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Review

Design of heterothermic muscle in fish

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Summary

Among the tremendous diversity of fish, there are a small number that are considered elite in their swimming performance. These include representatives from the tunas, billfish and sharks. In addition to being elite swimmers, these fish share numerous specialized anatomical features including the structure of their swimming muscles and some form of regional endothermy, termed heterothermy. These heterothermies fall into two classes: those that maintain elevated temperatures in swimming muscles and those that have muscle-derived tissues specialized for delivering warm blood to the brain. Because these versions of heterothermy are manifest in fish whose swimming performance is considered elite, it has been parsimonious to hypothesize that heterothermy is part of an integrated high-performance design. Recognizing that the design of skeletal muscle is hierarchical, the design of heterothermic muscle in fish will be examined within a hierarchical framework. This paper will examine, in order, the specific anatomical specializations, the performance of muscle as a biomaterial and then as a dynamic mechanical structure or device – in each case looking at the extent to which heterothermy is part of an integrated high-performance design or is perhaps just a happy accident. This examination will reveal how difficult it is to make a case for the central importance of heterothermy in the design of these swimming muscle systems.

Key words: fish, swimming, biomechanics, evolution, heterothermy, muscle.

Introduction

The tremendous evolutionary success of fishes has resulted in an extreme diversity of form and design. However, in almost every case, the design specializations shown by fishes are all still elaborations of features generic to the lower vertebrate classes. One design feature that forms a notable exception is seen in those few fish that maintain body temperatures (T_b), or some part of the body, in excess of ambient temperatures (T_a). Specifically, elevated core temperatures have been demonstrated in 13 species of scombrid fishes of the tribe Thunnini, such as yellowfin and bluefin tunas (Carey, 1973; Graham, 1975; Graham and Dickson, 2000) as well as some sharks within the families Lamnidae (e.g. makos) and Alopidae (e.g. threshers) (Carey and Teal, 1969; Carey et al., 1982) and some billfish in the families Istiophoridae and Xiphiidae (Carey, 1982; Block et al., 1993). Indeed, in the literature, these fish have been described as ‘mammal-like’ solely on the basis of these elevated temperatures, acknowledging the special character of this design feature (Stevens and Neill, 1978; Graham, 1983; Korsmeyer et al., 1996).

Of specific interest to this paper, tunas and sharks that maintain elevated temperatures do so within the mass of red, or oxidative, muscle used in steady swimming that is in addition to the red muscle seen in non-heterothermic fishes. These fish also possess a complex circulatory anatomy that retains heat within the muscle. In the context of all this design, it has been presumed that the maintenance of elevated temperatures is adaptive in improving muscle power output during swimming (Graham, 1975; Stevens and Neill, 1978). This assertion, however satisfyingly parsimonious it might be, has never been critically questioned. This paper will examine the role heterothermy plays in the swimming biomechanics of heterothermic fish with an eye to testing this assertion.

This goal turns out to be challenging for several reasons, but among them is simply defining the issue in a manner that allows a discrete question to be framed. There are a lot of things that make these heterothermic tunas and sharks special, so how does one decide how they relate to each other? Or do they relate to each other at all? For example, all the fish that display heterothermy are considered elite, high-performance swimmers. In addition to elevated T_b, they possess a number of correlated anatomical specializations that are distinctive to the swimming machinery (which will be described in more detail below). Is heterothermy a primary design feature and itself adaptive? Given that a strip of muscle *in vitro* shows

increased mechanical performance over a limited range of increasing temperatures (i.e. a *within*-species comparison) (e.g. Rome and Swank, 1992; Rome et al., 1992a,b), there is a general expectation that heterothermic fish will perform better than non-heterotherms simply because they are warmer (i.e. an *across*-species comparison). On that basis alone, heterothermy has been called adaptive. An alternative hypothesis might be that the biomechanical consequence of the anatomy is the principal design feature and that heterothermy is a happy by-product. To help form that discrete question, it is worth putting some boundaries on the scope of this paper.

One thing to keep in mind is that the fish discussed in this paper do not maintain a constant T_b over a wide range of T_a, as do mammals and birds. Tuna, for example, appear to maintain a roughly constant thermal gradient (T_b–T_a) rather than constant T_b, with T_b from as little as 4 °C to as much as 20 °C above T_a (Carey, 1973; Dewar et al., 1994). So, the characterization 'mammal-like' seems inaccurate. Also, these fish are maintaining these elevated T_b values in specific, regional tissues rather than generally in large portions of the body. Tuna and the lamnid sharks from which measurements have been made elevate the temperatures of their oxidative, red swimming muscle and viscera (Carey and Teal, 1964, 1969; Carey, 1973), while butterfly mackerel (genus *Gasterochisma*) and billfish keep only limited components of the central nervous system warm (Carey, 1982). Since this paper examines the biomechanics of swimming muscle, it will not address brain heater organs directly. Because these fish show a more limited, regional endothermy than that displayed by mammals and birds, it is more correctly referred to as heterothermy, and it will be so in this paper.

In discussing heterothermic swimming muscle, it is also worth pointing out that what little experimental work that does exist is almost entirely from work on tuna. Other than documenting that some lamnid sharks are heterothermic (Carey and Teal, 1969; Carey, 1973) and that they possess a high-capacity cardiovascular delivery system similar to that seen in tunas (Korsmeyer et al., 1997; Lai et al., 1997; Bernal et al., 2001), there is little discrete experimental work on the biomechanics of shark muscles. So, while this paper will continue to refer to heterothermic swimming muscle in fish, the reader should keep in mind that there is a big assumption lurking here about the similarities between these sharks and tunas that remains to be validated rigorously.

Now that we have described what this paper is not about, we can frame our question as well as a strategy for achieving an answer. The question is: what is the role of heterothermy in the design of the swimming muscle of these high-performance fish? Given the prominence of mechanics in the performance and design of muscle, it seems logical to start evaluating the design of the muscle in a biomechanical framework. With that in mind, the anatomical design of the swimming muscle in tuna will be reviewed first. Then, the properties of the muscle as a biomaterial will be described. I will then review the properties of the muscle as a dynamic biomechanical structure. At each point, we can ask how the tuna is distinctive from other fish and what role heterothermy plays, in terms of measurable performance, in that distinctiveness. Finally, I will synthesize these components into a clear statement that describes the design of the swimming muscle in these fish and the role heterothermy plays in that design.

Structural design of swimming muscle in these fish

Design of the muscle

Fish myotomes are anatomically complex on several levels, each of which limits one's ability to predict quantitatively how they work as well as making direct biomechanical measurements difficult (Bone, 1978; Katz and Jordan, 1997; Katz and Shadwick, 2000). Originally, the serially arranged myotomes were modeled as simple blocks, one connected to the next all the way down the body (Bone et al., 1995). One result of this early model is that the propulsive wave formed by body undulation is the direct consequence of the activation, and the subsequent contractions, of the muscles down the side of the body. Another feature of this model is that body bending is simply the result of muscle shortening at the same location on the body. But the muscle is geometrically much more complex than simple blocks (Nursall, 1956). Fig. 1 is a diagram of the anatomy of fish myotomes. In side view, the myotomes appear as folded chevrons that bend several times across the dorsal/ventral extent of the fish (Fig. 1A). In cross section, however, the steak appears to consist of a series of concentric rings (Fig. 1B,C). If one merges those two geometries, one sees that the myotomes are a series of stacked cones arranged in series from the posterior margin of the skull to the final caudal myotomes. In fact, there are four sets of cones on each side of most teleost fishes. The most dorsal and most ventral cones on each side have their apexes pointing towards the tail. The larger, intermediate pair of cones have their apexes pointing towards the head. These middle sets of cones are separated by a robust connective tissue structure called the mid-lateral septum (Fig. 1C).

This anatomy has a number of mechanical consequences, most significant of which is that force generated within any myotome has several possible trajectories, making discrete mechanical measurement of any single muscle difficult (Johnsrude and Webb, 1985) (for a review, see Katz and Shadwick, 2000). Individual myotomes are separated by a collagenous fabric-like sheet called a myoseptum that forms the origin and insertions for muscle fibers from adjacent myotomes (Willemse, 1966). So, some force is transmitted across from muscle to muscle. Force is also transmitted along the myoseptum to adjacent skin and spinal column and can act to bend the body locally (Wainwright, 1983). There are also complex connective tissues within the muscle that provide additional force pathways from the muscle to the skeleton (see below).

