cycle, the smallest phase shift between the onset of EMG activity and maximum muscle length during each tailbeat and undergoes the smallest strain or length change. For both trout and largemouth bass, work-loop experiments indicate that the majority of power for steady swimming is generated by the posterior muscle, as has been observed in other species.

Key words: fish, swimming, power production, largemouth bass, *Micropterus salmoides*, rainbow trout, *Oncorhynchus mykiss*, electromyography, sonomicrometry, red muscle.

Introduction

Over the last decade, a debate has developed concerning how fish use their red or slow-twitch, aerobic muscle for swimming. The debate has centered on longitudinal variations in power production, with a variety of interpretations on whether the principal source of power during swimming is the anterior musculature, the posterior musculature or a generalized feature of all of the red myotome.

Body form and swimming mode predictably affects how the red muscle is used to power swimming. Wardle et al. (1995) reviewed the literature on estimates of power production during swimming. They described a spectrum of fish swimming modes on the basis of body curvature during swimming. They concluded that fish that swim with high body curvature, such as eels, will use primarily their anterior myotome to power steady swimming and that the stiffer-bodied fishes, such as scup, will rely more on their posterior myotome.

The variety of techniques that have been used to study swimming in various fish species has also contributed to the formation of multiple hypothesis on how fish power steady swimming. Using data on *in vivo* muscle activity and contraction kinetics with various forms of modeling, van Leeuwen et al. (1990), Wardle and Videler (1993) and van Leeuwen (1995) concluded that mackerel (*Scomber scombrus*), saithe (*Pollachius virens*) and carp (*Cyprinus carpio*) power their steady swimming primarily through the use

of the anterior red musculature. The posterior red muscle was theorized to act as a stiffened rod that transmitted force from the anterior muscle to the tail blade (see Wardle et al., 1995). Alternatively, using *in vivo* muscle activity data for *in vitro* work-loop measurements of power production (Josephson, 1985), Rome et al. (1993) argued that, in scup (*Stenotomus chrysops*), the power for swimming is generated by the posterior musculature and that the anterior musculature does not generate power, but may act to stabilize the head. Johnson et al. (1994) used the same techniques for one posterior position in largemouth bass (*Micropterus salmoides*) and showed that the posterior muscle of this species does generate some power for swimming. They suggested that the results for largemouth bass were similar to those for scup.

The different conclusions about longitudinal variation in power production by fish red muscle are not entirely divided by technique. Hammond et al. (1998) used the work-loop technique with *in vivo* data on muscle activity during swimming and reported that rainbow trout (*Oncorhynchus mykiss*) use their anterior muscle for swimming, at least at the maximum steady swimming speed. Alternatively, Shadwick et al. (1998), using a modeling technique that employed *in vivo* muscle activity data and contraction kinetics to estimate power production, suggested that, in pacific mackerel (*Scomber japonicus*), power for swimming is generated along the length

of the fish. Like the studies of van Leeuwen et al. (1990), Wardle and Videler (1993) and van Leeuwen (1995), no actual measurements were made of power production by red muscle in pacific mackerel (Shadwick et al., 1998).

In the present study, the goal was to use the techniques of Rome et al. (1993) and Coughlin and Rome (1996) to examine power production during swimming in two species, rainbow trout (*Oncorhynchus mykiss*) and largemouth bass (*Micropterus salmoides*). Although both these species have moderately compressed bodies with similar tail size (approximately 10% of total length), they differ in head size and in the number of vertebrae. Largemouth bass have approximately 30 vertebrae (Jayne and Lauder, 1995), while rainbow trout have more than 50 vertebrae (Nelson, 1994). Also, the head of largemouth bass is much longer than that of trout. A longer head and fewer vertebrae suggest that largemouth bass should swim with less body curvature than trout. On the basis of these morphological differences and the work of Johnson et al. (1994), largemouth bass are predicted to swim much like scup, with the majority of power produced by the posterior musculature. However, the work of Hammond et al. (1998) on large rainbow trout suggests that trout may swim by generating more power for swimming with the anterior musculature. That result will be tested here.

The methods used here require detailed data on *in vivo* muscle activity during swimming. This was collected through the use of electromyography and sonomicrometry. For rainbow trout, electromyography and sonomicrometry were used to detail muscle activity; for largemouth bass, data on muscle activity were available from the literature (Jayne and Lauder, 1995). When muscle activity is accurately characterized, the data can be used in *in vitro* experiments on live muscle bundles. Using the work-loop technique (Josephson, 1985), oscillatory work and power production can be measured.

Materials and methods

Experimental animals

Rainbow trout, *Oncorhynchus mykiss* (Walbaum), were obtained from the Huntsdale Fish Culture Station (Carlisle, Pennsylvania, USA) of the Fish and Boat Commission of the Commonwealth of Pennsylvania. Trout were maintained on a diet of prepared fish feed (Ziegler Trout Grower) in a recirculating aquarium system at 10 °C. Large juvenile rainbow trout, termed smolts, were used in this study. The mean total length (L) of trout used was 25.6 ± 1.5 cm ($N=11$) for swimming studies and 24.6 ± 2.0 cm ($N=5$, means \pm S.D.) for the *in vitro* physiology experiments. These two groups were not significantly different in total length ($t=1.09$, $P=0.294$). Largemouth bass, *Micropterus salmoides* (Lacépède), were obtained from a commercial fish farm in Chester County, Pennsylvania, USA. The mean total length of largemouth bass used in physiology experiments was 18.2 ± 1.9 cm, which was similar to the mean total length of largemouth bass (19.8 cm) used by Jayne and Lauder (1995). Largemouth bass were maintained on a diet of live food in a recirculating aquarium

system at 20 °C. All handling of experimental animals was reviewed by the Widener University IACUC in accordance with the National Research Council's *Guide for the Care and Use of Laboratory Animals*.

Swimming studies on rainbow trout

For each fish, electromyograms and sonomicrometry signals were recorded from the red muscle at two out of three longitudinal positions. The anterior (ANT), middle (MID) and posterior (POST) positions were respectively 35%, 55% and 75% of the total length from the anterior tip or snout. An additional electromyogram (EMG) electrode in each fish monitored white muscle activity at the MID position. Fish were anesthetized with tricaine methanesulfate (MS-222) at a dosage of 50 mg l^{-1} . Twisted wire (Teflon-coated Medwire) electrodes were inserted into the muscle using a hypodermic needle. Grass EMG amplifiers filtered the EMG signal with a bandwidth of 10–1000 Hz and a 60 Hz notch filter. The placement of electrodes into the red muscle was verified through dissection after each experiment. Omnidirectional, 2.0 mm piezoelectric crystals (Triton Technology) were implanted just in front of and just behind each EMG electrode. They were inserted subcutaneously and anchored *via* sutures. Typically, the crystals were 5–6 mm apart (Coughlin et al., 1996a). Sonomicrometry signals were recorded (Triton Technologies; model 120) together with EMGs for fish swimming at speeds of $1.0\text{--}4.0 L s^{-1}$ (in increments of $0.5 L s^{-1}$). Fish were swum in a recirculating flow chamber. The temperature-controlled flume has a 0.40 m test section of 0.15 m internal diameter clear acrylic pipe. A calibrated direct current motor permitted speeds of $0.10\text{--}1 \text{ m s}^{-1}$. The order of swimming speeds was randomized.

Sonomicrometry and EMG signals were collected using a PC and a Keithley-Metrabyte DAS-1601 input/output board. The signals were analyzed using custom-designed software to define several variables of muscle activity at each swimming speed. Tailbeat frequency and body curvature were determined at each swimming speed. The tailbeat frequency of swimming for a given fish at a specific speed was found from the period of the sonomicrometry signal. Body curvature was expressed as λ_B , the wavelength of body curvature in units of total body length. Higher values of λ_B indicate relatively less curvature, and λ_B is calculated as mechanical wave speed divided by tailbeat frequency. Mechanical wave speed was found through the sonomicrometry signal by determining the transit time of the peak in muscle length progressing from anterior to posterior. The maximum steady swimming speed was defined as the highest swimming speed at which no white muscle was recruited. For each position at each speed, the duty cycle of EMG activity was determined as the duration of the EMG burst expressed as a proportion of the tailbeat period. The onset and offset times for EMG activity were determined manually from the raw EMG recordings. Data were only used if EMG activity could unambiguously be differentiated from background noise. The sonomicrometry signal of muscle activity was analyzed to determine muscle strain, which is defined as \pm the percentage

length change from muscle resting length. Lastly, phase was determined from a comparison of the EMG and sonomicrometry signals. Phase is the relative timing of EMG onset relative to peak muscle length (onset of shortening) expressed as a proportion of tailbeat period. A negative phase means that muscle activity (EMG) begins before muscle shortening in each tailbeat cycle.

