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New Data on Axial Locomotion in Fishes: How Speed Affects Diversity of Kinematics and Motor Patterns[1]

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SYNOPSIS. Despite considerable recent progress in understanding the function of the axial muscles and skeleton in fishes, generalizing from these results has been hindered by the great phylogenetic diversity of taxa, the lack of quantitative morphometric data on axial musculoskeletal structure, and limited analysis of the full range of locomotor behaviors exhibited within any one taxon. This paper reviews novel results from our studies of two taxa within a single monophyletic clade, the sunfish family Centrarchidae. Integrated analyses of lateral displacement, lateral bending, and axial muscle activity reveal widespread effects of swimming speed both within a particular mode of swimming and among different behavioral modes. The longitudinal position along the body of the fish also commonly affects kinematics, muscle activity and the timing of electromyograms (EMGs) relative to kinematics. EMGs and kinematic events propagate from head to tail for both steady and kick and glide swimming. In contrast, during the escape response, the onset of EMGs forms a standing wave pattern, whereas kinematic events are propagated. Several novel features of the axial motor pattern are summarized for the kick and glide mode of unsteady swimming. For example, the onset of white fiber EMGs lags significantly behind that of the red fibers at the same longitudinal position, and red fibers are inactivated at higher unsteady swimming speeds. Muscle activity propagates posteriorly via the sequential activation of myomeres, but there are statistically significant differences in the timing of EMGs from the contractile tissue opposite a single vertebra. During relatively slow kick and glide swimming, the extreme dorsal and ventral portions of myomeres are not active. Estimates of the longitudinal extent of the fish with simultaneous muscle activity indicate that EMGs from an individual myomere usually have temporal overlap with more than 20 neighboring myomeres on the same side of the fish. Consequently, the functional units for axial locomotion of fishes do not correspond simply to the anatomical units of individual myomeres. Rather the *in vivo* motor pattern is a primary determinant of the functional units involved in swimming.

INTRODUCTION

The body plan of all vertebrates includes a segmented architecture of the axial skeleton, muscle and nerves and the segmental pattern of the axial muscles is probably best exemplified by the myotomes of fishes. For generalized fishes, lateral undulation of the axial structures is the primary means of generating propulsive forces over a wide range of swimming speeds. Thus, a central issue for understanding the locomotion of fishes is how movements and muscle activ-

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ity are coordinated among these serially homologous axial structures.

Blight (1977) emphasized that the waveform of undulating swimmers was a complex result of: 1) the mechanical properties of the body, 2) the resistance of the fluid to movement, and 3) the pattern of muscle activity. Furthermore, the interactions between these three factors may be so complex that one might observe such unexpected results as longitudinal propagation of kinematics events resulting from a standing wave pattern of muscle activation (Blight, 1977). Consequently, it is important to relate movements to muscle activity for a diversity of undulatory swimmers over a wide range of swimming speeds in order to determine generalities of the underlying mechanisms of swimming. Previous electromyographic studies have measured *in vivo* axial muscle activity during steady undulatory swimming of such diverse fishes as lampreys, sharks, eels, trout, carp, and scup (Williams *et al.,* 1989; Bone, 1966; Grillner and Kashin, 1976; Van Leeuwen *et al.,* 1990; Rome *et al.,* 1993).

Recent reviews of this literature (*e.g.,* Wardle *et al.,* 1995) have attempted to synthesize these results and propose a general model that is consistent with current data. However, the utility of such a synthesis is compromised by a number of factors. First, the tremendous phylogenetic diversity and consequent highly variable body shape and numbers of axial segments across taxa greatly limits our ability to compare taxa that share common underlying morphological traits. Hence, differences observed in locomotor kinematics between any pair of taxa may be due to any one of a large number of underlying morphological differences. Second, for most previously studied taxa, there are only poor data on the structure of relevant underlying axial components. Thus, we lack quantitative data for the taxa mentioned above on myomere structure, its relationship to the underlying axial skeleton, and on longitudinal changes in axial structures such as ribs and haemal and neural arches. Consequently, nearly all kinematic analyses of locomotion discuss bending of the body in isolation from skeletal morphology, and treat the axial skeleton as though it were homogeneous along its length. Third, experimental analyses, with a few important exceptions (*e.g.,* Williams *et al.,* 1989; Van Leeuwen *et al.,* 1990), have generally analyzed relatively few sites along the body. Kinematic data are often summarized by measuring movement of the tail tip in ventral view, while electromyographic data are frequently obtained from only two or three locations along the body. As a result, we know very little about recruitment patterns of white fibers in relation to the better studied red locomotor muscle, and even less about the function of white fibers in different locations within a myomere. Fourth, few studies have investigated the diversity of locomotor behaviors exhibited by fishes over a wide speed range: from slower speed steady undulatory locomotion through burst and glide swimming at higher speeds to the rapid escape response involving the greatest movement velocities. The analysis of behavioral diversity is of particular importance because generalizations of muscle function that are sound for one mode, such as steady undulatory locomotion, may be inappropriate for a different mode such as burst and glide swimming.

Over the past several years, we have attempted to address the issues raised above by analyzing a wide diversity of locomotor behaviors in taxa within the endemic North American sunfish Family Centrarchidae (Gibb *et al.,* 1994; Jayne and Lauder 1993, 1994*a, b,* 1995*a, b, c*; Jayne *et al.,* 1996; Johnson *et al.,* 1994; Lauder and Jayne, 1996). The centrarchids are a well-defined monophyletic group of perciform teleost fishes with considerable interspecific variation in external shape but only slight variation in the numbers of vertebrae (Lauder and Liem, 1983; Mabee, 1993; Scott and Crossman, 1973). We have focused our comparative analyses on two taxa: the largemouth bass, *Micropterus salmoides,* which has a generalized body shape, and the bluegill sunfish, *Lepomis macrochirus,* which has a deep-bodied shape characteristic of many maneuvering specialists.