Fish, in general, are also remarkable in having an almost complete separation of muscle fiber types at the gross anatomical level. Oxidative, or red, muscle fibers, used for long-duration, low-intensity activity, are located in a small

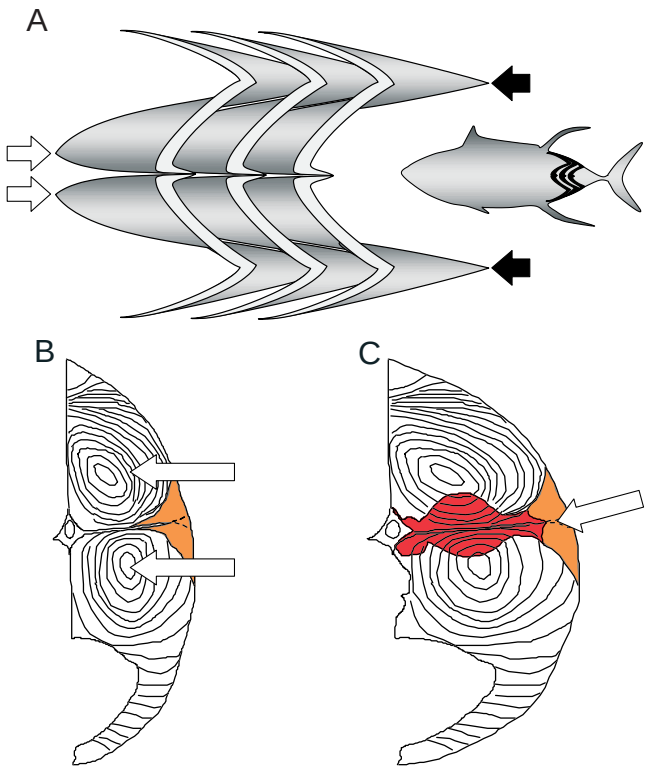


Fig. 1. (A) Structure of the myotomes in side or fillet view. This diagram shows three myotomes each separated by the removal of two intervening myotomes to demonstrate the nested nature of the cones. The silhouette of the fish indicates the orientation of the myotomes within the fillet. Each anterior-pointing cone is indicated with a white arrow and each posterior-pointing cone is indicated with a black arrow. (B) Diagram of the myotomes from a generic non-heterothermic fish in cross section, or steak view. The red, oxidative muscle is in a small wedge in close apposition to the skin along the mid-lateral line (indicated in orange). The remainder of the muscle consists of white, glycolytic fibers within the cones. Sectioning through the nested cones produces the concentric ring structure visible in this view (white arrows). (C) Diagram of the myotomes of a heterothermic yellowfin tuna (*Thunnus albacares*) in cross section, or steak view. This diagram shows the distribution of red muscle that is common to tunas, where there is an internal loin of red muscle fibers (in red) in addition to the superficial wedge of red fibers seen in other fish (orange). The location where the mid-lateral septum passes through this section is indicated with a white arrow.

wedge that runs along the body under the skin along the mid-lateral line (Fig. 1B). The glycolytic, or white, muscle fibers, used for high-intensity sprinting, make up the remaining volume of muscle (Rome et al., 1984; Johnston et al., 1993). Studies looking at patterns of muscle activation indicate that red fibers are the only fibers active at slow swimming speeds and that, as speed increases, white fibers are differentially recruited (Bone, 1966; Rome et al., 1984; Brill and Dizon, 1979). It is not clear that this separation is absolute, and it is possible that red fibers are still active at higher speeds (Coughlin and Rome, 1996), although it has been argued that they are unable to contribute significant amounts of work at the tailbeat frequencies used in sprinting (van Leeuwen, 1992). In some teleost fishes, there is a distinct, additional layer of 'pink' muscle that has an intermediate anatomical location, biomechanical function and biochemical character (Coughlin and Rome, 1996; Johnston et al., 1974).

In addition to this anatomy shown by fish in general, fish with heterothermic swimming muscle have an additional loin of red muscle that lies within the fillet, medial to the skin and lateral to the spinal column (Fig. 1C). This internal loin of red muscle is in a location that in non-heterothermic fish is composed of white fibers, and this turns out to have numerous mechanical consequences (Knower et al., 1999; Shadwick et al., 1999) (see below). As a group, fish with the additional loin of internal red muscle have more total red muscle than other fish (Graham et al., 1983; Bernal et al., 2001). However, measures of the percentage of body mass that is red muscle are confounded by differences in body size, developmental age and lifestyle. In non-heterotherms, red muscle makes up between 2 and 6% of body mass, while heterotherms have between 4 and 13% of body mass composed of red muscle (Webb, 1975; Graham et al., 1983; Videler, 1993). Although the median value for heterotherms is higher, the overlap in these ranges prevents an unqualified statement. Importantly, heterothermic sharks have convergently developed an internal loin of red muscle in a similar location to that seen in tuna (Carey and Teal, 1969). This internal loin of muscle is a shared character among fish with warm swimming muscle and is distinctive from other fish, suggesting that an examination of the mechanical consequences of this muscle design will provide insights into the shared design characteristics: muscle mechanics, high-performance swimming and heterothermy.

Design of the connective tissues

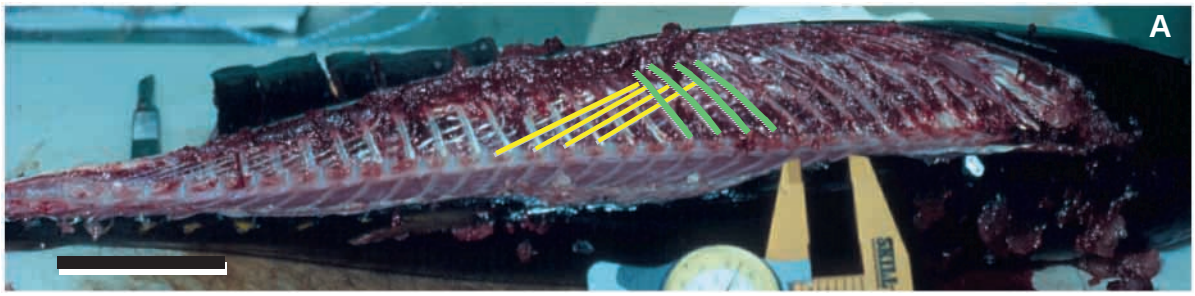
Superimposed on this muscle anatomy is a complex hierarchy of connective tissue structures located within the axial musculature. Most explicitly, Westneat et al. (1993), in analyzing scombrid connective tissue previously described by Kishinouye (1923), Kafuku (1950) and Fierstine and Walters (1968), arrived at a model to explain the function of the organized tendons within the mid-lateral septum of tuna. Briefly, red muscle fibers that lie within the warm, internal loins of muscle attach to collagen fibers that coalesce into a tendon near the skin. That tendon extends posteriorly, then obliquely and medially towards an insertion on the spinal column several vertebrae caudal to the location of the muscle fibers (Fig. 2A). The suggested mechanical function of these oblique tendons is a departure from the model of blocks of myotomal muscle attaching one to the next down the body of other fish in that these tendons form a muscle–tendon–bone trajectory for force transmission like that seen in the appendicular musculo-skeletal systems of vertebrates. This anatomical force trajectory also suggests that the force of the muscle is applied across several vertebrae – rather than strictly in the same anatomical location as the muscle fibers themselves.

Although quite reasonable, this model remains untested.

Indeed, the surgical requirements of introducing force transducers into the mid-lateral septum of intact, swimming fish seems quite challenging. It is also worth pointing out that the oblique tendons within the mid-lateral septum of tuna are distinctive among fish in being particularly well developed, and tuna are the only fish for which a model has been developed for their mechanical function. However, some form of this structure is almost ubiquitous among teleost fish and, if the proposed mechanical role for heterotherms proves true, it will probably prove true for other fish as well. No obvious analog has been identified in heterothermic sharks (Bernal et al., 2001).

What does make heterothermic tunas distinct from other teleost fish is the progressive replacement of the most caudal myotomes with tendon (Fierstine and Walters, 1968) (Fig. 2B). The great lateral tendons are formed from the collagenous myoseptal sheets in the caudal portion of the body. These tendons run from the caudal myotomes, span the caudal peduncle and insert on the hypural bones of the caudal fin. The mechanical role of these tendons has been explored by Knower et al. (1999) in two species of endothermic tuna (skipjack tuna *Katsuwonus pelamus* and yellowfin tuna *Thunnus albacares*) swimming in a water-tunnel treadmill. Tension in the tendons was transduced using a tendon buckle force transducer after the method described by Biewener et al. (1988). This work has shown that, during steady swimming, these tendons are substantially loaded. More significant than the magnitudes of these loads is the observation that tension in these tendons begins while only the most anterior myotomes are active, as indicated by simultaneous electromyography. This suggests that force generated in these most anterior myotomes is transmitted along the length of the fish to the caudal tendons across the intervening, inactive myotomes during swimming (Knower et al., 1999). In tuna, this long-range force transmission is an additional trajectory of force from the anterior muscles to the tail blade.

