Principles of Actuation in the Muscular System of Fish

Lawrence C. Rome

Abstract—**Over the last 20 years, there have been tremendous intellectual and technological advancements in the fields of muscle biophysics, biomechanics, and musculoskeletal modeling. These advances have fueled a revolution in integrative muscle physiology. Whereas 20 years ago the notion of understanding the function and design of a muscular system from the molecular to the whole animal level was a dream, it is now becoming a reality. Fish represent an exceptional model for understanding the function and design of the muscular system of vertebrates. There are two fundamental reasons for this preeminence. First, the unique anatomical separation of the different muscle fiber types has made fish the most tractable model (i.e., the use and properties of the different muscle fiber types can be most easily studied). Second, fish utilize the broadest range of movement than any vertebrate. This diversity of movement imposes a wide array of challenges on the muscular system of fish and at the same time enables physiologists/biomechanists to observe how these challenges have been met. These features have permitted us to extract a number of general principles of actuation and control that have evolved over millions of years. Rather than summarizing the considerable literature on fish muscle function and fish swimming, this paper will focus narrowly on a relatively few studies that permit us to extract principles of actuation. These principles may in turn provide some insights into the design and construction of autonomous underwater vehicles (AUVs).**

Index Terms—**Fish, muscle design, swimming.**

I. Introduction

ANIMALS perform a great variety of motor tasks, and fish are especially noteworthy. Their motor tasks range from making explosive movements taking less than ~25 ms, to sustained swimming over thousands of miles in the ocean, to producing sound at several hundred hertz for communication. These activities require very different outputs from the muscles [1], [2]. Accordingly, research over the past several decades has revealed that vertebrate muscle tissue has enormous diversity, perhaps more than any other tissue.

Recently, with the advent of new integrative muscle physiology techniques, research has focused on comparing these diverse muscle properties to the function muscles must actually perform *in vivo* [3], [4]. This has led to two important conclusions. First, there is an excellent matching between the properties of the muscles and the mechanical performance that is required of the muscles *in vivo*. Second, no one type of muscle can perform all the required motor activities effectively—rather, different types of muscles (along with different muscular anatomies) are required to perform the full repertoire of motor activities in which animals engage [5]. These facts no doubt underlie the large diversity of muscle properties observed within and between species.

Insights developed about the function and design of the fish muscular system can, in principle, aid efforts in building autonomous underwater vehicles (AUVs). First, the biophysical mechanisms and ultrastructural arrangement of myofilaments and sarcomeres, which permit muscle to generate force and to shorten, may be transferable to the design and synthesis of artificial muscle. Second, the unique geometry of the muscle attachments within fish may provide insights into how artificial muscles should be attached in AUVs. Third, examining how various components of the muscular system (at different levels of organization) are varied to permit a wide range of movement may provide strategies that can be utilized in AUVs. Finally, it may be possible to use actual components of the fish muscular system (i.e., the fish muscle itself) to power AUVs. Based principally on laboratory work on carp, scup, and toadfish over the past 20 years, this chapter will focus on a relatively few studies of the fish muscular system that permits one to extract a series of principles of actuation, characterize some fundamental differences between artificial and real muscles, and assess the possibility of using fish muscle in a man-made device.

II. Fish Provide an Exceptional Experimental Model for Exploring Muscle Function

Breakthroughs in the understanding of muscle function and muscular system design have been fueled in a large part by the use of fish as an experimental model. In all vertebrates, there is considerable diversity of the physiological/mechanical properties of skeletal muscle cells (muscle fibers) within a given animal. Muscle fibers with like properties are usefully grouped together and categorized as separate muscle fiber types. There are at least three fiber types in all vertebrates, each of which represents a biological actuator with different physiological/mechanical properties. To understand how these actuators power different activities, it is obviously important to know 1) which are recruited (activated) for which motor activities; and 2) what are their characteristic physiological/mechanical properties. Prior to the use of fish, characterizing the properties of these different fiber types and how they are used to perform different functions was problematic. Mammalian muscle is typically heterogeneous, that is, slow-twitch muscle fibers (slow contracting) are interspersed with fast-twitch muscle fibers (fast contracting)

Manuscript received May 21, 2004; accepted February 10, 2005. This paper was supported by National Institutes of Health (NIH) grants (AR38404 and AR46125), Office of Naval Research (ONR) grant (N000140310568), and a grant from the University of Pennsylvania Research Foundation. Associate Editor: J. Lynch.

The author is with the Department of Biology, University of Pennsylvania, Philadelphia, PA 19104 USA, and also with the Marine Biological Laboratory, Woods Hole, MA 02543 USA (e-mail: lrome@sas.upenn.edu).

Digital Object Identifier 10.1109/JOE.2005.852346

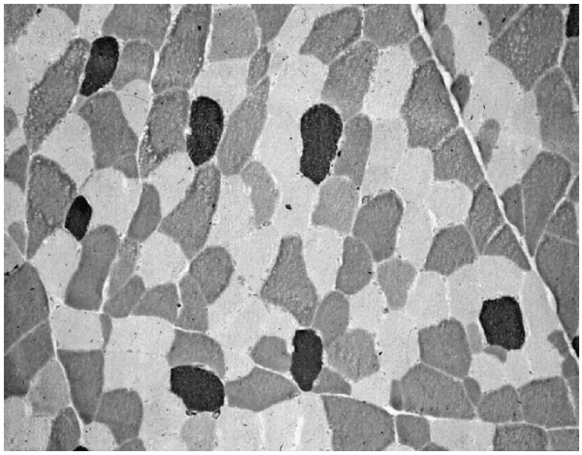

Fig. 1. Cross section of horse muscle stained histochemically for different muscle fiber types.

(Fig. 1). Experimentally, this makes it very difficult to identify which fibers are active during particular motor activities [i.e., electromyography (EMG) electrodes implanted in muscles will pickup signals from fibers of all types, making it extremely difficult to discriminate which types are powering a particular movement [6]—note that there has been recent development of new techniques [7]–[9]]. In addition, any given bundle of fibers dissected from a muscle will necessarily contain more than one fiber type, making it difficult to differentiate the properties of one fiber type from another [10]. Speculation about the properties of different fiber types and how they are used during activities such as running and weight lifting are rampant in the field of exercise physiology; however, these conclusions have generally been based on indirect evidence.

In fish, by contrast, the different muscle fiber types are organized into large, homogenous, and anatomically separated regions that are obvious to the naked eye Fig. 2(c) [11]–[14]. This enables researchers to overcome both obstacles mentioned above for studying the mammalian muscular system [15]. First, EMG electrodes can be implanted into these anatomically separate regions to monitor which swimming activities are powered by each fiber type (see Fig. 2) [16]–[18]. Second, one can dissect bundles of fibers, which are all of the same type, and hence one can, in a relatively straightforward manner, determine the mechanical, biochemical, and ultrastructural properties of each muscle fiber type [Fig. 2(a) and (b)] [19]–[23]. It should be noted that in some species (e.g., salmonids) this separation may not be complete (i.e., red muscle fibers are interspersed with white muscle fibers). Consequently, prior to using a particular species as an experimental model, its fiber type distribution must be determined. Finally, as illustrated below, fish undergo the widest range of movement of any vertebrate, providing considerable challenges to the design of the muscular system. Because of these advantages, the fish muscular system has become widely used in studies of comparative muscle design [2], [24], [25].

III. Muscle Fiber Types

In this section, four different fish muscle fiber types are briefly defined and how they are used *in vivo* is discussed. The remainder of the chapter explores the differences in properties and usage in greater detail. This part focuses on three trunk muscle fiber types used for swimming, along with a single muscle fiber type associated with the swimbladder and used for sound production. It should be noted that additional fiber types are found attached to the jaws, eyes, and fins [26], [27]. In addition, some muscles have lost their ability to generate force altogether, evolving into heater organs [28], [29]. Discussion of these additional fiber types goes beyond the coverage here.

A. Mechanical Properties

Muscle fiber types are defined by both their mechanical properties and their metabolic properties. The mechanical properties can be expressed by measurements of the maximum velocity of shortening $(V_{\max})$, the rate of activation and force generation, and the rate of muscle relaxation. The rate at which muscle uses energy is also generally proportional to the overall speed of the muscle [30]. Muscles used for slow motor activities (e.g., maintaining posture or performing slow movements) typically activate and relax slowly, have a low $V_{\max}$, and use energy slowly. These are called slow-twitch muscle fibers. Muscle used for fast and powerful movements activate and relax quickly, have a high $V_{\max}$, and use energy rapidly. These are called fast-twitch muscles. Muscles used for rapid eye movements or to generate sound for communication activate and relax extremely rapidly, have a high $V_{\max}$, and use energy extremely rapidly. These are called "superfast-twitch muscles" [19].

B. Metabolic Properties

Slow-twitch fibers are thought to be recruited even during low intensity activity and hence are used a large percentage of the time [31]. They must therefore be highly aerobic to prevent build up of anaerobic byproducts (e.g., lactic acid) that cause fatigue. In mammals, slow-twitch fibers with high aerobic capacities are called "slow-twitch oxidative fibers" (SO, Type I). In fish, they are called "slow-twitch red fibers" (the red color in fish muscle is due to the presence of high densities of myoglobin, mitochondria, and capillaries necessary to support a high oxygen consumption rate) [21], [24] [32]–[35]. At the other end of the spectrum, "fast-twitch glycolytic" muscles (FG or Type IIb in mammals) are the last fiber types to be recruited and thus are used only occasionally (for rapid acceleration or escape) [36]–[38]. They use energy very rapidly—at a rate that cannot be maintained aerobically. Thus, they use glycolytic metabolism almost exclusively, which results in rapid fatigue. In most fish, this muscle is white (due to very low densities of myoglobin, mitochondria and capillaries) and hence is referred to as "fast-twitch white muscle." There is also an intermediate fiber type that is both fast and is used aerobically (e.g., for long distance fish swimming and bird flying). In mammals, these are called "fast-twitch oxidative glycolytic" (FOG) or Type IIa fibers. In fish, they are called "pink muscle" [39]. This coloration is due to intermediate densities of myoglobin, mitochondria, and blood supply. In fish, the pink muscle forms a thin sheet that sits between the red and the white muscles. Finally, superfast-twitch muscles can be either highly aerobic or anaerobic depending on their function. Two aerobic muscles are the shaker muscle of rattlesnakes (which shakes its tail for many hours) [40], [41] and the swimbladder muscle of the midshipman (*Porichthys notatus*; which produces a long and continuous mating call [42]–[45]). The swimbladder muscle of the

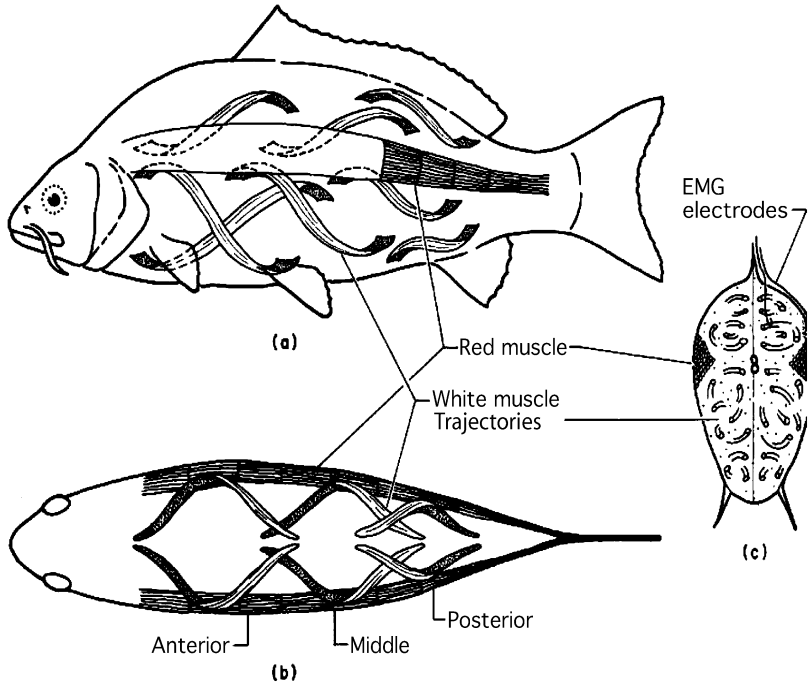

Fig. 2. Deposition of different muscle fiber types in carp. From [15].

oyster toadfish (*Opsanus tau*), in contrast, has a low aerobic capacity, reflecting that its mating call is intermittent [46]–[48].

IV. Recruitment of Different Fiber Types

In the preceding paragraph, the general usage of different fiber types was discussed. Prior to work on fish, the recruitment pattern of different fiber types was rarely measured during locomotion. However, taking advantage of the anatomical separation of the muscle fiber types in fish has made it relatively straight forward to measure recruitment. In experiments on swimming carp (*Cyprinus carpio*), at relatively slow steady swimming speeds only slow-twitch red fibers were recruited, and at high speeds the fast-twitch white fibers were additionally recruited [18], [49].

Furthermore, when fish recruited the white muscle, they shifted from "steady" swimming to "burst and coast" swimming [50]. Subsequent work on marine scup (*Stenotomus chrysops*) showed that the intermediate pink muscle was additionally recruited at intermediate steady swimming speeds [51]. Thus, as the fish swims faster, faster muscle fiber types are additionally recruited, but the slower types remain activated. The swimming speed at which faster muscle types are recruited seems to be well explained by the biomechanics of the muscle and swimming (see further discussions below).

V. Muscle Structure

The muscle structure can be viewed at multiple levels, ranging from the gross level, to the cellular, and eventually down to the ultrastructural or molecular level. There is a great deal of variation in muscle at each of these levels, some of which are associated with different fiber types.

