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FISH SWIMMING: PATTERNS IN MUSCLE FUNCTION

JOHN D. ALTRINGHAM* AND DAVID J. ELLERBY
School of Biology, University of Leeds, Leeds LS2 9JT, UK
*e-mail: j.d.altringham@leeds.ac.uk

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Summary

Undulatory swimming in fish is powered by the segmental body musculature of the myotomes. Power generated by this muscle and the interactions between the fish and the water generate a backward-travelling wave of lateral displacement of the body and caudal fin. The body and tail push against the water, generating forward thrust. The muscle activation and strain patterns that underlie body bending and thrust generation have been described for a number of species and show considerable variation. This suggests that muscle function may also vary among species. This variation must be due in large part to the complex interactions between muscle mechanical properties, fish body form, swimming mode, swimming speed and phylogenetic relationships. Recent work in several laboratories has been directed at studying patterns of muscle power output *in vitro* under simulated swimming conditions. This work suggests that the way that fish generate muscle power and convert it into thrust through the body and caudal fin does indeed vary. However, despite the differences, several features appear to be common to virtually all species studied and suggest where future effort should be directed if muscle function in swimming fish is to be better understood.

Key words: fish, kinematics, muscle, swimming.

Introduction

Fish swim using undulatory movements of their body and/or their paired and unpaired fins. In undulatory swimming, a backward-travelling wave of bending is generated by the sequential activation of the segmental myotomes from head to tail. As the body bends, and the bends travel down the fish, the body and caudal fin push against the water, generating forward thrust. The relationship between the timing of muscle activation and the muscle strain cycle that underlies body bending varies significantly amongst species studied. The way in which muscle is being used to generate thrust may therefore vary along the fish and among species (for reviews, see Wardle et al., 1995; Gillis, 1998; Katz et al., 1999). Exploring and understanding this variation requires a knowledge of muscle mechanical properties, fish body form, swimming mode, swimming speed and phylogenetic relationships and of the complex interactions between them. *In vitro* patterns of muscle power output, under simulated swimming conditions, have been determined for several fish species (e.g. Altringham et al., 1993; Rome et al., 1993; Johnson et al., 1994; Hammond et al., 1998). The most obvious conclusion is that different species use their myotomal muscle to generate thrust in subtly different ways. However, several features are common to most species, and future work may reveal patterns that will lead to a more integrated view of fish swimming. This paper summarises current understanding of how fish use their lateral muscle during steady swimming, highlighting areas of consensus and of confusion, and key areas for future research.

Swimming muscle anatomy and physiology

The body musculature of fish is arranged into segmental myotomes which have a complex three-dimensional structure (for a review, see Videler, 1993). The myotomes form stacked cones in which the muscle fibres follow complex helical trajectories from one myotome to the next along the fish (Fig. 1). Fibres are oriented at angles of up to 40° to the longitudinal axis of the fish. Alexander (1969) described two patterns in some detail, one in selachians and primitive teleosts, the other in higher teleosts. Alexander's modelling led him to suggest that this complex arrangement enabled all fibres across the body section to undergo similar strains during body bending: the arrangement could therefore be seen as a gearing system. More recent modelling by van Leeuwen (1999) provides new insights into this complex structure.

The muscle can be divided into two principal types, fast-twitch or white muscle, and slow-twitch or red muscle. Some species have a distinctive intermediate layer of pink muscle (Johnston, 1981) and, on a histological and sometimes a physiological basis, several other types have been identified (e.g. Bone, 1978; Johnston, 1981). Fast muscle makes up the bulk of the fish, typically 80–100% of the fish cross section at a given point. The proportion of slow muscle is related to the ecology of the fish: constantly swimming pelagic species have more slow muscle than benthic species (Boddeke et al., 1959; Videler, 1993). The slow muscle is usually confined to a zone beneath the lateral line (Fig. 2), making up an increasing proportion of the body cross-section towards the tail (Videler, 1993).

