

Structure, Function and Neural Control of Pectoral Fins in Fishes

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Abstract—Fin-based propulsion systems perform well for both efficient cruising and high maneuverability in fishes, making them good models for propulsors of autonomous underwater vehicles. Labriform locomotion in fishes is actuated by oscillation of the paired pectoral fins. Here we present recent research on fin structure, fin motion and neural control in fishes to outline important future directions for this field and to assist engineers attempting biomimicry of efficient, maneuverable locomotion in shallow surge zones. Three areas of structure and function are discussed in this review: (1) the anatomical structure of the fin blade, skeleton, and muscles that drive fin motion, (2) the rowing and flapping motions that fins undergo for propulsion in fishes, and (3) the neuroanatomy, neural circuitry, and electrical muscle activity (EMG) that are characteristic of pectoral fins. Research on fin biomechanics, muscle physiology and neural control is important to the comparative biology of locomotion in fishes and application of fin function for aid in aquatic vehicle design. Recommendations are made regarding fin propulsor designs based on the fin shape, activation pattern and motion. Research on neural control of fins is a key piece in the puzzle for a complete understanding of comparative fin function and may provide important principles for engineers designing control systems for fin-like propulsors.

I. INTRODUCTION

THE basic mechanisms of pectoral fin function are now understood in several species of fish [1]–[4], and there is considerable research interest focused on the design, mechanics, and hydrodynamics of animal propulsors due to the potential relevance of efficient

animal designs for practical applications in underwater vehicle technology. However, several areas of pectoral fin function remain to be explored. The pectoral fins of fishes (paired fins on the shoulder girdle) have been shown to provide efficient locomotion in coral reef fishes over a wide range of speeds [4], [5]. Swimming performance (speed endurance tests for fishes) show that pectoral propulsors are capable of generating thrusts that can power speeds up to 10 body lengths/second in some species [4]. In addition, these species are highly maneuverable in complex three-dimensional reef habitats. Efficiency, speed, performance and maneuverability are key aspects of pectoral locomotion that make reef fishes an excellent model system for the study of animal behavior and evolution and at the same time provide design ideas for underwater vehicle technology.

Previous research on morphology, behavior and hydrodynamics of the pectoral fins provides predictions regarding correlations between fin structure and function [1]–[6]. Pectoral fin mechanisms operate along a continuum from a fore-aft rowing stroke used for high transient thrust and maneuverability to a dorsoventral flapping stroke that is characteristic of high speed, endurance and high efficiency. Although pectoral fins appear to share the same basic mechanical design across many taxa, structural contrasts associated with the rowing-flapping functional axis include low aspect ratio (AR) fins for rowing and high AR fins for flapping, and a more vertical angle of insertion of the pectoral fin onto the body in rowing specialists. Flapping species also have forceful leading edge control through larger arrector ventralis and dorsalis

muscles, a higher mechanical advantage due to basal processes on the fin rays, relatively larger muscles that power the downstroke, and radials (support bones) that move as a unit. Rowers on the other hand, have muscles specialized for increased control across multiple fin rays rather than the leading edge, a lower mechanical advantage of fin rays, radials supporting the fin base that allow flexibility of fin motion, and more powerful muscles that power the upstroke. The integration of structure, muscle physiology, and neurobiology holds promise for testing these hypotheses.

Among the tools being used to explore pectoral fin function are anatomical research [1], [6], kinematics [2], [4], [8]-[12], electromyography [13]-[14], and both experimental and computational fluid dynamics [3], [7], [15], [16]. These research areas are revolutionizing our understanding of how fins work and clarifying the biological and hydrodynamic foundations of aquatic locomotion. However, there has been little synthesis of the function and control of pectoral fins from the perspective of detailed fin anatomy, fin motion, and fin neurobiology in an effort to develop a more complete model of fin function. Deeper understanding of these areas provides future goals for basic research on the comparative biology of locomotion, and sets useful targets for engineers interested in biomimicry of fish fins for vehicle applications. Here we discuss three key areas of biology of pectoral fin locomotion: (1) the anatomical structure of the fin blade, skeleton, and muscles that drive fin motion, (2) the motions of rowing and flapping that fins undergo for propulsion in fishes, and (3) perspectives on fin neural circuits and the muscle activity patterns (EMG) of pectoral fins.

II. MORPHOLOGY OF FINS: FIN BLADE, MUSCLE, TENDON AND BONE

The pectoral fin of teleost fishes is homologous to the upper limb or arm of tetrapods, and is supported by the shoulder girdle. The main features of pectoral fin structure (Fig. 1) consist of a pectoral or shoulder girdle skeleton, a row of 4 radials that form a basal support for the fin, a cartilage pad upon which the fin rays rotate, a series of fin rays with complex bases, and a set of muscles that powers the motion of the fin rays. Considerable variation is present in the pectoral girdle, the shape of the fin, and the anatomy of the muscles (Fig. 2-3). The pectoral girdle (Fig. 1A, Fig. 2) is the anchor upon which the pectoral muscles originate. The anteroventral surfaces of the cleithrum, both laterally and medially, as well as scapula and coracoid, are the sites of attachment for abductor and adductor

musculature (Fig. 1B, Fig. 3). The first pectoral fin ray is a short, thick ray that articulates with the scapula in a synovial joint. The first and second pectoral rays are tightly connected by connective tissues to form a single rotational element that forms the leading edge of the pectoral fin (Fig. 1A). Most pectoral rays have their bases imbedded in a fibrous pad that separates them from the underlying radials. Pectoral fin shape (Fig. 2) is determined largely by relative fin ray length- in most fishes the anterodorsal rays are the longest and the rays taper in length from dorsal to ventral to form a wing-shaped fin.

Fin shape has large consequences for fin thrust mechanics, related to a trade-off between efficiency of fast swimming and maneuverability in slowly swimming species. Walker and Westneat [4], [5] demonstrated that a rowing stroke is capable of producing stronger thrust transients for maneuvers when it is performed with a more rounded, distally broadened, paddle-shaped fin. In contrast, a more slender, tapering, wing-like fin is most efficient for swimming at higher sustained speeds using a dorso-ventral flapping stroke. There are several key parameters of fin shape that are associated with fin motion and locomotor strategy, including fin aspect

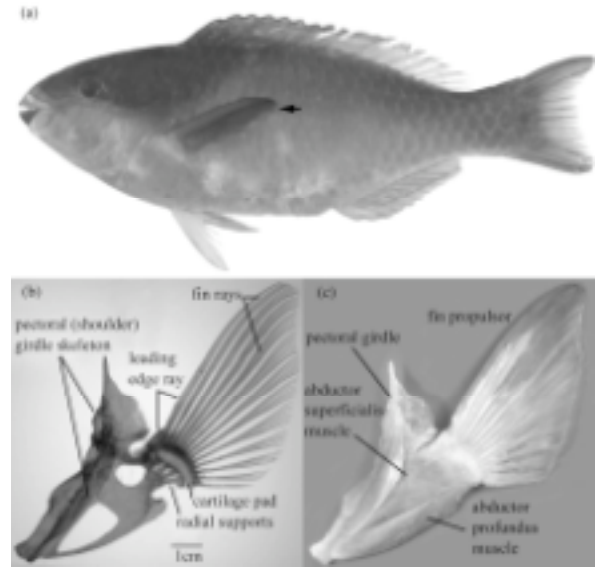


Fig. 1. Anatomy of the pectoral fin in a highly maneuverable coral reef fish, the parrotfish, *Scarus forsteni*. (a) position of the pectoral fin (arrow) illustrated with a photo of a parrotfish, *Scarus forsteni*. (b) skeletal structure including shoulder girdle support, fin base and leading edge anatomy, and the structure of fin rays of *Scarus frenatus*. (B) Lateral muscles that power the downstroke of the fin, including the broad superficialis and profundus that pull on the bases of many fin rays to bring the fin down and forward.