Physiological studies on rainbow trout and largemouth bass

For muscle mechanics experiments, fish were killed by spinal transection. Live *in vitro* muscle preparations were dissected from the longitudinal bands of red muscle running down each side of the fish. Strips of red muscle were extracted from just above and below the lateral line of the fish. For rainbow trout, muscle preparations were dissected from the three longitudinal positions, in strips that were approximately 20% of fish total length, centered at the positions defined above. ANT muscle preparations came from 0.25–0.45L, MID preparations from 0.45–0.65L and POST preparations from 0.65–0.85L. For largemouth bass, ANT muscle strips were extracted approximately 0.35–0.50L, MID bundles from 0.55–0.70L and POST bundles from 0.70–0.80L. These ranges correspond approximately to positions 2–3, 4–5 and 6–7 described by Jayne and Lauder (1995).

Muscle preparations were eventually reduced to a single myotome in length through dissection using a stereomicroscope. Muscle was kept at 4 °C and maintained in a physiological saline solution (see Altringham and Johnston, 1990). Live bundles from trout were typically 3–4 mm in length and 0.25 mm² in cross-sectional area, whereas those from largemouth bass were usually 2–3 mm in length with a similar cross-sectional area to that for trout. A description of histological techniques is given below. The bundles were tied into a muscle mechanics system using 9-0 gauge silk thread. The muscle was tied *via* connective tissue to stainless-steel pins attached to a Cambridge Technology 300S servosystem at one end of the mechanics apparatus and to an ENTRAN load cell (2–20 g) at the other end. For trout, the temperature was maintained at 10 °C, while for largemouth bass it was 20 °C. The temperature for largemouth bass was chosen on the basis of the work of Jayne and Lauder (1995), while the temperature for trout represents a middle value in the range of environmental temperatures preferred by these fish (4–15 °C). Trout show reduced survival when maintained outside this temperature range. Experimental control and data collection were carried out using a PC, Keithley-Metrabyte DAS-1601 input/output board and custom-designed software.

For each bundle, the optimal length for maximal tetanic force production was found first (D. J. Coughlin, J. Burdick, K. A. Stauffer and F. E. Weaver, in preparation). Muscle length, total stimulus duration, pulse duration and pulse amplitude (voltage) were optimized to give maximum force output. Maximal isometric tetanic force was usually obtained using a 200 ms duration stimulus of 3 ms duration pulses at a frequency of 125 Hz. Isometric twitch contractions were then measured at the optimal length using a single pulse. Maximal

twitch and tetanus force values were then measured, and the force traces were analyzed for activation and relaxation times. For tetanic contractions, time of activation (t_A) was defined as the time from 10% to 90% of maximum force, and time of relaxation (t_R) was the time from 90% to 10% of force. Twitch time (t_{TW}) was the time from stimulation to 90% recovery (10% of peak twitch force remaining) in twitch contractions.

Work-loop experiments (Josephson, 1985) were used to measure work and power output of muscle during oscillatory activity. Peak work per oscillatory cycle and maximum oscillatory power were found across a range of frequencies (e.g. 2–7 Hz). Positive work is produced by muscle during the shortening phase of each oscillatory length change cycle. Negative work is the work done to muscle to lengthen it. Net work per cycle is the difference between the positive work of shortening and the negative work of lengthening. Power is the product of the net work per oscillation cycle and the oscillation frequency. For all the experiments reported here, work and power were expressed in mass-specific terms by dividing the work or power production of a muscle bundle by the mass of that bundle. A modified triangular waveform was used; peak values of the waveform were smoothed to avoid abrupt changes in length. This waveform was chosen because it represented a uniform length change pattern (i.e. constant strain for a series of cycles) that approximated the triangular waveform observed in swimming fish (see Fig. 1). Values of muscle strain, stimulation duration and stimulation phase were optimized to maximize power production at each frequency. Optimal frequency of oscillation was defined as the frequency of maximum power production (\dot{W}_{max}). To control for fatigue in the muscle preparation, work-loop trials that generated maximum power at a given frequency were run consecutively with trials for \dot{W}_{max} at the optimal frequency.

Work-loop experiments were carried out using *in vivo* muscle activity data. For trout, the *in vivo* muscle activity was found during the swimming experiments. Fifteen sets of *in vivo* conditions resulted from recordings made at three longitudinal positions for five swimming speeds. A red muscle bundle from a given position was run through work-loop experiments under conditions for a range of swimming speeds for that position. In addition, the bundle was run through a limited set of conditions for the other two positions. For instance, work-loop experiments carried out on ANT bundles would include the *in vivo* ANT conditions for five swimming speeds (1.0, 1.5, 2.0, 2.5 and 3.0 L s⁻¹) and the MID and POST conditions for two swimming speeds (typically 2.5 and 3.0 L s⁻¹).

For largemouth bass, *in vivo* data on red muscle activity during steady swimming were reported by Jayne and Lauder (1995) for six positions (positions 2–7). Thirty sets of *in vivo* conditions resulted from recordings made at six longitudinal positions for five swimming speeds. Muscle at position 1 in their study, the most anterior position, was not active during swimming (Jayne and Lauder, 1995). For largemouth bass ANT muscle bundles, *in vivo* work-loop experiments were carried out using the *in vivo* conditions of positions 2 and 3 for five swimming speeds (0.7, 1.2, 1.6, 2.0 and 2.4 L s⁻¹). For

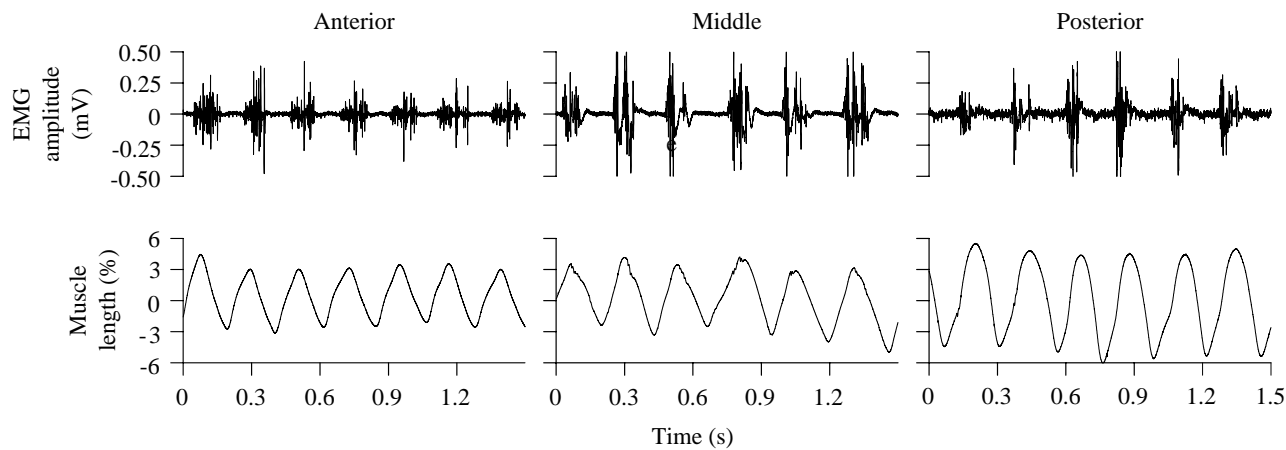


Fig. 1. Electromyography and sonomicrometry records from rainbow trout. Electromyograms (EMGs) from red muscle in rainbow trout swimming steadily at $3.0 L s^{-1}$ (where L is total body length; 3.9 Hz tailbeat frequency) are plotted for the anterior, middle and posterior body positions (respectively 0.35, 0.55 and $0.75 L$). In addition, muscle length change recordings collected simultaneously using sonomicrometry are shown for each position. Examination of the EMGs shows that duty cycle decreases from anterior to posterior, while examination of the length change recordings reveals an increase in muscle strain from anterior to posterior. These sample recordings are from several fish.

MID bundles, work-loop experiments were carried out using the *in vivo* conditions of positions 4 and 5 for the same five swimming speeds. Lastly, for POST bundles, work-loop experiments were carried out using the *in vivo* conditions of positions 6 and 7 for the five speeds.

To control for fatigue, power was measured under the optimized conditions for \dot{W}_{max} . Power output under *in vivo* conditions was then expressed as a percentage of \dot{W}_{max} . Power output of bundles could then be corrected for fatigue by tracking any drops in \dot{W}_{max} , which were typically less than 10%.