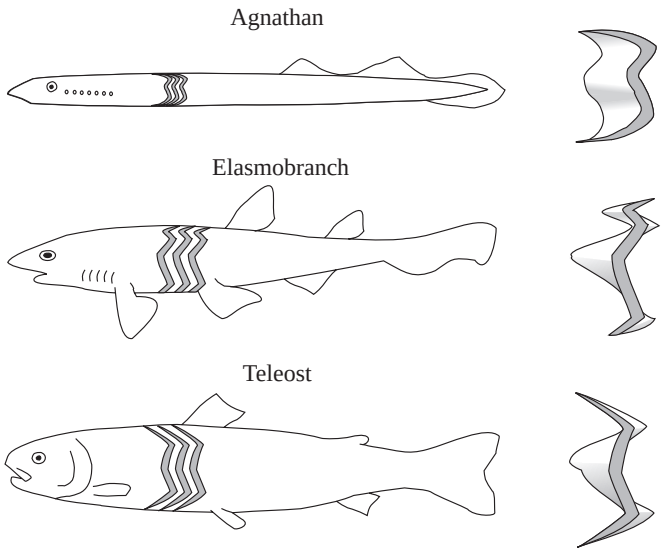

Fig. 1. Myotomal structure of the lateral muscle. Isolated myotomes are shown to the right of the fish.

However, some species have different distributions of slow muscle, the functional significance of which is often not known.

In recent years, it has become increasingly evident that these two muscle types are not homogeneous. A longitudinal slowing of twitch kinetics from anterior to posterior has been observed in most (but not all: see Johnston at al., 1993; Hammond et al., 1998) species studied (e.g. Wardle et al., 1989; Altringham et al., 1993; Davies and Johnston, 1993; Davies et al., 1995; Rome et al., 1993; Altringham and Block, 1997). For example, there is a twofold increase in fast and slow muscle twitch contraction times along the length of the smooth hound shark *Mustelus californicus* (Fig. 3). Twitch contraction time decreases with increasing depth in the large internal mass of slow muscle in the yellowfin tuna (Altringham and Block, 1997).

Muscle activation patterns during swimming

Electromyography (EMG) is routinely used to monitor when muscle is active. Slow swimming is powered by the slow muscle. This makes sense, since the mechanical properties of slow muscle are too slow to generate useful work at high tailbeat frequencies (Rome et al., 1988; Altringham and Johnston, 1990a). In all fish studied, slow steady swimming is characterised by activation of the musculature on alternate sides of the body (for a review, see Videler, 1993). Anterior muscle is activated first, and a wave of activation travels from head to tail. The wave of deactivation typically travels more rapidly, so that anterior muscle is active for longer (Figs 4, 5) (Videler, 1993; Wardle et al., 1995; Gillis, 1998). As swimming speed and tailbeat frequency increase, deeper faster fibres are recruited (e.g. Bone et al., 1978; Johnston and Moon, 1980). These show similar patterns of activation, with a backward-travelling wave of activation and a longer activation period in anterior myotomes (Wardle and Videler, 1993; D. J. Ellerby and J. D. Altringham, in preparation).

Body kinematics during swimming

Muscle activity, the arrangement and properties of skeletal and other passive elements, and the interaction between the fish and the reactive forces of the water all combine to cause a wave of body curvature which passes down the fish (for a review, see Videler, 1993). The amplitude of this wave increases as it travels down the body to a maximum of approximately 10 % of body length. The number of waves on the body at a given time varies between approximately 0.7 and 1.7 in different species (Videler, 1993; Wardle et al., 1995). It is this backward-travelling wave of curvature that must push against the water to generate thrust. Since the water yields as the fish pushes against it, the wave must travel backwards faster (v=wave speed) than the fish swims forwards (u=fish swimming speed). Increases in swimming speed are due primarily to increases in tailbeat frequency. This means that data obtained at different swimming speeds can often be compared by normalising them to tailbeat period (e.g. Wardle and Videler, 1993). Stride length, the distance moved in one tail beat, is typically approximately 0.9 body lengths, but varies from 0.5 to 1 body lengths between species. When forward swimming speed is equal to backward wave speed, u/v=1 and there is said to be no slip. Some slippage usually occurs, so u/v is less than 1 and increases as stride length increases (Videler, 1993) and there is less slip.