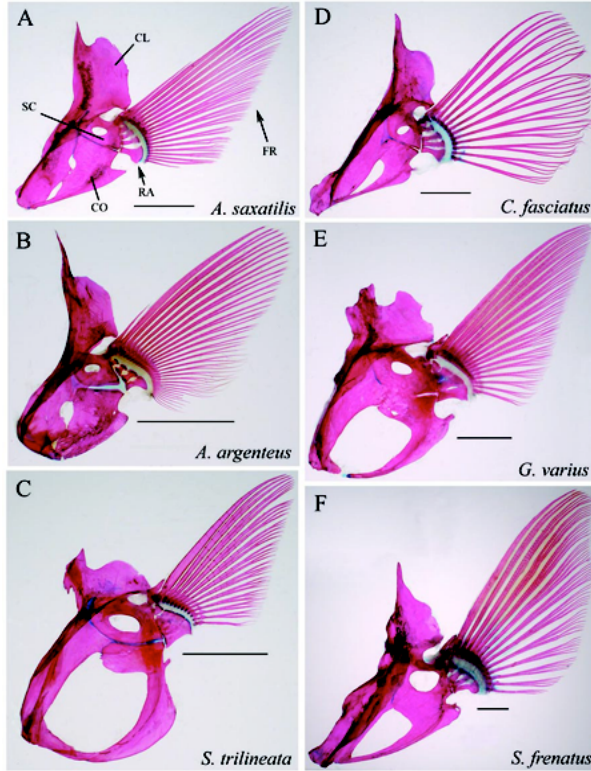


Fig. 2. Skeletal diversity of cleared and stained pectoral girdles and pectoral fin shapes in lateral view of labroid species. **A:** *Abudefduf saxatilis*, **B:** *Amphistictus argenteus*, **C:** *Stethojulis trilineata*, **D:** *Cheilinus fasciatus*, **E:** *Gomphosus varius*, **F:** *Scarus frenatus*. CL, cleithrum; CO, coracoid; FR, fin rays; RA, radials; SC, scapula. Scale bar = 1 cm.

ratio, fin chord lengths, and the distribution of fin area. Aspect ratio varies among fish species from a low of about 2 in fishes with paddle-shaped fins and a rowing stroke to a high of 4 or 4.5 in several flapping species [6], [17]. Higher aspect ratio fins typically have a relatively long leading edge and are narrower distally. Flappers are characterized by a higher aspect ratio and a longer leading edge relative to trailing edge, and the distribution of fin area is different among species. Fin base area is largest in flappers and smallest in rowers, indicating that the center of fin area is located closer to the fin base in flappers [4].

Fin ray morphology also reflects locomotor strategy among reef fishes. Fin rays of all species have at least the first two fin rays that are non-branched, and these are usually fused together to form a stiff leading edge. Leading edge stiffness appears to be variable, with high aspect ratio, wing-like fins having higher stiffness than broader fins. Although this remains to be tested by measuring fin ray stiffness, a stiff leading edge will enhance the development of flow circulation around the fin undergoing a steep flapping stroke with rapid stroke reversal [4].

Six major pectoral muscles actuate the fin during

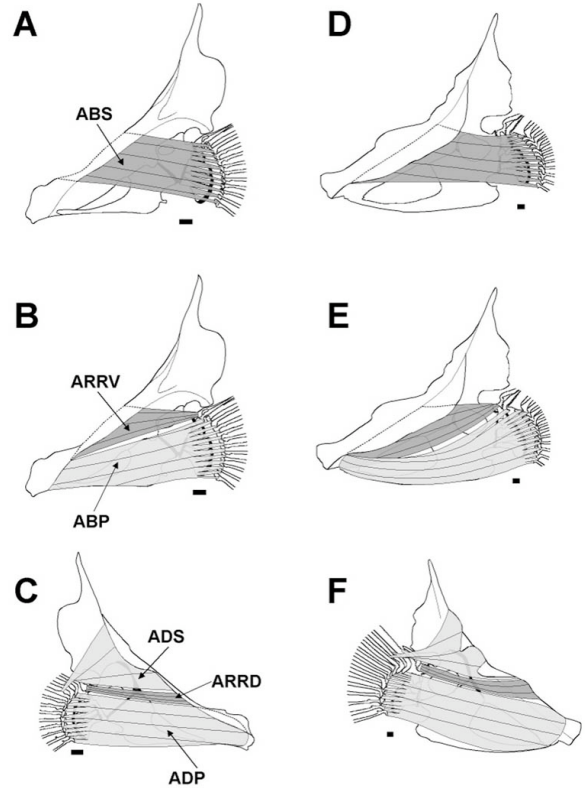


Fig. 3. Muscle morphology in a wrasse (A-C) that uses a fore-aft rowing stroke and a parrotfish (D-F) that uses a lift-based flapping stroke for pectoral locomotion. (A,D) Structure of the abductor superficialis muscle on the lateral face of the pectoral fin. (B, E) Arrector ventralis (upper dark shaded muscle) and abductor profundus (lower light-shaded muscle). (C, F) Adductor superficialis (upper light-shaded muscle) arrector dorsalis (middle dark shaded muscle) and adductor profundus (lower light-shaded muscle) on the medial face of the pectoral fin.

locomotion [1], [6]. Three muscles form the abductor complex that abducts the fin in the downstroke. The abductor superficialis and abductor profundus (Fig. 3) are broad, flattened muscles that originate on the anterolateral face of the cleithrum. The abductor superficialis inserts via abductor tendons onto all pectoral rays (excluding the first ray), and the profundus inserts on all rays. The arrector ventralis (Fig. 3) also attaches along the anterolateral edge of the cleithrum, lying medial to the abductor superficialis. The arrector ventralis inserts onto the anterior base of the first pectoral ray by a stout tendon. The adductor complex (Fig. 3) is composed of three major muscles and two smaller muscles. The adductors superficialis and profundus originate on the anteromedial surface of the cleithrum and insert via adductor tendons onto the pectoral rays (excluding the first ray). These muscles are antagonists to the abductors superficialis and profundus. The arrector dorsalis originates anteroventrally on the medial face of the cleithrum and inserts onto the anterior base of the first pectoral ray by

a stout tendon, as an antagonist to the arrector ventralis.

Muscle mass is proportional to force generation ability, and pectoral muscle masses can vary widely across species. Recent research [6] showed that the pectoral fin musculature comprises 0.68 – 8.24% of the total body mass. Two coral reef species, *Stethojulis trilineata* and *Zanclus cornutus* have the largest pectoral musculature so far measured among reef fishes, 6.84% and 8.24% respectively. The majority of species ranged from 0.34 – 1.22%. The ratio of abductor (downstroke) muscles to adductor (upstroke) muscles ranged from 0.72 to 1.46. The relative mass of abductors and adductors provides an estimate of the total amount of muscle tissue dedicated to downstroke and upstroke power. Most wrasses and parrotfish have a abductor/adductor ratio less than one, though other flappers have a larger abductor musculature. These differences highlight the relative importance of the upstroke (for fishes with a more massive set of adductors) or downstroke (for other flappers with high relative mass of abductors) for thrust production [6].

Future biomechanical models of fin morphology can make use of structural information and muscle mechanics to provide a means for testing functional concepts gleaned from the diversity described above. The mechanical design of the pectoral girdle, musculature, and fin ray levers will be integrated by a mechanical model based on morphometrics (Fig. 4) that reflect functionally important fin dimensions in order to quantify differences in mechanical advantage, velocity advantage, angle of attack, and stroke plane angle. Such models are a useful tool for predicting the mechanical results of changes in morphology and motor patterns in musculoskeletal systems [18], [19]. Comparisons of kinematics, muscle actions, skeletal mechanisms, and fin shapes in the context of mechanical models will be crucial for mechanical analyses of pectoral fin propulsion.

The design of propulsors for aquatic vehicles employing fin mechanisms for thrust and maneuverability may benefit from the mechanical design principles of the biological structures described above. A range of fin shapes is available for biomimicry of both efficient lift-based locomotion and for developing high thrust transients for rapid aquatic maneuvers. The structure of the skeleton and particularly the saddle-joint and shape of the critical leading edge of the fin is a system potentially worth imitating in a human-engineered propulsor. The attachments, lines of force, and relative force magnitudes of the pectoral muscles are also available for artificial muscle engineers or other mechanisms of driving fin propulsors.