Histology of muscle bundles

Determination of the live muscle fiber area of muscle bundles was carried out at the end of each experiment, as described by Coughlin et al. (1996b) and D. J. Coughlin, J. Burdick, K. A. Stauffer and F. E. Weaver (in preparation). Bundles were stained with Trypan Blue to identify dead tissue, embedded in gelatin and frozen with liquid nitrogen. The frozen bundles were sectioned at $16 \mu m$ and stained with succinate dehydrogenase (SDH) for mitochondrial content. Areas stained dark blue were dead tissue. Live tissue that had stained dark brown corresponded to aerobic muscle fibers. The live fiber area of all bundles used in this research were dominated (>95%) by red muscle fibers. Neither species has an obvious pink layer, such as that in scup (Zhang et al., 1996). Live fiber mass was estimated by multiplying live fiber area by the muscle bundle length and then multiplying by 1.05 to compensate for the slightly higher density of muscle mass relative to water. This approach has been used previously (Rome et al., 1993).

Results

Swimming studies on rainbow trout

Simultaneous recording of muscle activity *via* EMGs and

muscle length change patterns *via* sonomicrometry allowed the characterization of red muscle activity patterns at three longitudinal positions for a range of swimming speeds (Fig. 1). Eleven fish were use in the swimming experiments. The maximum steady swimming speed, or the fastest swimming speed before the recruitment of white muscle, was $2.77 \pm 0.08 L s^{-1}$ (mean \pm S.E.M.). Data on swimming at $3.0 L s^{-1}$ were included here because six of the 11 fish did not recruit white muscle at that speed, and white muscle recruitment was relatively weak in the other five fish at that speed.

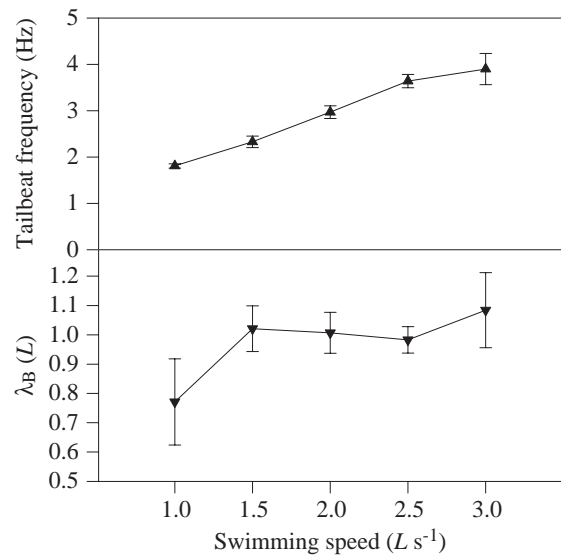


Fig. 2. Tailbeat frequency and body curvature during steady swimming in rainbow trout. Mean tailbeat frequency ($N=11$) increases significantly ($P<0.001$) with swimming speed. The wavelength of body curvature (λ_B) is largely constant (approximately $1 L$), but tends to decrease with swimming speed. L , total body length.

Tailbeat frequency increased twofold with an increase in swimming speed from $1.0 L s^{-1}$ to $3.0 L s^{-1}$; swimming speed significantly affected tailbeat frequency (Fig. 2; $F=17.50$, $P<0.001$). There appeared to be a gradual increase in body curvature λ_B with swimming speed (Fig. 2). However, λ_B was not significantly affected by swimming speed ($F=0.83$, $P=0.544$, power=0.244) and, across most speeds, λ_B was approximately $1L$ (Fig. 2).

Both longitudinal position and swimming speed affected the pattern of *in vivo* muscle activity variables. Longitudinal position significantly affected the duty cycle of EMG activity, muscle strain and the phase of EMG activity relative to the length change cycle, while swimming speed affected only phase and strain significantly (Table 1; Fig. 3). The duty cycle of muscle activity during swimming decreased from anterior to posterior at a given swimming speed. The duration of EMG bursts is significantly longer in the anterior musculature, with duty cycle ranging from 0.3 to 0.4 in the anterior to 0.15 to 0.3 in the posterior musculature (Table 1; Fig. 3). However, duty cycle did not vary significantly with swimming speed. Phase

showed a significant negative shift from anterior to posterior: the onset of EMG activity occurred earlier in each length change cycle at the more posterior positions. Phase was also significantly affected by swimming speed, with a more negative phase shift observed at higher swimming speeds (Table 1; Fig. 3). The strain (\pm percentage muscle length change) of muscle during swimming also increased significantly from anterior to posterior, and strain increased significantly with swimming speed (Table 1; Fig. 3). Longitudinal position and swimming speed had no interactive effects for any of the three dependent variables.

Physiological studies on rainbow trout and largemouth bass Contraction kinetics

Before carrying out work-loop experiments on rainbow trout and largemouth bass red muscle bundles, basic contractile properties were measured. In rainbow trout, the mean force generated by muscle bundles in isometric tetanic contractions was $169.6 \pm 19.7 \text{ kN m}^{-2}$ (mean \pm S.E.M., $N=15$). Longitudinal position did not significantly affect force ($F=0.12$, $P=0.89$).

Fig. 3. (A) Red muscle activity during steady swimming in rainbow trout at 10°C . Duty cycle, the proportion of electromyogram (EMG) activity during each tailbeat period, decreases from anterior to posterior, but does not vary with swimming speed. Phase, the timing of EMG activity relative to maximum muscle length during each tailbeat cycle, is expressed as a proportion of the tailbeat period. Phase shifts negatively from anterior to posterior, such that posterior muscle shows the most negative phase shift (such that EMG activity is evident earlier in each tailbeat period). Phase also shifts negatively with increasing swimming speed. Muscle strain (\pm percentage change in muscle length, ML) increases significantly from anterior to posterior and from low to high swimming speeds. Values are means \pm S.E.M., $N=5-6$. Asterisks indicate individual swimming speeds at which there is a significant effect of longitudinal position on a given variable (ANOVA); $*P<0.05$, $**P<0.01$. (B) For comparison, the red muscle data of Jayne and Lauder (1995) for largemouth bass swimming steadily at 20°C are also plotted. L , total body length.

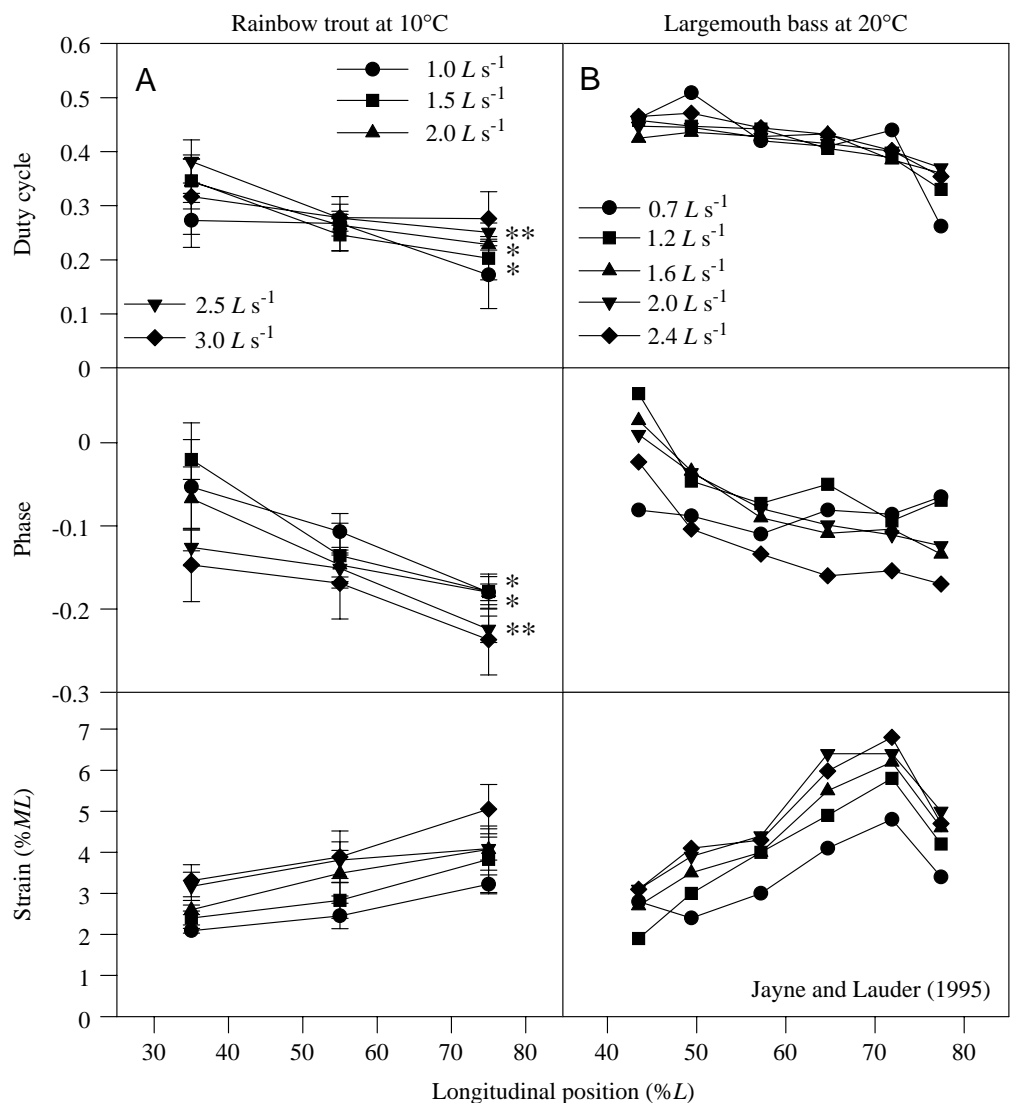


Table 1. Statistical tests on *in vivo* muscle activity variables and mass-specific power production in rainbow trout and largemouth bass