A. Gross Level

The gross structure sets the gearing of muscles. That is, how much body movement a given shortening of muscle can produce. This gearing is set by both the orientation of the fibers within the muscle and the placement of the origin and insertion of the muscle. One fiber arrangement is "parallel," in which the fibers run parallel to the long axis of the body—this is evident in the red and pink muscles of fish. Another orientation is a complex helical arrangement found in the white muscle of fish (Fig. 2) [15], [52]–[54]. Different fiber arrangements can have a marked effect on the function of muscle. In fish, for instance, parallel orientation to the long axis endows the red and pink muscles with a relatively low gear ratio, whereas the helical structure of the white muscle endows it with a high gear ratio. The different gear ratios are equivalent to low and high gears on a bicycle. This difference, together with differences in $V_{\max}$, has a dramatic effect on the muscle function in fish (see further discussions below).

B. Cellular Level

At the cellular level, the space within a muscle fiber is largely occupied by three components in differing proportions (force-generating myofibrils, the Ca^{2+}-pumping sarcoplasmic reticulum (SR), and oxygen-consuming/ATP-generating mitochondria). While each of these structures performs necessary cellular functions, a critical tradeoff exists since an increase in the space occupied by one structure (and its function) comes at the expense of another. This competition for space puts limitations on the properties of different fiber types [5], [55]. A fourth component, stored metabolic substrates such as glycogen and fat, is generally small and is ignored here.

Aerobic muscle fibers, red and pink, must have a high density of mitochondria. Indeed, the mitochondria make up 25–50% of the volume of the red muscle in fish [21], [56]. The volume of

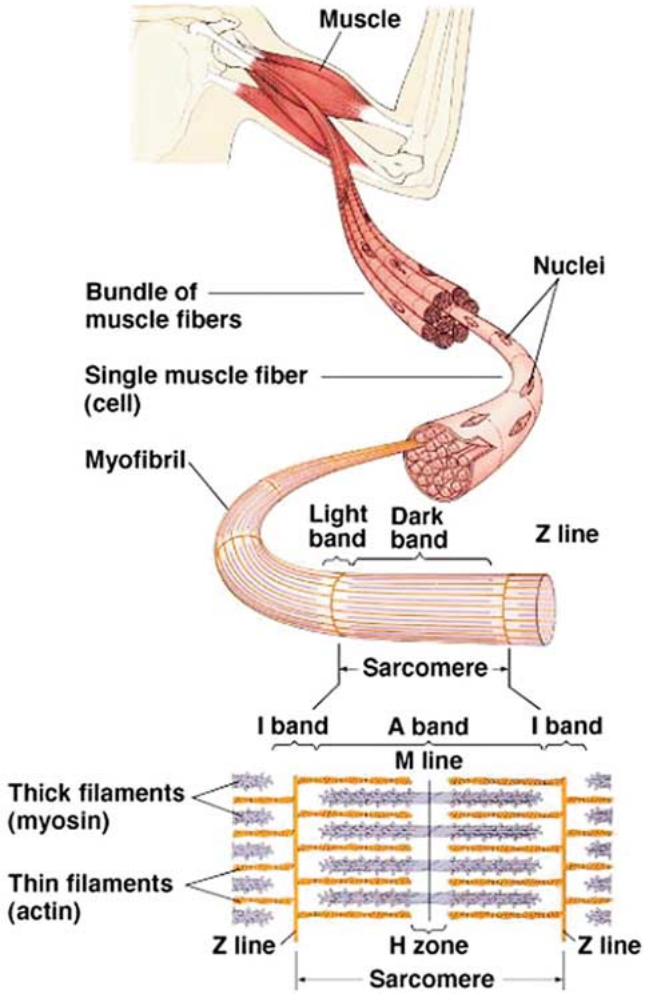

Fig. 3. Adapted from Human Anatomy and Physiology by Marieb, Fifth Ed., 2001.

the mitochondria, in turn, reduces the space available for the force-generating myofibrils, and hence red fibers generate less force than white fibers. Superfast fibers require high volumes of SR for rapid cycling of Ca^{2+}. Thus, myofibrillar volume is reduced accordingly, contributing to a reduction in force (see further discussions below).

C. Ultrastructural/Molecular Level

The force-generating myofilaments consist of myosin thick filaments and actin thin filaments that interdigitate with one another (Fig. 3). The thick filaments are 1.6 μm long in vertebrates [57]. Because the distribution of myosin heads along thick filaments is similar, all vertebrates have the same number of myosin heads. However, there are different types (isoforms) of myosin, and these different types (slow, fast, and superfast) confer many of the observed differences in mechanical properties (e.g., different $V_{\max}$s). The thin filaments are made primarily of actin monomers that are identical in different fiber types, but the number of monomers in a filament, and hence its length, can vary. Whereas thin filaments are generally 1.0 μm long in fish and most other vertebrates [58], mammalian thin filaments can be longer (1.2–1.3 μm long), which leads to a change in the sarcomere–length tension relationship, but no effect on $V_{\max}$.

The thin filament also contains the regulatory proteins that control the activation and relaxation of muscle. These consist of the troponin complex (troponin C, troponin T, and Troponin I) as well as the tropomyosin. Again, different muscle fiber types have different isoforms of these proteins, which alter their performance (see muscle activation, force generation, and muscle relaxation). A detailed discussion of these proteins is beyond the scope of this paper.

D. Structural Arrangement of Muscles

Muscle has a highly organized crystal-like geometry that extends all the way from the ultrastructure of the crossbridges and myofilaments to the whole muscle. Some components are arranged in parallel while others are in series (Fig. 3). This geometry has an enormous impact on the design and function of muscle. In addition, by knowing the geometry, one can employ a "bottom up" approach by starting with an understanding of crossbridge function and integrating, in a systematic way, up to the whole animal. In contrast, one can also employ a "top down" approach by working backwards from making measurements on a moving animal and systematically deducing how single crossbridges are operating. Knowing this geometry and having the ability to go from ultrastructure to the whole animal (and back again) are important facets of the muscular system that allow us to understand its design and thus to extract principles of actuation.

1) Crossbridges on One-Half of a Thick Filament are in Parallel: Muscle force is generated by crossbridges—projections from the myosin thick filament that bind to specific sites on the thin filaments and generate force. The crossbridges extend from the thick filament to the thin filament, parallel to, but independent of, one another. Because of this, the forces are additive (similar to a tug of war using a rigid object like a pipe rather than a rope). Thus, the force generated by a thick filament is equal to the force per crossbridge times the number of attached crossbridges on one-half of the thick filament (it turns out that the crossbridges on the other half of the thick filament are in series with those on the first side, and hence the force is not additive).

Force generation declines as sarcomere length (SL) increases beyond the point of optimal overlap of the thick and thin filaments. This behavior is explained by the "sliding filament hypothesis" [59]–[61] that provides the most fundamental explanation of muscle function. The sliding filament hypothesis assumes that 1) crossbridges are independent force generators, 2) each crossbridge generates the same force, and 3) crossbridges are uniformly distributed on the thick filament. Hence, as the sarcomere is lengthened, there is progressively less and less overlap between the thick and thin filaments, thus fewer crossbridges can attach and generate force. Eventually, the sarcomere becomes so elongated that there is no longer an overlap between the filaments. At this point, crossbridge attachment is impossible and the force drops to zero (Fig. 3).

2) Sarcomeres are in Series: Sarcomeres are placed end to end (Z line to Z line), like links in a chain. Hence, the force generated in one sarcomere is the same for each sarcomere in the chain. Although a chain of 10 000 sarcomeres has a large number of total crossbridges in it, the force generated by the chain is determined by the force generated by any one sarcomere, and that force in turn is determined by the number

of crossbridges in parallel on one-half of the sarcomere as stated above.

Because sarcomeres are in series, however, this means that the length changes and consequently velocities will be additive. This is a necessity for turning microscopic movements into macroscopic movements needed for locomotion. For instance, if one has 10 000 sarcomeres in series, each with a length of 2 μm, then a 0.1-μm shortening of each sarcomere will result in a $10\,000 \times 0.1\ \mu\mathrm{m} = 1\ \mathrm{mm}$ or 5% shortening of the string. More crucially, the speed at which thin filaments move past thick filaments is very slow in absolute terms: in a fast muscle, it would be 10 $\mu\mathrm{m/s}$ (note that this would cause the Z lines to move toward each other at twice the speed or 20 $\mu\mathrm{m/s}$). This is far too slow to produce a useful movement. However, the chain of sarcomeres will shorten at 20 cm/s $(10\,000 \times 20\ \mu\mathrm{m/s})$, which can produce the large-scale movements associated with locomotion. The amplification mechanism for length changes shows that to obtain high velocities it is necessary to have many sarcomeres in series.

3) Myofilaments, Myofibrils, and Muscle Fibers are in Parallel: Muscle fibers typically extend from one tendon to another, independent of surrounding muscle fibers. Hence, fibers are in parallel and the force generated by one fiber is directly transmitted to the tendons. One way to increase the force generated by a muscle is to simply put more fibers in parallel.

At the cellular level, a muscle cell is made up of thin strings of myofilaments (myofibrils) running parallel to each other. In between these myofibrils are the SR, mitochondria, and other cellular components. Within a myofibril, there is a set of thick filaments that is parallel to one another as well as a set of thin filaments that is parallel to each other. Because each of these components are parallel, if one cuts through a cross section of the muscle, it is the number of thick filaments in the cross section that ultimately sets the total force a muscle can generate (note that because thick filaments are parallel in myofibrils, myofibrils, in turn, are parallel in cells, and cells, in turn, are parallel in muscles; then all the thick filaments in the cross section of the muscle will be in parallel with one another; Fig. 3).

This regular geometry permits one to move from force generation in a whole muscle (or whole animals) to force generation by a single crossbridge. For instance, assume a fish muscle with a 1-cm^2 cross section can generate 30 N of force. Because thick filaments are arranged in parallel and there are about $5 \times 10^{10}\ \mathrm{thick\ filaments/cm}^2$ or $500/\mu\mathrm{m}^2$, it follows that each thick filament generates 600 pN of force. Because there are 150 crossbridges/half thick filament, then each crossbridge generates ~4 pN of force. With the recent development of laser trap technology, the force generated by single crossbridges can now be measured and the values obtained are similar to the one calculated above. Laser traps and *in vitro* motility assays can also measure the speeds of single actin filaments moving past single myosin heads. They reveal values almost identical to those calculated from the quotient of the macroscopic shortening speed of the muscle and the number of sarcomeres in series.

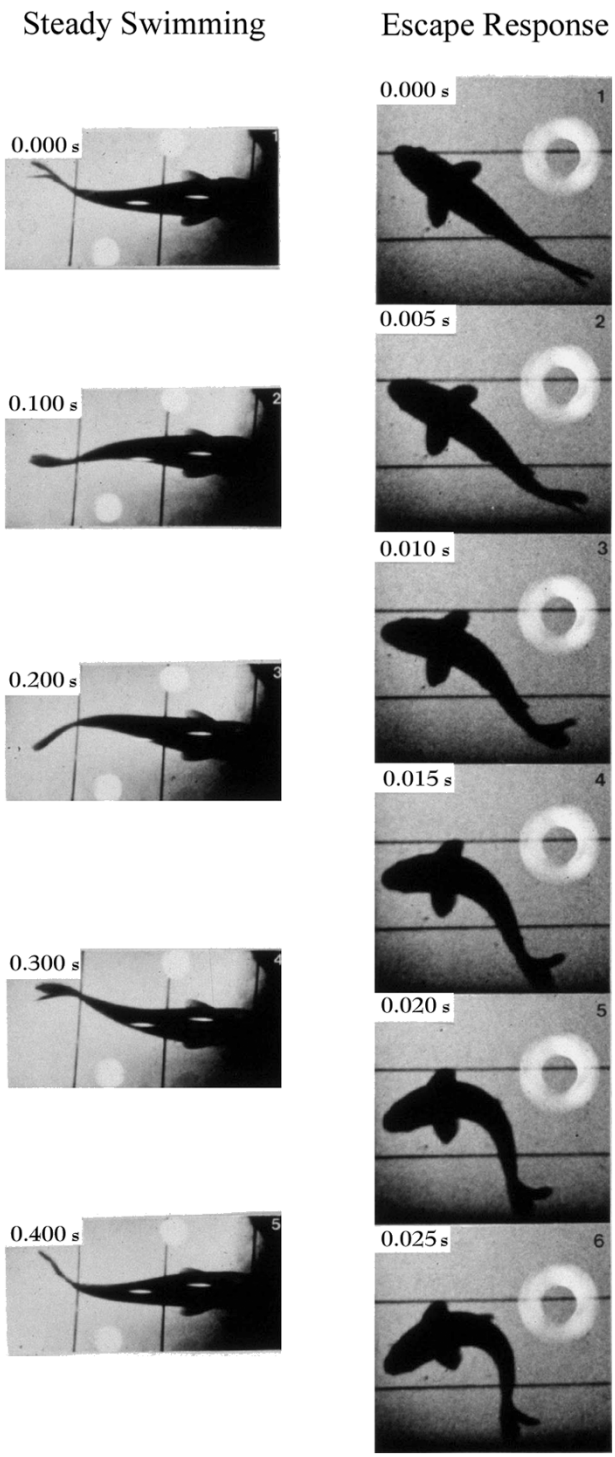

Fig. 4. High-speed motion picture frames shot at 200/s. Note that while consecutive frames are shown for the escape response, only every 20th frame is shown for steady swimming. From [15].

VI. Design of the Fish Muscular System

Having described some of the basic elements of the fish muscular system, the authors will now examine more functional aspects and point out along the way the insights that the fish muscular system has provided to the field of muscle design in general. Fish have been a very helpful model in elucidating how muscular systems are designed. The reason is threefold. First, fish undergo a wide range of motor movements from swimming (see Fig. 4) to sound production at 200 Hz, and these can be easily elicited and quantitatively analyzed. Second, these motor movements are powered by different muscle fiber types permitting exploration of the function of different fiber types. And

most importantly, one can experimentally determine 1) which fiber types are powering a particular activity, 2) what length change and stimulation pattern they undergo, and 3) the mechanical properties of the different fiber types [10].