The force is generated in the rostral muscle and transmitted to the caudal great lateral tendons, but what transmits the force over that distance? In these high-performance fish, it is likely that the skin is a mechanically important component in the specialized connective tissue design. Fish skin has been recognized as a potentially important mechanical tissue by several investigators (Motta, 1977; Hebrank, 1980; Videler, 1993; Wainwright, 1983; Long et al., 1996), and its importance as an ‘exotendon’ was demonstrated in sharks. Mechanical tests on teleost skin, including that of the heterothermic skipjack tuna (Hebrank and Hebrank, 1986), indicated that the tissue had a fairly low stiffness in the longitudinal direction when tested unidirectionally, suggesting potentially poor performance as a tendon. We cannot rule out the possibility of



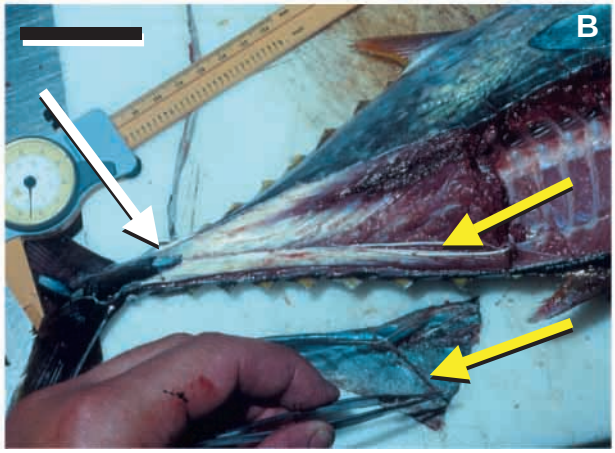


Fig. 2. (A) Dissection photograph of a yellowfin tuna (*Thunnus albacares*) showing the location and structure of the mid-lateral septum. The head is on the right and the tail on the left, and the dorsal half of the left fillet has been removed to reveal this view from above. As described by Westneat et al. (1993), the anterior oblique tendons run outwards and posteriorly and are composed of tendon precipitated around ribs. Four of them are highlighted in green. Posterior oblique tendons run inwards and posteriorly, and four of these are highlighted in yellow. Scale bar, 5 cm. (B) Dissection photograph of the posterior region of a yellowfin tuna (*Thunnus albacares*) with the skin removed to reveal the dwindling posterior muscle volume and the progressive replacement of muscle with tendon. These tendons form from myosepta, but progressing towards the peduncle (white arrow) they completely replace the muscle and form dense, twisting ropes of solid tendon. The yellow arrows indicate the long tendons from the subdermal sheath that originate in the myosepta but form mechanical connections to the skin, indicated by the tendons still attached to the skin after an attempt to peel them away. This also suggests a potential trajectory for forces generated in anterior myotomes (see text). The presence of a mechanical connection can be seen in the way the skin ‘tents up’ when the tendon is pulled on with forceps in the lower, reflected flap of skin. Scale bar, 5 cm.

the skin acting as a longitudinal force transmitter however, since, if the shortening muscle bulges the skin, it may be stretched in the dorso-ventral direction, resulting in a tendency to shorten in the longitudinal direction. This force transmission mechanism was proposed by Wainwright (1983) and Videler (1993) and tested in preliminary work by Müller and Blickhan (1991) on trout. The helical layering of collagen fibers within the skin means that a single fiber connects a point on one edge of the skin (i.e. on the dorsal or ventral midline) with a more posterior point on the opposite edge (Videler, 1993), also suggesting that this loading of the skin would probably transmit forces longitudinally.

Other anatomical evidence that indicates a mechanical role for the skin includes the observation that the skin of tuna is firmly anchored to the myosepta of the axial muscles above and below the region of the lateral red muscle. In addition, the skin is tightly anchored to the superficial lateral caudal tendons (Fig. 2B), termed the subdermal sheath by Westneat et al. (1993), which inserts directly onto the caudal fin. This suggests that forces generated by the anterior muscles and transmitted *via* the skin could be applied directly to the caudal fin. Sharks are known to have robust skin, heavily invested in collagen fibers; there is no documentation of great lateral tendons. It has recently been suggested that the skin in heterothermic sharks could serve the same mechanical role as the lateral tendons in tuna (Bernal et al., 2001). Direct *in vivo* measurements of the mechanics of the skin have yet to be made in tunas or heterothermic sharks.

Design of the circulatory system

In addition to the connective tissue framework within the fillet, the swimming muscles of tunas and sharks are penetrated by a sophisticated architecture of blood vessels. The presence of specialized vascular structures and their role in heterothermy has been documented since 1835, and the history of the study of these structures and their function has been reviewed in great detail by Fudge and Stevens (1996). Therefore, they need only be briefly summarized here.

The vessels show a tremendous complexity in their structure and are clearly an important part of the overall design of heterothermic muscle in these fish. It is important to keep in mind that the anatomical design reflects the dual roles of supplying the muscle's metabolic need for oxygen as well as conducting, or limiting the conduction of, heat from these tissues. In spite of this, just the presence of the special circulation associated with the deep red muscle has prompted some to suggest that thermogenesis is a primary function for the internalized muscle – surely so much correlated morphological specialization would not have occurred if thermogenesis were not a principal component in the evolution of these fish (Block et al., 1993). However, some have argued that the conclusions drawn between heterothermy and performance in these fish, no matter how compelling or satisfying, are weak (Brill et al., 2000).

Among tuna, there are a variety of large-scale patterns in the design of the circulatory supply to the thermogenic red muscle. In general, the deep red muscle is supplied from some

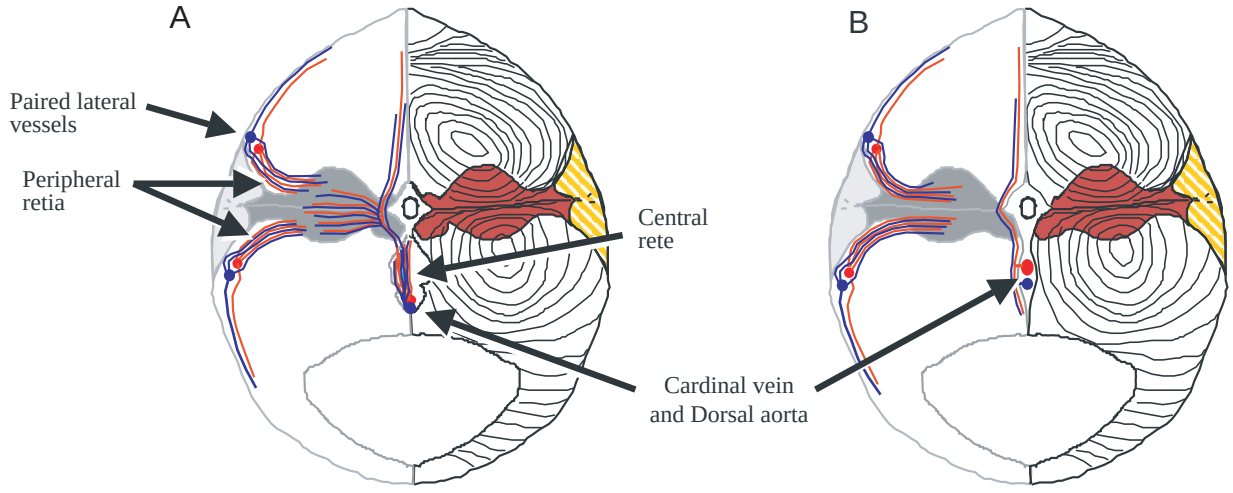


Fig. 3. (A) Diagram of a yellowfin tuna (*Thunnus albacares*) in cross section or steak view indicating the structural components of the blood vessels that make up the specialized supply for the internal red muscle. The right half of the diagram is similar to Fig. 1C to show the muscle anatomy and allow comparison. In the left half, the muscle anatomy has been removed and the superimposed vascularity is displayed. Arterial vessels are in red and venous vessels are in blue. In yellowfin, the deep red muscle is supplied by large lateral vessels that lie close to the skin, at the margins of the superficial red muscle and the skin. In addition, there is a central rete composed of vessels attached to the posterior cardinal vein and dorsal aorta, from which vessels also enter the deep red muscle. (B) Diagram of the anatomy of a bluefin tuna (*Thunnus thunnus*) in steak view similar to that in A. Like the yellowfin tuna, the bluefin tuna has peripheral retia, but it lacks the central rete. Importantly, comparison of these figures shows that the vascularity of the deep red muscle is diverse among the heterothermic fish, even between these closely related tuna.

combination of two sources, large pairs of vessels located along either side of the body and/or branches from the central hemal canal that contains the aorta and cardinal vein (Fig. 3). In different members of the tribe Thunnini, as well as the heterothermic sharks, different combinations of these blood supplies are developed to different degrees to supply the metabolically active red muscle as well as being further specialized with retia to isolate the heat generated there. For example, yellowfin tuna (*Thunnus albacares*) have both a highly developed central and peripheral rete, while bluefin tuna (*Thunnus thunnus*) have highly developed peripheral retia, but little or no central rete (Graham and Dickson, 2000).