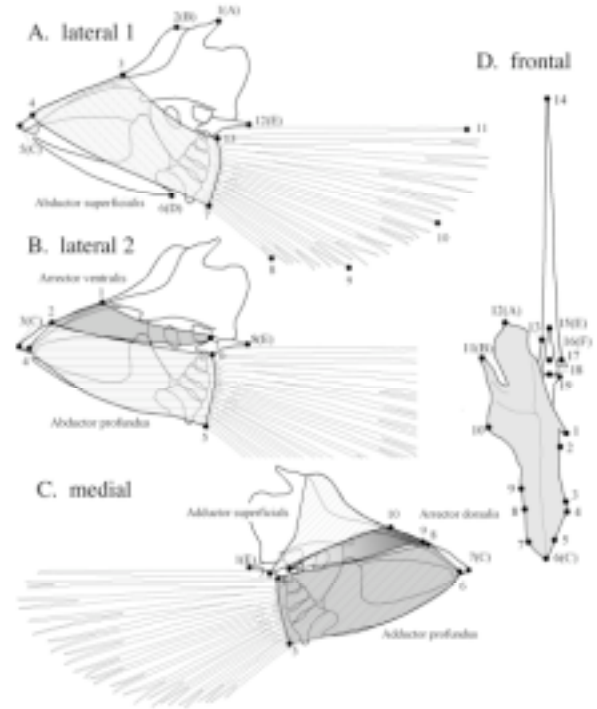


Fig. 4. Morphometric protocol for quantifying the mechanical design of the fin, and specifying structural parameters for a 3-dimensional biomechanical model of the fin. (A) lateral view of abductor superficialis, with metrics of muscle and fin; (B) lateral view with superficialis removed, and metrics of arrector ventralis and abductor profundus; (C) medial view of three major adductor muscles, with metrics of muscle dimensions; (D) frontal view to provide 3D coordinate system for computer modeling of muscle actions, torque, mechanical advantage, and fin stroke parameters.

III. KINEMATICS OF PECTORAL FIN PROPULSION

Two modes of oscillatory pectoral fin propulsion are generally recognized, rowing and flapping [20], [21]. Rowing is a largely fore-aft movement in which the pectoral fin swings forward largely parallel to the flow in a low drag configuration and then sweeps backwards perpendicular to the flow in a high-drag position. By contrast, flapping is a largely dorsoventral fin motion in which the fin develops thrust on both the downstroke and upstroke. Kinematic analyses of pectoral fin locomotion using both rowing and flapping strokes showed significant differences between stroke plane and angle of attack during rowing and flapping (Walker and Westneat 2000; 2002). The rowing-flapping dichotomy is in reality a continuum and although some species are extreme rowers or flappers, many species appear to be intermediates.

Rowing and flapping employ different mechanisms for generating thrust [5], [9], [21]. During the power stroke of rowing, the fin is pulled back broadside to the flow of water. The resistance to moving the fin against the local flow creates a large

pressure drag at the fin, which, being directed anteriorly, is felt as thrust at the body's center of mass [9]. During steady forward swimming using a flapping stroke, the oscillation of the fin creates a vertical component to the flow over the fin. By maintaining the fin at a small angle to this local flow, a net circulation around the fin is generated, causing a lift force normal to the flow. The component of lift in the direction of swimming is felt as thrust at the center of mass [8], [22].

Detailed kinematic data that provide a three-dimensional perspective on complex fin motion have been collected on few fishes. For the flapping stroke of the bird wrasse (Fig. 5), fin beat frequency, stroke angle, and 3-dimensional angular rotation of the leading edge increased with swimming speed (Fig. 6 A-B). As velocity increased, the durations of abduction (Fig. 6C) and adduction (Fig. 6D) decrease. The percentage of the stride of each part of the fin stroke is similar across swimming speeds, with abduction comprising about 60% of the stroke duration at all speeds (Fig. 6E). This pattern in *G. varius* is different from that found in *Lepomis* [11] and *Cymatogaster* [8] in which the percent stride time for abduction decreased and that for refractory period increased. This result suggests that bird wrasses gain thrust from their abduction phase across a range of speeds.

The pectoral fin tip traces a figure-8 path that is nearly perpendicular to the body axis and direction of motion (Fig. 7). At the end of adduction the fin is pressed against the lateral body surface. The fin then rotates rostrally to peel the leading edge away from the body in preparation for abduction (Fig. 5). At maximal abduction, the leading edge of the fin flips rapidly dorsally to produce the first stage of adduction (Fig. 5E). A lateral view of the path of the fin tip relative to the fish's body (Fig. 7B) shows that the stroke plane angle of the leading edge during abduction is close to 90° (vertical), and the average stroke plane angle set by anterior- and posterior-most fin excursions was 70° to the horizontal. A lateral view of the fin tip relative to the water velocity (Fig. 7C) reveals the stride length of a fin beat, the total distance traveled during one beat cycle. Stride length increased nearly linearly with swimming speed in the bird wrasse, with a slope close to 1.0.

The velocity of the center of mass in the direction of swimming (Fig. 7D) is roughly constant during abduction, decreases by several cm/s during the fin flip transition from abduction to adduction, and then increases sharply during adduction. This suggests that during abduction, drag on the extended fins is largely offset by thrust from lift or acceleration

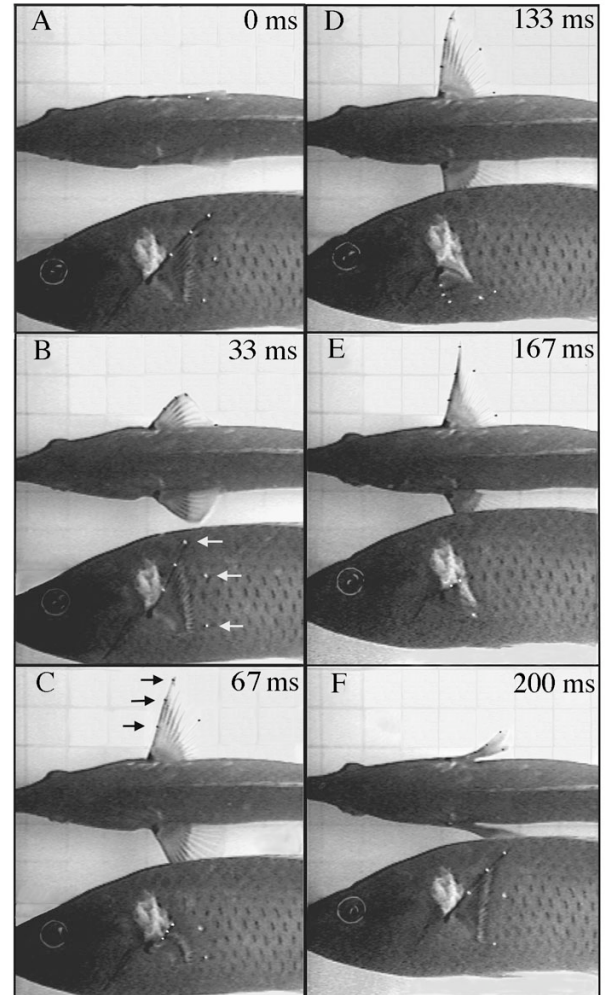


Fig. 5. Video images of pectoral locomotion by the bird wrasse *Gomphosus varius* in lateral view and dorsal (mirror) view, with a labeled left pectoral fin. (A) Fin is adducted. (B) Start of abduction, in which the dorsal view shows lateral motion of the fin tip and lateral view shows protraction of the fin. Fin markers in lateral view (see white arrows) appear light against the dark body. (C) Mid-abduction stage at which the fin is cambered in lateral view and approaches maximal anterior rotation in dorsal view. Fin markers in dorsal view (see dark arrows) appear dark against the white grid. (D) Near maximal abduction, the twisting of the fin is apparent and the overall angle of attack of the fin is low. (E) The fin flip during which the leading edge of the fin is brought rapidly upward and backward to begin adduction. (F) Fin is nearly fully adducted.

reaction, and that most propulsive force for accelerating forward is generated during adduction. The velocity of the center of mass of the body in the Y-direction (dorsoventral axis) reveals that the body of the bird wrasse bounces up and down in response to oscillating lift vectors (Fig. 7E). The body rose during abduction and fell during adduction, a behavior similar to other lift-based aquatic locomotion such as that of penguins.