Putting the pieces together: the relationship between strain and EMG cycles and patterns of muscle power output

Swimming movements resulting from muscle contraction and body kinematics reflect the underlying muscle strains although, as we will see, body curvature and underlying muscle strain may not always be in phase. When muscle is activated, it can develop force and shorten, hence performing work. However, active muscle can also lengthen when work is done

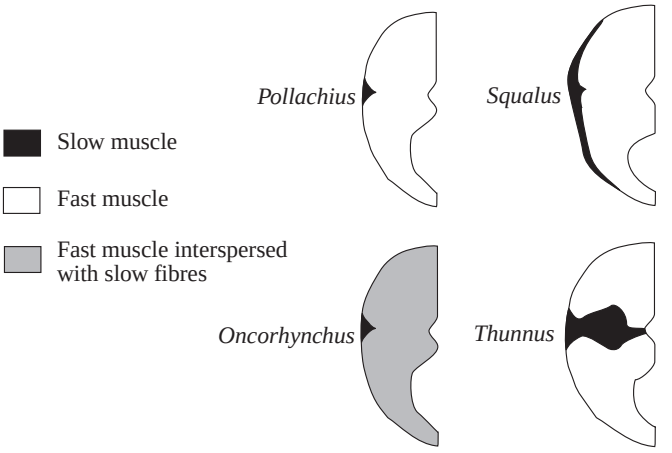

Fig. 2. Diagrammatic transverse sections to show the distribution of slow-twitch (red) and fast-twitch (white) muscle. Cross sections were taken at approximately 0.35 body lengths from the snout. Intermediate pink fibres are omitted because of their comparatively small cross-sectional area.

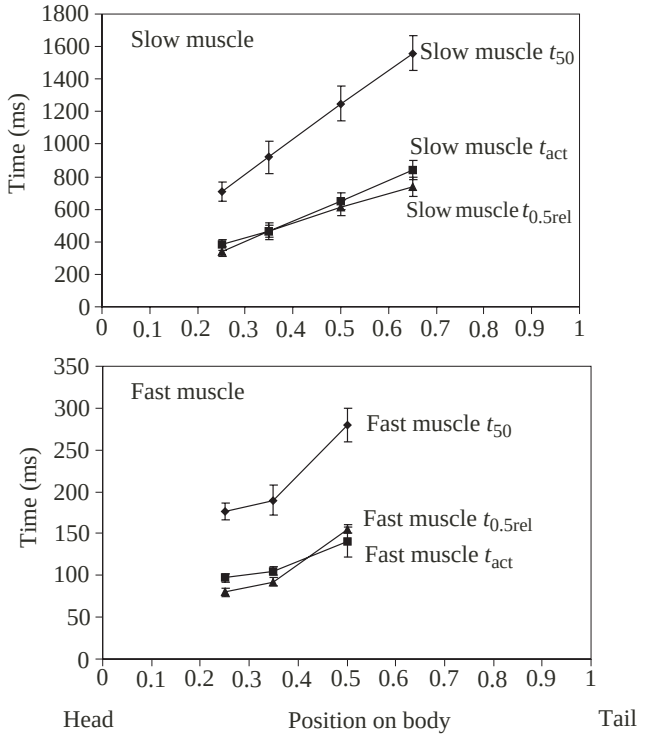

Fig. 3. Twitch contraction times along the length of the smooth hound shark *Mustelus californicus*. t_{act}, time to peak force (■); $t_{0.5rel}$, time from stimulus to 50 % relaxation (▲); $t_{50}=t_{act}+t_{0.5rel}$ (◆). All values are means ± S.E.M. (N=4–6) (J. D. Altringham, H. Dewer and B. A. Block, unpublished data).

against it by antagonistic muscles, passive skeletal elements or external forces in the surrounding water. The role played by muscle in powering swimming is not a simple one. The power generated by muscle along most of the length of the fish must be transmitted to the water largely or entirely in the region of the tail (Videler, 1993; Wardle et al., 1995). To understand how this is happening, we need to follow the time course of muscle strain and force during swimming, since work is force times distance moved, and power is work per unit time. Strain can be calculated from body kinematics (e.g. Hess and Videler, 1984; Rome et al., 1993; Katz and Shadwick, 1998), from X-ray videography (Shadwick et al., 1998) or by direct measurement using sonomicrometry (e.g. Hammond et al., 1998; Wakeling and Johnston, 1999).