Fish produce a wide range of movements [15]. The SL change of the muscle depends largely on the curvature of the spine. High-speed motion pictures of carp swimming at 20 cm/s reveal that there is very little curvature in the backbone (Fig. 4, left panels). In contrast, during the escape response (C-start), there is a large amount of curvature in the backbone (Fig. 4, right panels). Note also the difference in time scales. During steady swimming, one tailbeat takes 400 ms (i.e., 2.5 Hz), whereas in the escape response the fish goes from straight to highly curved in only 25 ms. How has the muscular system evolved so that it can produce both of these types of movements effectively?

A. Myofilament Overlap and $V/V_{\max}$—Two Design "Constraints" of the Muscular System

From the cell physiology, one may anticipate that there are some rules [2], [62] that are followed when an animal muscular system evolves. During full activation, the force generated depends on the amount of overlap between the myosin thick filament and the actin thin filament, or more precisely, the number of myosin crossbridges that can interact with actin sites [60]. Force is maximal when there is optimal overlap between the filaments so that the maximum number of myosin heads can attach to actin. Force falls as the sarcomere length increases, and the overlap and number of myosin heads that can interact declines. Force also declines when the sarcomeres become too short, reflecting a possible interference in force generation by myosin heads (Fig. 5).

It would seem sensible that during evolution the gear ratio of the animal's muscle fibers and their myofilament lengths are varied so that no matter what movements the animal makes the muscle would operate at optimal myofilament overlap (i.e., where the muscle generates near maximal force; see Fig. 5). As such, gear ratio and myofilament lengths can be viewed as the design parameters (those components that can be varied during evolution). Myofilament overlap can be viewed as a design constraint (i.e., the rule by which the variation in parameters is adjusted). As both design parameters are anatomical features of the muscle, one being at the organ level and the other at the molecular level, this can be viewed as a structural design consideration.

There is also a dynamic design consideration that takes into account the fact that muscle shortens during locomotion. When a muscle is isometric (i.e., it is being held at constant length), it generates maximal force. However, to move limbs or bend the body, muscles must shorten. Muscle shortening is also necessary to perform mechanical work—a requirement of increasing the mechanical energy of a body (e.g., during jumping) and for overcoming drag (e.g., during flying or swimming).

The relationship between the force and the velocity is described by the force–velocity curve (Fig. 6). The force muscle generates a function of the velocity when it shortens (V), or more precisely a function of $V/V_{\max}$ [63]. The faster the muscle shortens, the less force it generates, until it generates zero force when shortening at its maximum velocity of shortening $V_{\max}$.

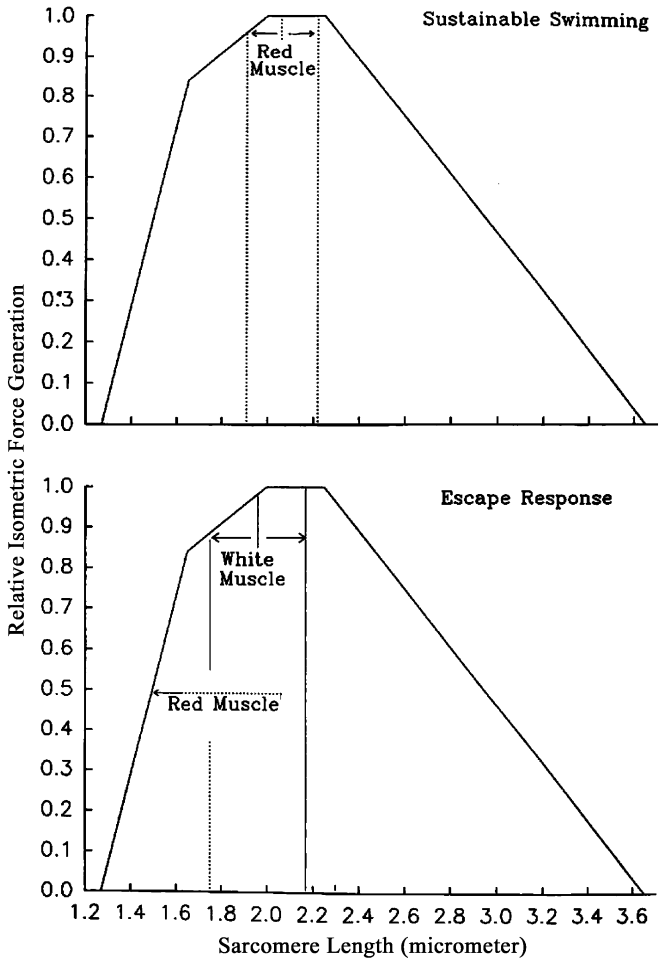

Fig. 5. Myofilament overlap in swimming carp. The figure shows where the fiber operated on the sarcomere–length tension curve of red and white muscle. From [52].

In addition and more importantly, the mechanical power that a muscle generates, the rate of energy usage, and the efficiency (mechanical power output/rate of energy usage) with which it generates mechanical power are functions of $V/V_{\max}$ as well (Fig. 6). As mentioned previously, animals have different fiber types (i.e., different $V_{\max}$s within the same animal). Hence, one might anticipate that the muscular system of animals who need to generate power (swimming fish, jumping frogs, flying birds) would be designed so that no matter what movement the animal makes the muscle fibers operate over a range of $V/V_{\max}$ values (0.15–0.40) where the fibers generate maximal power with near maximal efficiency. Thus, the design parameters $V_{\max}$ and fiber gear ratio are varied in such a way that they operate under the design constraint of $V/V_{\max}$.

It is important to emphasize that myofilament overlap and $V/V_{\max}$ are potential constraints, which are derived exclusively from experiments on isolated muscle. It was necessary to determine whether animals actually use their muscles over this narrow range of values during their full range of locomotion, which had never been previously determined.

B. Myofilament Overlap

Experiments on fish have provided considerable insight into myofilament overlap in vertebrates. During caudal fin propul-

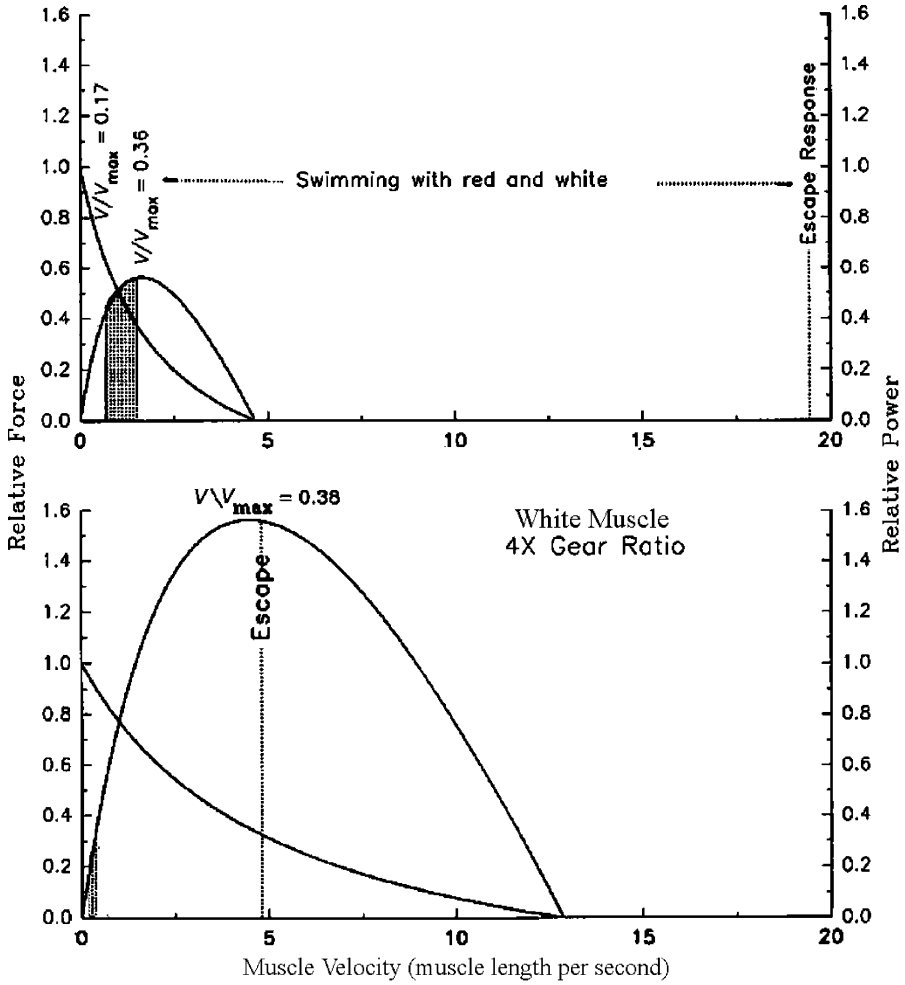

Fig. 6. $V/V_{\max}$ in swimming carp. Force–velocity and power–velocity curves are shown for the red and white muscle. Where fibers operate during different swimming activities is illustrated. From [15].

sion, most fish bend their backbone. By a combination of high-speed motion pictures and anatomical and mathematical approaches that relate SL to the backbone curvature, it was found that at low swimming speeds in carp (Fig. 4), the red muscle, which powers this movement, undergoes cyclical SL excursions between 1.89 and 2.25 μm centered around an SL of 2.07 μm [Fig. 5(a)] [15], [50], [52]. Further, using quantitative electron microscopy, it was found that the thick and thin filament lengths of the red (1.52 and 0.96 μm) and white (1.56 and 0.99 μm) muscles in carp are similar to that in frog [58]. Using the frog SL–tension relationship to approximate that of the red and white muscles shows that the red muscle operates over a range of SLs where no less than 96% maximal tension is generated [Fig. 5(a)] [15], [50], [52].

The most extreme movement that carps make, the escape response [pictured in Fig. 4(b)], involves a far greater curvature of the backbone than steady swimming. If the red muscle was powering this movement, it would have to shorten to an SL of 1.4 μm, where low forces and even irreversible damage can occur [Fig. 5(b)] [15], [52]. Rather, it is the white muscle that performs the movement because the white muscle has a different fiber orientation than the red. The red muscle fibers run parallel to the long axis of the fish (Fig. 2) just beneath the skin. The white muscle fibers, by contrast, run in a helical orientation with respect to the long axis of the fish.

As predicted in [53] and experimentally verified in [52], the helical orientation endows the white fibers with a fourfold higher gear ratio than the red fibers (i.e., the white muscle can produce a given backbone curvature while undergoing only 1/4 of the SL excursion). Thus, to power this most extreme movement of fish, on average the white muscle must shorten to an SL of 1.82 μm, and at this SL the muscle generates about 94% maximal force [Fig. 5(b)].

As shown above, the myofilament overlap is never far from its optimal level even in the most extreme movements. It appears, therefore, that animals are designed in such a way that no matter what the movement, the muscles used generate nearly optimal forces. As such, myofilament overlap can be considered a design constraint (i.e., a part of the system that is kept constant). Given the movements that fish need to make, two design parameters (fiber gear ratio and myofilament lengths) are adjusted during evolution such that the muscle fibers being used always operate at near maximal myofilament overlap and force generation [2], [52].

C. $V/V_{\max}$

The two main fiber types in fish, red muscle and white muscle, have different $V_{\max}$ values in addition to the aforementioned different gear ratios (note that pink muscle, which is abundant in some species, has intermediate properties and appears to follow

the same set of design rules [64]). The first question that was asked is why do animals have different fiber types and are the faster fibers used to power faster movement (higher Vs) while operating at the same $V/V_{\max}$?

As illustrated in Fig. 6, it was found by [15] that the $V_{\max}$ of carp red muscle was 4.65 muscle lengths/s (ML/s) and the $V_{\max}$ of carp white muscle was 2.5 times higher, 12.8 ML/s. During steady swimming, the red muscle is used over ranges of velocities of about 0.7 to 1.5 ML/s [Fig. 6(a), shaded part of the curve [15], [50], [65]]. This corresponds to a $V/V_{\max}$ of 0.17–0.36, which is where maximum power is generated. At higher swimming speeds (higher Vs), the fish recruited their white muscle because the mechanical power output of the red muscle actually declines.

It is clear from Fig. 6(a) that the red muscle cannot possibly power the escape response. To power the escape response, the red muscle would have to shorten at 20 ML/s, which it clearly cannot do, as this is four times its $V_{\max}$. Even if the white muscle was placed in the same orientation occupied by the red (i.e., same gear ratio), it could not power the escape response either, because its $V_{\max}$ is only about 13 ML/s. However, because of its fourfold higher gear ratio, the white muscle needs to shorten at only 5 ML/s to power the escape response [Fig. 6(b)]. This corresponds to a $V/V_{\max}$ of about 0.38, which is where the white muscle generates maximum power [15], [52].

If the white muscle does so well at producing fast movements, then why don't fish have only one fiber type and let the white muscle power the slow swimming movements as well? The white muscle could certainly power slow swimming, but it is not used because its high $V_{\max}$ and fourfold higher gear ratio would make its $V/V_{\max}$ at slow swimming speeds so low [i.e., 0.01–0.03; shaded portion of Fig. 6(b)] that the muscle's efficiency would be nearly zero.

Thus, the red and white muscles form a two-gear system. To achieve a wide repertoire of movements, fish must use different fiber types with different $V_{\max}$s and different gear ratios to power different movements. The red muscle powers slow movements while the white muscle powers very fast movements, both while working at the appropriate $V/V_{\max}$ (0.17–0.38). The effectiveness of the white muscle to power fast movements depends on the product of its gear ratio and $V_{\max}$. In terms of backbone curvature, the white muscle can produce tenfold faster movements (2.5-fold higher $V_{\max}\times$ fourfold higher gear ratio) than the red muscle. If the red muscle had the same gear ratio as the white, it could not produce the escape response, nor could the white muscle if it had the gear ratio of the red. What is needed is both the correct $V_{\max}$ and the correct gear ratio (see also, [66]) to produce the full repertoire of movements [15], [52].