Three-dimensional kinematic data allowed calculation of three variables important to hydrodynamic thrust mechanics: angle of attack, advance ratio, and the reduced frequency. Calculating

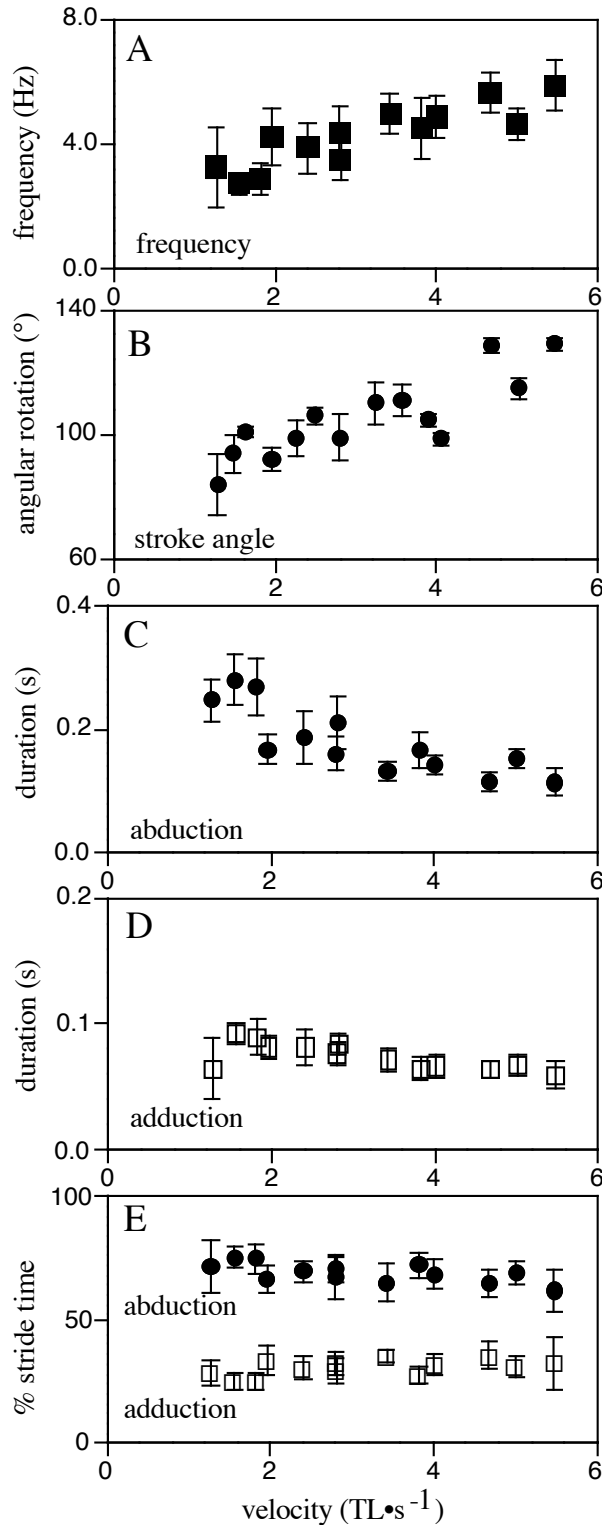


Fig. 6. Kinematic profiles of pectoral fin motion in *Gomphosus varius* across a speed range of 1-6 lengths per second. The frequency (A) of fin beats increases with swimming speed. The stroke angle (B) increases with increased swimming speed, whereas the durations of the abduction phase (C), and adduction phase (D) decrease with increasing swimming speed. However, the percentage of stride time (E) expressed as a percentage of the total beat duration is constant across this velocity range.

the angle of attack of a flapping appendage is difficult, requiring 3-dimensional coordinates from multiple positions on the fin and calculation of the resultant water velocity (the vector sum of the freestream, flapping, and induced velocities) and the potential for flexible fin membranes to develop camber (anteroposterior arching of the fin). Despite these problems, angles of attack have been calculated for proximal and distal chords [2]. The angle of attack is highly variable depending upon its position along the fin length (proximal or distal) and upon swimming speed. The angles of attack are strikingly different during the downstroke and upstroke, and during peak velocity the fin is twisted along its length like a propeller. During abduction the angle of attack of the proximal chord with respect to the direction of forward motion was greater than that of the distal chord. During adduction, the reverse was true. To calculate the hydrodynamic thrust generated by the twisted fin acting as a propeller blade, the net flow circulation around the fin during both abduction and adduction must be calculated or measured. This will require an integrated approach that will incorporate both flow circulation for lift and the changes in flow vectors due to acceleration reaction. Recent approaches using particle imaging hydrodynamics [3] and computational methods [7] will likely resolve these questions.

A measure of the ability of the fin to generate circulation around the wing for lift-based thrust is provided by the advance ratio, the ratio of forward speed to fin tip speed. The advance ratio for bird wrasses ranged from 0.5 at low velocities up to about 1.7 at high swimming speeds, indicating that forward speeds are high enough relative to fin speed for lift generation. These values are in the range of other flapping fliers that generate flow circulations around the wing for lift generation, including insects and aquatic birds [21].

The importance of the acceleration reaction in locomotor mechanics is summarized by the reduced frequency parameter, calculated as fin beat frequency multiplied by fin chord length divided by swimming speed. *Gomphosus varius* swam with a reduced frequency of about 1.5 at low speeds, decreasing to 0.6 at high velocities. Unsteady effects due to acceleration of fluid during oscillation of an appendage are considered important above 0.5. These results suggest that both lift and acceleration reaction forces play important roles in the flapping locomotion of fishes, the two perhaps contributing differentially to the overall thrust budget as forward velocity increases.

Fewer data are available for rowing fin motions, in which the fin is feathered during the forward stroke and pushed rearward broadside. However, simulation