The peripheral blood supply consists of large artery and vein pairs that run in the rostral–caudal direction along the body in four tracts – two tracts on either side, each just under the skin at the approximate junction of the peripheral red muscle margins and the skin (Fig. 3). Closely spaced, small vessels branch from these large vessels and penetrate the fillet. These small vessels run along the margins between the peripheral red muscle and the large bodies of white muscle. At the margins of the peripheral red and internalized red muscles, the small vessels branch into numerous fine vessels that feed the capillary beds within the internal loins of red muscle. Significantly, as the vessels traverse the distance between the large lateral vessels and the deep red muscle, they form a sheet of alternating veins and arteries that flow in antiparallel orientation, forming the heat-exchanging retia that are so distinctive to the heterothermic fishes. It is the close apposition between these vessels that allows the heat to be concentrated within the deep red muscle. It seems significant that heterothermic sharks show not only a similar distribution of red muscle to the heterothermic tuna but also a similar distribution of blood vessels and retia to isolate heat generated within the deep red muscle (Carey, 1973; Bernal et al., 2001).

The muscle as a biomaterial

Now that the anatomical structure has been described, we can examine the mechanical performance of these muscles. The first rational step is to evaluate how the muscle performs when examined as a biomaterial.

How might that be evaluated? Muscle does several mechanical jobs; it shortens, it generates force, it does both at the same time so it does mechanical work, and it does work in a finite period of time so it generates power. As a consequence of its characteristic properties, the shape of the force/velocity curve for example (Katz, 1939), it cannot simultaneously do all these jobs maximally. Is there a specific job upon which muscle's design capitalizes? Biewener and Gillis (1999) have made the case that muscle use generally falls into two categories: muscles that generate maximal force isometrically and muscles that generate maximal power, which is applied to the outside world. Therefore, it is reasonable to search the literature and ask how heterothermic muscle compares with non-heterothermic fish muscle with respect to its ability to generate force, on the one hand, and power, on the other.

Unfortunately, in fish muscle, all the anatomical features reviewed in the previous section make direct measurements of mechanical performance difficult (Katz and Shadwick, 2000), so the strategy has been to perform mechanical tests *in vitro* using data on *in vivo* strain (strain=length change normalized by original resting length) and excitation to make a prediction about how the muscles work in the fish. Specifically, it has become common to use the oscillatory work loop technique pioneered by Josephson (1985). This technique amounts to imposing a time-varying strain on an isolated strip of muscle, imposing a correlated pattern of electrical stimulation and measuring the force developed by the sample. When the results are plotted on the force/length plane, the area within the trajectory that results describes the work done by the muscle on the outside world (positive work) or the work done by the outside world on the muscle (negative work). If the temporal patterns of strain and excitation in the experiments are reflections of those observed in real life, the power output is believed to represent what the muscle does *in vivo*. In the course of performing some of these experiments, it has been possible to record the peak isometric stress (force/cross-sectional area) of the muscle, and we can then compare those performance metrics as well (Altringham and Johnston, 1990; Johnson and Johnston, 1991a). In other cases (tuna for example), the values of peak stress for other fish were used to calibrate the power values (Altringham and Block, 1996; Katz et al., 2001) and, therefore, are unavailable for comparison.

Published measures of biomechanical performance for muscle from a variety of fish species are presented in Fig. 4. Fig. 4A displays the peak isometric stress in red and white muscle from a variety of fish that live in a range of T_a. Fig. 4B shows maximal power produced in oscillatory work loop experiments in red and white muscle in a variety of fish including heterothermic tuna. Temperature affects the performance of muscle during *in vitro* experiments, and wide variability exists in literature values with respect to the experimental temperatures and the environmentally relevant temperatures. In an effort to maintain a rational basis for comparison, only data collected at the temperature at which the fish were acclimated are reported here.

Although there are numerous subtleties and points where one could debate the importance of differences, there are some impressive general statements to be made. For example, in spite of all the differences between species and approaches in separate laboratories, there is a lot of congruence in the data. Red muscle generates a peak stress of approximately 130–160 $kN\,m^{-2}$, while white muscle generates approximately 175–250 $kN\,m^{-2}$. Red muscle generates approximately 10–30 $W\,kg^{-1}$ fish, and white muscle is reported to generate approximately 20–40 $W\,kg^{-1}$ fish, tuna included. While it is unfortunate that there are few data with which to compare peak isometric stress in heterothermic fish, it is quite impressive that there is so much agreement among fishes. Importantly, there is no indication that heterothermic tuna have a higher power output than other, non-heterothermic fish.

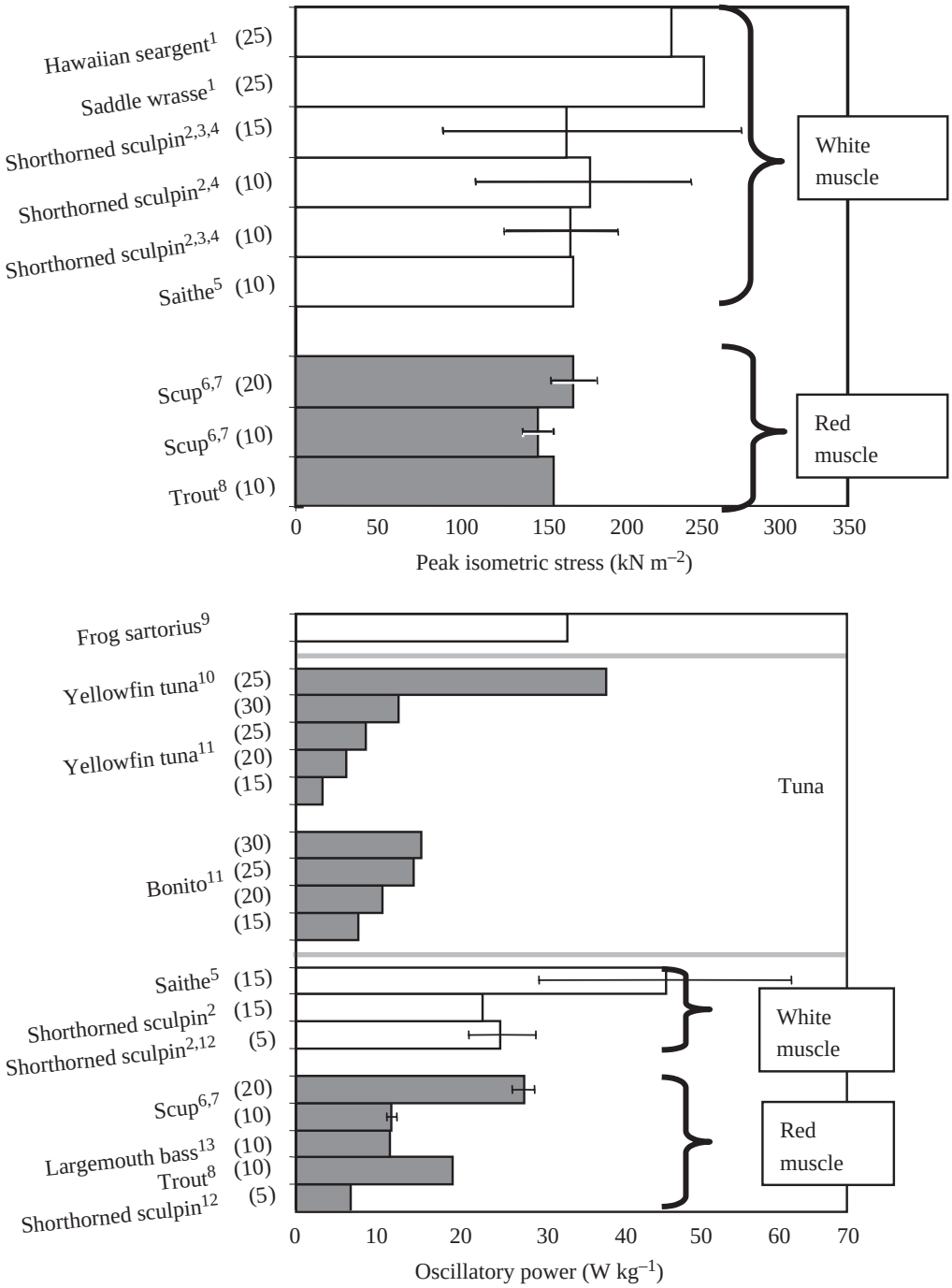


Fig. 4. Bar graph summarizing values of peak stress and oscillatory power output from muscles tested *in vitro*. Shaded bars, red muscle; white bars, white muscle. (A) Values for peak stress (force/cross-sectional area) in kN m^{-2} for a variety of fish that cover a range of temperatures. (B) Power output in W kg^{-1} fish. Data are reported only for muscles tested at temperatures that were the same as the acclimation temperature of the intact fish and are given in parentheses next to the fish name. In those cases where more than one study reported values, the range of values is indicated with error bars. For comparison, a value for frog sartorius is provided. Fish species for which data were reported include Hawaiian seargent (*Abudefduf abdominalis*), saddle wrasse (*Thalassoma duperrey*), shorthorned sculpin (*Myxocephalus scorpius*), trout (*Oncorhyncus mykiss*), scup (*Stenotomus chrysops*), largemouth bass (*Micropterus salmoides*), yellowfin tuna (*Thunnus albacares*), bonito (*Sarda chiliensis*) and saithe (*Pollachius virens*). [1]Johnson and Johnston, (1991b); [2]Beddow and Johnston (1995); [3]Johnson and Johnston, (1991a); [4]Langfeld et al. (1989); [5]Altringham et al. (1993); [6]Coughlin et al. (1996b); [7]Rome et al. (1999); [8]Hammond et al. (1998); [9]Stevens (1988); [10]Katz et al. (2001); [11]Altringham and Block (1996); [12]Altringham and Johnston (1990); [13]Johnson et al. (1994).