Additional studies have revealed that fast and slow swimming species of fish [67], [68], fish swimming at low and high temperatures [50], [65]–[68], and even jumping frogs [4] also use their muscle at optimal $V/V_{\max}$ (0.17–0.36). This provides additional evidence that $V/V_{\max}$ is an important design constraint.

It appears from these examples that many animals use their muscles over a narrow range of myofilament overlap and over a narrow range of $V/V_{\max}$, where muscle generates maximum force and maximum power with optimal efficiency. Therefore, during evolution, three design parameters (gear ratio, $V_{\max}$, and myofilament lengths) appear to have been adjusted so as to obey these design constraints. Hence, these design constraints appear to constitute two of the rules by which muscular systems have evolved [1], [2].

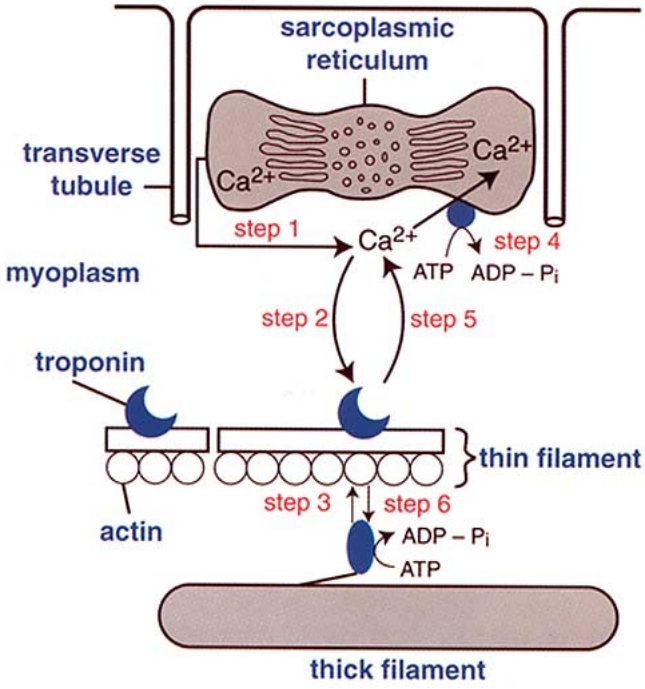

Fig. 7. Steps in muscle activation and relaxation.

D. Muscle Activation, Force Generation, and Relaxation

As successful as myofilament overlap and $V/V_{\max}$ are in explaining muscle design, it is important to realize at this point that the SL–tension curve and the force–velocity, power–velocity, and energy utilization–velocity curves are steady-state properties of maximally activated crossbridges. As such they do not account for the fact that muscle must be turned on and off during locomotion. Perhaps different from artificial muscles, the processes of activation and relaxation (i.e., turning on and off) exert a major effect on the mechanical function of real muscle in living animals and thus must be considered in the overall design. Hence, to fully understand the design of the muscle system, it is important to consider nonsteady state properties of muscle.

Different muscle fiber types are designed to activate, generate force, and relax over a large range of frequencies. Here, the author examines the modifications of muscles to operate at different frequencies. Muscle is turned on by the release of calcium (Ca^{2+}) from the sarcoplasmic reticulum (SR, which stores Ca^{+2}) into the myoplasm. Ca^{+2} in turn binds to troponin, removing the inhibition from the thin filament and thereby allowing the myosin crossbridges to attach and generate force (Fig. 7).

For the muscle to relax, the process must be reversed; Ca^{+2} must unbind from troponin so that inhibition can be returned to the thin filament. Thus, the myoplasmic calcium must be lowered and this is done by Ca^{+2} being pumped into the SR. Ca^{+2}

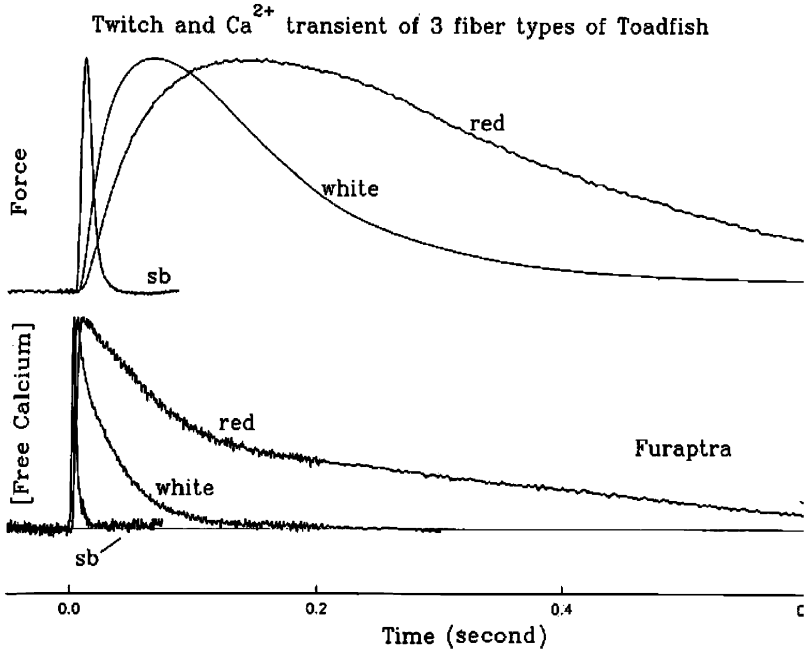

Fig. 8. Twitch force and calcium transient from three muscle fiber types in toadfish whose speed varies by 50-fold. Note that sb refers to swimbladder. From [69].

must then unbind from troponin and finally the crossbridges must detach.

To reveal how these processes are adjusted to allow muscle to operate over a large range of frequencies, fish again have been advantageous because in a single species the properties of superfast muscles used to produce sound could be compared to slow- and fast-twitch locomotory muscles used for swimming [69]. The male toadfish (*O. tau*) produces a "boatwhistle" mating call 10–12 times/min for many hours to attract females to its nest. A tone is generated by oscillatory contractions of the muscles encircling the fish's gas-filled swimbladder at 200 times/s [47], [70]. Such high-frequency stimulation of typical locomotory muscles (which relax relatively slowly) would produce a completely fused (i.e., constant force) tetanus because they would be unable to relax between stimuli. Because maintained tension would simply compress the bladder and prevent it from vibrating and producing sound, sonic muscles must be specifically modified to turn on and off rapidly.

The muscle activation–relaxation rates vary by ~50-fold between locomotory and sonic fiber types in toadfish [69]. Toadfish red muscle (used for slow steady swimming at ~2 Hz) has a twitch half-width (the time duration at the 50% force level) of about 500 ms compared to approximately 200 ms for white muscle (used for burst swimming at ~1 Hz) and about 10 ms for the swimbladder muscle (top panels of Fig. 8).

For any muscle to activate and relax rapidly, two conditions must be met. First, calcium, the trigger for muscle contraction, must enter the myoplasm rapidly and be removed rapidly (Fig. 7, steps 1 and 4). Second, myosin crossbridges must attach to actin and generate force soon after the Ca^{2+} level rises and then detach and stop generating force soon after the Ca^{2+} level falls (Fig. 7, steps 2, 3, 5, and 6).

The time course of Ca^{2+} release and reuptake during contractions can be determined by injecting muscle cells with a fluorescent Ca^{2+} sensitive dye and tracking fluorescence with time (Fig. 8, bottom). The Ca^{2+} transient in the sonic muscles is the fastest ever measured for any fiber type (a half-width of ~3.4 ms at 16 °C and 1.5 ms at 25 °C) [69]. The importance of the Ca^{2+} transient duration in setting the twitch duration can be seen in Fig. 8, which shows that between the slow-twitch red fibers and the superfast-twitch swimbladder fibers, the half-widths of the Ca^{2+} transient and the twitch sped up in parallel (by ~50-fold).

The significance of a fast Ca^{2+} transient is most apparent during repetitive stimulation. During stimulation of slow red muscle at a modest 3.5 Hz (Fig. 9, left), the time course of Ca^{2+} uptake is so slow that $[Ca^{2+}]$ does not have time to return to baseline between stimuli. Even the lowest myoplasmic $[Ca^{2+}]$ between stimuli was above the threshold required for force generation in this fiber type, thus resulting in a partially fused tetanus. By contrast, the swimbladder's Ca^{2+} transient is so rapid that even with a 67-Hz stimulation, the $[Ca^{2+}]$ returns to baseline between stimuli is complete (Fig. 9, right; note the 50× faster time base). In addition, $[Ca^{2+}]$ is below the threshold for force generation for more than half of the time in all but the first stimulus. Hence, the Ca^{2+} transient is sufficiently rapid to permit the oscillation in force required for sound production.

Even though $[Ca^{2+}]$ returns rapidly to baseline, the swimbladder fiber could not relax quickly unless its troponin rapidly released the bound Ca^{2+} (Fig. 7, step 5). Indeed, kinetic modeling indicates that if the swimbladder troponin had the same off rate for Ca^{2+} (k_{off}) as fast-twitch fibers, then occupancy of its troponin sites with Ca^{2+} would not decline sufficiently rapidly to permit the observed rapid fall in force. Experiments on the Ca^{2+} sensitivity of troponin suggest that the swimbladder muscle has a threefold lower affinity troponin than fast-twitch muscle, and hence a threefold faster k_{off}. With this higher k_{off}, the modeled rate of troponin deactivation no longer appears limiting. Thus, the less sensitive troponin with its more rapid k_{off} may be another modification for faster relaxation [69].

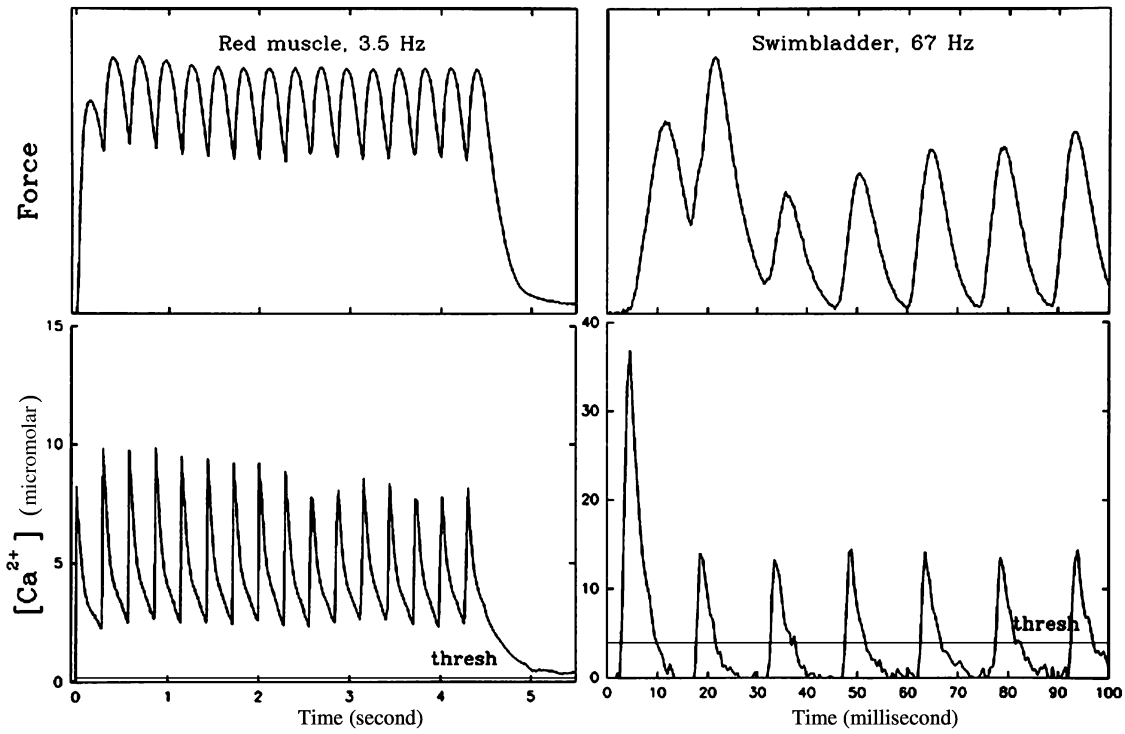

Fig. 9. Force and calcium transients of red and swimbladder muscles during repetitive simulation. From [69].

The final requirement for force to drop quickly following the dissociation of Ca^{2+} from troponin is a fast crossbridge detachment rate (Fig. 7, step 6). Indeed, the maximum velocity of shortening (V_{max}; which is thought to be affected by crossbridge detachment rate) of swimbladder muscle (~12 ML/s) is exceptionally fast, 5- and 2.5-fold faster than toadfish red and white muscle. Further, direct measurement of the crossbridge detachment rate shows it to be exceptionally fast (~110 s^{-1} or about 50 times faster than the toadfish red fibers and the well-studied rabbit fast fibers). This fast detachment rate would permit the rapid relaxation rate observed [5].

The toadfish experiments have thus identified three kinetic variables that change progressively as twitch speed increases from the slow twitch of red fibers to the superfast twitch of swimbladder fibers. 1) The duration of the Ca^{2+} transient must become shorter, which in turn requires more rapid calcium release and reuptake. This is achieved principally by an increased density of SR Ca^{2+} pumps. 2) Troponin needs a faster off rate for Ca^{2+}, which requires molecular modification of troponin to a lower affinity type. 3) Crossbridges must detach more rapidly, which involves molecular modification of myosin.