In this paper we provide an overview of several novel findings that have resulted from our studies of these two closely relat-

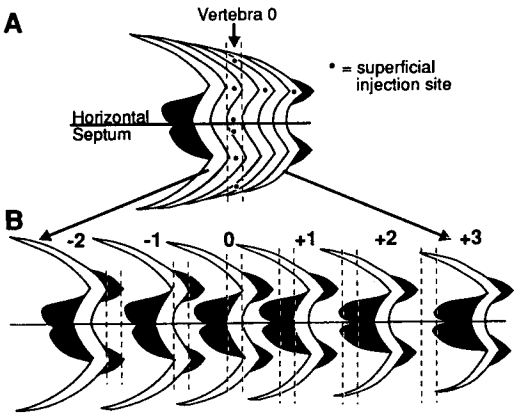

FIG. 1. Left lateral view (anterior to left) of the myomeres of *Micropterus salmoides* in the region used to study activity of white myomeric muscle during kick and glide swimming. White areas are the most superficial surfaces of the myomeres which are visible after removing only the skin. Black regions indicate medially projecting parts of the myomere that overlap longitudinally with adjacent myomeric muscle segments. (A). Dots indicate the superficial positions used to inject EMG electrodes. Note that the myomere containing an electrode is highly dependent on both the depth and dorso-ventral position of the electrode. (B). An exploded view of the myomeres shown in A with vertical dashed lines indicating the location of a single reference vertebra. Numbers above myomeres indicate the segmental location of each myomere relative to reference vertebra 0. By using the dashed vertical lines to align the myomeres, one can reconstruct the normal myomeric relationships shown in panel A. Modified from Jayne and Lauder (1995*c*).

ed species of centrarchid fishes performing undulatory swimming over a wide range of speeds. For similarly sized individuals of these two centrarchid species we have performed an extensive series of experiments using electromyography synchronized with high-speed videotapes to determine both *in vivo* muscle activity and kinematics for effectively the entire range of swimming speeds for which axial structures are used.

AXIAL MORPHOLOGY

The most conspicuous anatomical units of the axial muscles of fishes are the W-shaped myomeres for which the top of the "W" is oriented anteriorly (Fig. 1). Although there is a 1:1 ratio between the numbers of myomeres and the numbers of vertebrae, the longitudinal extent of an individual myomere commonly spans several vertebrae. Remarkably, in centrarchid fishes, the longitudinal span of a single myomere may encompass up to 30% of the length of the vertebral column (Jayne and Lauder, 1994*b*). White fibers in a single myomere may thus influence vertebral movement at many segments. Myomeres also have a convoluted shape that results in portions of adjacent myomeres overlapping similar to a series of nested cones. Consequently, in a fish such as the largemouth bass, electromyographic (EMG) electrodes opposite a single vertebrae could be in any one of six different muscle segments, depending on both the depth and dorso-ventral position (Fig. 1).

Fish also generally have a spatial segregation of different fiber types of the axial muscles which has served as an excellent model for studying fiber type recruitment of vertebrate muscle (Rayner and Keenan, 1967; Hudson 1973; Johnston *et al.*, 1977; Bone *et al.*, 1978; Johnston and Moon, 1980; Rome *et al.*, 1984). Longitudinally-oriented, slow red muscle fibers are generally located superficially near the horizontal septum. In the largemouth bass the superficial red muscle may be less than 2% of the total body mass (Johnson *et al.*, 1994), whereas the entire axial muscle mass in fishes commonly ranges from 40–60% of the total body mass (Bone, 1978). However, the exact locations and amounts of red muscle vary considerably depending on the species and other factors such as the season of the year (Bone, 1978; Johnston, 1983; Kolok, 1992).

The size and shape of both the myomeres and vertebrae commonly vary significantly along the length of an individual fish (Jayne and Lauder, 1994*b*). The amount of water affected by laterally undulating bodies is proportional to body depth which also has significant longitudinal variation (Jayne and Lauder, 1994*b*). Thus, we have employed experimental procedures that systematically examined the effects of longitudinal position on both EMG and kinematic data (Jayne and Lauder 1993, 1994*a*, 1995*a*, *b*, *c*). We have carefully confirmed the positions of EMG electrodes by post-mortem dissections and radiographs, and measurements from radiographs allow partitioning of com-

puter-reconstructed midlines of fish into line segments corresponding to the lengths of individual vertebrae.

EFFECTS OF SPEED ON SWIMMING BEHAVIOR

As swimming speed increases, the structures used to propel a fish commonly change, and the manner in which these structures are used also changes with speed (Webb, 1994). For generalized species of ray-finned fishes and the centrarchid species that we have studied, the following sequence of behaviors can be observed from the slowest to fastest speeds: 1) steady pectoral fin swimming without axial undulation, 2) steady speed swimming with both pectoral fins and lateral axial undulation, 3) steady axial undulations without pectoral fin movements, 4) kick and glide swimming involving irregular rapid tail beats followed by an interval of gliding with no axial movement, and 5) the Mauthner-initiated escape response which is also referred to as the C-start. Not only do behavioral modes change with swimming speed, but a single behavioral mode commonly spans a considerable range of swimming speeds. Thus, studying muscle function and kinematics by systematically accounting for locomotor speed among and within behavioral modes of swimming facilitates determining: 1) whether the potential variation associated with speed occurs as a continuum or as a series of discrete states, and 2) whether a single speed is adequate to characterize all speeds of swimming within a behavioral mode.

STEADY SWIMMING

Maximal lateral displacement and bending are out of phase

Lateral displacement of undulating bodies is an important quantity since it is related to transverse velocity and momentum transferred to the water. Lateral bending is also of central importance for understanding axial muscle function because bending is proportional to the amount of stretching undergone by the contractile tissue which in turn affects force production. However, few studies of axial locomotion have quantified both lateral displacement and bending and their phase relationships.