		Longitudinal position	Swimming speed	Position × speed interaction
Rainbow trout	Duty cycle	10.618 (<0.001)	1.097 (0.369, 0.319)	0.442 (0.890, 0.184)
	Phase	19.845 (<0.001)	3.346 (0.016)	0.599 (0.774, 0.249)
	Strain	6.260 (0.004)	2.592 (0.047)	0.174 (0.994, 0.096)
	Power	97.246 (<0.001)	67.407 (<0.001)	4.021 (<0.001)
Largemouth bass	Power	30.655 (<0.001)	13.600 (<0.001)	0.845 (0.654, 0.586)

Two-way analyses of variance (ANOVAs) on the effects of longitudinal position and swimming speed were tested for the dependent variables duty cycle, phase and strain from the trout swimming experiments.

A two-way ANOVA was also performed on data from trout and largemouth bass work-loop experiments used to measure power output of *in vitro* muscle bundles stimulated with the conditions measured *in vivo*.

F-values are provided along with significance in parentheses. The second number in parentheses is the power calculation, where appropriate. For rainbow trout, there were three positions and five speeds. Total degrees of freedom is 69 for duty cycle, phase and strain and 74 for mass-specific power. For largemouth bass, there were six positions and five speeds, and the total degrees of freedom is 119.

Similar results were observed in largemouth bass, with the mean force generated in isometric tetanic contractions by muscle bundles being $186.4 \pm 33.6 \text{ kN m}^{-2}$ ($N=18$). Again, longitudinal position did not significantly affect force ($F=0.151$, $P=0.861$). The ratio of peak isometric twitch force to peak tetanic force was not affected by longitudinal position in either species. In trout, this ratio was 0.525 ± 0.025 ($F=0.03$, $P=0.072$), while in largemouth bass the ratio was 0.279 ± 0.030 ($F=0.20$, $P=0.819$). The peak force ratio was significantly different between the two species, however, with that for trout ratio being approximately double that for largemouth bass ($t=6.103$, $P<0.001$). This observation may simply relate to temperature differences. Muscle operating at colder temperature, such as the trout muscle examined here, typically shows a higher ratio of twitch to tetanic force (e.g. Rome and Swank, 1992).

Both rainbow trout and largemouth bass red muscle showed significant effects of longitudinal position on contraction kinetics. The relaxation time of red muscle stimulated tetanically increased significantly from anterior to posterior in both species (Fig. 4). Similarly, the twitch time also increased significantly from anterior to posterior in both species (Fig. 4). Activation time was not significantly affected by longitudinal position.

Muscle work output

When red muscle bundles are activated under the *in vivo* conditions observed in the swimming fish (Fig. 3), work-loop measurements of muscle performance could be made. Work per cycle is represented by the area of work loops and was characterized for each longitudinal position for a range of swimming speeds (Fig. 5). In rainbow trout, there was a gradual increase in work per cycle (or work-loop area) along the length of the fish (Fig. 5). The observed variations in shape correlate with the gradations in *in vivo* conditions. The posterior muscle bundles experience longer strains, giving wider work loops, and they have greater negative phase shifts

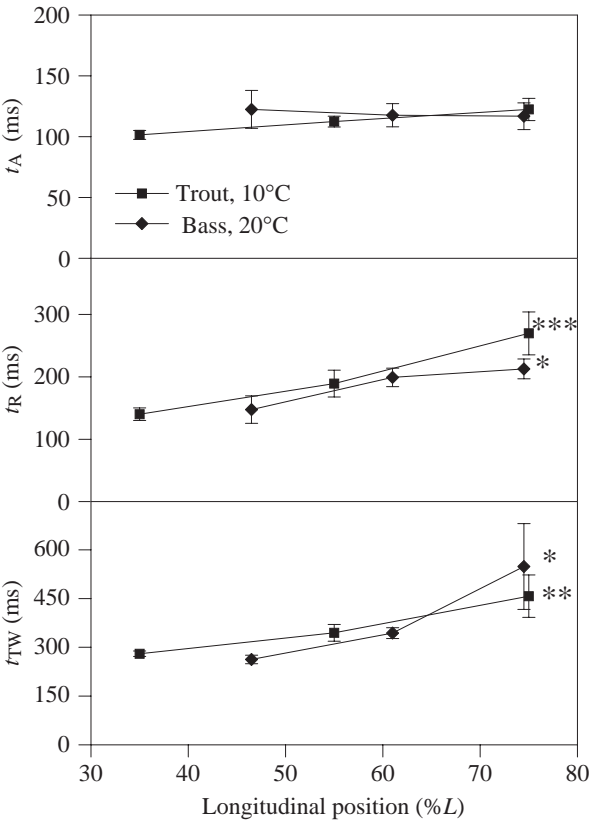
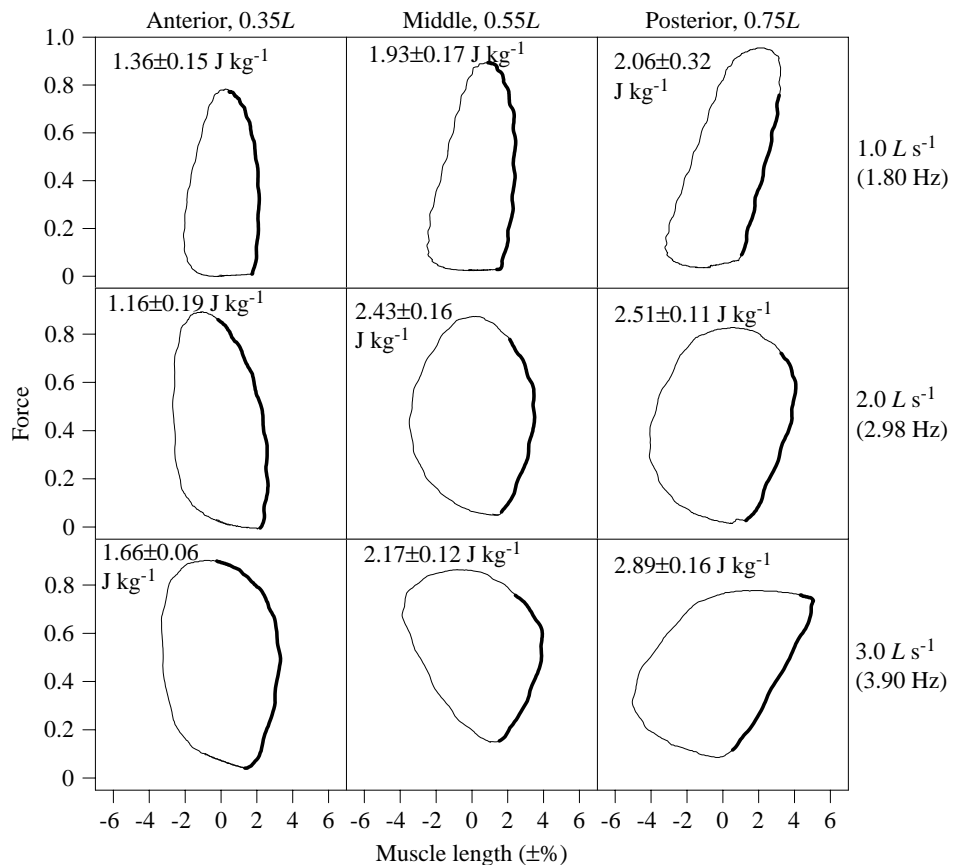


Fig. 4. Contraction kinetics of red muscle from rainbow trout (10 °C) and largemouth bass (20 °C). Mean (\pm S.E.M.) values are given for $N=5$ for each position in trout and $N=6$ for each position in largemouth bass. Asterisks indicate a significant effect of longitudinal position on a kinetic variable (ANOVA); * $P<0.05$, ** $P<0.01$, *** $P<0.001$. In both species, relaxation time (t_R , time from 90% to 10% of force) and twitch time (t_{TW} , time from stimulation to 90% recovery; i.e. 10% of peak twitch force remaining) increase significantly from anterior to posterior. Anterior muscle has faster kinetics than posterior muscle. t_A , time from 10% to 90% of maximum force; L , total body length.