E. Evaluating Muscle Function by the Workloop Technique

Optimal Workloops: Changes in all of these parameters in concert enable swimbladder fibers to perform mechanical work at high operating frequencies (100 Hz at 15 °C to over 200 Hz at 25 °C) [5], [69]. In contrast, vertebrate locomotory muscles lack these properties, and thus the red and white swimming muscles of toadfish cannot perform work over 2 and 12 Hz, respectively. This is illustrated in Fig. 10, which shows the power output of the three fiber types as a function of frequency in "optimized" workloop experiments. In workloop experiments, the muscle is

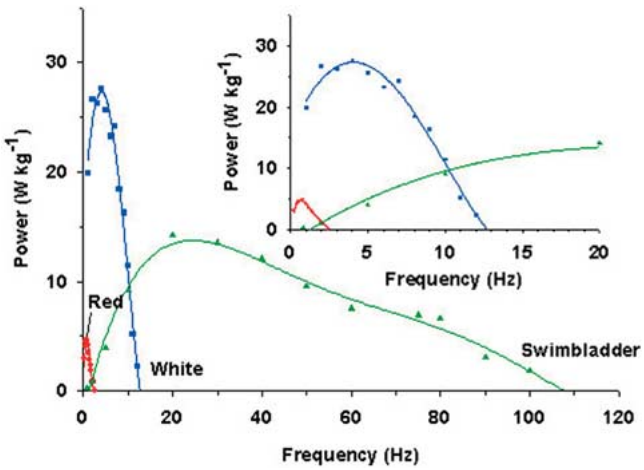

Fig. 10. Maximal power output derived from optimized workloops as a function of oscillation frequency for three fiber types in toadfish. From [71].

driven under a particular length change (usually a sinusoid) and the muscle is stimulated for a particular duration and at a particular phase relative to the length change. In "optimized" workloop experiments, the strain, stimulation duration, and stimulation phase are all optimized to maximize net work (and hence power) at each frequency (N. B., for the determination of the maximum net power output of the muscle, the frequency too must be optimized). The rate of relaxation clearly has a dominant effect on the frequency of operation (recall that there is a 50× change in the Ca^{2+} transient and relaxation rate between swimbladder and red muscle, but only a fivefold difference in V_{max}). The fact that the ratio of the maximum operating frequency is much closer to the ratio of relaxation speeds than the ratio of V_{max} shows the importance of activation and relaxation

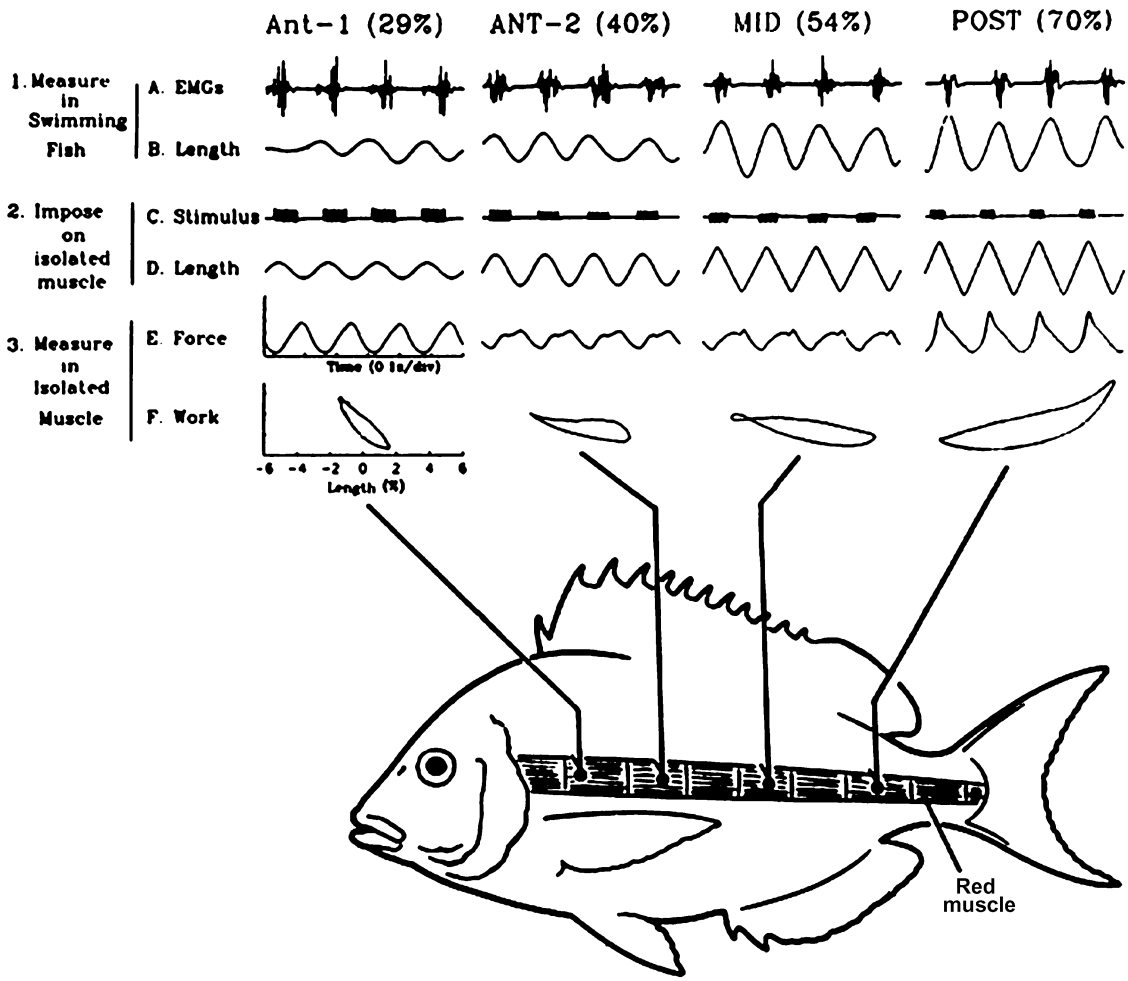

Fig. 11. EMGs and muscle length changes of the red muscle of scup while swimming at 80 cm/s. From [3].

rates in setting the operational ability of the muscle. Note that to compensate for the 50-fold difference in frequencies with only a fivefold change in $V_{\max}$, the strain in swimbladder at 100 Hz must be reduced to only $\sim$1/10 that of the red muscle at 2 Hz [71].

1) In vivo Workloops: Although the processes of activation and relaxation have a large effect in "optimal" workloops, surprisingly, under "*in vivo*" workloop conditions (where the muscle strain, stimulation phase, stimulation duration, and frequency are constrained to those values found when the fish is swimming), the rates of activation and relaxation have an even greater effect on muscle performance. Fig. 11 shows the *in vivo* workloops of the red muscle at four different positions (Ant-1, Ant-2, Mid, and Post) along the length of a scup swimming at 80 cm/s at 20 °C. The first step was to measure the muscle length change and stimulation pattern (i.e., EMGs) the red muscle undergoes at each position during swimming. The second step was to remove the muscle from these four different regions and drive each through the length changes and stimulation pattern it sees *in vivo*. The authors then measured the resulting force and work generated by the muscle [3]. The work is signified by the area of the loop. Fig. 11 shows that the amount of work per tailbeat varies considerably with position—small levels are generated at the head and large levels at the tail. The principal determinant of these differences is the muscle strain, which is large ($\pm$5.7%) at the tail because of the large backbone curvature, but small ($\pm$1.6%) towards the head because the fish holds the front of his body stiff during swimming. There are more subtle effects as well: the stimulation duration is much longer in the front of the fish, giving the muscle very little time to relax between tailbeats. In fact, if you take muscle from the Mid or Post positions and drive it under the length and stimulation conditions of the Ant-1 region, the muscle would not generate any net work [i.e., it would generate net negative work (the muscle absorbs more mechanical energy during lengthening than it produces during shortening)]. It is only because the Ant-1 muscle is endowed with a faster relaxation rate than the Mid or Post that allows it to generate any power, albeit on a small scale.

The importance of relaxation rate as a determinant of muscle function is clearly illustrated by the effect of temperature on muscle and locomotory performance in scup [72], [73]. Although under optimized workloop conditions scup muscle at 10 °C generates about 44% of that at 20 °C, when the muscle is constrained to "*in vivo*" conditions, the power level at 10 °C varies from about 10% to none at all (i.e., at some swimming speeds and anatomical positions, the muscle generates negative work). The reason is as follows: when the fish swims at low

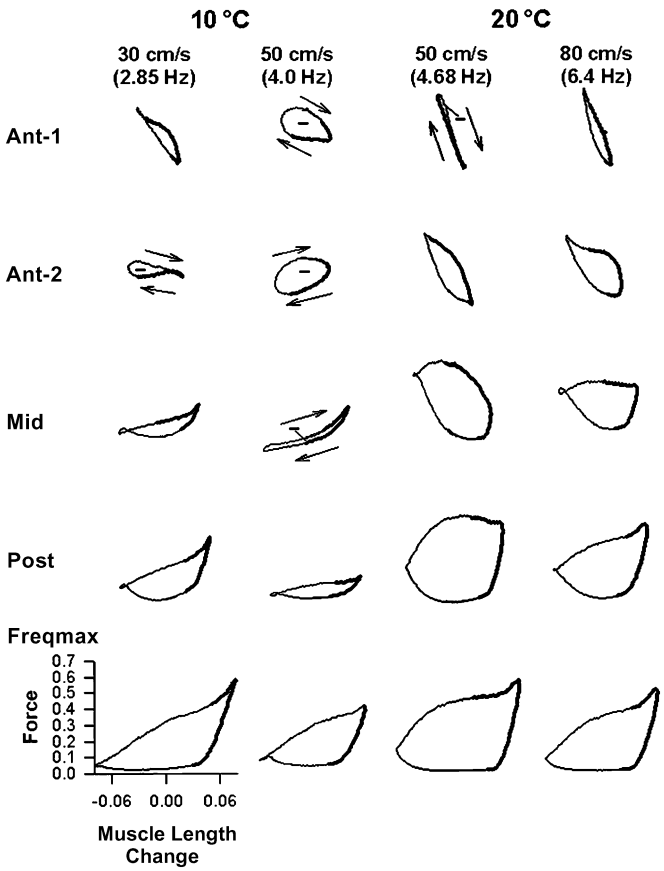

Fig. 12. *In vivo* workloops from scup red muscle at four locations. Optimized work loops for each frequency (Freqmax) are shown at the bottom. From [74].

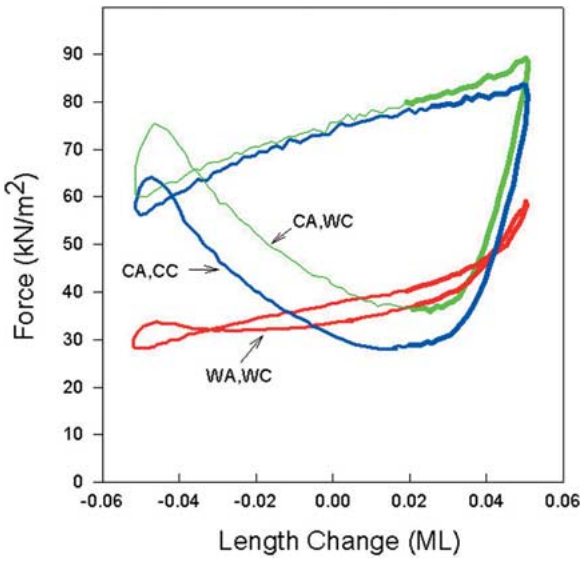

Fig. 13. CA,CC: cold-acclimated muscle driven under cold-acclimated conditions; WA,WC: warm-acclimated muscle under warm-acclimated conditions; CA,WC: cold-acclimated muscle under warm-acclimated conditions. From [77].

temperature, the rate of muscle relaxation is slowed by a factor of 3. During "optimized" workloop experiments, this slowing can be counteracted by reducing the duration of the stimulus or by reducing the oscillation frequency of the length change (i.e., in scup maximum power is achieved at 2.5 Hz at 10 °C and 5 Hz at 20 °C). During swimming at a given speed, however, scup swim with the nearly same tailbeat frequency and the same stimulation duration at 10 °C as at 20 °C (see the middle two columns, Fig. 12). Hence, the muscle at 10 °C is not given any additional time to relax and thus is often not completely relaxed when relengthened by muscle on the contralateral side. Because the active muscle generates greater forces when being stretched than when shortened, this results in a more negative work than positive work, and thus there is net negative work production (signified by a clockwise workloop in Fig. 12).

This creates a problem for scup swimming at low temperatures. This effect is countered in the short term by recruiting a faster muscle fiber type (e.g., pink muscle), which has a faster relaxation rate than the red muscle at a given temperature. Therefore, the pink muscle can generate positive work under the same *in vivo* conditions where the red muscle generates negative work, and in total can generate sixfold more power than the red musculature while swimming at 50 $\mathrm{cm\ s^{-1}}$ at 10 °C [64], [74], [75].

Scup can also deal with this problem over a long time scale (weeks), which occurs during their annual migrations between inland waters and the Gulf Stream. Thermal acclimation to low temperatures permits the nervous system to reduce the stimulation duration during swimming [76] and permits the mechanical properties of the muscle to become faster [77], both of which increase the power output of red muscle during swimming at 10 °C (see Fig. 13).

Finally, the *in vivo* workloop technique represents a novel approach for assessing the amount of mechanical power that fish need to generate in order to swim. By combining the *in vivo* workloop values with the distribution of different fiber types down the length of the fish [78], the authors can estimate the total mechanical power generated by the fish's musculature at swimming speeds where the muscle fiber type recruited as well as the activity level is known [77]. Eventually, these data can be compared to power values derived from new hydrodynamics measurements (e.g., digital particle image velocimetry or DPIV—see Section X) to provide a robust assessment of the power needed for swimming—a value that until now has been elusive.