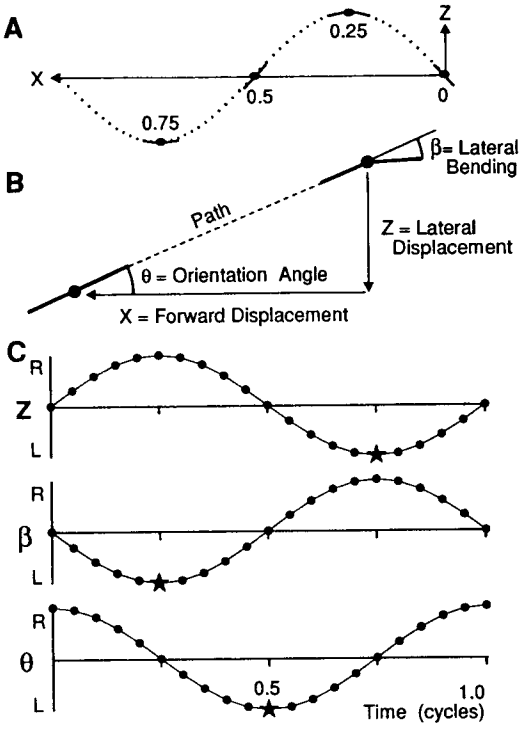

FIG. 2. Kinematic variables and *a priori* expectations for phase relationships among kinematic variables for an undulating body that conforms to the sinusoidal path that it travels. (A). Orientation of axes. The thin dotted line represents the path traveled by two midline segments which are shown at four different times (in cycles). X indicates the overall direction of forward travel, and Z indicates lateral displacement. In A and B the large dot represents the joint between two adjacent midline segments (thick lines). (B). Methods for calculating the angles of orientation (θ) and lateral bending (β) are shown for a time between 0.25 and 0.5 cycles. (C). Plots of Z, β and θ versus time for the case illustrated in panel A. R and L indicate right. and left. When a site is maximally displaced to the right (time = 0.25), one would expect it to be bent maximally concave to the left. Stars indicate landmark kinematic events whose elapsed times were used for calculations of phase shifts. Kinematic analyses of each tail beat cycle were usually based on minimum of 20 video images that were spaced at equal time intervals. Modified from Jayne and Lauder (1995*a*).

If an undulating body simply conforms to the sinusoidal path that it travels (Fig. 2A), then lateral bending of the body (β) is maximally concave to the left at the same time that lateral displacement (Z) is maximally to the right (Fig. 2A, 0.25 cycles). Furthermore, the angle between an individual body segment and the path traveled by

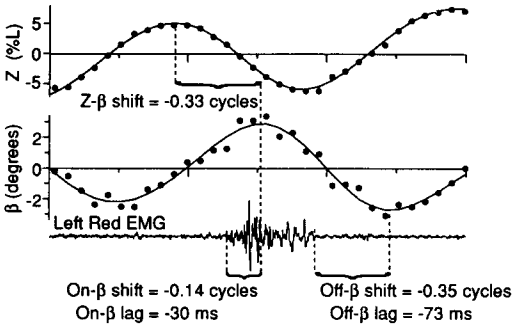

FIG. 3. Lateral displacement (Z in % total length), bending (β), and left side muscle activity versus time for a *Micropterus salmoides* swimming steadily at 2.4 lengths/sec with a tail beat frequency of 4.8 Hz. Sign conventions for Z and β are as in Figure 2. Z-β shift indicates the phase shift between Z and β. Values of phase shifts (On-β shift; Off-β shift) and time lags (On-β lag; Off-β lag) between muscle activity and lateral bending would be expected to equal zero if EMGs occurred during the shortening of contractile tissue. From data in Jayne and Lauder (1995*b*).

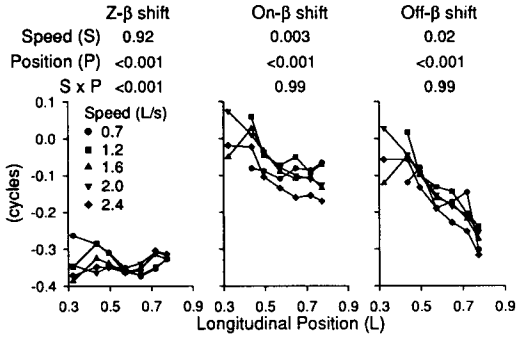

FIG. 4. Mean values of phase shift variables (defined in Fig. 3) for each combination of 5 speeds of steady swimming and 7 standardized longitudinal locations of red muscle in *Micropterus salmoides*. Below each phase shift variable the results of analyses of variance (Jayne and Lauder, 1995*b*) are summarized by giving the P values for each term of the ANOVA. Values of phase shifts differed significantly from the *a priori* expectation for kinematics, and they also indicate that timing of EMGs does not correspond simply to the time of muscle shortening.

that segment (Fig. 2B, orientation angle, θ) would be greatest when the body segment crosses the axis of overall forward progression (Fig. 2A, 0.5 cycles). For this simple theoretical case of sinusoidal bending and movement (Fig. 2A), Figure 2C illustrates the *a priori* expectations for timing differences (phase shifts) among the different kinematic variables. The expectation of synchronous maximal lateral bending and displacement (Fig. 2) has even lead some workers to measure only lateral displacement and then use it as a surrogate for lateral bending (Frolich and Biewener, 1992; Ritter, 1992).

Interestingly, none of the experimentally determined phase relationships among pairs of kinematic variables for the largemouth bass (Jayne and Lauder, 1995*a*) agrees simply with the expectations (Fig. 2C) for an undulating body that conforms to the path that it travels. Figure 3 shows an example of how the time of maximal lateral displacement (Z) to the left is not coincident with maximal lateral bending (β) to the right for a single longitudinal location and swimming speed.