There is a reasonable argument that comparing tuna with all these other fish may be an unfair phylogenetic comparison. Since the evolutionary histories of all these species are so distinct from that of heterothermic tuna, it is also possible that

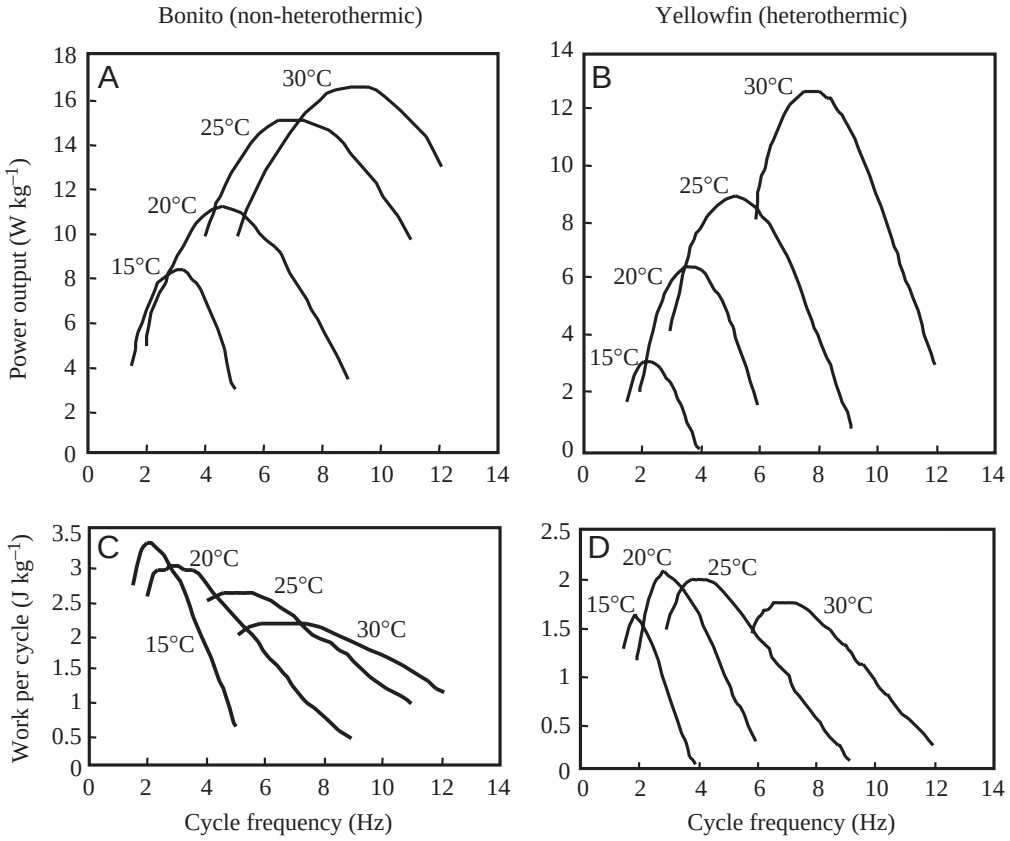


Fig. 5. Results of *in vitro* measurements of power output from red muscle using the oscillatory work loop technique for the non-heterothermic bonito (*Sarda chiliensis*) (A,C) and the heterothermic yellowfin tuna (*Thunnus albacares*) (B,D). Data are from Altringham and Block (1996). (A,B) Power in $W kg^{-1}$ fish for four experimental temperatures, each tested over a range of cycle frequencies. (C,D) The data from A,B normalized by cycle frequency to estimate work per cycle. Normalization by cycle frequency separates the effect of temperature on the force-generating capacity of the muscle from the effect of temperature on the time constants of force development and decay. The results show that yellowfin and, except at the highest temperature bonitos as well, have a modest temperature-dependence in the maximum work per cycle they can generate at the different temperatures. The data also show that, when compared at the same temperatures and frequencies, the non-heterothermic red muscle performs at least as well as the heterothermic red muscle.

factors other than heterothermy determine the specializations and performance of their muscle design. The only case in which this comparison was made between two closely related fishes, one heterotherm and one non-heterotherm, is the comparison of red muscle power outputs of bonito (*Sarda chiliensis*), a non-heterothermic scombrid, and yellowfin tuna (*Thunnus albacares*), a heterothermic scombrid (Altringham and Block, 1996). These authors report power output for red muscle tested in oscillatory work loop experiments at a variety of cycle frequencies and temperatures. Their data are reproduced in Fig. 5A,B. In an effort to remove the temporal characteristics of the muscle from the effect of temperature, I have normalized their power values by cycle frequency to produce an estimate of work per cycle in $J kg^{-1}$ (Fig. 5C,D). Three things emerge from an evaluation of these data. First, within-species comparisons showed that red muscle did produce more power at higher temperatures. Second, red muscle from neither fish was very temperature-dependent on the basis of work per cycle, although the non-heterotherm showed a decrease in performance at the highest temperatures. Finally, and most impressively, in making any across-species, point-to-point comparison of work or power production under similar conditions of temperature and cycle frequency, the values for the heterotherm were lower than those for the non-heterotherm by a substantial amount. It does seem reasonable at this point that, in terms of the mechanical performance of this biomaterial, being heterothermic does not make it better. This, of course, makes it hard to develop an argument that heterothermy is adaptive.

In the absence of data, it remains to be seen whether these results for tuna will be reflected in the data for heterothermic sharks.

The muscle as a dynamic structure

The mechanical characteristics of the complex anatomy seen in fish myotomes have been reviewed in numerous articles (Johnston, 1983; Wainwright, 1983; Videler, 1993; Wardle et al., 1995; Katz and Shadwick, 2000). In addition, the mechanical consequences of the distribution of red muscle seen

in tuna have recently been examined in detail (Shadwick et al., 1999; Knower et al., 1999; Katz et al., 2001). Therefore, in presenting what follows, we can afford the briefest of reviews.

As stated above, the complex anatomy of the folded and nested myotome cones make discrete measurements of mechanics a challenge. So, in the past, the study of myotome mechanics has relied on the same inferences as the *in vitro* experiments described above, only in reverse. As pointed out, critical to this approach is the acquisition of reliable data on the temporal patterns of strain and excitation. Although data on these parameters for tunas have only recently been collected, similar data for non-heterothermic fish have been available for some time. It is worth summarizing the situation in non-heterotherms so that the degree of distinctiveness seen in tuna will be appreciated.

Studies to describe the temporal patterns of electrical excitation, based on electromyography, are numerous, with differences in fish species studied, techniques used, muscle fibers assayed and temperatures (Bone, 1966; Rayner and Keenan, 1967; Brill and Dizon, 1979; Wardle and Videler, 1993; Jayne and Lauder, 1995a,b; Shadwick et al., 1998; Hammond et al., 1998; Gillis, 1998). In spite of the diversity of work, some general statements emerge. First, electromyographic (EMG) activity arrives at the myotomes in an anterior-to-posterior sequence. Although it is inappropriate to say that the EMG activity has a wave velocity along the body since the activity is not transmitted through the muscle directly, the time of onset does proceed along the body at a rate. In most fish, the rate of onset progression generally exceeds the rate of offset progression. Consequently, the time the muscle is active as a fraction of a complete cycle (i.e. the duty cycle) decreases from anterior to posterior. In eels, which are capable of passing several wavelengths of undulation simultaneously along their body during swimming (D'Aout and Aerts, 1999), the progression of activity offset is almost the same as that of onset, and the duty cycle is close to constant along the body (Gillis, 1998). Tuna, in contrast, pass only one wavelength on the body at a time, and have EMG activity offsets that occur simultaneously on one side of the body (Knower et al., 1999). It is appropriate to point out that the differences in duty cycle and onset timing between different fish and between different ends of the same fish have motivated numerous suggestions about mechanical specializations for the muscles, some of which are incompatible. A synthesis is emerging that, in a steadily swimming fish, red muscle in all parts of the body is activated similarly and in a manner that maximizes the amount of work done by the muscle on the outside world (for reviews, see Katz and Shadwick, 1998, 2000). There are no published data that describe the degree to which the patterns of muscle activation seen in heterothermic tuna are reflected in any heterothermic shark.