Fig. 5. Sample data for rainbow trout red muscle for *in vitro* work-loop experiments based on the *in vivo* muscle activity data (Fig. 3). The body positions of both the *in vivo* data and the muscle bundles used in the *in vitro* experiments are given across the top; swimming speeds and tailbeat frequencies (in parentheses) are given along the right side. The mean work output per oscillation cycle (\pm S.E.M.) is given for $N=5$ at each position and swimming speed. All the work loops shown run counterclockwise; experiments were at 10°C . Bold type indicates the period of stimulation. Muscle strain is indicated by the width of the work loops, with peak muscle length represented by the rightmost extreme of each loop. Greater phase shift is indicated by the onset of stimulation occurring before peak muscle length. L , total body length. Workloop force is normalized to maximal tetanic force.



and a shorter duty cycle, resulting in an increase in force prior to the onset of shortening. The effects of activation conditions on work and power production are established through an examination of sample work loops for anterior and posterior conditions. For instance, at $2.0 L s^{-1}$, force generation in anterior muscle increases as the muscle shortens and does not peak until almost the end of shortening. This limits the work per cycle and, therefore, power production compared with posterior muscle (Fig. 5). Typically, for a given swimming speed, work per cycle by posterior muscle is 50–100% greater than by anterior muscle. This increase is also reflected in a comparison of the mass-specific power production under the *in vivo* conditions with power production under the optimal conditions for a given muscle bundle. For instance, at $3.0 L s^{-1}$, anterior muscles stimulated under their *in vivo* conditions generate 24% of \dot{W}_{\max} ; alternatively, posterior muscle bundles stimulated under their *in vivo* conditions generate close to 40% of \dot{W}_{\max} .

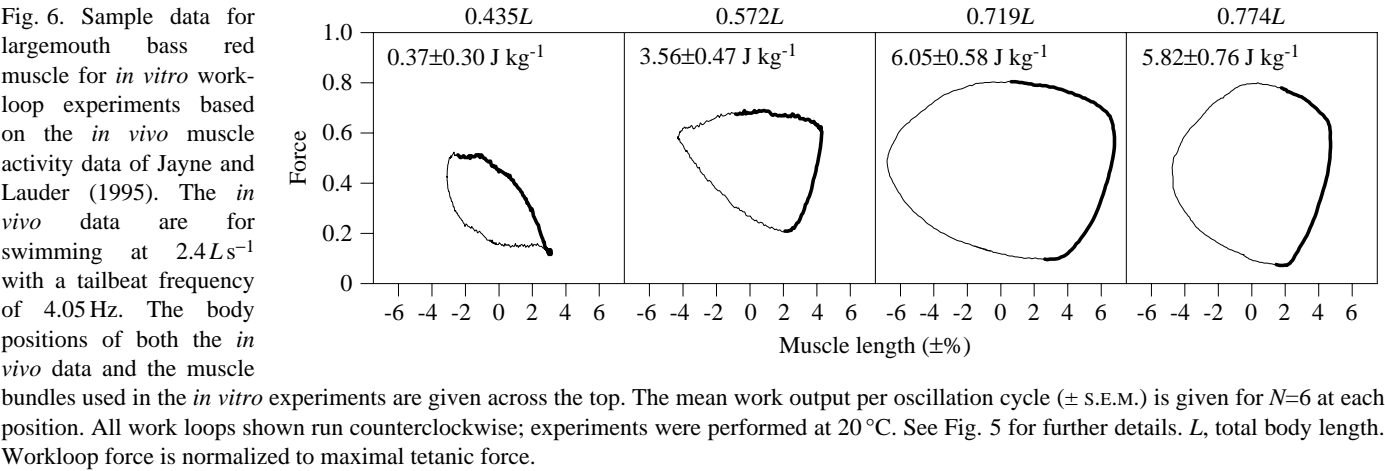
Similar patterns are observed by comparing work loops for one position across a range of swimming speeds. As speed increases, so does strain, giving wider work loops. Also, with an increase in swimming speed, the phase again shifts more negatively and the duty cycle decreases. The impact of these variations in muscle activity at different swimming speeds is a 15–40% increase in work per cycle from the lowest to the highest speed (Fig. 5).

For largemouth bass, the effect of longitudinal position on

work per cycle is more dramatic. At a given swimming speed, work loops at more posterior positions differ substantially from those at anterior positions (Fig. 6). As reported by Jayne and Lauder (1995), the strain of red muscle in swimming largemouth bass shows greater variation along the length of the fish than in the trout data reported here (Fig. 3). The work loops of anterior and posterior muscle of largemouth bass therefore differ more obviously in terms of width. Duty cycle and phase also differ with longitudinal position in largemouth bass and also affect work per cycle (Fig. 6). Work per cycle increased from anterior to posterior by five- to 15-fold (500–1500%) at a given swimming speed in largemouth bass (Fig. 6), a considerably greater increase than for trout. The increase in power with increasing swimming speed at a given position in largemouth bass was similar to that for trout, averaging 40% from the lowest to the highest swimming speed.

Muscle power production

Mass-specific power production, determined by dividing the product of work per cycle and the frequency of oscillation by muscle bundle mass, varied with both swimming speed and longitudinal position. In rainbow trout, speed and position both significantly affected mass-specific power output of red muscle bundles stimulated under the *in vivo* condition. As with work per cycle, posterior muscle produced more power than anterior muscle (Table 1; Fig. 7). At a given swimming speed, the



difference in power production by muscle from anterior and posterior sites was identical to that of work per cycle: posterior muscle produced 50–100 % more mass-specific power. Swimming speed also affected power production, with power increasing with speed. The difference in power production between low and high swimming speeds was considerably more than for work per cycle because of the higher oscillation frequencies at higher speeds. At a given position, muscle stimulated under the *in vivo* conditions for swimming at $3.0 L s^{-1}$ produced an average of 90 % more power than for swimming at $1.0 L s^{-1}$. In addition, there was an interactive effect between swimming speed and longitudinal position on power production: position had a greater effect on power output at higher swimming speeds (Fig. 7).

Power production by largemouth bass showed similar trends to that for rainbow trout. As with work, however, the variations in power with longitudinal position were more dramatic in largemouth bass. At all swimming speeds, there was a significant effect of longitudinal position on power output

(Table 1). The posterior muscle produced more power than the anterior muscle; there was a 10- to 15-fold increase in mass-specific power output from the front to the back of the fish. As with trout, longitudinal position also had a significant effect on power output (Table 1). More mass-specific power was produced at higher speeds for a given position (Fig. 7). Lastly, unlike in trout, there was no interactive effect between swimming speed and position with regard to power output. Substantially more power was produced by posterior muscle than by anterior muscle at all swimming speeds (Fig. 7).

To examine the effects of longitudinal variations in contraction kinetics on estimates of work per cycle and power production in rainbow trout, muscle bundles from each position were stimulated under the conditions observed at other positions. Anterior muscle generates more work per cycle than posterior muscle for most sets of *in vivo* muscle activity conditions (Fig. 8). For instance, anterior muscle generates significantly more work per cycle than posterior muscle when both are stimulated under the anterior muscle conditions for