Figure 4 shows the mean values of phase shift variables for each of seven longitudinal locations and five swimming speeds of the largemouth bass. Analysis of variance of the values of the phase shift between lateral displacement and bending (Z-β shift) reveals highly significant variation along the vertebral column, and speed and longitudinal location also have highly significant interactive effects on this kinematic variable (Fig. 4). Rather than a predicted phase shift of one-half cycle between Z and β, most mean values of Z-β shift for the largemouth bass are between −0.4 and −0.3 cycles (Fig. 4). If values of Z-β shift of the tail fin are included with values from sites along the vertebral column, then swimming speed also has a statistically significant effect on this phase relationship (Jayne and Lauder, 1995*a*). Swimming speed has little to no effect on values of Z-β shift at intermediate longitudinal locations (Fig. 4; Jayne and Lauder, 1995*a*). For the longitudinal sites that are significantly affected by speed, increasing speed generally decreases the difference between the observed (Fig. 4) and expected (−0.5 cycles, Fig. 2) values of Z-β shift. Given our results of phase shifts between displacement and bending that differ from the *a priori* value by 10–25% of a cycle, we recommend against using displacement as a surrogate of bending.

Orientation of the fish midline and path differ and are out of phase

The angles of orientation of the fish midline (θ_{body}) and the path traveled (θ_{path}) have another phase relationship that differs from the expectation shown in Figure 2. Rather than the steepest angle of the body occurring as it crosses the axis of forward travel, θ_{body} and θ_{path} may be out of phase by as much one-tenth of a cycle (Jayne and Lauder, 1995*a*). Besides being out of phase, the amplitudes of θ_{body} and θ_{path}, differ such that the midline of the fish has a measurable angle of attack that fluctuates regularly between positive and negative values within each tail beat cycle. Interestingly, the relatively stiff hypural region of the tail of the largemouth bass has consistently larger magnitudes for the angle of attack compared to the relatively compliant distal caudal fin, which comes much closer to having matched values for the amplitudes of θ_{body} and θ_{path} as well as having nearly no phase shift between these two variables (Jayne and Lauder, 1995*a*).

Speed and longitudinal position affect the timing of red EMGs relative to muscle shortening

Lateral bending can be used to estimate of the amount of stretch undergone by the axial muscles of fish and the timing of muscle activation (EMG or *in vitro* stimulation) relative to stretch can have substantial effects on the force production and power output of muscle (Rome *et al.*, 1988; Rome and Sosnicki, 1991; Coughlin, 1996). Hence, it is important to quantify the timing differences between EMGs and lateral bending, and the methodology for doing this is fundamentally similar to that which was used for timing differences between pairs of different kinematic variables. Figure 3 shows how the timing differences are calculated between the onset and offset of EMGs and stretch of the muscle as indicated by lateral bending. Phase shift variables (On-β shift, Off-β shift) use a relative time scale (cycles), whereas time lag variables (On-β lag, Off-β lag) use an absolute time scale (msec) to express timing differences. Values of zero for all of the phase shift and time lag variables that relate EMGs to lateral bending would correspond to simple activation of the contractile tissue while it shortens. However, as Figure 3 shows for a single recording site, the timing of the EMG can depart considerably from activation during shortening of the muscle fibers.

Figure 4 summarizes the mean values of both On-β shift and Off-β shift for each of seven longitudinal locations at five different swimming speeds for the largemouth bass. With the exception of some of the most anterior sites in the largemouth bass (Fig. 4), mean values of both On-β shift and Off-β shift are negative which indicates that red muscle is activated while it is being lengthened and electrical activity ceases before the muscle is maximally shortened. Furthermore, for increases in swimming speed and for more posteriorly located sites, analyses of variance show significant increases in the magnitude of these phase shifts such that progressively greater portions of the EMGs occur during lengthening of the muscle tissue (Fig. 4; Jayne and Lauder 1995*b*). Several previous studies (Grillner and Kashin, 1976; Williams *et al.*, 1989, Van Leeuwen *et al.*, 1990; Rome *et al.*, 1993) that have documented longitudinal variation have not detected any effects of swimming speed on the timing of EMGs relative to lateral bending, or else they have often not employed experimental designs and analysis to definitively determine the effects of swimming speed on phase relationships. For the largemouth bass, our observations indicate that a neither a single site nor a single swimming speed is adequate to characterize muscle function during steady swimming.

For each combination of swimming speed and longitudinal position (Fig. 4), the mean phase differences between the onset of activity and the beginning of shortening (On-β shift) are generally less than those between EMG offset and maximal shortening (Off-β shift). Furthermore, the most posterior sites at the fastest swimming speeds have the greatest phase shift between EMG and the shortening cycle of muscle. For example, the red muscle just anterior to the hypural bones in the tail of a largemouth bass swimming at 2.4 lengths

per second has mean values of −0.17 and −0.31 cycles for On-β shift and Off-β shift, respectively, which indicates that approximately the first one-half of the EMG occurs as the muscle is still being lengthened and then the EMG ceases before the muscle has shortened enough to return to its resting length (Fig. 3).

Because both cycle duration and phase shift (lag/cycle duration) variables change significantly with speed, it is also useful to examine the absolute lag times (in ms rather than cycles) between EMG and bending. For the largemouth bass, most values of On-β lag and Off-β lag are between 0 and −50 msec and −10 and −80 msec, respectively, and their magnitudes change significantly with both longitudinal location and swimming speed (Jayne and Lauder, 1995*b*). For *in vitro* preparations of the red muscle of largemouth bass under experimental conditions similar to *in vivo* studies of muscle, the mean times to peak tension and one-half relaxation during isometric twitch are 43 and 67 msec, respectively (Johnson *et al.*, 1994). However, the experimentally observed values of EMG-bending lag times are not constant and they do not correspond simply to these values for twitch that indicate the lags between electrical activity and force production. For some species of fish, the times to relaxation of the muscle increase posteriorly (Altringham *et al.*, 1993) in a fashion that is consistent with progressive posterior increase in the magnitude of Off-β lag that we have observed *in vivo* for the largemouth bass. Exactly how the different *in vivo* stimulation regimes of red muscle may affect time course of force development and relaxation remains an open and interesting question for this system.