The other critical piece of information in determining the mechanics of the muscles *in vivo* is the temporal pattern of muscle strain. In the past, estimates of strain were based on measures of local body curvature, which were related to strain by assuming that the body bent like a homogeneous beam and applying the relationship specific to bending beams:

$$\varepsilon = \kappa y , \quad (1)$$

where ε is strain, κ is body curvature and y is the distance of the muscle of interest from the neutral axis – a line close to the location of the spinal column that neither stretches nor shortens when the body bends (Young, 1989). Using this relationship amounts to accepting the hypothesis that the fillet of a fish bends like a homogeneous beam. There are three important considerations in adopting that hypothesis. The first is that estimates of strain are oriented in the long axis of the beam. However, it is known that muscle fibers assume a range of orientations within the fillet (Alexander, 1969) and might therefore undergo strain in excess of estimates using this relationship. Second, it estimates strain only at the longitudinal location where κ and y are calculated. If the muscle applies its action at a remote location, equation 1 will be inadequate. The third important consequence of treating the fillet like a beam is that it assumes that strain is distributed homogeneously along a gradient between maximal values at the skin (i.e. maximum y) and zero at the spine (i.e. y=0). Therefore, we have an *a priori* prediction that, if the tuna body bends like a homogeneous beam, the internal location of the heterothermic muscle will limit muscle strain amplitude simply because it is closer to the spine (i.e. smaller y). Equation 1 has often been used in the calculation of muscle strain in fish (Hess and Videler, 1984; Altringham et al., 1993; Rome et al., 1993; Videler, 1993; Jayne and Lauder, 1995b; Johnson et al., 1994; Wardle et al., 1995). However, it has been pointed out that the calculation of local body curvature requires care, and simplifications can lead to widely incompatible interpretations of muscle function (Katz and Shadwick, 1998).

Recently, the technology has become available to test quantitatively the hypothesis inherent in the use of equation 1. For example, using high-speed X-ray videography with gold beads surgically distributed within the myotomes of mackerel swimming in a small water tunnel, Shadwick et al. (1998) showed that equation 1 accurately predicted strain within the myotomes of these non-heterothermic scombrid fish. More recently, sonomicrometry has been used to show that the fillet of representative teleost species undergoes strain as would be predicted if it were a homogeneous beam.

Sonomicrometry is a technique in which pairs of small (approximately 2 mm in diameter) transducers are surgically placed in the muscle. One of the crystals is excited electrically and induced to transmit an ultrasound pulse (5 MHz) that travels through the muscle. The other crystal is a receiver and converts the arriving acoustic pulse to an electrical signal. The travel time of the acoustic pulse, when multiplied by the speed of sound through muscle, gives a high-resolution estimate of the distance between the crystals. If the travel path is aligned with the shortening axis of the adjacent muscle fibers, it is also a high-resolution estimate of muscle shortening (Ohmens et al., 1993; Katz et al., 1999). If the hypothesis is that the fish are bending like homogeneous beams, the test is to measure strain

using a technique such as sonomicrometry and to film the swimming fish at the same time so that curvature and body thickness (maximum *y*) can be calculated for the same location and time.

In spite of the concerns mentioned above, the beam bending hypothesis was validated using this approach for superficial red muscle in the scup, a non-heterotherm (Coughlin et al., 1996a), and in both peripheral red muscle and deep within the white muscle cones of the non-heterothermic milkfish (Katz et al., 1999). In the case of the peripheral red muscle, strains were approximately 6 % from resting length during steady swimming and almost 12 % during sprinting bursts. As predicted by equation 1, strains in the muscle half-way between the skin and spine are half as large as those in the most peripheral muscle. In addition, there was no indication that red muscle strain occurred out of phase with local body bending (Coughlin et al., 1996a; Katz et al., 1999). Thus, we conclude that these non-heterothermic fish deform during swimming, as would a bending beam that experienced the same history of undulation. If this result were also true for tuna, it would make the important prediction that the deep loin of warm red muscle in tuna is limited in its ability to shorten and, as a consequence, in its ability to contribute mechanical work per cycle.

When this approach of simultaneous sonomicrometry and videography was applied to tuna swimming in water-tunnel treadmills, a substantial difference from other fish was observed. Working with skipjack tuna (*Katsuwonus pelamus*), Shadwick et al. (1999) documented that, in the deep heterothermic muscle, strain was between 5 and 8 % in amplitude, with the larger values observed in the more posterior myotomes (substantially larger than the 2–3 % predicted by beam theory). Even more impressive was that the phase of shortening observed in the muscle was shifted by almost 17 % of a complete cycle later than predicted by local body bending. More recently, a direct comparison was made between the deep and shallow red muscle in the heterothermic yellowfin tuna (*Thunnus albacares*) (Katz et al., 2001). Strain amplitude and phase measured in the superficial red muscle using sonomicrometry were statistically indistinguishable from those predicted by beam theory, a result similar to that seen in

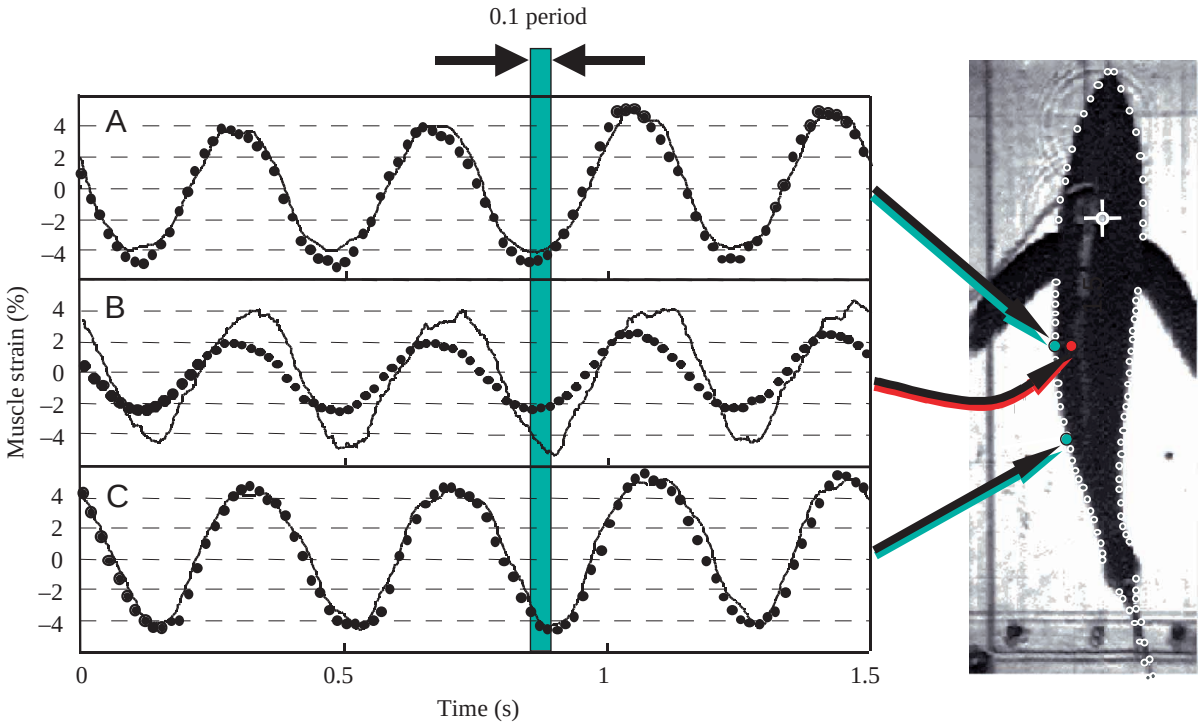


Fig. 6. Comparison of red muscle strain calculated from videography using beam theory (filled circles) and from sonomicrometry (continuous lines) for a yellowfin tuna swimming at 2.5 fork lengths s^{-1} (*FL* s^{-1}). The image on the right of the figure is an example overhead video image of a yellowfin tuna swimming in a water-tunnel treadmill. The dots on the lateral outline of the fish mark the locations of the digitized points used to calculate body bending and thickness, which are then used to calculate muscle strain using equation 1. The approximate locations of the sonomicrometers within superficial muscle are indicated by green dots superimposed on the image, and the location of the sonomicrometer within the deep red muscle is indicated with a red dot. The association between muscle strain data collected at these locations is indicated by arrows. (A) Muscle strain calculated at 0.5*FL* for superficial red muscle located in close apposition to the skin. (B) Muscle strain calculated at 0.5*FL* for deep red muscle located within the myotome. (C) Muscle strain calculated at 0.7*FL* for superficial red muscle in close apposition to the skin. The width of the vertical green bar indicates the magnitude of the phase shift between video and sonomicrometry estimates of muscle strain in the deep red muscle. The phase shift was calculated as the difference in argument for the principal harmonic component of a Fourier transform of the two time series and, in this case, was approximately 0.1 of a complete strain cycle, a value very close to the phase difference in muscle strain for the superficial muscle in the two longitudinal locations.

the superficial red muscle of other non-heterothermic fish. In the deep loin of red muscle, however, the amplitude was approximately double that predicted by beam theory, and the phase of the shortening cycle was retarded relative to the cycle of local bending by 10 % of a cycle, as indicated by simultaneous videography.