F. Muscle Energetics

As illustrated above, locomotory muscle can be limited in activation and relaxation rates, but can also be built to be very fast. Why not have all fast muscles? The reason is simple, there is always a tradeoff between speed and energetic cost—the faster the muscle, the more energy is used [13], [14], [25], [38], [79]. Here, muscle energy usage is briefly examined. The energetic cost of contractions is set by two components—the ATP used by the crossbridges to generate force (which accounts for about 50–70% of the total) and the ATP used by $\mathrm{Ca^{2+}}$ pumps to pump released $\mathrm{Ca^{2+}}$ back into the SR (which accounts for the remainder [30]; Fig. 7). Fibers used for high frequencies have high ATP utilization rates when active because the rate of ATP utilization by both of these components is rapid. For instance, swimbladder fibers appear to pump $\mathrm{Ca^{2+}}$ back into the SR at

about 50 times the rate of red muscle fibers. Thus, the swimbladder fiber's Ca^{2+} pumps use ATP 50-fold faster than those of the red muscle. Further, the crossbridges of swimbladder fibers use ATP about six times faster than red muscle fibers. Thus, during sound production (where Ca^{2+} is being continuously pumped and crossbridges are continuously generating force and splitting ATP), the swimbladder will use ATP at a far greater rate than the red muscle.

Interestingly, because of the swimbladder's high SR volume and high crossbridge detachment rate constant, it generates only a small fraction ($\sim$1/10) of the force of the red muscle. The fact that it also uses energy at a much faster speed results in the cost of force generation being about 20 times higher in swimbladder than in red muscle. This makes it far too costly for this superfast muscle to be used to power relatively slow movements such as swimming. By contrast, the locomotory red and white muscles are far too slow to power high frequency sound production. Hence, these different muscles represent mutually exclusive designs to power different activities [5], [71].

VII. Principles of Actuation

From the preceding description of the design and function of the fish muscular system, a series of principles of actuation emerge.

1) Geometric amplification: piconewton-level crossbridge forces, hundreds of nanometer-level filaments sliding at μm/s-level speeds are amplified into to kilogram-level forces, centimeter-per-second-level length changes at tens of centimeter-level speeds by placing many thick filaments in parallel and many sarcomeres in series. As illustrated above, the forces, length changes, and shortening speeds that take place for one crossbridge on one thick filament in one sarcomere are extremely small and without amplification cannot power locomotion. Although there are many functional differences between muscle fiber types at the molecular level, it is this geometric amplification that is the primary transformer from the molecular nanometer/piconewton world to macroscopic movement in animals.
2) For muscles that must generate mechanical power, the muscular system is designed so that muscle fibers operate at optimal myofilament overlap and optimal $V/V_{\max}$, where maximum power is generated. Work on the red and white muscle of carp and the red and pink muscle of scup (as well as work on frogs) illustrates that muscles operate where they generate maximum power.
3) No one actuator can power all motor activities. Multiple actuators are required to produce a wide range of movements. This is well documented in the comparison of the red and white swimming muscles in carp (and scup). The results show that red muscle cannot shorten fast enough to produce the rapid escape response whereas the white muscle is too energetically costly to use during slow swimming. Also, the comparison of the locomotory and sound-producing muscles of toadfish shows that they operate over mutually exclusive ranges of frequencies, and thus have mutually exclusive function.
4) Differential gearing is an important element of muscular system design. Comparison of steady swimming and the escape response in carp shows that changing only the actuator (i.e., from red muscle to white muscle) is not sufficient to produce the wide range of observed movements. Attaching the muscle with different gear ratios is necessary as well.
5) Muscle fiber types are configured differently at the molecular level to provide the appropriate macroscopic behavior for the required motor behavior. The comparison of the three muscle fiber types in toadfish shows that specific molecular alterations are necessary to enable the muscle to power different activities (i.e., from swimming to superfast sound production).
6) In addition to the mechanical properties of actuators, energetic and metabolic properties are also important design parameters and must be integrated into the overall design of the actuator. Fish, like AUVs, have to be able to perform their motor activities for a low energetic cost (food is the limitation for fish, battery life for the AUV). This fact provides another reason why fish have more than one actuator. Because increased muscle speed results in increased energetic cost, a basic tenet in the design of muscular systems is that muscle speed is set to be sufficiently fast to perform a given activity, but not faster than necessary, as this would entail a large waste of energy [80]. Thus, although the white muscle could easily generate the mechanical power needed for slow steady swimming, it would require far more energy to do so than the red muscle, and hence the red muscle is used for slow swimming. Further, the white muscle uses energy so rapidly that there is no way that the cardiovascular system could supply oxygen and nutrients rapidly enough to use this muscle continuously. Hence, all attempts to do so have been abandoned and the white muscle uses anaerobic metabolism and is reserved for infrequent short duty cycle movements. The more efficient red muscle is used for continuous activity and thus is equipped with metabolic support machinery (mitochondria and blood supply). Thus, the mechanical, energetic, and metabolic characteristics are all adjusted for the function of the muscle.
7) Muscles often perform cyclical activities so that the kinetics of muscle activation and deactivation (relaxation) are equally important to steady-state stress and strain rate characteristics in defining muscle performance. Hence, the mechanical properties of muscle (and artificial muscle) need to be evaluated using both the "optimized" and "*in vivo*" workloop techniques. The traditional way of evaluating muscle (and artificial muscle) is to examine the maximum stress it can generate, its maximum strain rate, and the relationship between stress and strain rate (which determines the maximum power output). However, during cyclical activity like swimming or sound production, the rates of muscle activation and relaxation greatly affect the mechanical performance, and this effect can only be quantified by the workloop technique. For instance, optimized workloop experiments of the different muscle fiber types in toadfish show that they

operate over a wide and effectively mutually exclusive range of frequencies. Further, the scup experiments show that even subtle changes in muscle or nervous system properties can manifest themselves as large changes in net power output during swimming. A fact that is only revealed during "*in vivo*" workloop experiments.

8) Multiple tradeoffs exist in the design of muscle for different activities. Tradeoffs should be expected and rigid guidelines may not be appropriate. Examination of toadfish swimbladder clearly shows that muscle performance should not be judged by single mechanical parameters such as maximum stress. Alterations at the molecular level to gain a high frequency response negatively impact macroscopic performance at lower frequencies. Using parameters such as maximum stress (or power), the swimbladder muscle would be viewed as ineffective, yet it is critically important to organismal fitness due to its functional role of producing sound for attracting mates. Also, as shown by the scup experiments, the suitability of muscle for its task can only be determined in the exact physiological and anatomical context of the animal performing the behavior (i.e., *in vivo* workloops). Thus, the only accurate way to evaluate the appropriateness of a muscle to perform a task is to drive it through the length change and stimulation pattern it undergoes during its *in vivo* function.

VIII. Comparing Artificial Muscle to Real Muscle

It is common for material engineers to characterize artificial muscle by four criteria: 1) the maximum stress; 2) the maximum power; 3) the maximum strain; and (4) the maximum strain rate. Values for artificial muscles usually compare favorably with that found for real muscle, and hence it is concluded that artificial muscle can substitute for real muscle. The preceding examination of the function of real muscle during locomotion, however, shows that these four aforementioned characteristics are by no means a complete description of real muscle performance. Indeed, they are so incomplete that in some situations they provide little insight into predicting whether a particular muscle type will be able to power a particular motor activity.

As illustrated above for scup and toadfish, and in actuation principle #7, the kinetics of activation and relaxation kinetics can play a significant role in defining the functional capacity of real muscle. One can obtain an indication of this by performing workloop experiments, but even "optimized workloop" measurements do not explain the full picture. This is because during many motor activities, anatomical, neurological, hydrodynamic, or other constraints may prevent animals from driving their muscles through conditions that are optimal for power generation. Hence, to accurately assess the real muscle's performance, one has to perform "*in vivo*" workloops. Accordingly, significant miscalculation can be made by simply assuming that muscle generates its maximum power output during all motor activities. These issues likely apply to artificial muscle performance as well. To assess an artificial muscle's capability to perform a particular task, the artificial muscle performance has to be measured when being driven under strains and frequencies over which it will be working. This is the only way to be certain that an overlooked constraint on performance will not, unexpectedly, affect performance during the desired activity.

IX. Can Fish Muscle be Used in an AUV?

Having examined these various principles, it is useful to address whether fish muscle, itself, could be used to actuate some movements in an AUV. As illustrated above, the mechanical capabilities of fish muscle are certainly suitable for use in an autonomous vehicle and the metabolic cost (and thus efficiency) is suitable as well. The metabolic delivery to isolated muscles, however, presents a significant problem.

Bundles of muscle fibers can be dissected from fish or other animals, but they cannot be any thicker than about 1 mm because oxygen would not be able to diffuse to the core of the bundle at a sufficient rate. There are of course much thicker muscles in the bodies of most animals. However, in animals, the oxygen is supplied to within several micrometers of the oxygen-consuming mitochondria by the circulatory system. Typically, when muscle fibers are dissected, the circulation system is removed and muscle fibers are "super-fused" with a Ringer solution containing oxygen and metabolites. Because of this thickness limitation, to generate high absolute force, the authors need to have many of these bundles in parallel, and in this lies the problem. It takes considerable effort to dissect and attach a large number of muscle bundles, and although they can last for several days, a whole new batch would have to be dissected again. Whole muscles can be removed from animals and artificially perfused by blood (or some solutions with high oxygen carrying capacity), but this takes considerable effort. In short, although the energy usage by muscle is modest for the amount of mechanical work it produces, delivering the metabolites and oxygen represents a significant limitation that must be addressed.

X. Future Directions

Although considerable progress has been made, there are a series of exciting new directions and technologies that are beginning to markedly improve the understanding of muscle design, function, and principles of actuation. First, biophysical approaches will continue to be utilized to understand the molecular basis of fish muscle function. For instance, new techniques permit the measure of step size and force generation from single motor molecules that will enable integration from the atomic level to the whole animal.

Second, a recently developed technique, DPIV, has been used to considerable extent already ([81]–[93]), and future use will provide a more fundamental understanding of muscle function during swimming (e.g., a limitation of the fish model is that historically one has not been able to measure force generation and work production in its fluid environment). For instance, it would be particularly important to measure the energy dissipated in the wake to compare the mechanical power required for swimming to that measured empirically by muscle physiology experiments.

Third, better optical/imaging methods [(e.g., higher resolution video, computerized axial tomography (CAT) scans,

magnetic resonance imaging (MRI)] will permit better understanding of the kinematics of fish swimming, particularly of fin function [94] as well as the three-dimensional (3-D) structure and movement of the white muscle (the complexity of the geometry of the white muscle has served as another limitation of the fish model).

Fourth, realistic musculoskeletal modeling, which has recently been applied to running cockroaches [95]–[99] and jumping frogs [100], will eventually be applied to fish swimming. Through realistic musculoskeletal modeling, one must explicitly define the geometry and physiology of the actuators and skeletal components, and through forward dynamic simulations, one can test both the understanding of musculoskeletal function and importance of various components to locomotion. This approach would be particularly important to better understand the exact functioning of the white muscle during swimming.

Fifth, new technologies to track the physiological function of animal locomotion in their natural environment (e.g., telemetry and satellite tracking) will provide important information about how the locomotory apparatus is actually used and under what important environmental factors (e.g., temperature) the system must operate [34], [101]–[107]. Only by understanding what function the locomotory system must perform in nature can we truly understand how it is designed.

Finally, one of the most exciting areas of research on fish involves the use of the genetic model, zebrafish. Research carried out by Fetcho *et al.*, in particular, has addressed important aspects of motor control. By using confocal microscopy, Ca^{2+}-sensitive dyes, and lasers in the transparent zebrafish, Fetcho *et al.* have been able to determine the function and firing sequence of various nerve cells during the escape response [108]–[110]. Further, because dyes are phototoxic (i.e., when illuminated by a laser), they have been able to test hypotheses by photoablating selected neurons and subsequently testing whole animal function [111]. More recently, Fetcho *et al.* have been able to engineer certain classes of cells to express Ca^{2+}-sensitive dyes so that the development of complex connections between nerves can be determined [112], [113]. Finally, as the genetic approaches evolve, one would anticipate the ability to modify specific molecular aspects of muscle function (i.e., cross-bridge kinetics) and to explicitly determine its effect on locomotory ability. This will provide an exceptional test of the principles that have been extracted in this chapter.

ACKNOWLEDGMENT

The author thanks Dr. E. Goldman, Dr. R. Essner, and Dr. J. Marx for reviewing, and helping to prepare the manuscript.

REFERENCES

[1] L. C. Rome, "Testing a muscle's design," *Amer. Sci.*, vol. 85, no. 4, pp. 356–363, 1997.

[2] L. C. Rome and S. L. Lindstedt, "Mechanical and metabolic design of the muscular system in vertebrates," in *Handbook of Physiology, Section 13, Comparative Physiology*, W. Dantzler, Ed. New York: Oxford Univ. Press, 1997, pp. 1587–1651.

[3] L. C. Rome, D. Swank, and D. Corda, "How fish power swimming," *Science*, vol. 261, no. 5119, pp. 340–343, 1993.

[4] G. J. Lutz and L. C. Rome, "Built for jumping: The design of frog muscular system," *Science*, vol. 263, no. 5145, pp. 370–372, 1994.

[5] L. C. Rome and S. L. Lindstedt, "The quest for speed: Muscles built for high frequency contractions," *News Physiol. Sci.*, vol. 13, no. 6, pp. 261–268, 1998.

[6] J. A. Hoeffer, G. E. Loeb, W. B. Marks, M. J. O'Donovan, C. A. Pratt, and N. Sugano, "Cat hindlimb motor neurons during locomotion— I. Destination, axonal conduction velocity, and recruitment threshold," *J. Neurophysiol.*, vol. 57, no. 2, pp. 510–529, 1987.

[7] J. M. Wakeling and D. A. Syme, "Wave properties of action potentials from fast and slow motor units of rats," *Muscle Nerve*, vol. 26, no. 5, pp. 659–668, Nov. 2002.