Propagated muscle activity occurs simultaneously along the entire length of the fish

During steady swimming of centrarchid fishes EMGs are propagated from the head towards the tail (Jayne and Lauder, 1994*a*, 1995*b*), and this appears to be universal for all species of fishes which have been studied. Paradoxically, the propagated axial motor patterns of centrarchid fish superficially

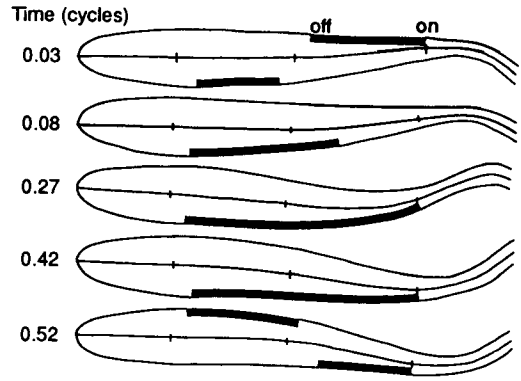

FIG. 5. Whole body summary of red axial muscle activity based on direct observation from thirteen recording sites (7 left and 6 right) in one individual *Micropterus salmoides* swimming steadily at 2.4 L/sec (cycle duration = 303 msec). Outlines of the fish were made directly from digitized video images. The three reference marks on the midline of the fish indicate the posterior border of the skull, the joint between the trunk and caudal vertebrae, and the most posterior intervertebral joint. The thick lines along the sides of the fish indicate muscle activity. Note that because muscle activity is propagated posteriorly, the posterior end of the thick line indicates onset of muscle activity and the anterior end is activity immediately prior to offset. Modified from Jayne and Lauder (1995*b*).

resemble a standing wave pattern of muscle activation because there is an interval when all of the superficial red muscle on one side is simultaneously active (Fig. 5, 0.27–0.42 cycles). This longitudinal extent of simultaneous active axial muscle segments is the result of EMG durations exceeding the total time taken to propagate activity from the most anterior to the most posterior site. The largemouth bass, trout, and carp are all subcarangiform swimmers with fairly generalized body shape for which the red muscle motor patterns can now be compared for steady swimming. Interestingly, the entire length of both carp (Van Leeuwen *et al.*, 1990) and the largemouth bass (Jayne and Lauder, 1995*b*) momentarily have simultaneous activity along an entire side, whereas this does not occur in the trout (Williams *et al.*, 1989) which has nearly twice as many body segments as carp and largemouth bass. Thus, comparative data are beginning to find structural correlates for some of the seemingly diverse motor patterns which have been observed for different species of fish.

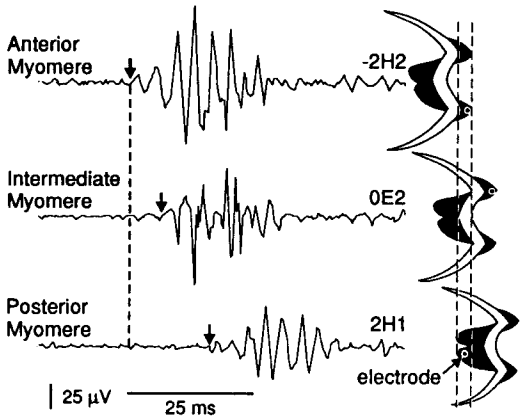

FIG. 6. Kick and glide EMGs recorded simultaneously from three different deep myomeric locations on the same side within a single individual of *Micropterus salmoides*. The EMGs are arranged from the most anterior to the most posterior myomere proceeding from the top to the bottom of the figure. Dots in the myomeres to the right of each EMG indicate the location of electrodes, and vertical arrows indicate onset times of EMG bursts. The first digit of the labels to the right of each EMGs correspond to myomeric numbers as defined in Figure 1B. E and H indicate epaxial and hypaxial, respectively, and the last digit of each EMG label indicates different portions of the myomere as shown in Figure 7. Note that EMGs from more posterior myomeres have later onset times indicating a posterior propagation of activity by sequential activation of the myomeres rather than simultaneous activation of all of the contractile tissue opposite a particular vertebra. Modified from Jayne and Lauder (1995*c*).

KICK AND GLIDE SWIMMING

Compared to other major behavioral modes of undulatory swimming, kick and glide swimming has been studied minimally; however, recent studies of this behavior (Jayne and Lauder 1994*a*, 1995*c*) are replete with novel and unexpected findings on motor pattern and fiber type recruitment. For centrarchid fishes (approximate total length = 20 cm), the transition from steady to kick and glide (=burst and coast) swimming occurs rather abruptly at relative swimming speeds near 3 lengths/sec, and this kinematically distinct behavior is correlated with the threshold of recruitment of faster fiber types.

White fiber activity is not synchronous at a single longitudinal position

Simultaneous recordings from vertical arrays of EMG electrodes (Figs. 1A, 6) in the deep white (fast) myomeric muscle (Jayne and Lauder, 1995*c*), reveal that not all of the contractile tissue opposite a single vertebra is activated simultaneously. When electrodes at a single longitudinal location are placed at different depth and/or dorsoventral position (Fig. 6,−2H2 *versus* 2H1), statistically significant differences in the timing of EMGs are present among electrodes that are in different myomeres. These timing differences indicate that muscle activity is posteriorly propagated by sequential activation of myomeres rather than activation all of the contractile tissue opposite a single skeletal segment. This sequential activation of myomeres, combined with the extensive longitudinal overlap of myomeres at different depths, accounts for the paradoxical observation that a more posterior electrode can have earlier onset and offset times than a more anterior site (Fig. 6, site 0E2 *versus* 2H1). Regression analysis confirms that over a limited longitudinal region these timing differences between EMGs from the myomeric musculature are best explained when electrode positions are indicated by myomeric number rather than alternative measures of longitudinal distance that ignore the myomere in which the electrode was placed (Jayne and Lauder, 1995*c*).