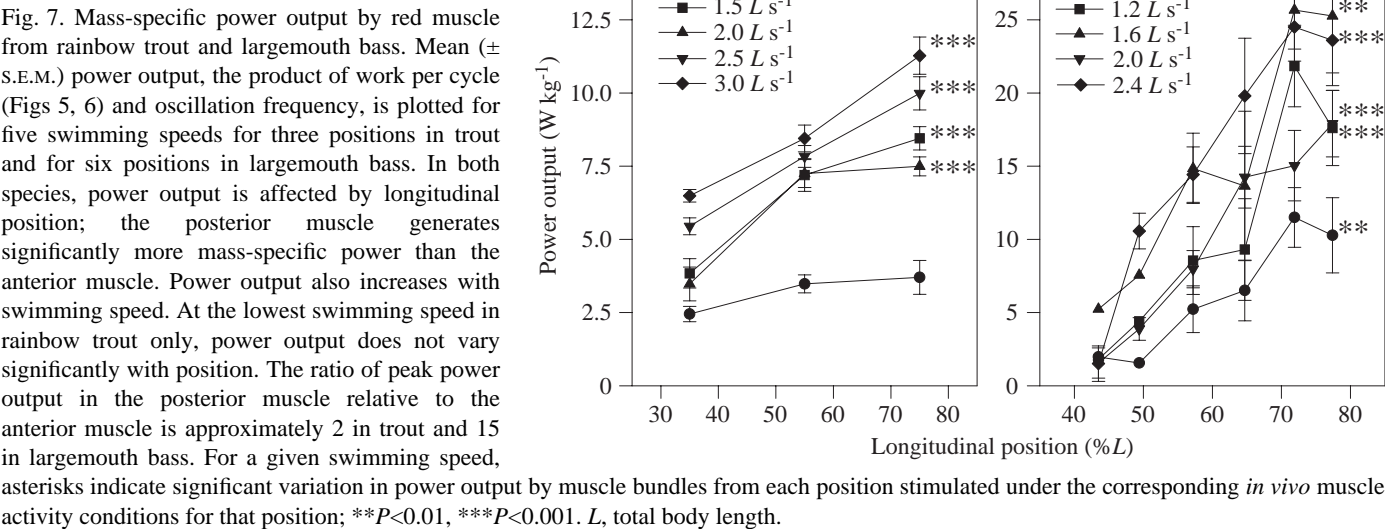
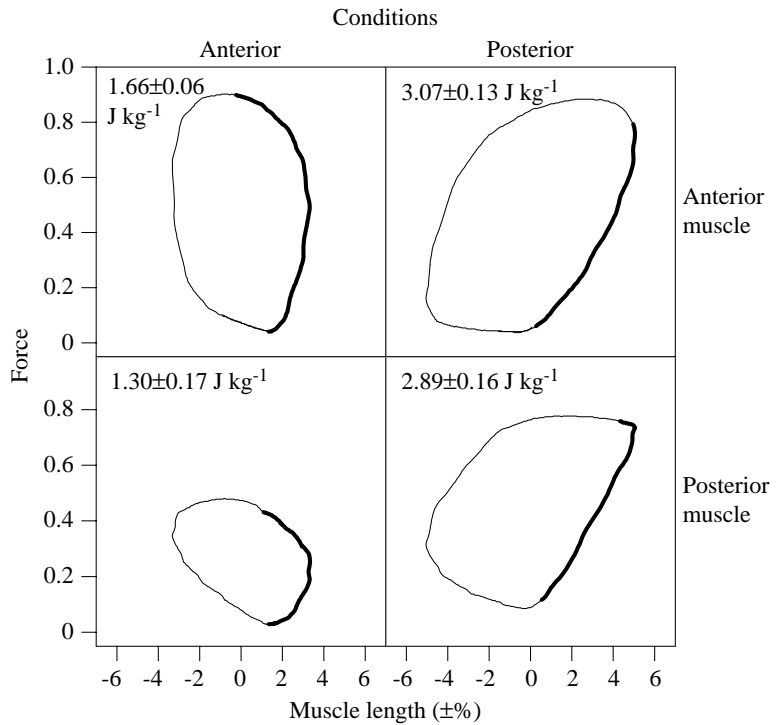


Fig. 8. Sample data for trout red muscle for *in vitro* work-loop experiments for swimming at $3.0 L s^{-1}$ with a tailbeat frequency of 3.9 Hz. The mean work output per oscillation cycle (\pm S.E.M.) is given for $N=4$ at each position and set of conditions. In the top row are work-loops for anterior muscle stimulated with both the conditions recorded at the anterior position (left) and those recorded at the posterior position (right). Similarly, the bottom row panels are for posterior muscle stimulated with both the anterior and posterior muscle activity conditions. Under the posterior conditions, work loops by anterior and posterior muscle are similar (right half of figure), and work per cycle does not differ significantly. Under the anterior conditions the anterior muscle, which has faster kinetics than the posterior muscle, generates significantly more work per oscillation cycle than the posterior muscle (left half of figure). Note that the representative work loop in the upper left panel was average in terms of power output, while that in the lower left panel is somewhat below average. All work loops shown run counterclockwise; all experiments were performed at 10 °C. See Fig. 5 for further details. Workloop force is normalized to maximal tetanic force. L , total body length.



swimming at $3.0 L s^{-1}$ ($t=2.31$, $P<0.05$, d.f.=8). However, there is no significant difference between work per cycle by anterior *versus* posterior muscle bundles when they are stimulated under the posterior muscle conditions for the same speed ($t=0.845$, $P>0.20$, d.f.=8). The same relationship is observed when work is converted to power (Fig. 9). There is a significant effect of muscle bundle position on power output for the stimulation conditions of anterior and middle muscle. Again, there is no difference in power production by the different muscle bundles when they are stimulated under the posterior muscle conditions (Fig. 9).

Discussion

Red muscle and steady swimming in trout, bass and scup

The function of red muscle during steady swimming in rainbow trout and largemouth bass is similar to that of red muscle previously described for scup. For all three species,

work-loop estimates of mass-specific power output during swimming suggest that the posterior musculature generates the majority of power for swimming. In scup, a survey of muscle fiber distributions in the swimming musculature (e.g. Zhang et al., 1996) allows a determination of absolute power output

Stimulation conditions:

- Anterior conditions, $3.0 L s^{-1}$
- Middle conditions, $3.0 L s^{-1}$
- ▲ Middle conditions, $2.5 L s^{-1}$
- ▼ Posterior conditions, $3.0 L s^{-1}$

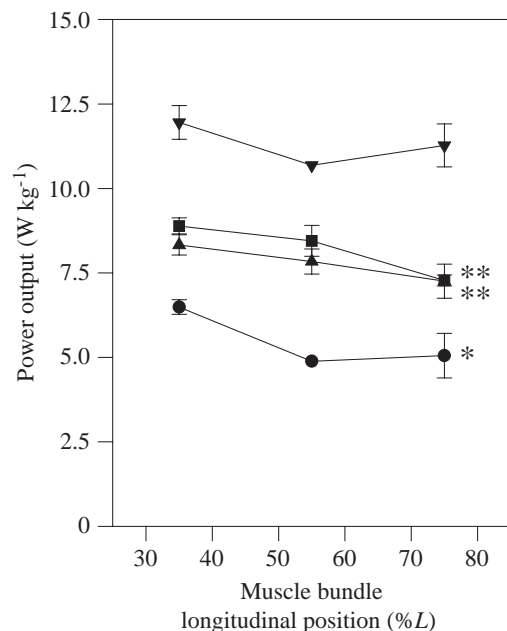


Fig. 9. Mass-specific power output by trout red muscle. Power output is plotted *versus* the location from which muscle bundles were taken. For the conditions recorded *in vivo* from the anterior position for swimming at $3.0 L s^{-1}$, where L is total body length, anterior muscle bundles generate significantly more power than those from the posterior for swimming. The same is true for middle *in vivo* conditions: mass-specific power output is greatest by anterior muscle. For the posterior *in vivo* conditions, there is no difference between anterior, middle or posterior muscle bundles. Asterisks indicate a significant variation in power output by muscle bundles from different positions stimulated under the *in vivo* muscle activity conditions for a given longitudinal position and swimming speed; * $P<0.05$, ** $P<0.01$. L , total body length.

along the length of the fish. This approach confirms that the posterior musculature generates the majority of power for swimming (Coughlin and Rome, 1996; Rome et al., 2000). In trout and largemouth bass, such a muscle fiber atlas does not yet exist, but examination of red muscle during dissection reveals that its cross-sectional area is greatest in the posterior of both species (D. J. Coughlin, unpublished observation). If the posterior muscle has the greatest mass and the greatest mass-specific power output, then the primary source of power for swimming is the posterior muscle. An important assumption made here is that red muscle mass in trout and largemouth bass is at least approximately evenly distributed along the length of the fish, if not skewed to the posterior as observed in scup.

In rainbow trout, largemouth bass and scup, the muscle activity patterns observed in the anterior red muscle of steadily swimming fish act as a constraint on power production compared with more posterior positions. The anterior muscle undergoes the lowest strain during swimming, has the longest duty cycle and has a smaller phase shift of activation time relative to peak muscle length. All three of these elements reduce the power production of the anterior muscle relative to the posterior muscle for a given fish at a given swimming speed. For instance, the limited shortening distance of anterior muscle results in the generation of less positive work during the shortening phase of the oscillation cycle, lowering power output (Coughlin and Rome, 1996). In addition, force production is limited in anterior muscle bundles by the less favorable phase conditions (Rome et al., 1993). Since the onset of muscle activity, measured using electromyography, is not until just before muscle shortening, the muscle will not generate maximum force until well into shortening. Anterior muscle shortens for a greater fraction of its length change at suboptimal force, leading to lower positive work and lower power output. In addition, a less negative phase and a longer duty cycle mean that anterior muscle will not begin to relax until late in the shortening phase of the length change cycle, resulting in residual force at the beginning of the lengthening phase (Rome et al., 1999). This residual force will require more negative work to be performed (by antagonists) to re-extend the muscle during the lengthening phase, reducing the net work per cycle and power output.