Force is more difficult to measure *in vivo*, particularly in the muscle of fish, which has no solid structures on which to anchor force transducers. However, if muscle activation patterns are known from EMG studies, *in vivo* patterns of force generation can be approximated *in vitro* by imposing *in vivo* strain and EMG cycles on isolated fibres. The force generated by a given muscle fibre at any time during a tailbeat cycle is a function of its level of activation, its length, its strain velocity and its recent strain history (see Josephson, 1999). Once we know the strain and force patterns during swimming, we can determine how much power is produced at different locations in a swimming fish and examine the temporal patterns in power production along the fish. For steady swimming, this has been achieved for only three species: saithe *Pollachius virens* (fast muscle, Altringham et al., 1993), scup *Stenotomus chrysops* (slow muscle, Rome et al., 1993) and rainbow trout *Oncorhynchus mykiss* (slow muscle, Hammond et al., 1998). Experiments have also been performed on largemouth bass *Micropterus salmoides* (slow muscle, Johnson et al., 1994), but limited *in vitro* experiments were conducted on muscle fibres from only one location. Many other studies have described swimming kinematics and/or EMG patterns.

Emerging trends

What patterns are emerging? EMG studies reveal one significant trend. Although the duration of muscle activity decreases towards the tail in all species studied, the trend is marked only in those species that swim with a long propulsive wavelength (Figs 4, 5) (Gillis, 1998). These are fish with a pronounced caudal fin, which generates most of the thrust. Anterior muscle is active for a large part of the locomotory cycle so, despite the decrease in EMG duration towards the tail, a large part of the muscle down one side of the fish is simultaneously active for part of the cycle. This is consistent with the bending of most of the body in one direction to produce the long propulsive wavelength. Eel and lamprey, which swim with a propulsive wavelength of significantly less than 1 body length, have relatively short anterior activation durations and show little or no decrease in burst duration towards the tail (Williams et al., 1989; Wardle et al., 1995). As this short activation burst travels down the fish, different regions of the body can be bent in opposing directions, hence the short propulsive wavelength.

Most species studied exhibit another common feature. EMG onset occurs earlier in the strain cycle in more posterior myotomes, in both slow and fast muscle (Figs 4, 5). Katz and Shadwick (1998) have shown that errors in kinematic analysis may have led to systematic errors in some studies. This may indeed be a factor, but the trend has been observed in many species, using a range of kinematic and direct measurement techniques (for a review, see Gillis, 1998; see also Hammond et al., 1998; D. J. Ellerby and J. D. Altringham, in preparation) and is probably a robust observation. Recent studies of the skipjack tuna *Katsuwonus pelamis* (Shadwick et al., 1999) provide an exception: the phase of EMG onset relative to shortening (determined by sonomicrometry) in the deep slow muscle barely changed along the body.

The phase relationship between strain and activation cycles determines how the muscle functions during swimming and the power it produces. Put simply, muscle active during shortening performs positive work, and muscle active during lengthening performs negative work, i.e. work must be done on the muscle to lengthen it. The majority of studies show that the muscle strain waveform during steady swimming approximates a sine wave. Phase can therefore be described in degrees, with a tailbeat cycle occupying 360 °, and the start of the cycle (0 °) assigned to the point when the muscle is lengthening through its mean length (Altringham and Johnston, 1990a). In all