During slow and moderate speeds of kick and glide swimming, activity is apparent in the central portions of the myomere including the cone-like structures that project posteriorly (Fig. 7, E2, H2) and anteriorly (Fig. 7, E1, H3); however, the extreme dorsal and ventral portions (Fig. 7, E3, H3) commonly lack activity (Fig. 7). In contrast, for the more rapid episodes of kick and glide swimming (Fig. 7) and the escape response, all portions of the deep myomeric musculature are activated (Jayne and Lauder, 1995*c*). Thus, some aspects of motor control of the axial musculature occurs at a finer level than the anatomical unit of an entire myomere.

The timing of red and white muscle activity differs at a single longitudinal location

When electrical activity in both red and white muscles was recorded in bluegill (*Le-*

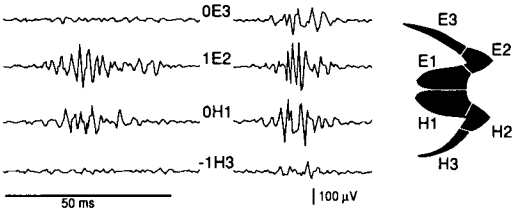

FIG. 7. Burst and glide swimming EMGs from deep myomeric muscle of a *Micropterus salmoides*. Labeling of EMG sites is as in Figures 1 and 6. EMG traces on the left were recorded during lower speed unsteady swimming, while EMG traces on the right reflect higher speed burst and glide locomotion. The left panel was recorded prior to the panel on the right from the same individual. Note that the recruitment of fibers in the extreme dorsal (E3) and ventral (H3) portions of the myomere may not always occur when there is activity at ipsilateral deep myomeric sites which are closer to the horizontal septum. Modified from Jayne and Lauder (1995*c*).

pomis macrochirus) at a single longitudinal location, several unexpected results were discovered. At swimming speeds near the threshold of recruitment of the white muscle fibers, the onset of superficial red muscle activity commonly precedes that of the underlying white by more than 50 msec (Fig. 8C; Jayne and Lauder, 1994*a*). The lag times between the onset of red and white muscle decrease linearly with decreased EMG duration, and decreases in EMG duration indicate faster swimming speed (Jayne and Lauder, 1994*a*). At the fastest speeds of kick and glide swimming, the onsets of red and white activity do not have measurable differences (Fig. 8B). In contrast to the onset time of red and white muscle, the offset times of red and white fibers do not differ significantly (Fig. 8C; Jayne and Lauder, 1994*a*). This combination of large differences in onset times and similar offset times of the red and white muscle is a pattern that can not be explained by the electrodes being located in different myomeres at the same longitudinal position. Instead, EMGs of the underlying white muscle have shorter durations than those of the superficial red muscle, and the differences between EMG durations equal the lag times between the onsets of activity.

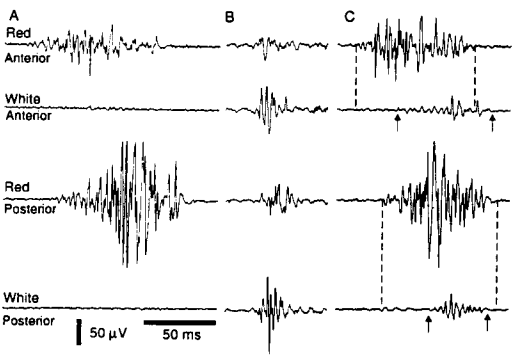

FIG. 8. EMGs recorded simultaneously from the red and white fibers on the same side of a *Lepomis macrochirus* at two longitudinal positions (labeled anterior and posterior) separated by eight body segments. (A). Steady swimming at approximately 2 L/sec. Note the complete absence of white activity. (B). A rapid burst preceding a glide. (C). Unsteady swimming at a speed intermediate to that in A and B. Dashed lines indicate the onset and offset of red muscle activity at each site whereas arrows indicate the onset and offset of white muscle activity. Near the threshold of white recruitment, the onset times of white muscle activity were delayed with respect to red, whereas the offset times of red and white at a single site were nearly synchronous. From Jayne and Lauder (1994*a*).

The intensity of red muscle activity decreases with increased speed

A common presumption for the swimming of fishes (*e.g.*, Rome *et al.*, 1988) is that the additional power required for faster speeds is attained by recruiting faster fiber types in addition to but not to the exclusion of slower fiber types. In other words, the intensity of recruitment of slow fiber increases up to a level yielding maximal power, whereupon the addition of a faster fiber type is then necessary to increase the power output to even higher levels. However, quantitative analysis of red and white EMGs of the bluegill sunfish shows that recruitment of slow fiber types actually decreases for the fastest speeds of kick and glide swimming (Fig. 8B).

A quantitative indication of the intensity of recruitment is obtained by dividing the rectified integrated area of an EMG burst by its duration, and analysis of this quantity for red and white muscle reveals the following sequence of muscle recruitment with increased speeds of undulatory swimming (Jayne and Lauder, 1994*a*). (1) Beginning with the slowest steady undulatory swimming, the intensity of red muscle activity

increases in the absence of white muscle activity. (2) The intensity of both red and white EMGs increases with increased speeds (of kick and glide swimming). (3) After red fibers are recruited maximally, the intensity of white recruitment increases and the intensity of red EMGs decreases. (4) With increased speed, the intensity of white EMGs continues to increase while the intensity of red EMGs remains near zero. Interestingly, this diminished recruitment of red muscle for the highest speeds of kick and glide swimming is not found in the escape responses (discussed in the next section) which have the highest tail beat frequencies of all of the swimming behaviors.