In scup, trout and largemouth bass, longitudinal position affects contraction kinetics: in all three species, anterior muscle relaxes more quickly than posterior muscle. This trait would affect power output by red muscle during swimming. Given the constraints described above, anterior muscle would benefit more than posterior muscle by the increased rates of relaxation. Faster relaxation would reduce the residual force in the muscle at the start of lengthening. In trout, this was demonstrated by stimulating anterior and posterior muscle bundles under both the anterior and posterior muscle conditions. The faster anterior muscle produces significantly more work per cycle and more mass-specific power than the posterior muscle when they are both stimulated under the less advantageous activation conditions of anterior muscle. Under the more advantageous

activation conditions of the posterior muscle, there is no significant difference in the power output of anterior and posterior muscle bundles (Figs 8, 9).

There are variations among species in the patterns of power production. The ratio of mass-specific power from the posterior compared with the anterior muscle is greater in scup and largemouth bass than in trout (Fig. 7). Interestingly, both largemouth bass and scup show greater variation in muscle strain from anterior to posterior than observed in trout. While largemouth bass and scup show a three- to fourfold increase in red muscle strain from anterior to posterior during steady swimming, the increase in trout is less than twofold (Fig. 3). The larger range in strain and the particularly low anterior strain of scup and largemouth bass muscle (e.g. <2 % at 0.28L in scup; Coughlin and Rome, 1996) leads to a greater increase in power output from anterior to posterior muscle. Katz et al. (1999) suggested that the strain pattern of scup was atypical and that many fish will have a smaller variation in red muscle strain from anterior to posterior. From this current research, it would seem that largemouth bass are similar in swimming form to scup. In terms of longitudinal patterns of muscle strain during steady swimming, however, trout are similar to milkfish (*Chanos chanos*) (Katz et al., 1999) and pacific mackerel (Shadwick et al., 1998), both of which show relatively modest increases in strain from anterior to posterior. Despite differences in patterns of strain, the posterior red muscle of largemouth bass and trout produces significantly more power than the anterior red muscle during steady swimming.

The results presented here for largemouth bass agree with those of Johnson et al. (1994). Their work found considerable mass-specific power produced by posterior muscle in the largemouth bass. The same result is reported here, along with power output data for more positions. However, the rainbow trout data reported here do not agree with published reports on trout swimming and red muscle function.

Rainbow trout swimming and development

The data for juvenile rainbow trout reported here conflict directly with the conclusions of Hammond et al. (1998) for swimming by adult rainbow trout. Hammond et al. (1998) argued that work per cycle and, therefore, the power output of anterior muscle exceeds that of posterior muscle for swimming at moderate to high steady swimming speeds. They support an argument made by others (e.g. Wardle et al., 1995) that the posterior muscle acts to transmit force from anterior to posterior. Hammond et al. (1998) report that posterior muscle has a greater negative work component during each tailbeat cycle. The relatively high force during lengthening in the posterior muscle occurs during the period of peak force and power output of the anterior muscle. This allows the output of the anterior muscle directly to affect the movement of the tail.

Why do the two studies of *in vivo* rainbow trout muscle function differ? Possible explanations include developmental differences in the fish used in each study and experimental error. Developmental differences in muscle activity and swimming will be dealt with first, while an important

experimental error will be discussed later. Patterns of muscle activation and body curvature during swimming differ between juvenile and adult trout. I argue below that the muscle activation patterns do not vary in a manner that explains the differences in power production, but that differences in body curvature between juvenile and adult trout might contribute to the observed differences.

If the data of Hammond et al. (1998) are transformed into the same units reported here, the duty cycle of muscle activity in adult trout ranges from 0.59 in the anterior to 0.50 in the posterior. These values are considerably higher than the data reported here for juvenile trout (Fig. 3). For instance, at 3.0 L s^{-1} , duty cycle ranges from 0.32 in the anterior to 0.28 in the posterior muscle. Similarly, phase differs between the two age groups. In adult trout, the phase of EMG activity shifted from -0.09 in the anterior to -0.17 in the posterior (Hammond et al., 1998), whereas the juvenile trout data ranged from a phase of -0.15 in the anterior to -0.24 in the posterior.

Variations in the temporal aspects of muscle activation will affect the power production of muscle. However, the differences between the data for adult and juvenile trout do not explain the direction of reported variations in power output. For instance, Hammond et al. (1998) attribute the low power output of posterior red muscle during swimming in trout to the relatively greater phase shift in muscle activation compared with the anterior. They argued that the force in the posterior muscle will peak during lengthening, thus reducing work per cycle and power output. However, the posterior red muscle of juvenile rainbow trout has an even greater phase shift than in adults, and this shift contributes to the relatively greater power output of posterior muscle compared with anterior muscle in juvenile trout. The critical issue is that muscle does not activate instantaneously. The greater phase shift of posterior red muscle allows force production to peak near the onset of shortening so that high force and high instantaneous power output are achieved early in shortening (e.g. posterior muscle, Fig. 5). A phase shift closer to zero means that force does not peak until well into shortening (e.g. anterior muscle, Fig. 5). The variation in duty cycle seems to play a similar role. If the duty cycle of anterior muscle of adult trout is almost 60% of the tailbeat period (Hammond et al., 1998), the anterior muscle will not relax until well after muscle lengthening has begun. The power output of muscle operating under such a stimulation pattern should suffer. That it does not in adult trout is not readily explainable, given the relatively long twitch times of the anterior red muscle of these fish. In smolts, the anterior muscle produces significantly less power under conditions that are so disadvantageous for power production. Understanding the effects of longitudinal variations in activation conditions on power output in adult trout might have been easier if Hammond et al. (1998) had included sample work loops.

The mechanical bending of the body during swimming provides an interesting clue about how juvenile and adult trout might differ in their swimming. Wardle et al. (1995) argue that the wavelength of body curvature during swimming (λ_B) is an indicator of how the red muscle is used for steady swimming.

Low values of λ_B (e.g. $<1.0L$) indicate greater body curvature during swimming and, Wardle et al. (1995) suggest, are associated with fish that use their anterior myotome to power steady swimming. From the data of Williams et al. (1989), Wardle et al. (1995) report a value of λ_B of $0.67L$ for trout. The smolts studied here showed considerably less body curvature during swimming, with values of λ_B of approximately $1.0L$. If smolts swim with a stiffer body than adults, then the contribution of the anterior muscle to powering swimming would be reduced. Less curvature in the anterior means that the contribution of anterior muscle to power output will be limited. The difference between red muscle power output in adult and juvenile trout swimming may stem from this difference in body curvature during swimming.

A developmental change in body curvature during swimming by rainbow trout has previously been reported by Webb et al. (1984), who found that λ_B decreases with growth as $\lambda_B = 1.43L^{0.83}$. From this equation, it follows that small juvenile trout (5 cm) would have λ_B values of approximately $1.1L$, while adults trout (50 cm) would have λ_B values of approximately $0.7L$ (Webb et al., 1984). The range of these values is similar to that described above for juvenile and adult trout (Wardle et al., 1995).

Scup swim with less body curvature than trout, with λ_B values of 1.0 – $1.35L$; λ_B also increases with swimming speed (Swank and Rome, 2000). The higher λ_B of scup correlates with swimming that is powered almost entirely by posterior musculature. In trout smolts, a λ_B of close to $1L$ is associated with swimming powered largely by the posterior myotome, but to which the anterior muscle also contributes. In larger trout, a lower λ_B is potentially associated with swimming powered by the anterior muscle (Hammond et al., 1998).

An important experimental problem with the work of Hammond et al. (1998) is that different-sized fish were used for the swimming and muscle mechanics components of the research. The fish used in the swimming experiments by Hammond et al. (1998) were much larger ($L \approx 42$ cm for swimming experiments; $L \approx 30$ cm for muscle mechanics experiments) than those used in this study ($L \approx 25$ cm for both swimming and mechanics). Since there are developmental variations in red muscle contraction kinetics in rainbow trout (D. J. Coughlin, J. Burdick, K. A. Stauffer and F. E. Weaver, in preparation), differences in size may contribute to variations in muscle function during swimming. As rainbow trout grow, the time needed by red muscle to activate and to relax lengthens (D. J. Coughlin, J. Burdick, K. A. Stauffer and F. E. Weaver, in preparation). Changes in red muscle contraction kinetics should affect muscle function. For instance, juvenile trout that have faster muscle swim steadily with tailbeat frequencies up to 4.0 Hz , while the approximately 42 cm adult trout swim steadily with tailbeat frequencies of 2.7 Hz or less. Also, when muscle activity conditions that limit power output are used for work-loop experiments (e.g. conditions recorded at the anterior position), the faster anterior muscle produces more power than the posterior muscle (Fig. 9).