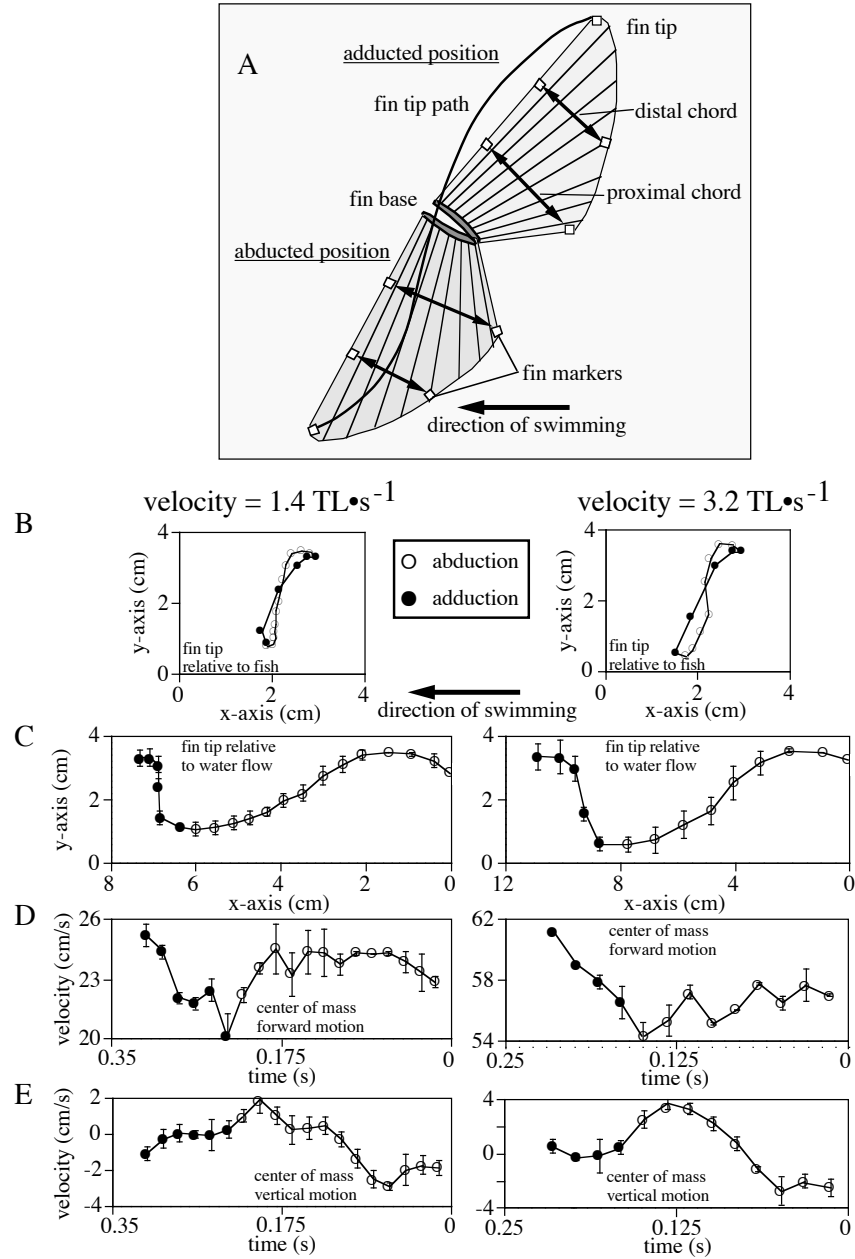


Fig. 7. Kinematic profiles of pectoral fin motion in *Gomphosus varius* at two different speeds; 1.4 and 3.2 body lengths per sec. The left fin of the fish is depicted during swimming from left to right in all plots. (A) Diagram of the pectoral fin at maximal abduction and maximal adduction to illustrate the positions of the fin markers at the fin tip and the ends of a proximal and distal chord along the fin. (B) Plot of the path of the fin tip from lateral view in relation to the body of the fish. Note the "figure-8" pattern and the steep stroke plane angle. (C) Plot of the path of the fin tip from lateral view in relation to the velocity of the water. The stride length is shown as the distance traveled along the x-axis. (D) Velocity of forward motion of the fish's center of mass during a single pectoral fin stroke. (E) Velocity of dorsoventral motion of the fish's center of mass during a single pectoral fin stroke. Abduction (open circles) is associated with the body rising due to lift on the fin.

experiments [5] demonstrated the primary differences between a rowing and flapping stroke. Rowing and flapping hydrodynamic models set upper and lower bounds on the mechanical performance of real limbs. The mechanical efficiency of a flapping appendage (ranging from about 0.2 to 0.6) was always higher than a rowing appendage (0.1 to 0.5) at equivalent hydrodynamic conditions. These efficiencies agree

quite well with experimental data, and the behavioral implications of this trade-off are seen in real fish fin motions [4]. A significant finding is that at slow speeds, flapping appendages are more efficient but rowing appendages generate more thrust. Large thrust, in turn, facilitates maneuverability. We suggest that the performance trade-off at slow speeds explains the presence of rowing in some aquatic vertebrates,

especially fishes.

Bioengineering may ultimately want to attempt to mimic the structure and motion of real animal fins to achieve the greatest range of function in fin-like propulsors of underwater vehicles. In particular, efficiency at high speeds requires a flapping stroke and high thrust and maneuverability at lower speeds is best attained by a rowing stroke. Stroke frequency, stroke plane angle, and 3-dimensional amplitude should be relatively easy to duplicate. However, the complex dynamic twisting and bending that fins perform during swimming is simultaneously critical to thrust forces of the fin and likely difficult to mimic. Research questions surrounding complex fin motions include the hydrodynamics of fin motions and the degree to which complex 3D motions are caused by active muscle contraction or passive mechanical properties of the fins. Study of motor control and neurobiology is a key to a complete understanding of fin function.

I. MOTOR PATTERNS AND NEURAL CIRCUITRY OF PECTORAL FINS

The mechanisms of neural control of pectoral locomotion in fishes are relatively unexplored, yet knowledge of muscle contraction patterns, neuroanatomy, and neural circuits are critical to developing models of pectoral fin function. The basic contraction pattern of pectoral muscles [13] is that of alternate activity of the antagonistic abductor and adductor groups (Fig. 8). Starting at the maximal adduction with fins against the body, the abduction phase begins with activity of the arrector ventralis muscle before the other abductors. The arrector ventralis rotates the fin forward to initiate the peel of the leading edge away from the body. The abductor superficialis and profundus are then active with the arrector ventralis to produce the downstroke of the fin. Immediately following maximum abduction, adduction begins with the fin flip, initiated by activity of the arrector dorsalis muscle. Then the adductor superficialis and profundus are active in synchrony with fin adduction (Fig. 8).

Frequency and amplitude of EMG activity increase with increasing swimming speeds. The durations of abductors are significantly greater than adductors, with the abductor profundus showing the longest duration. However, EMG durations do not change significantly as a function of forward velocity. Rather, the inter-EMG lag time between cycles decreases with increased speed. The onset times of the abductor profundus and superficialis relative to arrector ventralis do not change significantly as a function of

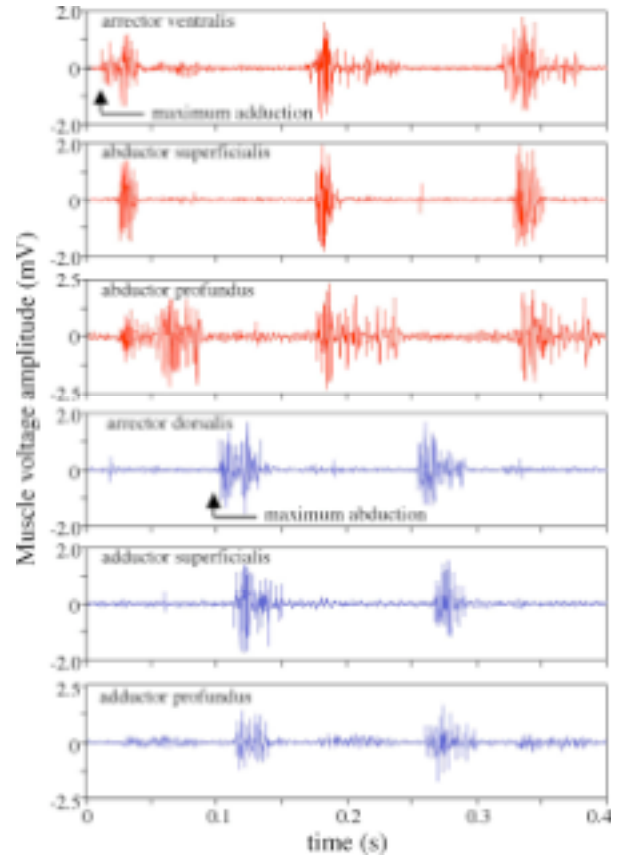


Fig. 8. Pectoral EMGs of a high efficiency flapping stroke in the bird wrasse at 3.8 TL/s. Alternate activation of downstroke (red) and upstroke (blue) muscle groups power the fin locomotor cycle. Kinematic maxima are shown. AV begins abduction, and the AbP shows long duration activity during the downstroke. The AD initiates activity of the adductors during the upstroke.

speed, but the onset times of the adductors relative to arrector ventralis decrease at higher velocities.

The motor patterns of fin flapping muscles give us substantial insight into the neuromotor basis of labriform swimming. The integration of EMG data with kinematics reveals that EMG activity of abductors is synchronous with the onset and action of abduction, and that adductor EMG is nearly synchronous with adduction. These results are in contrast to EMG data collected for undulatory axial locomotion [23], the activity of pectoral muscles in bird flight [24], and the activity of the flight muscles of insects [25]. These previous studies have shown that EMG activity in axial fish muscle and flight muscle begins substantially before the behavior that the muscle is responsible for producing. Arrector ventralis activity is synchronous with initiation of abduction, arrector dorsalis activity is synchronous with the fin flip beginning adduction, and the large antagonistic abductor and adductor muscles are active during the major rotational motions of the fin in downstroke and upstroke.