Larger motoneurons are a neuro-anatomical correlate of faster muscle fiber types in fishes (Fetcho, 1986), and the size order of recruitment model states that, with increased speed of movement, the rank order for recruiting additional motoneurons is the same as that based on the size of the motoneurons (Henneman *et al.*, 1965). With the exceptions of some studies involving specialized non-locomotor behaviors (Smith *et al.*, 1977; Nardone *et al.*, 1989), the size order of recruitment model has been widely supported by previous studies of vertebrate motor systems including the axial muscles of fishes which have often been studied over a limited range of swimming speeds. However, earlier models of fiber type recruitment must now be refined and expanded to account for the diminished recruitment of slow fibers as detected by the quantitative analysis of the EMGs of fish during a natural locomotor behavior (Jayne and Lauder, 1994*a*).

ESCAPE RESPONSE

Red muscle is recruited maximally

The most intense axial muscle activity that we have observed occurs during the escape response during which both red and white fibers are recruited maximally (Jayne and Lauder, 1993). Unlike the propagated muscle activity of slower swimming behaviors, the onset of the initial EMG (=agonist contraction in Foreman and Eaton, 1993) of the escape response occurs simultaneously along the entire side of the fish (Jayne and Lauder, 1993). The initial recruitment of the major side red fibers would seem to be mechanically sub-optimal because these fibers take more than 40 msec to develop peak tension (Johnson *et al.*, 1994), and the contralateral EMG (=antagonist contraction in Foreman and Eaton, 1993) during stage 2 of the escape response can occur less than 20 msec after the onset of the initial EMG. Thus, initial activity of the red fibers seems likely to oppose the action of the later, contralateral muscle activity. Hence, unlike the diminished red muscle activity observed for rapid kick and glide swimming, maximal activation of red muscle during escape responses does not conform in any simple way to expectations for optimal performance based on work loop studies (*e.g.*, Altringham and Johnston, 1990) which have shown how activating slow fibers above a certain frequency may be counter-productive. The escape response involves specialized neural circuitry that apparently is not used in other locomotor behaviors (Eaton *et al.*, 1991), and recent *in vitro* recordings from the motoneurons of the red muscle (Fetcho and O'Malley, 1995) are consistent with the unexpected *in vivo* finding of activating a slow fiber type during a very rapid movement (Jayne and Lauder, 1993).

Fish do not form a C during C-starts

Escape responses are often also referred to as C-starts (Eaton *et al.*, 1991) because of the gross appearance of the fish soon after the initial EMG. A true C-shape would involve the entire length of the fish simultaneously being maximally concave towards one side; however, a quantitative analysis of midline kinematics indicates that such a shape is never attained during the escape responses of centrarchid fishes (Jayne and Lauder, 1993). Although much of the length of the fish is concave towards the side of the initial EMG, a considerable portion of the posterior axial skeleton and nearly all of the caudal fin are flexed laterally towards the opposite side (Fig. 9). Close examination of other published figures (*e.g.*, Eaton *et al.*, 1977) of escape responses suggests that it is generally the case that adult fish are not entirely concave towards one side (but recent data on larval

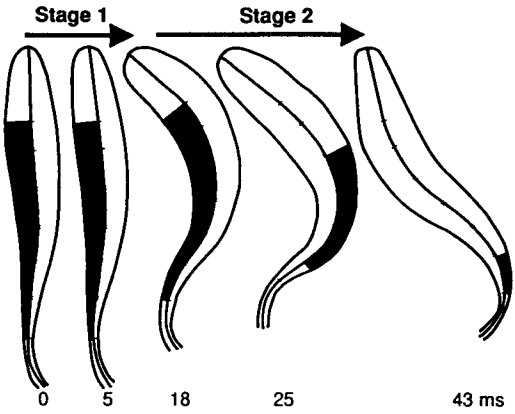

FIG. 9. Summary of movement and muscle activity during the escape response of *Lepomis macrochirus*. The muscle activity and outlines of the dorsal view of the fish are from a single individual. Times in msec are indicated below each figure (0 msec = onset of stage 1 EMG). The thick dark areas along the side of the fish represent synchronous red and white muscle activity. X marks along the midline indicate the longitudinal location of electrodes. From anterior to posterior, the three remaining marks on the midline indicate the posterior margin of the skull, vertebra 5, and the beginning of the caudal fin, respectively. Note that there is never a time when the entire length of the fish is maximally concave to one side along its entire length. Modified from Jayne and Lauder (1993).

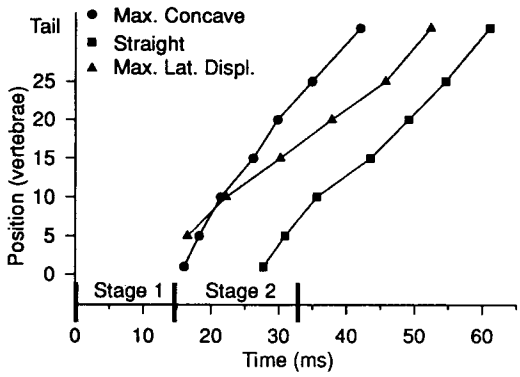

FIG. 10. Mean times of landmark kinematic events during the escape response of *Lepomis macrochirus* (Jayne and Lauder, 1993). 0 msec indicates the onset of the stage 1 EMG, and the additional vertical bars along the time axis indicate the mean values of the earliest onset of a stage 2 EMG and the latest offset of a stage 2 EMG along the entire length of the fish. Max. concave refers to the time at which a midline position was bent maximally concave toward the side of the stage 1 EMG and maximum lateral displacement is also towards the side of the stage 1 EMG. Note that the kinematic events are propagated even though the onset of the stage 1 EMG occurs simultaneously along the entire length of the fish.

fishes may prove an interesting exception [Hale, 1996]).