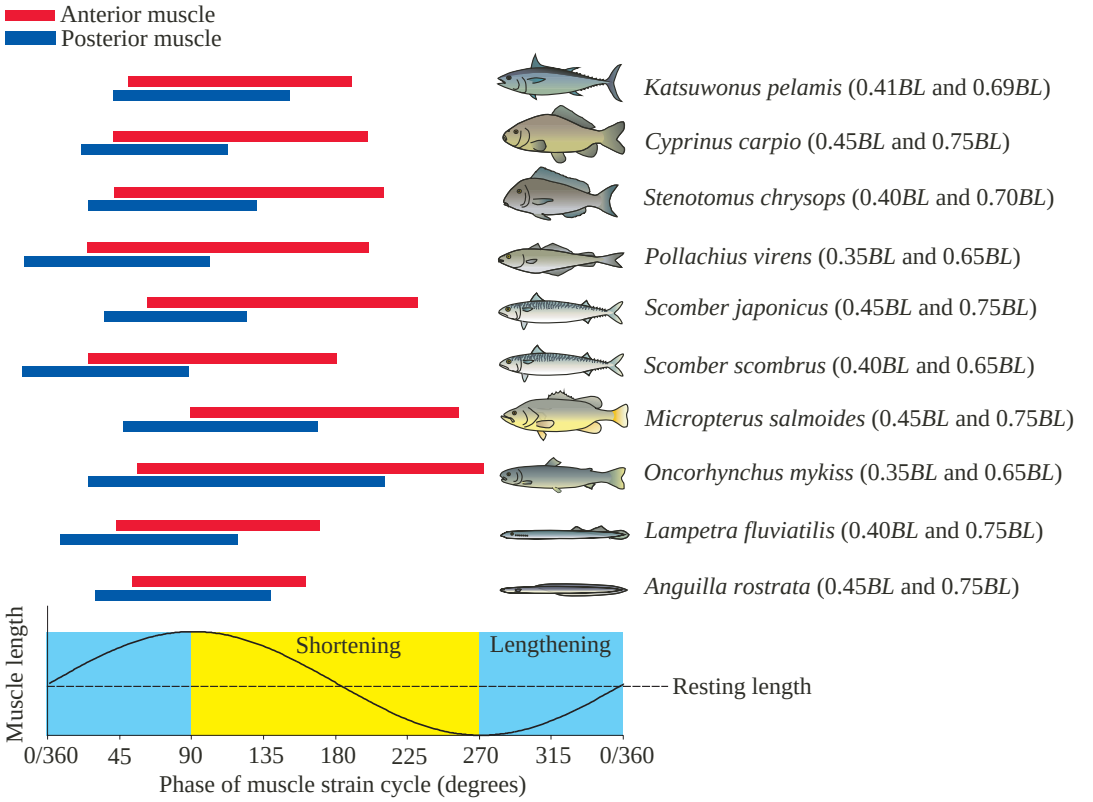

Fig. 4. Activation of anterior and posterior slow muscle in a range of fish taxa. Activation is shown relative to the muscle strain cycle. The position on each species from which data were recorded is expressed as a proportion of the body length (*BL*) from the snout. There is a general decrease in propulsive wavelength down the list of species. Electromyographic timing data are derived from Knower et al. (1999) (*Katsuwonus pelamis*), van Leeuwen et al. (1990) (*Cyprinus carpio*), Rome et al. (1993) (*Stenotomus chrysops*), Hammond (1996) (*Pollachius virens*), Shadwick et al. (1998) (*Scomber japonicus*), Wardle and Videler (1993) (*Scomber scombrus*), Jayne and Lauder (1995) (*Micropterus salmoides*), Hammond et al. (1998) (*Oncorhychus mykiss*), Williams et al. (1989) (*Lampetra fluviatilis*) and Gillis (1998) (*Anguilla rostrata*).

species studied to date, anterior muscle is activated late in the lengthening phase (0–90 °) and before the onset of shortening (90 °). These results are summarised in Figs 4 and 5. The onset of muscle activity in anterior myotomes is typically at approximately 45 °, and the muscle receives a small stretch when active prior to shortening. This stretch can increase force and power production during the subsequent shortening phase (e.g. Altringham and Johnston, 1990b). Muscle activity ends during shortening (approximately 180–250 °), and force falls rapidly during shortening. The rapid onset of shortening enables the muscle to operate at frequencies above those predicted from isometric twitch kinetics (Altringham and Johnston, 1990b). Lou et al. (1999) have shown that this shortening during the post-stimulation decline of force leads to maximum recovery of work stored in the muscle series elastic component. This will increase power output independently of power enhancement by stretch.