EMG data show that there is fine motor control of both fin shape, fin twist, and the position of individual fin rays during both downstroke and upstroke. The interaction of motor control and muscle forces with the mechanical properties of the fin and its motion is a key unanswered question. Further study of nerve function, muscle contraction, and fin behavior will address this research goal and will provide bioengineers additional biological data for designing fin control systems.

Few studies have examined pectoral fin neural control in fishes [26], [27], although techniques are available for analyzing nerve structure and activity. Triple staining pectoral fins for bone, cartilage, and nervous tissue (Fig. 9) reveals the gross neuroanatomy of the fin mechanism. The pectoral fin is innervated by the dorsal and ventral roots of several anterior spinal cord segments that descend from the cord to enter the pectoral girdle as a combined brachial plexus (Fig. 9). Labeling of pectoral motoneurons [26] showed that the majority of motor axons extend from the ventral root of segment 3, and 1 or 2 other vertebral segments. Sensory and motor axons then branch to serve the pectoral muscles. Currently, there are no data on the activity of the motor axons of pectoral fin nerves. However, experiments are possible with direct recording of action potentials in the pectoral nerves using hook electrodes [28] applied both above and below the fusion of the spinal nerves to form the brachial plexus. Nerve recordings generated in synchrony with muscle activation will allow interpretation of components of the neural circuit that controls the pectoral muscles. Such experiments can provide data on neural control signals and muscle responses to generate a more complete picture of neuromuscular function in aquatic locomotion.

In addition to nerve staining, other preparations

using zebrafish have produced key advances in our understanding of pectoral fin neuroanatomy and muscle function. New approaches permit precisely labeling fin motoneurons and fin muscles. Fins are well formed by the larval stage with cartilaginous fin rays and muscles developed to actuate the fins. The larval zebrafish fin is relatively simple with two major muscles. The extensor muscle, the abductor pectoralis, is located on the rostral side of the fin and pulls the fin forward when it contracts. The flexor muscle, the adductor pectoralis, is located on the caudal side of the fin and pulls the fin back against the body when it contracts. Figure 10a-c shows confocal sections through these muscles in a transgenic fish that expresses green fluorescent protein in muscle fibers ($\square$ - actin GFP [29]). As can be seen in the planar views of the extensor and flexor muscles (Figure 10a and b), muscle fibers run in a sheet on the fin extending up the fin from its base. Other approaches are available for labeling motoneurons in the fin, allowing simultaneous imaging of the muscles and parts of the circuits that control them.

Rhythm generating circuits are integral to many vertebrate behaviors including an array of locomotor movements. The best understood vertebrate rhythm generating network, the axial locomotor system in fishes and aquatic amphibians, mediates left-right alternations of axial muscle contraction. The primary locomotor rhythm in tetrapods and some fishes involves flexion and extension of the limb or fin [30]. For tetrapod limbs, considerable progress has been made in understanding the neuroanatomy and ontogeny of limb movement [30]-[33], but the complexity of the mammalian spinal cord and limbs makes studies of circuit organization difficult. An *in vitro* walking preparation for *Necturus* [30] has been fruitful for studying the neural basis of tetrapod limb movements

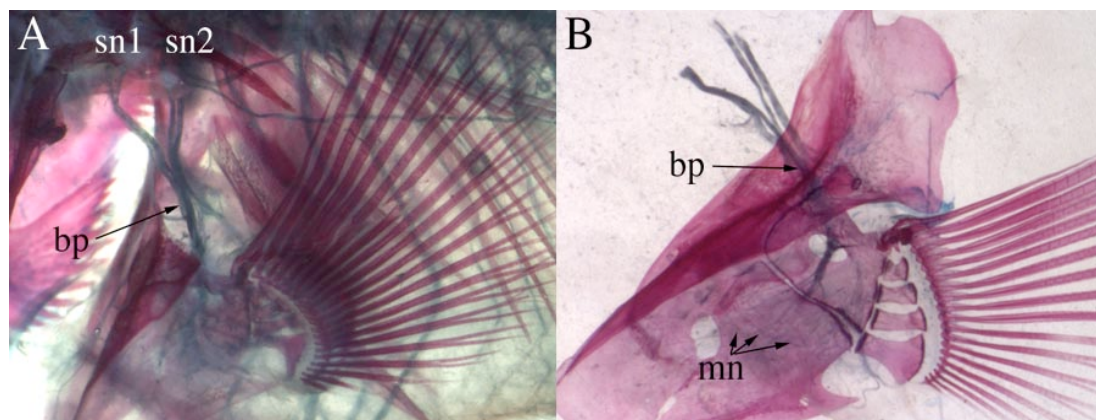


Fig. 9. Neuroanatomy of the pectoral fin. (A) The pectoral fin is innervated by both sensory and motor neurons descending from the first and second spinal nerves (sn1, sn2) that join to form the brachial plexus (bp) that enters the pectoral fin region medially. (B) the brachial plexus splits medially and half passes through the scapular foramen to serve the lateral abductor muscles. Populations of motor neurons (mn) branch out to serve the main pectoral muscles both medially and laterally.

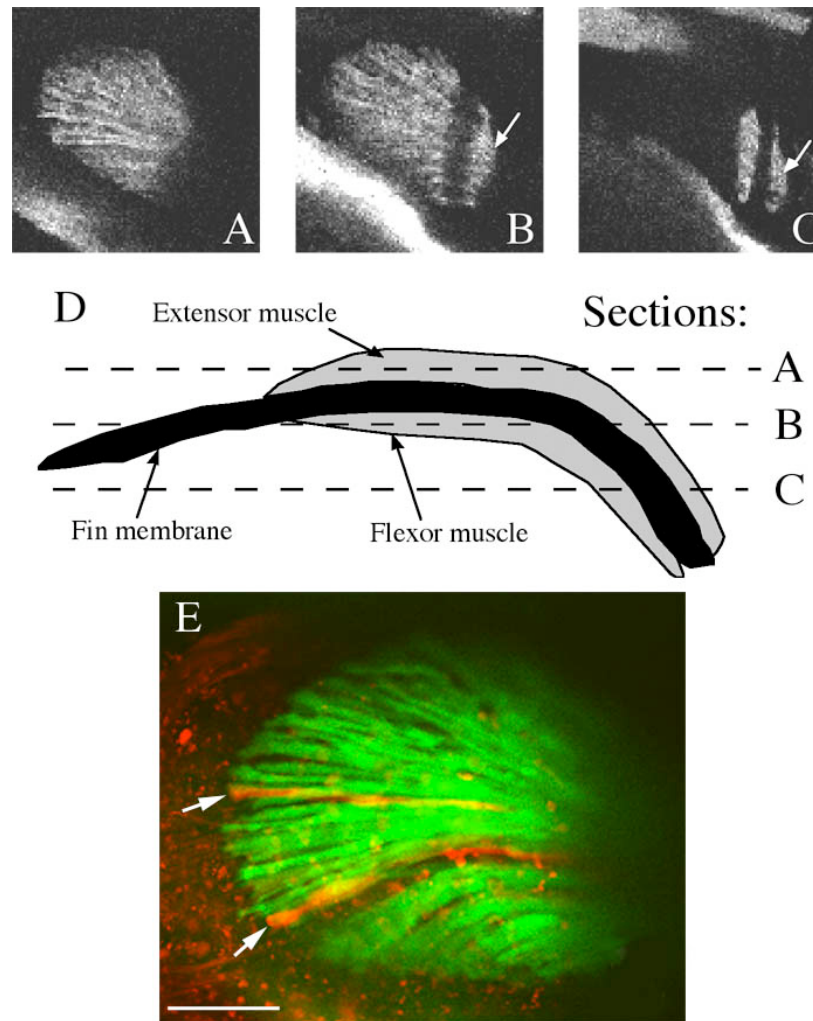


Fig. 10. Optical sections through pectoral fin muscle of an α -actin transgenic zebrafish expressing GFP with rostral to the right. (A) Planar section through the extensor muscle. (B) Flexor muscle (left) and cross section through extensor muscle (right, with arrow). (C) Cross sections through the flexor muscle (left) and extensor muscle (right with arrow). (D) Orientation of the muscle sections A through C on the entire pectoral fin. (E). Muscle fibers labeled with Texas Red dextran (indicated by arrows) in the extensor muscle of the α -actin GFP transgenic showing labeling specificity. Scale bar = 50 μ m.

by isolating interneuron centers for movements [34], [35]. Despite broad interest in their organization, it has been difficult to propose how individual cells are connected within a circuit.