Fig. 6 is an example of simultaneous calculations of muscle strain using beam theory and measured using sonomicrometry for three locations in the left-side fillet of a yellowfin tuna. Transducers were placed in the shallow red muscle at 50 % of fork length (*FL*), in deep red muscle at the same longitudinal position and in shallow red muscle at 70 %*FL*. These data show the close agreement between muscle strain predicted by beam theory and measured with sonomicrometry in the superficial red muscle. In this case, the strain observed in the shallow red muscle was approximately 5 %, with no significant phase difference at either longitudinal location. In contrast, the strain in the deep muscle was retarded by approximately 10 % of a cycle and had an amplitude almost double that predicted by beam theory. Indeed, the difference in phase between deep and peripheral red muscle was substantial enough that there were clear moments when muscle in one region was shortening at the same time as muscle in the other was lengthening. This indicates that a substantial amount of shearing of the intervening white muscle is occurring – substantial enough to allow approximately twice as much strain as would otherwise occur.

One consequence of this phase difference is that strain in the deep red muscle was more in phase with that in the peripheral red muscle at 70 %*FL* than with that in the peripheral red muscle in the same longitudinal location. Interpolation of these results for several fish reveals that the deep red muscle at 0.5*FL* undergoes strain approximately in phase with the superficial muscle 0.18*FL* farther posterior. This result suggests that the location of the action of the deep muscle is substantially posterior to its anatomical position. Westneat et al. (1993) report that the complex tendon system that exists within the mid-lateral septum of bigeye tuna (*Thunnus obesus*) spans approximately 0.16*FL*. As noted above, those authors suggested that at least some portion of this tendon system transmits force from red muscle to more posterior locations on the spinal column. The data presented in Fig. 6 provide circumstantial evidence that the mid-lateral tendons are a principal force trajectory for the contractions of the deep red muscles.

Using the sonomicrometry data as an input for a series of *in vitro* work loop experiments on the deep red muscle indicated that the twofold difference in strain between beam theory and sonomicrometry results in a doubling of work output (Katz et al., 2001). An additional increase in strain amplitude to 8 % produced only modest increases in work output by the muscle. Therefore, the strains seen in the heterothermic muscle of yellowfin tuna are approximately optimal. That these internally located loins of red muscle are able to produce maximal work and power is a feature of the anatomical design that allows the large amplitudes of strain. Specifically, the deep red muscle is separated from the skin. If additional red muscle were in close apposition to the skin, with its relatively rigid connective tissue attachments, we would expect its strain to track that of the skin, as it does in other fish. Thus, for the first time, the measurable improvement in performance attributable to this anatomical specialization was explicitly documented. Importantly, there is nothing about the improved biomechanical performance of this anatomical design that is specifically determined by T_b.

Biomechanics *versus* heterothermy in design

In trying to coordinate all this information about performance into a coherent model of design, it is easy to become confused by the many scenarios that have been invoked to characterize the evolution of heterothermic muscle. For example, it has been suggested that heterothermy in these fish evolved to maintain the body temperature and muscle performance at times when the predatory fish enters relatively colder water in search of prey (Block et al., 1993). However, an analysis of imposed temperature changes in captive tuna shows that the heart is not protected from low T_a and that the aerobic performance of tuna in colder water is thus not expected to remain high (Brill et al., 2000). Indeed, whenever one encounters such a specialized and multi-component physiological system, there is the temptation to introduce some evolutionary scenario that, as the example above suggests, leaves one tackling intractable logic problems that are virtually untestable.

In an attempt to resolve a design strategy for the heterothermic swimming muscle of fish, consider the following design pressure as an imperative: increase red muscle. We can consider some of the consequences of this simple idea and see whether those consequences are reflected in the design of heterothermic muscle in these fish. There are two sides of this imperative. The first is *how* it is achieved in the design and whether it explains the observed features of the design. The second is how is this imperative reacting to selection, or *why* 'more red muscle'? Although the idea that the tuna represents a design for increased red muscle has been advanced before on the basis of it being a parsimonious idea (Graham and Dickson, 2000; Altringham and Shadwick, 2001), it has not been critically examined as a discrete evolutionary model in the context of biomechanical data.

How is the design achieved?

If a design imperative does exist where fish with increased red muscle are at a selective advantage, then there are a number of constraints that must be incorporated into the evolving design. The first is the constraint that the body is bounded. One cannot add red muscle outside the skin, so any additional red muscle must be added within the existing myotome structure. In the absence of our understanding of beam theory, this comment would be as trivial as it sounds. However, because of beam behavior, any additional red muscle added within the myotome structure would be limited in its ability to undergo strain, and consequently to generate

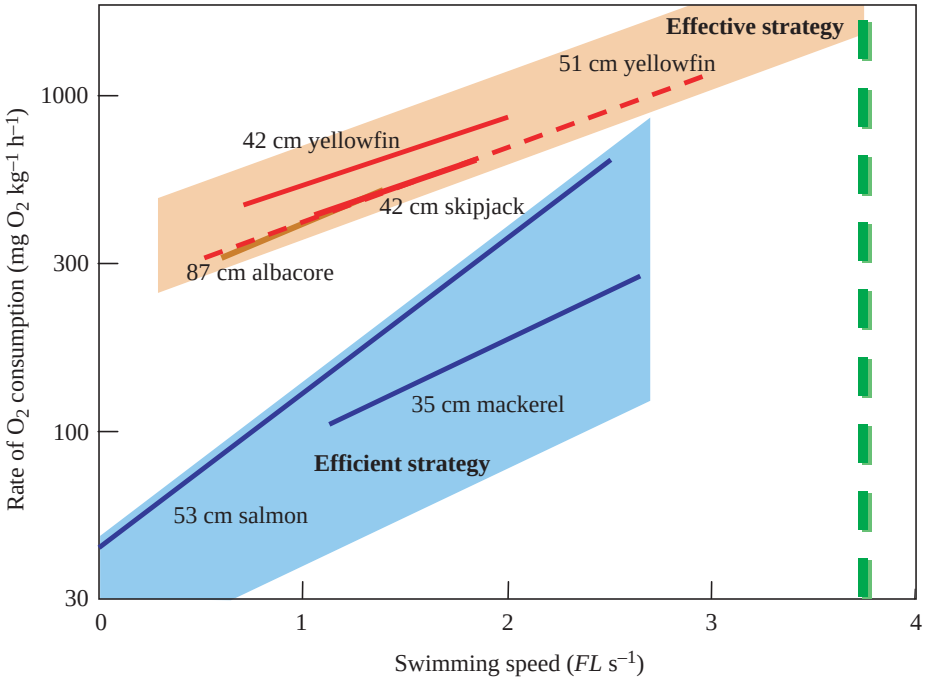


Fig. 7. Plot of the rate of oxygen consumption as a function of swimming speed for a selection of heterothermic and non-heterothermic species. Heterothermic tuna are indicated by red lines, and non-heterotherms are indicated by blue lines. The colored regions indicate broad distinctions between strategic differences in design. These performance characteristics are hard to measure experimentally and should not treated as quantitative measures of performance limits. The 'effective' strategies have higher aerobic swimming speeds, but consume more O_2 at any speed. The 'efficient' strategies have lower aerobic swimming speeds, but consume less O_2 at any speed than heterothermic fish. The broken green line indicates the top aerobic speed predicted by Korsmeyer et al. (1996) based on modeled estimates of tissue O_2 delivery and consumption. Data are presented for sockeye salmon (*Oncorhynchus nerka*) (Brett and Glass, 1973), Atlantic mackerel (*Scomber scombrus*) (Lucas et al., 1993), yellowfin tuna (*Thunnus albacares*) (Dewar and Graham, 1994), skipjack (*Katsuwonus pelamus*) (Gooding et al., 1981) and Pacific albacore (*Thunnus alalunga*) (Graham et al., 1989).

swimming power, in the absence of any specializations such as those seen in tuna. As discussed with respect to equation 1, this is a strict limitation imposed by the behavior of beams. The only way to circumvent this is to allow the strain in the additional red muscle to be uncorrelated with the local strain of the myotome in a manner that allows larger amplitudes. This seems unlikely if the additional muscle is in close apposition either to the relatively stiff skin or to the spinal column. Therefore, if the fish is to increase the amount of red muscle, its only option is that some portion of the volume within the otherwise white-fibered myotome cones should express the red phenotype. Furthermore, if these fibers are to shorten out-of-phase with local strain and therefore apply their force at some distant location (a result indicated by the data in Fig. 6, where there are times when deep red muscle shortens while local tissues should be lengthening), then some connective tissue element must exist to transmit that force – the surrounding muscle cannot be stiff to transmit the force and also be compliant to allow the required shear at the same time. So, the observed connective tissue structures of tuna are not a coincidence; rather, they are a functional requirement of the location of the additional red muscle. Therefore, on the basis of mechanical function alone, the location of the red muscle and of its associated connective tissue are anticipated as a consequence of the design imperative to increase red muscle. It is worth pointing out that, to this point, the design imperative makes no demand that the additional muscle should be heterothermic.