Muscle operating under these conditions has been shown to produce maximum net power output (e.g. Altringham and Johnston, 1990a,b; Altringham et al., 1993; Hammond et al., 1998). Power output may be negative for a small part of the tailbeat cycle, but is large and positive for most of it in anterior

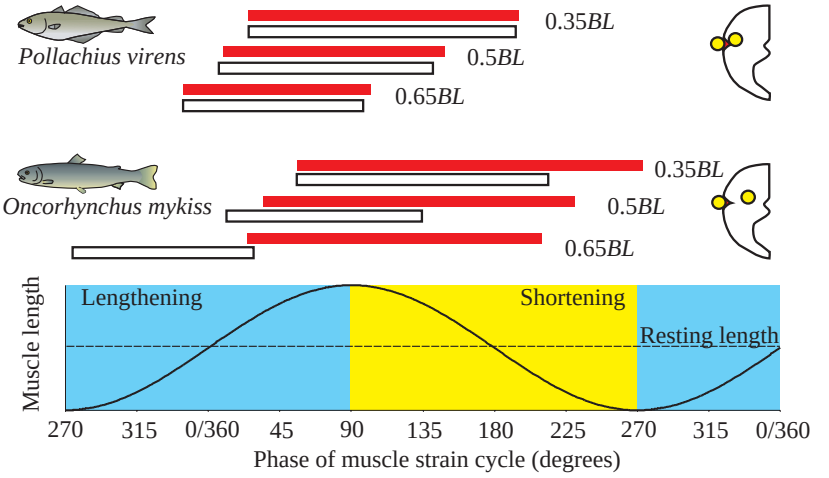

Fig. 5. Relative timing of activation in slow (red bars) and fast (white bars) muscle. Data were recorded at points 0.35, 0.5 and 0.65 body lengths (*BL*) from the snout. Cross sections shown to the right of the bars show the depth of the sampling points in the lateral muscle. Electromyographic timing data were derived from Hammond (1996) (*Pollachius virens*), Hammond et al. (1998) (*Oncorhynchus mykiss* slow muscle) and D. J. Ellerby and J. D. Altringham (in preparation) (*Oncorhynchus mykiss* fast muscle).

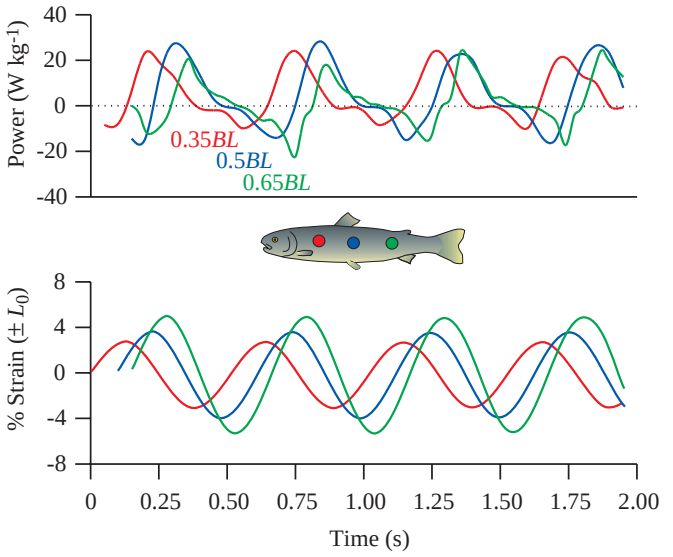

Fig. 6. Instantaneous power output of slow muscle and corresponding strain recordings over three oscillatory cycles at a tailbeat frequency of 2 Hz. Recordings are from preparations of *Oncorhynchus mykiss* at three body positions 0.35, 0.5 and 0.65 body lengths (*BL*) from the snout. L_0 is muscle length when the body of the fish is straight (Hammond et al., 1998).