[8] J. M. Wakeling, M. Kaya, G. K. Temple, I. A. Johnston, and W. Herzog, "Determining patterns of motor recruitment during locomotion," *J. Exp. Biol.*, vol. 205, no. Pt 3, pp. 359–369, Feb. 2002.

[9] J. M. Wakeling, S. A. Pascual, B. M. Nigg, and V. von Tscharner, "Surface EMG shows distinct populations of muscle activity when measured during sustained sub-maximal exercise," *Eur. J. Appl. Physiol.*, vol. 86, no. 1, pp. 40–47, Nov. 2001.

[10] L. C. Rome, "Some advances in integrative muscle physiology," *Comp. Biochem. Physiol.*, vol. 120, no. 1, pp. 51–72, 1998.

[11] J. D. Altringham and I. A. Johnston, "Modelling muscle power output in a swimming fish," *J. Exp. Biol.*, vol. 148, pp. 395–402, 1990.

[12] T. A. Beddow and I. A. Johnston, "Plasticity of muscle contractile properties following temperature acclimation in the marine fish *Myoxocephalus scorpius*," *J. Exp. Biol.*, vol. 198, no. 1, pp. 193–201, 1995.

[13] N. A. Curtin and R. C. Woledge, "Efficiency of energy conversion during sinusoidal movement of white muscle fibres from the dogfish *Scyliorhinus canicula*," *J. Exp. Biol.*, vol. 183, no. 1, pp. 137–147, 1993.

[14] ——, "Efficiency of energy conversion during sinusoidal movement of red muscle fibres from the dogfish *Scyliorhinus canicula*," *J. Exp. Biol.*, vol. 185, no. 1, pp. 195–206, 1993.

[15] L. C. Rome, R. P. Funke, R. M. Alexander, G. J. Lutz, H. D. J. N. Aldridge, F. Scott, and M. Freadman, "Why animals have different muscle fibre types," *Nature*, vol. 335, no. 6193, pp. 824–827, 1988.

[16] Q. Bone, J. Kicenuik, and D. R. Jones, "On the role of the different fibre types in fish myotomes at intermediate swimming speeds," *Fish. Bull.*, vol. 76, pp. 691–699, 1978.

[17] B. C. Jayne and G. V. Lauder, "Red muscle motor patterns during steady swimming in largemougth bass: Effects of speed and correlations with axial kinematics," *J. Exp. Biol.*, vol. 198, no. 7, pp. 1575–1587, 1995.

[18] L. C. Rome, P. T. Loughna, and G. Goldspink, "Muscle fiber activity as a function of swim speed and muscle temperature in carp," *Amer. J. Physiol.*, vol. 247, no. 2 Pt 2, pp. r272–r279, 1984.

[19] D. Appelt, V. Shen, and C. Franzini-Armstrong, "Quantization of Ca ATPase, feet and mitochondria in super fast muscle fibers from the toadfish, *Opsanus tau*," *J. Muscle Res. Cell Motil.*, vol. 12, pp. 543–552, 1991.

[20] B. Block, T. Imagawa, K. P. Campbell, and C. Franzini-Armstrong, "Structural evidence for direct interaction between the molecular components of the transverse tubule/sarcoplasmic reticulum junction in skeletal muscle," *J. Cell Biol.*, vol. 107, no. 6, pp. 2587–2600, 1988.

[21] K. M. O'Brien, C. Skilbeck, B. D. Sidell, and S. Egginton, "Muscle fine structure may maintain the function of oxidative fibres in haemoglobinless Antarctic fishes," *J. Exp. Biol.*, vol. 206, no. Pt 2, pp. 411–421, Jan. 2003.

[22] W. K. Riemenschneider and B. D. Sidell, "Cold acclimation induces proliferation of sarcoplasmic reticulum without increase in Ca2+-ATPase activity in white axial muscle of striped bass (*Morone saxatilis*)," *J. Exp. Zool.*, vol. 292, no. 3, pp. 231–240, Feb. 2002.

[23] K. M. O'Brien and B. D. Sidell, "The interplay among cardiac ultrastructure, metabolism and the expression of oxygen-binding proteins in Antarctic fishes," *J. Exp. Biol.*, vol. 203, no. Pt 8, pp. 1287–1297, Apr. 2000.

[24] F. Lou, N. A. Curtin, and R. C. Woledge, "Isometric and isovelocity contractile performance of red muscle fibres from the dogfish *Scyliorhinus canicula*," *J. Exp. Biol.*, vol. 205, no. Pt 11, pp. 1585–1595, Jun. 2002.

[25] F. Lou, W. J. Der Laarse, N. A. Curtin, and R. C. Woledge, "Heat production and oxygen consumption during metabolic recovery of white muscle fibres from the dogfish *Scyliorhinus canicula*," *J. Exp. Biol.*, vol. 203, no. Pt 7, pp. 1201–1210, Apr. 2000.

[26] H. A. Akster, "Ultrastructure of muscle fibres in head and axial muscles of perch (*Perca fluviatilis* L.)," *Cell Tissue Res.*, vol. 219, no. 1, pp. 111–131, 1981.

[27] H. L. M. Granzier, J. Wiersma, H. A. Akster, and J. W. M. Osse, "Contractile properties of a white- and a red-fibre type of the *M. hyohyoideus* of the carp (*Cyprinus carpio* L.)," *J. Comp. Physiol.*, vol. 149, pp. 441–449, 1983.

[28] B. Block, "Evolutionary novelties: How fish have built a heater out of muscle," *Amer. Zool.*, vol. 31, no. 4, pp. 726–742, 1991.
[29] J. M. Morrissette, J. P. Franck, and B. A. Block, "Characterization of ryanodine receptor and Ca2+-ATPase isoforms in the thermogenic heater organ of blue marlin (*Makaira nigricans*)," *J. Exp. Biol.*, vol. 206, no. Pt 5, pp. 805–812, Mar. 2003.
[30] R. C. Woledge, N. A. Curtin, and E. Homsher, *Energetic Aspects of Muscle Contraction*. New York: Academic, 1985.
[31] E. Henneman, G. Somjen, and D. O. Carpenter, "Functional significance of cell size in spinal motor neurons," *J. Neurophysiol.*, vol. 28, pp. 560–580, 1965.
[32] K. D'Aout, A. Curtin, T. L. Williams, and P. Aerts, "Mechanical properties of red and white swimming muscles as a function of the position along the body of the eel *Anguilla anguilla*," *J. Exp. Biol.*, vol. 204, no. Pt 13, pp. 2221–2230, Jul. 2001.
[33] S. Egginton, C. Skilbeck, L. Hoofd, J. Calvo, and I. A. Johnston, "Peripheral oxygen transport in skeletal muscle of Antarctic and sub-Antarctic notothenioid fish," *J. Exp. Biol.*, vol. 205, no. Pt 6, pp. 769–779, Mar. 2002.
[34] D. J. Marcinek, J. Bonaventura, J. B. Wittenberg, and B. A. Block, "Oxygen affinity and amino acid sequence of myoglobins from endothermic and ectothermic fish," *Amer. J. Physiol., Regul. Integr. Comp Physiol.*, vol. 280, no. 4, pp. R1123–R1133, Apr. 2001.
[35] D. J. Ellerby, J. D. Altringham, T. Williams, and B. A. Block, "Slow muscle function of Pacific bonito (*Sarda chiliensis*) during steady swimming," *J. Exp. Biol.*, vol. 203, no. Pt 13, pp. 2001–2013, Jul. 2000.
[36] I. A. Johnston and G. K. Temple, "Thermal plasticity of skeletal muscle phenotype in ectothermic vertebrates and its significance for locomotory behaviour," *J. Exp. Biol.*, vol. 205, no. Pt 15, pp. 2305–2322, Aug. 2002.
[37] J. M. Wakeling, K. M. Kemp, and I. A. Johnston, "The biomechanics of fast-starts during ontogeny in the common carp *Cyprinus carpio*," *J. Exp. Biol.*, vol. 202, no. Pt 22, pp. 3057–3067, Nov. 1999.
[38] F. Lou, N. A. Curtin, and R. C. Woledge, "Elastic energy storage and release in white muscle from dogfish *Scyliorhinus canicula*," *J. Exp. Biol.*, vol. 202, no. Pt 2, pp. 135–142, Jan. 1999.
[39] I. A. Johnston, W. Davison, and G. Goldspink, "Energy metabolism of carp swimming muscles," *J. Comp. Physiol.*, vol. 114, pp. 203–216, 1977.
[40] P. J. Schaeffer, K. E. Conley, and S. L. Lindstedt, "Structural correlates of speed and endurance in skeletal muscle: The rattlesnake tailshaker muscle," *J. Exp. Biol.*, vol. 199, no. Pt 2, pp. 351–358, 1996.
[41] K. E. Conley and S. L. Lindstedt, "Rattlesnake tail-shaking: Minimal cost per twitch in striated muscle," *Nature*, vol. 383, pp. 71–73, 1996.
[42] A. H. Bass and J. R. McKibben, "Neural mechanisms and behaviors for acoustic communication in teleost fish," *Prog. Neurobiol.*, vol. 69, no. 1, pp. 1–26, Jan. 2003.
[43] J. L. Goodson and A. H. Bass, "Vocal-acoustic circuitry and descending vocal pathways in teleost fish: Convergence with terrestrial vertebrates reveals conserved traits," *J. Comp. Neurol.*, vol. 448, no. 3, pp. 298–322, Jul. 2002.
[44] D. A. Bodnar, A. D. Holub, B. R. Land, J. Skovira, and A. H. Bass, "Temporal population code of concurrent vocal signals in the auditory midbrain," *J. Comp. Physiol., A Neuroethol. Sens. Neural Behav. Physiol.*, vol. 187, no. 11, pp. 865–873, Dec. 2001.
[45] J. R. McKibben and A. H. Bass, "Peripheral encoding of behaviorally relevant acoustic signals in a vocal fish: Harmonic and beat stimuli," *J. Comp. Physiol., A*, vol. 187, no. 4, pp. 271–285, May 2001.
[46] M. L. Fine, K. L. Malloy, C. B. King, S. L. Mitchell, and T. M. Cameron, "Movement and sound generation by the toadfish swimbladder," *J. Comp. Physiol.*, vol. 187, no. 5, pp. 371–379, 2001.
[47] M. L. Fine, "Seasonal and geographical variation of the mating call of the oyster toadfish *Opsanus tau* L.," *Oecologia*, vol. 36, pp. 45–57, 1978.
[48] P. Edds-Walton, L. Mangiamele, and L. C. Rome, "Boatwhistles from oyster toadfish (*Opsanus tau*) around Waquoit Bay, Massachusetts," *J. Bioacoustics*, vol. 13, pp. 153–173, 2002.
[49] L. C. Rome, P. T. Loughna, and G. Goldspink, "Temperature acclimation improves sustained swimming performance at low temperatures in carp," *Science*, vol. 228, pp. 194–196, 1985.
[50] L. C. Rome, R. P. Funke, and R. M. Alexander, "The influence of temperature on muscle velocity and sustained performance in swimming carp," *J. Exp. Biol.*, vol. 154, no. 1, pp. 163–178, 1990.
[51] D. J. Coughlin and L. C. Rome, "Muscle activity in steady swimming scup, *Stenotomus chrysops* is a function of fiber type and body position," *Biol. Bull.*, vol. 196, no. 2, pp. 145–152, 1999.
[52] L. C. Rome and A. A. Sosnicki, "Myofilament overlap in swimming carp—II. Sarcomere length changes during swimming," *Amer. J. Physiol., Cell Physiol.*, vol. 260, no. 2, pp. C289–C296, 1991.
[53] R. M. Alexander, "The orientation of muscle fibres in the myomeres of fishes," *J. Mar. Biol. Assoc.*, vol. 49, pp. 263–290, 1969.
[54] J. L. van Leeuwen, M. J. M. Lankheet, H. A. Akster, and J. W. M. Osse, "Function of red axial muscle of carp (*Cyprinus carpio* L.): Recruitment and normalised power output during swimming in different modes," *J. Zool. (Lond.)*, vol. 220, pp. 123–145, 1990.
[55] S. L. Lindstedt, T. McGlothlin, E. Percy, and J. Pifer, "Task-specific design of skeletal muscle: Balancing muscle structural composition," *Comp. Biochem. Physiol.*, vol. 120, no. 1, pp. 35–40, 1998.
[56] I. A. Johnston, "Dynamic properties of fish muscle," in *Fish Biomechanics*, P. W. Webb and D. Weihs, Eds. New York: Praeger, 1983, pp. 36–67.
[57] S. G. Page and H. E. Huxley, "Filament lengths in striated muscle," *J. Cell Biol.*, vol. 19, no. 2, pp. 369–390, 1963.
[58] A. A. Sosnicki, K. Loesser, and L. C. Rome, "Myofilament overlap in swimming carp—I. Myofilament lengths of red and white muscle," *Amer. J. Physiol., Cell Physiol.*, vol. 260, no. 2, pp. C283–C288, 1991.
[59] Y. E. Goldman and A. F. Huxley, "Actin compliance: Are you pulling my chain?," *Biophys. J.*, vol. 67, no. 6, pp. 2131–2133, 1994.
[60] A. M. Gordon, A. F. Huxley, and F. J. Julian, "The variation in isometric tension with sarcomere length in vertebrate muscle fibers," *J. Physiol. (Lond.)*, vol. 184, pp. 170–192, 1966.
[61] A. F. Huxley and R. Niedergerke, "Structural changes in muscle during contraction: Interference microscopy of living muscle fibers," *Nature*, vol. 173, pp. 971–973, 1954.
[62] L. C. Rome, "The mechanical design of the muscular system," in *Comparative Vertebrate Exercise Physiology*, J. H. Jones, Ed. Orlando, FL: Academic, 1994, pp. 125–179.
[63] A. V. Hill, "The dimensions of animals and their muscular dynamics," *Sci. Prog.*, vol. 38, no. 150, pp. 209–229, 1950.
[64] D. J. Coughlin, G. Zhang, and L. C. Rome, "Contractile dynamics and power production of pink muscle of the scup," *J. Exp. Biol.*, vol. 199, pp. 2703–2712, 1996.
[65] L. C. Rome and A. A. Sosnicki, "The influence of temperature on mechanics of red muscle in carp," *J. Physiol. (Lond.)*, vol. 427, pp. 151–169, 1990.
[66] J. M. Wakeling and I. A. Johnston, "White muscle strain in the common carp and red to white muscle gearing ratios in fish," *J. Exp. Biol.*, vol. 202, no. Pt 5, pp. 521–528, Mar. 1999.
[67] L. C. Rome, I. Choi, G. J. Lutz, and A. A. Sosnicki, "The influence of temperature on muscle function in fast swimming scup—I. Shortening velocity and muscle recruitment during swimming," *J. Exp. Biol.*, vol. 163, pp. 259–279, 1992.
[68] L. C. Rome, A. A. Sosnicki, and I. Choi, "The influence of temperature on muscle function in the fast swimming scup—II. The mechanics of red muscle," *J. Exp. Biol.*, vol. 163, pp. 281–295, 1992.
[69] L. C. Rome, D. A. Syme, S. Hollingworth, S. L. Lindstedt, and S. M. Baylor, "The whistle and the rattle: The design of sound producing muscles," *Proc. Natl. Acad. Sci.*, vol. 93, no. 15, pp. 8095–8100, 1996.
[70] A. B. Bass and R. Baker, "Evolution of homologous vocal control traits," *Brain Behav. Evol.*, vol. 37, pp. 1–15, 1991.
[71] I. S. Young and L. C. Rome, "Mutually exclusive muscle designs: Power output of locomotory and sonic muscles of the oyster toadfish (*Opsanus tau*)," *Proc. R. Soc. Lond., B*, vol. 268, no. 1480, pp. 1975–1980, 2001.
[72] L. C. Rome and D. Swank, "The influence of temperature on power output of scup red muscle during cyclical length changes," *J. Exp. Biol.*, vol. 171, pp. 261–281, 1992.
[73] D. Swank and L. C. Rome, "The influence of temperature on power production during swimming—I. *In vivo* length change and stimulation pattern," *J. Exp. Biol.*, vol. 203, no. Pt 2, pp. 321–333, 2000.
[74] L. C. Rome, D. Swank, and D. J. Coughlin, "The influence of temperature on power production during swimming—II. Mechanics of red muscle fibres *in vivo*," *J. Exp. Biol.*, vol. 203, pp. 333–345, 2000.
[75] D. J. Coughlin and L. C. Rome, "The role of pink and red muscle in powering steady swimming in scup, *Stenotomus chrysops*," *Amer. Zool.*, vol. 36, pp. 666–677, 1996.
[76] L. C. Rome and D. Swank, "The influence of thermal acclimation on power production during swimming—I. *In vivo* stimulation and length change pattern of scup red muscle," *J. Exp. Biol.*, vol. 204, pp. 409–418, 2001.
[77] D. Swank and L. C. Rome, "The influence of thermal acclimation on power production during swimming—II. *In vivo* mechanics of scup red muscle," *J. Exp. Biol.*, vol. 204, no. Pt 3, pp. 419–430, 2001.
[78] G. Zhang, D. Swank, and L. C. Rome, "Quantitative distribution of muscle fiber types in the scup *Stenotomus chrysops*," *J. Morphol.*, vol. 229, no. 1, pp. 71–81, 1996.