Another important constraint that must be addressed is that no muscle will operate aerobically without an adequate circulatory supply. It is definitional to the characterization 'aerobic' that the performance of red muscle is determined by the supply of O_2 and substrates. It has been shown experimentally that the ability of red muscle to do work is determined by O_2 delivery, even in perfusion-limited systems (Wagner, 2000). Therefore, any design pressure that mandates an increase in the amount of red muscle will not be successful in the absence of a sufficient parallel increase in the capacity of the circulatory system to feed that extra muscle. In terrestrial vertebrates, it is known that aerobic exercise promotes angiogenesis in working muscle and that it has a genetic, and therefore heritable, component. Specifically, it has been shown in mammals that increased work rate in red muscle promotes the expression of vascular endothelial growth factor (VEGF), basic fibroblast growth factor (bFGF) and transforming growth factor (TGF beta-1) mRNA (Breen et al., 1996; Richardson et al., 1999), all with angiogenic properties. It remains to be seen whether exercise has the same

angiogenic consequences in fish. If a similar result is seen in fish, however, then it suggests an evolutionary scenario for the circulatory structure observed in the deep red muscle of tunas. Because the increase in O_2 delivery with increased angiogenesis has a positive effect on performance, and because the functional link between that demand and angiogenesis is heritable and therefore subject to selection, one would expect a large directional selection pressure towards ever denser vascular supply correlated with the imperative of increased red muscle.

This directional selection towards increased blood vessel density is rationalized in response to increased demand for aerobic muscular work; a biomechanical imperative. This scenario is not dependent on any design imperative to maintain elevated T_b. Once the machinery for increased O_2 delivery is in place in the form of a dense vascular plexus, the system is pre-adapted for retaining heat within the muscles as long as the vessels are in close apposition with flow in adjacent vessels going in opposite directions. However, this system will be competent only if the muscle is already some distance from the skin and its high conductive heat loss (Fudge and Stevens, 1996; Ellerby et al., 2001). The data in Fig. 5A,B suggest that, within a species, an increase in temperature results in a modest increase in muscle power output. Thus, it is reasonable to hypothesize that retia are designed to capture by-product heat within the deep muscle. However, this is only possible in a design pre-adapted for developing those retia within an existing dense vessel structure. This, in addition to the lack of any benefit imparted by heterothermy in any across-species comparison, suggests that heterothermy is not a significant component of the selection history that originally resulted in the addition of red muscle deep within the swimming muscle in these fish.

Why ‘ more red muscle’?

One potential motivation for having more red muscle is simply the need to maintain higher aerobic speeds than potential prey species or competitive predators. The idea of increased aerobic scope has been discussed as a rationalization for the suite of physiological specializations of tuna in a variety of selection scenarios (e.g. Korsmeyer et al., 1996). The idea is familiar to the study of the physiological ecology of terrestrial vertebrates (Taigen, 1983; Hayes and Garland, 1995). It is the simple model that, if a predator can maintain a higher aerobic speed than its prey, or any competitive predator, then it will almost always be successful. This defines an ‘effective’ strategy. The penalty, of course, for this increased top aerobic speed in tuna is a greater metabolic rate at any aerobic swimming speed to pay for all the extra red muscle (Dewar and Graham, 1994; Korsmeyer et al., 1996). As an alternative strategy, predators can adopt an ‘efficient’ model, maintaining relatively small red muscle power plants that make lower demands on the metabolism of the swimmer. As a consequence, these more efficient designs, such as salmon, will have a lower metabolic consumption than a similarly sized heterotherm at any swimming speed. However, if maximum aerobic speed is limited by the smaller mass of red muscle, the probability of failure in an individual predatory action is higher.

Fig. 7 shows the relationship between metabolic rate (rate of O_2 consumption) and swimming speed for a sample of heterotherms and non-heterotherms. Superimposed on these data are areas summarizing the differences between the ‘efficient’ and ‘effective’ strategies. Calculation of top aerobic speed is difficult, and the distinction between aerobic and non-aerobic speeds is often made on the basis of time to fatigue rather than on the discrete muscles used (Videler, 1993). In addition to technique, the speed transition is dependent on body form, water temperature and, particularly, body size (Videler, 1993). Looking at fish over a similar size range (>0.3 m), a selection of non-heterothermic fish show a transition speed at which they switch from aerobic to anaerobic speeds between 2.5 and 3 $FL\,s^{-1}$ (Webb, 1975; Videler, 1993). Observations on swimming milkfish (*Channos channos*) showed a gait transition from presumed aerobic steady swimming to increasingly anaerobic burst-and-glide swimming at approximately 2.75 $FL\,s^{-1}$ (Katz et al., 1999), although explicit O_2 consumption was not measured. These fish were of similar size to the tuna for which data are available.

Tuna, in contrast, show steady aerobic swimming up to 3.25 $FL\,s^{-1}$, and models suggest that the maximum value could be as high as 3.7 $FL\,s^{-1}$ (Korsmeyer et al., 1996). The technical problems in getting a 50 cm fish to swim at 3.7 $FL\,s^{-1}$ have made it difficult to explore systematically the transition from aerobic to sprint swimming. However, in water-tunnel treadmill experiments, yellowfin tuna have been observed to switch from a steady gait to a bursting, sprinting gait at approximately 3.25 $FL\,s^{-1}$ (S. L. Katz, personal observation). This suggests that, in a competitive situation with other similarly sized, non-heterothermic predators such as the charcharhinid sharks that participate in feeding with tuna in the tropical eastern Pacific, tuna will be more successful because they can hunt at higher speeds without fatigue. Although the final predatory strikes in tuna are vigorous and probably anaerobic, they spend significant periods covering large distances as well as herding prey into tight masses or ‘bait-balls’ that improve the effectiveness of the final predatory strikes (S. L. Katz, personal observations).

In the absence of a comprehensive energy budget, it is difficult to argue how relatively important these activities might be, but chasing and herding are highly ordered activities and probably substantial in cost. For those that do not like competition as an evolutionary force, this also suggests that, when chasing prey, tuna can maintain aerobic swimming at a speed at which the prey has begun to sprint anaerobically, resulting in rapid fatigue, capture and death – although body size plays a large role here as well. So the tuna, a predator whose power plant design is less efficient, should invariably be successful, or more effective, in the open sea where prey refugia are absent. This model has each tuna acting as its own wolfpack, but not in any environment where prey can hide.

If this is a strategy that is more effective, is there a reason

why more examples are not observed? It is worth remembering that this is an integrated design, fundamentally different from non-heterotherms. The tuna is not at one end of some efficiency continuum. The efficient strategy has low amounts of red muscle, low maximum aerobic speeds, lower metabolic rates and no internalized red muscle with its elaborate connective tissue and vascular accessories. The tuna is distinct in all these ways and represents a different strategy based on effectiveness. Importantly, if this scenario is a fair representation of reality, we are left with no primary role for heterothermy in the evolution of these designs. It may be that heterothermy really is nothing more than a happy accident after all.

This work has grown out of work, collaborations and discussion over a number of years with Robert Shadwick, Keith Korsmeyer, Doug Fudge, Torre Knower, Jeff Graham, Chin Lai, Harry Rappoport, Kobi Tai, Stephen Wainwright, James Covell, J. R. Carrington and Douglas Syme. This paper benefits directly and indirectly from the tremendous work and generosity of the Kewalo Research Facility of the National Marine Fisheries Service Honolulu Laboratory, Hawaii, and in particular Richard Brill. Some of the experimental results in this paper were funded by a grant from NSF (IBN95-14203).

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