Similar challenges exist for fin neural circuits, and major questions remain regarding basic pectoral fin circuitry and the central mechanisms of generation and coordination of rhythmic motion in fin systems. However, the pectoral fin is a simpler system than limbs, and may yield significant insight into the design of locomotor neural circuits. Zebrafish demonstrate a range of behaviors during fin-based locomotion that correspond to tetrapod limb-based locomotion, including alternating and synchronous limb movement. Neurally, the zebrafish spinal cord organization is simpler than that of tetrapods with

fewer cells, many of which have been described morphologically [36], [37]. The fin system's accessibility makes it possible to approach questions of rhythm coordination and fin stroke control.

Similar to the lamprey and tadpole axial systems, there is evidence that inhibitory interneurons are important for coordinating the activity of extensor and flexor centers in fin and limb neural circuits [38]. Inhibitory neurotransmitters glycine and GABA suppress rhythmic activity and antagonists of those receptors, strychnine for glycine and bicuculline for GABA_A, changed the alternating EMG activity of extensors and flexors to simultaneous EMG bursts. The inhibitory interneurons that appear to function in limb movement and other interneurons used in the response have not been identified morphologically. However, four broad classes of interneurons involved

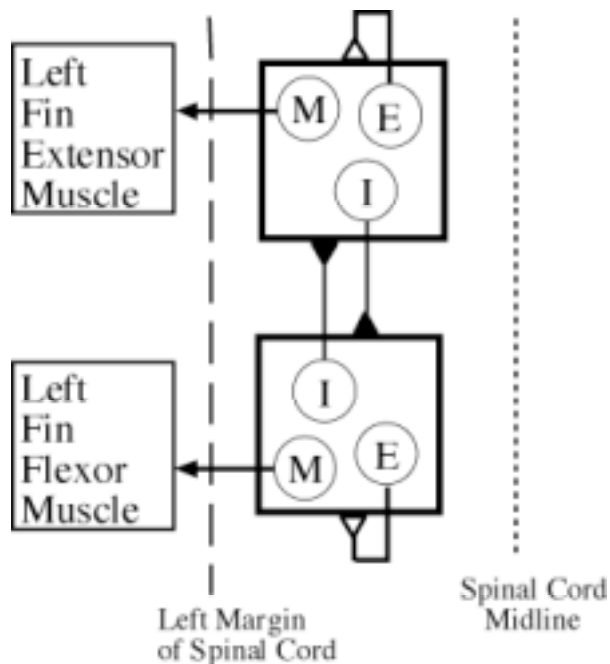


Fig. 11. Model of circuit for the extensor/flexor rhythm in fin locomotion based on the left/right axial rhythm generating circuit in lampreys and tadpoles. E=excitatory interneurons, I=inhibitory interneurons, M=motoneurons.

in rhythmic limb movement have been identified electrophysiologically in *Necturus* based on their activity during the extension/flexion cycle, one during limb extension, one during flexion and one at each of the transitions between the two movements [34].

By analogy to the axial rhythm generating circuit, a model for limb rhythmic activity has been proposed (Fig. 11). A simple model is postulated for the extensor/flexor fin locomotor rhythm based on the left/right axial circuit of lampreys and tadpoles and models of the extensor/flexor rostral scratch circuit of turtles [38]. Excitatory interneurons activate all cells in a half center causing inhibitory interneurons that cross between the half centers to inhibit activity in the other half center prevent antagonist muscle contraction. Excitatory interneurons also cause motoneurons to initiate agonist muscle contraction. The physiologically defined cell types [34] may correspond to the four interneurons (excitatory extensor, excitatory flexor, inhibitory extensor and inhibitory flexor) proposed in this model. In addition to ipsilateral cells and circuits, contralateral input appears necessary to generate a normal ipsilateral rhythm in some limb rhythms [38]. Empirical measurements of nerve activity, muscle function, and behavior combined with testing models of neural circuits will help reveal the role of interneurons involved in limb rhythms and the extensor/flexor circuits of aquatic propulsors.

Testing the motor circuits of pectoral fin locomotion is an important step in understanding limb neural circuits, and will have important impacts on both basic research and the applied goals of engineers designing control systems for vehicle propulsors. At a broader level, understanding the neural control of complex locomotor behaviors is one of the central goals of neurobiology [38], [39], [40], with considerable progress being made in recent years using model systems and novel imaging techniques. The contributions to this volume identify a new field of applied neurobiology that integrates biomechanics [this paper], central pattern generation and motor control [41] with sensory systems and engineering design [42], [43] that may derive new ways of designing and controlling underwater vehicles.

I. CONCLUSION

We have reviewed pectoral fin locomotion in the areas of structure, kinematics, and neural control. For each area, we identify important areas for future basic research and for applied uses in bioengineering of fin-based propulsors for underwater vehicles. The morphology of pectoral fin skeletons and muscles can be analyzed from the point of view of quantitative biomechanical modeling, allowing for broadscale comparison of alternative structural conformations among species. Pectoral fin structure holds great promise for the design of propulsors that can provide high efficiency and high maneuverability to aquatic vehicles in shallow surge zone applications. Kinematics studies of pectoral fin motion provide the information needed to test hypotheses of fin function and analyze hydrodynamics of fin-based locomotion. In addition, biomimicry of real fin motions may greatly improve the thrust and efficiency of propulsors designed for aquatic vehicles. Finally, the neural circuits and motor control of pectoral muscles is a critical unexplored area of fin function. Numerous questions remain regarding sensory-motor control of fins, the circuits for setting up fin oscillatory motion, and the role of neural control in the fine details of fin motion. These areas are of simultaneous interest to biologists interested in animal function and engineers considering control systems for biologically based vehicle propulsors.