The term "C-start" has probably been intended as an approximate rather than literal description of the shape of the fish, but this terminology potentially can obscure an observation that is critical to understanding the relevant physiology of muscle: namely, the initial activity of the posterior myomeres occurs during lengthening rather than shortening of the muscle fibers. Hence, the simultaneous initial activation of lateral muscle along one entire side of the fish (Fig. 9), does not cause simultaneous shortening of all muscle fibers on the same side of the fish. Furthermore, the initial lateral bending of the posterior body away from the side with the initial EMG suggests that the axial muscles are inadequate to overcome the resistance of water that opposes such a rapid lateral acceleration, and the large caudal fin area is probably an important contributing factor to the increased resistance at the posterior end of the fish.

A standing wave of muscle activity produces a propagated kinematic wave

A recurrent theme for studies of axial locomotion (Gray, 1968; Blight, 1977) is whether events along the length of the animal propagate or occur as a standing wave. The onset of the initial EMG during escape responses does occur as a standing wave. However, as shown in Figure 10, kinematic events of the midline of the fish propagate from head to tail, and this lead Jayne and Lauder (1993) to suggest alternative definitions for the stages of the escape response based on EMG events rather than kinematic events. Blight (1977) provided compelling conceptual arguments for how standing patterns of muscle activity could produce traveling kinematic waves; however, the experimental work of Blight (1976) did not actually quantify the timing of EMGs at different longitudinal locations. Long *et al.*, (1994) used a standing pattern of axial muscle stimulation in a recently killed fish and obtained forward propulsion as a result of a traveling kinematic wave. Consequently, the quantitative analysis of the escape re-

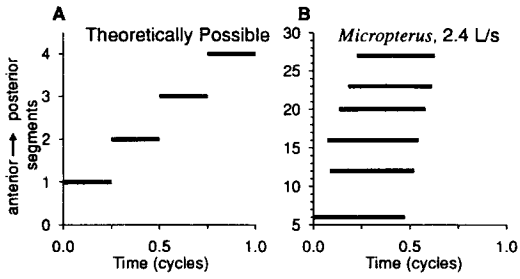

FIG. 11. Posteriorly propagated axial motor patterns. The y-axis indicates the number of the axial muscle segment counting from anterior to posterior, and the thick horizontal bars indicate the time course of the EMG for a particular muscular segment. (A). A theoretically possible motor pattern for which there is no overlap in the timing of EMGs from adjacent muscular segments. (B). Experimentally observed activity for the superficial red muscle during the steady swimming of *Micropterus salmoides* swimming steadily at 2.4 L/sec (Jayne and Lauder, 1995*b*). Note the extensive longitudinal overlap for the timing of the experimentally observed muscle activity.

sponse EMGs and midline kinematics of the bluegill sunfish (Jayne and Lauder, 1993) now provide compelling data supporting the hypothesis that standing patterns of muscle activity can indeed produce propagated waves of bending during the axial swimming of an intact animal.

CONCLUSIONS

Results from this recent work on the axial locomotion of the centrarchid fishes suggest several refinements to methodology that will enhance the ability to make meaningful comparisons between different studies and species of fishes. Because of the complicated phase relationships between times of lateral displacement and bending, neither of these kinematic quantities is an adequate substitute for the other. Precise location, confirmation and description of electrode location are essential in light of the heterogeneity of muscle activity that can occur for the contractile tissue opposite a single vertebra. Both locomotor speed and longitudinal position may have complicated effects on the phase relationships among kinematic variables and between EMGs and kinematic events. The unexpected variation in muscle function encountered with variable speeds of swimming within the centrarchids provides a cautionary note regarding the importance of carefully accounting for the behavior of intact animals before generalizing about the function of a complex system.

TABLE 1. *Longitudinal overlap of axial muscle activity for posteriorly propagated motor patterns of* Lepomis macrochirus* *(based on Jayne and Lauder 1994a).*

Swimming behavior (speed)	Fiber type	Lag of EMG onset (msec/myomere)	EMG duration (msec)	Overlap of EMG (Myomeres)
Steady (1.6 L/sec)	red	5.4	112	21
Steady (2.0 L/sec)	red	3.9	102	26
K&G (moderate)	red	3.1	88	28
K&G (moderate)	white	3.2	62	19
K&G (rapid)	white	0.9	33	37

K&G = kick and glide.
* *L. macrochirus* has 23 W-shaped myomeres.

An important conceptual issue raised by this work on axial locomotion is the extent to which anatomical units correspond to functional units in intact animals. Alexander (1969) suggested that an important structural attribute of the axial muscles of fish was the helically oriented trajectory of fibers that extends across several adjacent myomeres. However, what rationale might be used to justify a functional entity that does not simply correspond to an anatomical unit such as the myomere? One approach for addressing this question is to determine the extent of adjacent muscle tissue that is simultaneously active. For example, the different times of red and white activity and the absence of activity in the extreme dorsal and ventral portions of myomeres suggest that it is too simplistic to think of individual myomeres as monolithic functional units.

Allowing for the heterogeneity of activity within myomeres, to what extent does one myomere function independently of other myomeres? Figure 11 illustrates a theoretically possible propagated axial motor pattern for which the activity of adjacent muscle segments has no temporal overlap. For such a case, it could be reasonable to consider myomeres as distinct functional units. However, for all of the axial motor patterns which have been experimentally observed (Fig. 11; Table 1) activity of any one myomere always has extensive temporal over-

lap with that of neighboring myomeres. In fact, centrarchid fishes commonly have significant time intervals for which the all the axial muscles along one entire side of the fish are simultaneously active (Figs. 5, 9; Table 1). Accounting for the lag between EMGs and relaxation of muscle would result in even greater longitudinal extents of simultaneous muscle function than predicted from EMGs. Consequently, to be realistic, future models of axial muscle function during the swimming of fishes will need to account for the interaction of several adjacent muscle segments and the heterogeneity of fiber activity within a myomere, rather than assuming that anatomical units are equivalent to functional units.

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