myotomes (Fig. 6). As stated in the previous paragraph, there is a variable but consistent trend towards earlier activation in the strain cycle in the more posterior myotomes of most fish. Earlier activation means that the negative power component of the tailbeat cycle probably increases along the body towards the tail (Fig. 6). Altringham et al. (1993) were able to show in saithe that peak power output in the fast muscle of anterior myotomes was coincident with peak forces in the actively stretched posterior myotomes and with the production of maximum thrust (Cheng et al., 1998). Modelling studies on carp (van Leeuwen et al., 1990; van Leeuwen, 1995) yielded similar conclusions. Two functions have been suggested for negative work production by posterior myotomes. This muscle may, for part of the tailbeat cycle, be stiffened to assist passive tissues in the transfer of power to the tail (van Leeuwen et al., 1990; Altringham et al., 1993). Long (1998) has suggested that the fish may be tuning body stiffness so that the resonant frequency of the body matches the tailbeat frequency. If tailbeat frequency approaches the natural resonant frequency of the body, the mechanical cost of movement should be minimised. These two functions are not mutually exclusive and may vary in significance among species. It should be stressed that, in all studies which have included *in vitro* experiments on muscle under simulated swimming conditions (saithe fast muscle, Altringham et al., 1993; scup slow muscle, Rome et al., 1993; trout slow muscle, Hammond et al., 1998), net power output was positive at all locations along the body. It is not simply a question of whether posterior muscle is a power producer or transmitter, as is sometimes stated in the literature. Muscle can perform several tasks sequentially or simultaneously. The division of labour can only be determined with any certainty by using the combined *in vivo*/*in vitro* approach described above, since swimming studies alone lack the essential muscle kinetic data.

Identifying the major source of swimming power is complicated by several factors. Muscle strain typically increases from ±2 % to ±8 % in the central 40–50 % of the body length during steady swimming (e.g. Hess and Videler, 1984; Rome et al., 1993; Hammond et al., 1998; Shadwick et al., 1999). Absolute muscle power output along the body will be determined by strain, the volume of active muscle, the phase relationship between strain and EMG activity and muscle contraction kinetics. The region of the fish producing most of the power for swimming will also depend upon swimming speed. Given the greater strain during swimming in posterior myotomes, it is not surprising that posterior muscle produces more power than anterior muscle in slowly swimming scup (Rome et al., 1993). This does not mean that slow muscle does not undergo some subtle change in function along the length of the body: Wardle et al. (1995) showed that, even in the scup, there is a significant negative power phase. The change in phase between strain and EMG cycles and the slowing of contraction kinetics down the body, in most species studied, is likely to have some functional significance. Just why contraction kinetics slow down is not known: a testable hypothesis is a major priority.

Fast muscle mass decreases dramatically in the caudal region because of the necessary streamlined shape of the fish. During fast swimming, the bulk of the fast muscle may be active (e.g. Johnston et al., 1977), and anterior muscle must be a major power source (Altringham et al., 1993). Much of this power will be transferred to the caudal fin through the skeleton, the myosepta and even the skin, but Cheng et al. (1998) calculated that muscle in the caudal region must sustain stresses up to twice those in anterior myotomes. Muscle stretched when active can indeed sustain stresses almost twice as great as maximum isometric stress (e.g. Edman et al., 1978), and a power transmission mechanism for muscle seems likely under these circumstances. Spierts et al. (1996) found a higher interfacial ratio (area of junctional sarcolemma/fibre cross-sectional area) for myotendinous junctions of posterior relative to anterior muscle fibres in the carp, suggesting an adaptation for higher stresses in the caudal region. Wakeling and Johnston (1999) showed that, despite an increase in the amplitude of spine curvature during fast starts of carp *Cyprinus carpio*, slow and fast muscle strain decreased as a result of a decrease in the width of the fish and a change in the gearing ratio in fast muscle along the body (see also van Leeuwen et al., 1990). The decreased strain and strain rate would facilitate high force generation (at the cost of lower power output), and they suggested that the gearing change predisposed the fast muscle to its changing function along the body. Even the most caudally placed fast muscle studied by Altringham et al. (1993) spent more than half of the tailbeat cycle generating positive power, and net power output was positive: muscle at this location still has a major power-producing role.