[79] T. G. West, N. A. Curtin, M. A. Ferenczi, Z. H. He, Y. B. Sun, M. Irving, and R. C. Woledge, "Actomyosin energy turnover declines while force remains constant during isometric muscle contraction," *J. Physiol.*, vol. 555, no. Pt 1, pp. 27–43, 2004.

[80] L. C. Rome, "Matching the muscular system for different tasks: Are muscular systems optimally designed?," in *Optimal Animal Design: The Optimization and Symmorphosis Debate*, E. R. Weibel, C. R. Taylor, and L. Bolis, Eds. Cambridge, U.K.: Cambridge Univ. Press, 1998, pp. 103–114.

[81] M. J. Wolfgang, J. M. Anderson, M. A. Grosenbaugh, D. K. Yue, and M. S. Triantafyllou, "Near-body flow dynamics in swimming fish," *J. Exp. Biol.*, vol. 202, no. Pt 17, pp. 2303–2327, Sep. 1999.

[82] E. J. Anderson, W. R. McGillis, and M. A. Grosenbaugh, "The boundary layer of swimming fish," *J. Exp. Biol.*, vol. 204, no. Pt 1, pp. 81–102, Jan. 2001.

[83] J. C. Liao, D. N. Beal, G. V. Lauder, and M. S. Triantafyllou, "Fish exploiting vortices decrease muscle activity," *Science*, vol. 302, no. 5650, pp. 1566–1569, Nov. 2003.

[84] ——, "The Karman gait: Novel body kinematics of rainbow trout swimming in a vortex street," *J. Exp. Biol.*, vol. 206, no. Pt 6, pp. 1059–1073, Mar. 2003.

[85] E. G. Drucker and G. V. Lauder, "Function of pectoral fins in rainbow trout: Behavioral repertoire and hydrodynamic forces," *J. Exp. Biol.*, vol. 206, no. Pt 5, pp. 813–826, Mar. 2003.

[86] G. V. Lauder and E. G. Drucker, "Forces, fishes, and fluids: Hydrodynamic mechanisms of aquatic locomotion," *News Physiol. Sci.*, vol. 17, no. 6, pp. 235–240, Dec. 2002.

[87] J. C. Nauen and G. V. Lauder, "Quantification of the wake of rainbow trout (*Oncorhynchus mykiss*) using three-dimensional stereoscopic digital particle image velocimetry," *J. Exp. Biol.*, vol. 205, no. Pt 21, pp. 3271–3279, Nov. 2002.

[88] ——, "Hydrodynamics of caudal fin locomotion by chub mackerel, *Scomber japonicus* (Scombridae)," *J. Exp. Biol.*, vol. 205, no. Pt 12, pp. 1709–1724, Jun. 2002.

[89] E. G. Drucker and G. V. Lauder, "Locomotor function of the dorsal fin in teleost fishes: Experimental analysis of wake forces in sunfish," *J. Exp. Biol.*, vol. 204, no. Pt 17, pp. 2943–2958, Sep. 2001.

[90] J. C. Nauen and G. V. Lauder, "Locomotion in scombrid fishes: Visualization of flow around the caudal peduncle and finlets of the chub mackerel *Scomber japonicus*," *J. Exp. Biol.*, vol. 204, no. Pt 13, pp. 2251–2263, Jul. 2001.

[91] E. G. Drucker and G. V. Lauder, "Wake dynamics and fluid forces of turning maneuvers in sunfish," *J. Exp. Biol.*, vol. 204, no. Pt 3, pp. 431–442, Feb. 2001.

[92] J. Liao and G. V. Lauder, "Function of the heterocercal tail in white sturgeon: Flow visualization during steady swimming and vertical maneuvering," *J. Exp. Biol.*, vol. 203, no. Pt 23, pp. 3585–3594, Dec. 2000.

[93] C. D. Wilga and G. V. Lauder, "Three-dimensional kinematics and wake structure of the pectoral fins during locomotion in leopard sharks *Triakis semifasciata*," *J. Exp. Biol.*, vol. 203, no. Pt 15, pp. 2261–2278, Aug. 2000.

[94] G. V. Lauder and E. G. Drucker, "Morphology and experimental hydrodynamics of fish fin control surfaces," *IEEE J. Ocean. Eng.*, vol. 29, no. 3, pp. 556–571, 2004.

[95] R. J. Full and A. N. Ahn, "Static forces and moments generated in the insect leg: Comparison of a three-dimensional musculo-skeletal computer model with experimental measurements," *J. Exp. Biol.*, vol. 198, no. 6, pp. 1285–1298, 1995.

[96] D. L. Jindrich and R. J. Full, "Dynamic stabilization of rapid hexapedal locomotion," *J. Exp. Biol.*, vol. 205, no. Pt 18, pp. 2803–2823, Sep. 2002.

[97] J. Schmitt, M. Garcia, R. C. Razo, P. Holmes, and R. J. Full, "Dynamics and stability of legged locomotion in the horizontal plane: A test case using insects," *Biol. Cybern.*, vol. 86, no. 5, pp. 343–353, May 2002.

[98] A. N. Ahn and R. J. Full, "A motor and a brake: Two leg extensor muscles acting at the same joint manage energy differently in a running insect," *J. Exp. Biol.*, vol. 205, no. Pt 3, pp. 379–389, Feb. 2002.

[99] M. H. Dickinson, C. T. Farley, R. J. Full, M. A. Koehl, R. Kram, and S. Lehman, "How animals move: An integrative view," *Science*, vol. 288, no. 5463, pp. 100–106, Apr. 2000.

[100] W. J. Kargo, F. Nelson, and L. C. Rome, "Jumping in frogs: Assessing the design of the skeletal system by anatomically realistic modeling and forward dynamic simulation," *J. Exp. Biol.*, vol. 205, pp. 1683–1702, 2002.

[101] A. M. Boustany, S. F. Davis, P. Pyle, S. D. Anderson, B. J. Le Boeuf, and B. A. Block, "Expanded niche for white sharks," *Nature*, vol. 415, no. 6867, pp. 35–36, Jan. 2002.

[102] B. A. Block, H. Dewar, S. B. Blackwell, T. D. Williams, E. D. Prince, C. J. Farwell, A. Boustany, S. L. Teo, A. Seitz, A. Walli, and D. Fudge, "Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna," *Science*, vol. 293, no. 5533, pp. 1310–1314, Aug. 2001.

[103] H. Dewar, M. Deffenbaugh, G. Thurmond, K. Lashkari, and B. A. Block, "Development of an acoustic telemetry tag for monitoring electromyograms in free-swimming fish," *J. Exp. Biol.*, vol. 202, no. Pt 19, pp. 2693–2699, Oct. 1999.

[104] J. M. Donley and R. E. Shadwick, "Steady swimming muscle dynamics in the leopard shark *Triakis semifasciata*," *J. Exp. Biol.*, vol. 206, no. Pt 7, pp. 1117–1126, Apr. 2003.

[105] D. A. Syme and R. E. Shadwick, "Effects of longitudinal body position and swimming speed on mechanical power of deep red muscle from skipjack tuna (*Katsuwonus pelamis*)," *J. Exp. Biol.*, vol. 205, no. Pt 2, pp. 189–200, Jan. 2002.

[106] D. Bernal, K. A. Dickson, R. E. Shadwick, and J. B. Graham, "Review: Analysis of the evolutionary convergence for high performance swimming in lamnid sharks and tunas," *Comp. Biochem. Physiol., Part A Mol. Integr. Physiol.*, vol. 129, no. 2–3, pp. 695–726, Jun. 2001.

[107] S. L. Katz, D. A. Syme, and R. E. Shadwick, "High-speed swimming. Enhanced power in yellowfin tuna," *Nature*, vol. 410, no. 6830, pp. 770–771, Apr. 2001.

[108] D. A. Ritter, D. H. Bhatt, and J. R. Fetcho, "In vivo imaging of zebrafish reveals differences in the spinal networks for escape and swimming movements," *J. Neurosci.*, vol. 21, no. 22, pp. 8956–8965, Nov. 2001.

[109] M. E. Hale, D. A. Ritter, and J. R. Fetcho, "A confocal study of spinal interneurons in living larval zebrafish," *J. Comp. Neurol.*, vol. 437, no. 1, pp. 1–16, Aug. 2001.

[110] J. R. Fetcho, K. J. Cox, and D. M. O'Malley, "Imaging neural activity with single cell resolution in an intact, behaving vertebrate," *Biol. Bull.*, vol. 192, no. 1, pp. 150–153, Feb. 1997.

[111] K. S. Liu and J. R. Fetcho, "Laser ablations reveal functional relationships of segmental hindbrain neurons in zebrafish," *Neuron*, vol. 23, no. 2, pp. 325–335, Jun. 1999.

[112] S. Higashijima, M. A. Masino, G. Mandel, and J. R. Fetcho, "Imaging neuronal activity during zebrafish behavior with a genetically encoded calcium indicator," *J. Neurophysiol.*, vol. 90, no. 6, pp. 3986–3997, Dec. 2003.

[113] K. S. Liu, M. Gray, S. J. Otto, J. R. Fetcho, and C. E. Beattie, "Mutations in deadly seven/notch1a reveal developmental plasticity in the escape response circuit," *J. Neurosci.*, vol. 23, no. 22, pp. 8159–8166, Sep. 2003.

Lawrence C. Rome was born in Boston, MA, in 1952. He received the A.B. degree in biology at Dartmouth College, Hanover, NH, in 1974 and the Ph.D. degree in biology from Harvard University, Cambridge, MA, in 1981.

Between 1982 and 1985, he received Postdoctoral Fellowships at the University of Hull, U.K., and the Harvard Medical School. He took his first professorial position at the University of Tennessee, Knoxville, in 1985 and then moved to the University of Pennsylvania, Philadelphia, in 1989, where he became Professor of Biology in 1998. He is also a Member of the Pennsylvania Muscle Institute, Philadelphia. Since 1986, he has worked in Woods Hole, MA, in summers as a Principal Investigator at the Marine Biological Laboratory and for a portion of the time as a Visiting Investigator at the Woods Hole Oceanographic Institution. His chief interest is integrating muscle function from the biophysical level to whole animal to understand how muscles are designed for different functions (including locomotion and sound production). He has used fish, frogs, and mammals of different body sizes as experimental models. Recently, he invented a backpack that generates electricity during walking and demonstrates improved ergonomics. He has published about 80 papers.

Prof. Rome is a member of the American Physiological Society, The Biophysical Society, and the Society for Experimental Biology (U.K.)