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REFERENCES

- [1] M. W. Westneat, "Functional morphology of aquatic flight in fishes: Mechanical modeling, kinematics, and electromyography of labriform locomotion," *Amer. Zool.*, vol. 36, pp. 582-598, 1996.
- [2] J. A. Walker and M. W. Westneat, "Labriform propulsion in fishes: Kinematics of flapping aquatic flight in the bird wrasse *Gomphosus varius* (Labridae)," *J. Exp. Biol.*, vol. 200, pp. 1549-1569, 1997.
- [3] E. G. Drucker and G. V. Lauder, "A hydrodynamic analysis of fish swimming speed: wake structure and locomotor force in slow and fast labriform swimmers," *J. Exp. Biol.*, vol. 203, pp. 2379-2393, 2000.
- [4] J. A. Walker and M. W. Westneat, "Performance limits of labriform propulsion and correlates with fin shape and motion," *J. Exp. Biol.*, vol. 205, pp. 177-187, 2002.
- [5] J. A. Walker and M. W. Westneat, "Mechanical performance of aquatic rowing and flying," *Proc. Roy. Soc. Lond. B.*, vol. 267, pp. 1875-1881, 2000.
- [6] D. H. Thorsen and M. W. Westneat, "Pectoral girdle form and function: Diversity of the musculoskeletal system of fishes with labriform propulsion," In review, *J. Morph.*, 2003.
- [7] R. W. Ramamurti, W. C. Sandberg, R. Lohner, J. A. Walker, and M. W. Westneat, "Computational fluid dynamics of flapping aquatic flight in the bird wrasse: 3-D unsteady computations," *J. Exp. Biol.*, vol. 205, pp. 2997-3008, 2002.
- [8] P. W. Webb, "Kinematics of pectoral fin propulsion in *Cymatogaster aggregata*," *J. Exp. Biol.*, vol. 59, pp. 697-710, 1973.
- [9] R. W. Blake, "The mechanics of labriform locomotion. I. Labriform locomotion in the angelfish (*Pterophyllum eimekei*): an analysis of the power stroke," *J. Exp. Biol.*, vol. 82, pp. 255-271, 1979.
- [10] P. J. Geerlink, "Pectoral fin kinematics of *Coris formosa* (Teleostei, Labridae)," *Neth. J. Zool.*, vol. 33, pp. 515-531, 1983.
- [11] A. C. Gibb, B. C. Jayne, and G. V. Lauder, "Kinematics of pectoral fin locomotion in the bluegill sunfish *Lepomis macrochirus*," *J. Exp. Biol.*, vol. 189, pp. 133-161, 1994.
- [12] E. G. Drucker and J. S. Jensen, "Pectoral fin locomotion in the striped surfperch. I. Kinematic effects of swimming speed and body size," *J. Exp. Biol.*, vol. 199, pp. 2235-2242, 1996.
- [13] M. W. Westneat and J. A. Walker, "Motor patterns of underwater flight: an electro-myographic study of the pectoral muscles in the bird wrasse, *Gomphosus varius*," *J. Exp. Biol.*, vol. 200, pp. 1881-1893, 1997.
- [14] E. G. Drucker and J. S. Jensen, "Kinematic and electromyographic analysis of steady pectoral fin swimming in the surfperches," *J. Exp. Biol.*, vol. 200, pp. 1709-1723, 1997.
- [15] P. R. Bandyopadhyay, "Maneuvering Hydrodynamics of fish and small underwater vehicles," *Integ. Comp. Biol.*, vol. 42, pp. 102-117, 2002.
- [16] P. R. Bandyopadhyay, J. M. Castano, J. Q. Rice, R. B. Philips, W. H. Nedderman, and W. K. Macy, "Low-speed maneuvering hydrodynamics of fish and small underwater vehicles," *J. Fluids Eng.*, vol. 119, pp. 136-144, 1997.
- [17] P. C. Wainwright, D. R. Bellwood, and M. W. Westneat, "Ecomorphology of locomotion in labrid fishes," *Env. Biol. Fishes*, vol. 65, pp. 47-62, 2002.
- [18] M. W. Westneat, "Transmission of force and velocity in the feeding mechanisms of labrid fishes," *Zoomorph.*, vol. 114, pp. 103-118, 1994.
- [19] M. W. Westneat, "A biomechanical model for analysis of force and motion in the mandible of fishes," *J. Theor. Biol.*, vol. 203, pp. 2003.
- [20] C. M. Breder, Jr., "The locomotion of fishes," *Zoologica*, vol. 4, pp. 159-291, 1926.
- [21] S. Vogel, "Life in Moving Fluids (2nd Ed.)," Princeton: Princeton University Press, 1994.
- [22] R. W. Blake, "Fish Locomotion," Cambridge University Press, Cambridge, 1983.
- [23] C. S. Wardle, J. J. Videler, and J. D. Altringham, "Tuning in to fish swimming: body form, swimming mode, and muscle function," *J. Exp. Biol.*, vol. 198, pp. 1629-1636, 1995.
- [24] K. P. Dial, G. E. Goslow, Jr., and F. A. Jenkins, Jr., "The functional anatomy of the shoulder of the European starling (*Sturnus vulgaris*)," *J. Morph.*, vol. 207, pp. 327-344, 1991.
- [25] M. S. Tu and M. H. Dickinson, "Modulation of negative work output from a steering muscle of the blowfly *Calliphora vicina*," *J. Exp. Biol.*, vol. 192, pp. 207-224, 1994.
- [26] P. Z. Myers, "Spinal motoneurons of the laval zebrafish," *J. Comp. Neurol.*, vol. 236, pp. 555-561, 1985.
- [27] L. R. Parenti and J. Song, "Phylogenetic significance of the pectoral/pelvic fin association in acanthomorph fishes: A reassessment using comparative neuroanatomy," In: M. L. J. Stiassny, L. R. Parenti, and G. D. Johnson, eds., "Interrelationships of Fishes," pp. 427-444, Academic Press, San Diego, 1996.
- [28] S. Shefchyk, D. McCrea, P. Kriellaars, P. Fortier, and L. Jordan, "Activity of interneurons within the L4 spinal segment of the cat during brainstem-evoked fictive locomotion," *Exp. Brain Res.*, vol. 80, no. 2, pp. 290-295, 1990.
- [29] S. Higashijima, H. Okamoto, N. Ueno, Y. Hotta, and G. Eguchi, "High-frequency generation of transgenic zebrafish which reliably express GFP in whole muscles or the whole body using promoters of zebrafish origin," *Devel. Biol.*, vol. 192, pp. 189-199.
- [30] M. Wheatley and R. B. Stein, "An in vitro preparation of the mudpuppy for simultaneous intracellular and electromyographic recordings during locomotion," *J. Neurosci. Methods*, vol. 42, pp. 129-137, 1992.
- [31] J. R. Cazalets, M. Borde, and F. Clarac, "Localization and organization of the central pattern generator for hindlimb locomotion in newborn rats," *J. Neurosci.*, vol. 15, pp. 4943-4951, 1995.
- [32] O. Kjaerulff and O. Kiehn, "Crossed rhythmic synaptic input to motoneurons during selective activation of the contralateral spinal locomotor network," *J. Neurosci.*, vol. 17, pp. 9433-9447, 1997.
- [33] P. Whelan, A. Bonnot, and M. J. O'Donovan, "Properties of rhythmic activity generated by the isolated spinal cord of the neonatal mouse," *J. Neurophysiol.*, vol. 86, pp. 2821-2833, 2000.
- [34] M. Wheatley, K. Jovanovic, R. B. Stein, and V. Lawson, "The activity of interneurons during locomotion in the in vitro *Necturus* spinal cord," *J. Neurophysiol.*, vol. 71, pp. 2025-2032, 1994.
- [35] J. Cheng, R. B. Stein, K. Jovanovic, K. Yoshida, D. J. Bennett, and Y. Han, "Identification, localization and modulation of neural networks for walking in the mudpuppy (*Necturus maculatus*) spinal cord," *J. Neurosci.*, vol. 18, pp. 4295-4304, 1998.
- [36] R. R. Bernhardt, A. B. Chitnis, L. Lindamer, and J. Y. Kuwada, "Identification of spinal interneurons in the embryonic and larval zebrafish," *J. Comp. Neurol.*, vol. 302, pp. 603-616, 1990.
- [37] M. E. Hale, D. A. Ritter, and J. R. Fetcho, "A confocal study of spinal interneurons in living larval zebrafish," *J. Comp. Neurol.*, vol. 537, pp. 1-16, 2001.
- [38] P. S. Stein, J. C. Victor, E. C. Field, and S. N. Currie, "Bilateral control of hindlimb scratching in the spinal turtle: contralateral spinal circuitry contributes to the normal ipsilateral motor pattern of fictive rostral scratching," *J. Neurosci.*, vol. 15, pp. 4343-4355, 1995.
- [39] J. R. Fetcho, "Morphological variability, segmental relationships, and functional role of a class of commissural

- interneurons in the spinal cord of goldfish," *J. Comp. Neurol.*, vol. 299, pp. 283-298, 1990.
- [40] M. E. Hale, "S- and C-start escape responses of the muskellunge (*Esox masquinongy*) require alternative neuromotor mechanisms," *J. Exp. Biol.*, vol. 205, pp. 2005-2016, 2002.
 - [41] F. A. Mussa-Ivaldi and S. A. Solla, "Neural primitives for motion control," *IEEE J. Ocean Eng.*, vol. In press, 2003.
 - [42] M. A. MacIver, "Neuromechanical design and active sensory systems in animals," *IEEE J. Ocean Eng.*, vol. In press, 2003.
 - [43] J. E. Colgate and K. M. Lynch, "Design and control of robotic swimming machines: A review," *IEEE J. Ocean Eng.*, vol. In press, 2003.