It can be argued (Katz and Shadwick, 1998) that tendon

would be better at transmitting power than active muscle, and this is indeed the case: muscle used in this way will be inefficient. However, most fish spend only a fraction of their time swimming under the conditions studied – that of constant-speed, straight-line motion. When turning or changing speed, muscle activation patterns are very different, and manoeuvrability requires muscle not tendon. Tuna are known to have replaced muscle in the caudal region with tendon, presumably as a more effective and energy-efficient mechanism of power transfer during steady swimming, but tuna are not very manoeuvrable. Tuna appear to be different in a number of ways. Another of their many adaptations as efficient high-speed cruisers is the presence of a large internal slow muscle mass between the lateral line and the vertebral column (Fig. 2). Countercurrent heat exchangers maintain elevated temperatures in this muscle, increasing power output (Altringham and Block, 1997). Recent work by Shadwick et al. (1999) shows that this mid-body muscle has near-synchronous onset of activation along the body, there is no significant phase change between strain and EMG cycles. The phase is presumed to be optimal for maximising power output on the basis of *in vitro* tuna muscle studies (Altringham and Block, 1997). Activation and shortening of this muscle appear to lead to local bending at more posterior locations, directing power towards the caudal fin, consistent with the view that tuna produce virtually all of their thrust at the tail blade. These forces may be transmitted by the unique posterior tendon arrangement described in tuna (e.g. Westneat et al., 1993).

The observation that muscle strain changes deep in the fish may not be in phase with local curvature (Shadwick et al., 1999) is an important one, both experimentally and functionally. Fast muscle strain can show significant regional variation (e.g. Wakeling and Johnston, 1999), which prompts caution in interpreting results from limited sampling sites, but also raises intriguing questions about its function. Fast muscle activity is highly dependent upon swimming speed. Jayne and Lauder (1995) have shown that activation in the largemouth bass is *via* sequential activation of myotomes, which span several vertebrae, rather than by simultaneous activation of tissue at one longitudinal location, for example that spanning a single vertebra. The extreme dorsal and ventral projections of the myotomes appeared to be activated only during the most extreme movements, suggesting a division of labour between different parts of the myotome. Differences in muscle properties with depth are probably significant but, as yet, they have been studied only in the atypical deep slow muscle of the yellowfin tuna (Altringham and Block, 1997). Consistent with the general pattern of recruitment of deeper fibres at higher swimming speeds, twitch contraction times decrease with depth.

Conclusions

All, or nearly all, muscle generates some power during swimming. This power is generated sequentially from anterior to posterior myotomes. In species that generate thrust at the tail blade, power must be transmitted towards the tail, and posterior muscle may have a role together with passive structures in power transmission. Posterior muscle may also serve to stiffen the body. These roles may vary in significance among species, but the change in phase between the EMG and strain cycles, and in muscle contraction kinetics, suggests some change in muscle function along the body. As yet, this is poorly understood. Variation among species clearly exists, and fish with novel muscle systems such as tuna may have novel solutions to the problem.

Fast muscle function is less well understood. It shares many of the features of slow muscle, notably a change in phase between the EMG and strain cycles, and in muscle contraction kinetics. The decreased muscle mass towards the tail places the power source for fast swimming far anterior to the tail, and a power-transmitting role for posterior fast muscle seems likely.

There is an abundance of published data, but comparison is often difficult. Few studies incorporate all the essential components, techniques and methods. Study species, sampling locations and experimental conditions vary too much to draw safe conclusions. A better understanding of muscle function will require a systematic study of strain and EMG patterns at several known locations in identified myotomes, at several locations along the length of the fish and at a range of swimming speeds. This will need to be followed up by *in vitro* studies of muscle function simulating *in vivo* conditions. Ideally, these experiments will be carried out in closely related species, but with different body forms and swimming modes.

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