Since contraction kinetics vary with development in rainbow

trout, it is critical to use the same age and size of fish for both *in vivo* swimming experiments and *in vitro* studies on isolated muscle bundles. If the contraction kinetics of a particular muscle type slow as the fish grows, then the muscle activity conditions collected for a given size of fish must be used to stimulate muscle bundles from the same size of fish to allow for confidence in conclusions about power output. As described above, the power output of muscle bundles under less advantageous activity conditions is affected by the contraction kinetics of the muscle (Fig. 9).

Steady swimming in fishes

The use of the work-loop technique to generate *in vitro* estimates of red muscle power production indicates that mass-specific power output varies along the length of the fish during steady swimming. For most of the few species for which both *in vivo* muscle activity conditions have been described and for which *in vitro* work-loop experiments have been carried out using those conditions, the results indicate that the majority of power is generated by the posterior red muscle during steady swimming, such as in scup (Rome et al., 1993; Coughlin and Rome, 1996; Rome et al., 2000), largemouth bass (Johnson et al., 1994; this study) and rainbow trout (this study). For these species, the model used for white muscle function does not apply to red muscle. For a number of species, Wardle et al. (1995) suggest that the anterior red muscle generates most of the power for steady swimming and that the posterior muscle functions as a stiffened rod to transmit power from the anterior to the posterior. This is not the case for juvenile rainbow trout, for scup and for largemouth bass. However, it may still be appropriate for some species.

The distinct morphology of the deep red muscle of endothermic scombrids may lead to different patterns of red muscle function during swimming from those observed in scup, largemouth bass and rainbow trout. The relatively large blocks of red muscle have long posterior oblique tendons that connect each red myomere to the backbone at a point considerably more posterior than in other fishes. Shortening in the anterior red muscle of scombrids will be communicated *via* a tendon to the posterior body segments (Westneat et al., 1993). If this deep anterior muscle undergoes relatively large length changes, it will result in greater caudal bending and tail movement than in non-scombrids such as scup and trout. For tuna, this means that the anterior muscle may contribute more directly to the movement of the tail and to thrust generation. Experimental evidence supporting this hypothesis has recently been published (Shadwick et al., 1999). In scup, shortening of the superficial red muscle results in local bending (Coughlin et al., 1996a). The same is presumably true for trout and largemouth bass. Force produced in the anterior is not readily transmitted to the posterior. Instead, the local bending propagates posteriorly as a mechanical wave. This wave grows in amplitude from anterior to posterior, ultimately resulting in tail movement and forward thrust. In these fish, the body of course also acts as a thrust-generating surface to various degrees, depending on body shape (for a recent discussion, see

Webb, 1998). The relative roles of anterior and posterior red muscle may also vary with values of λ_B and muscle contraction kinetics.

In conclusion, red muscle function during steady swimming in rainbow trout and largemouth bass was evaluated using *in vitro* work-loop techniques together with *in vivo* muscle activity conditions. For both species, the majority of power for swimming comes from the posterior. However, the ratio of mass-specific power produced by the posterior muscle relative to that produced by the anterior muscle in largemouth bass is greater than that in trout. That is, the variation in power output is more substantial in largemouth bass than in trout.

I thank Bruce Jayne for providing access to largemouth bass red muscle data. I thank Dennis Ricker, Chief (retired), Division of Trout Production of the Pennsylvania Fish and Boat Commission, and Paul Drumm, Manager, and David Jordan of the Huntsdale Fish Culture Station for supplying rainbow trout. I also thank Widener University undergraduate students Jason Mitchell, Shannon McGlinchey, Katherine Saporetto and Karen Stauffer for laboratory assistance. This work was supported by an NSF-RUI Grant (Research at Undergraduate Institutions, IBN-9604140) and by a Provost Grant and Faculty Development Grants from Widener University.

References

- Altringham, J. D. and Johnston, I. A. (1990). Scaling effects on muscle function: power output of isolated fish muscle fibres performing oscillatory work. *J. Exp. Biol.* **151**, 453–467.
- Coughlin, D. J. and Rome, L. C. (1996). The roles of pink and red muscle in powering steady swimming in scup, *Stenotomus chrysops*. *Am. Zool.* **36**, 666–677.
- Coughlin, D. J., Valdes, L. and Rome, L. C. (1996a). Muscle length changes during swimming in scup: sonomicrometry verifies the anatomical high-speed cine technique. *J. Exp. Biol.* **199**, 459–463.
- Coughlin, D. J., Zhang, G. and Rome, L. C. (1996b). Contraction dynamics and power production of pink muscle of scup (*Stenotomus chrysops*). *J. Exp. Biol.* **199**, 2703–2712.
- Hammond, L., Altringham, J. D. and Wardle, C. S. (1998). Myotomal slow muscle function of rainbow trout *Oncorhynchus mykiss* during steady swimming. *J. Exp. Biol.* **201**, 1659–1671.
- Jayne, B. C. and Lauder, G. V. (1995). Red muscle motor patterns during steady swimming in largemouth bass: effects of speed and correlation with axial kinematics. *J. Exp. Biol.* **198**, 657–670.
- Johnson, T. P., Syme, D. A., Jayne, B. C., Lauder, G. V. and Bennett, A. F. (1994). Modeling red muscle power output during steady and unsteady swimming in largemouth bass. *Am. J. Physiol.* **267**, R481–R488.
- Josephson, R. K. (1985). Mechanical power output from striated muscle during cyclical contraction. *J. Exp. Biol.* **114**, 493–512.
- Katz, S. L., Shadwick, R. E. and Rapoport, H. S. (1999). Muscle strain histories in swimming milkfish in steady and sprinting gaits. *J. Exp. Biol.* **202**, 529–541.
- Nelson, J. S. (1994). *Fishes of the World*; third edition. New York: John Wiley & Sons.
- Rome, L. C. and Swank, D. (1992). The influence of temperature on

- power output of scup red muscle during cyclical length changes. *J. Exp. Biol.* **171**, 261–281.
- Rome, L. C., Swank, D. and Corda, D.** (1993). How fish power swimming. *Science* **261**, 340–343.
- Rome, L. C., Swank, D. M. and Coughlin, D. C.** (2000). The influence of temperature on power production during swimming. II. Mechanics of red muscle fibers *in vivo*. *J. Exp. Biol.* **203**, 333–345.
- Shadwick, R. E., Katz, S. L., Korsmeyer, K. E., Knower, T. and Covell, J. W.** (1999). Muscle dynamics in skipjack tuna: timing of red muscle shortening in relation to activation and body curvature during steady swimming. *J. Exp. Biol.* **202**, 2139–2150.
- Shadwick, R. E., Steffensen, J. F., Katz, S. L. and Knower, T.** (1998). Muscle dynamics in fish during steady swimming. *Am. Zool.* **38**, 755–770.
- Swank, D. M. and Rome, L. C.** (2000). The influence of temperature on power production during swimming. I. *In vivo* length change and stimulation patterns. *J. Exp. Biol.* **203**, 321–331.
- van Leeuwen, J. L.** (1995). The action of muscles in swimming fish. *Exp. Physiol.* **80**, 177–191.
- van Leeuwen, J. L., Lankheet, M. J. M., Akster, H. A. and Osse, J. W. M.** (1990). Function of red axial muscles of carp (*Cyprinus carpio*): recruitment and normalized power output during swimming in different modes. *J. Zool., Lond.* **220**, 123–145.
- Wardle, C. S. and Videler, J. J.** (1993). The timing of the electromyogram in the lateral myotomes of mackerel and saithe at different swimming speeds. *J. Fish Biol.* **43**, 347–359.
- Wardle, C. S., Videler, J. J. and Altringham, J. D.** (1995). Tuning in to fish swimming waves: body form, swimming mode and muscle function. *J. Exp. Biol.* **198**, 1629–1636.
- Webb, P. W.** (1998). Swimming. In *The Physiology of Fishes*; second edition (ed. D. H. Evans), pp. 3–24. New York: CRC Press.
- Webb, P. W., Kostecki, P. T. and Stevens, E. D.** (1984). The effects of size and swimming speed on locomotor kinematics of rainbow trout. *J. Exp. Biol.* **109**, 77–95.
- Westneat, M. W., Hoese, W., Pell, C. A. and Wainwright, S. A.** (1993). The horizontal septum: mechanisms of force transfer in locomotion of scombrid fishes (Scombridae: Perciformes). *J. Morph.* **217**, 193–204.
- Williams, T. L., Grillner, S., Smoljaninov, V. V., Wallen, P., Kashin, S. and Rossignol, S.** (1989). Locomotion in lamprey and trout: relative timing of activation and movement. *J. Exp. Biol.* **143**, 559–566.
- Zhang, G., Swank, D. M. and Rome, L. C.** (1996). Quantitative distribution of muscle fiber types in the scup. *J. Morph.* **229**, 71–81.