Geared for the Open Ocean
Unique Tendons in Tuna Stretch to Tune Fiber Strains During Cruising Swimming

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SUMMARY

Tuna slow-twitch red muscle powers the sustained cruising of these pelagic nomads and is distinct from that of other fish. Red muscle of tuna has (1) a more medial position, (2) a higher temperature than the rest of the fish, (3) a main horizontal septum, which is a mechanical structure comprising (a) posterior oblique tendons, which are long tendons that connect the red muscle to the spine and tail, and (b) epiplural ribs that connect the spine and the muscle-tendon unit. To investigate the biomechanical implications of this structure, we asked whether the tendons stretch during cruising swimming. We measured muscle, tendon, rib and spine geometry from fresh dissected Pacific Bluefin, Albacore, and Yellowfin tunas and then used these measurements to make a two-dimensional musculoskeletal computer model. We then used the model in a kinematic simulation of cruising swimming at 1 body length/sec. We calculated that the muscle fibers would need to strain by ±11.7% if the tendons did not stretch, which is more than double the value observed experimentally by in vivo sonomicrometry. We conclude that the tendons do stretch appreciably during cruising. We hypothesize that, as with terrestrial animals, stretch of the elastic tendons allows the muscle fibers to be activated at their optimal lengths and to contract at slower shortening velocities. Tuna red muscle, with the supporting structure of the ribs and tendons, and a short moment arm relative to spine bending, is geared for continuous cruising in the open ocean.

INTRODUCTION

Tuna red muscle is distinct from that of other fish. Red muscle of tuna has (1) a more medial position, giving it a shorter moment arm relative to spine bending, (2) an elevated temperature above the rest of the body, (3) long posterior oblique tendons that connect the red muscle to the spine and tail, and (4) bony ribs that connect the spine and the muscle tendon structure. While the elevated temperature of the tuna's red muscle has been studied extensively, the mechanics of the tuna's long tendons have not. In humans and other terrestrial animals, long compliant tendons allow muscle fibers to maintain an optimal fiber length over a larger range of joint motion, and allow fibers to shorten at lower velocities [e.g., 1-3]. In tuna, red muscle operates at length ranges and velocities that optimize its work output [e.g., 8]. We hypothesize that the tendons stretch to allow the red muscle fibers to stay closer to their optimal length
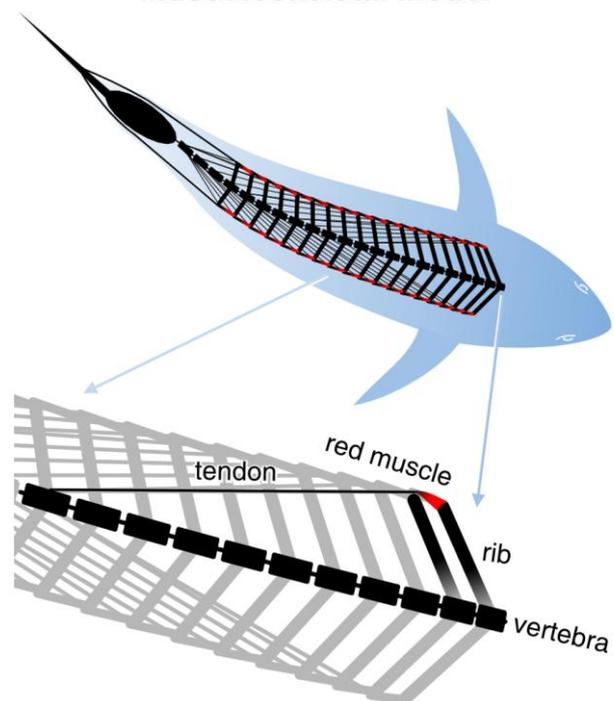
Figure 1: We created a scalable two-dimensional musculoskeletal model of the medially-located red muscle.

during cruising. Although the fiber strain of the red muscle has been measured in-vivo [8] during cruising, the tendon kinematics are unknown. In fact, the unique muscle-rib-spine-tendon structure of tuna has not been biomechanically analyzed beyond an anatomical description [9]. Therefore, the goals of this study were to: (1) collect novel geometric measures of tuna red muscle, tendon, ribs, and spine, (2) create a musculoskeletal model and kinematic simulation, and (3) assess whether tendons stretch during cruising and (4) synthesize how the biomechanics impacts sustained swimming in this highly migratory fish..

METHODS

We made a scalable two-dimensional musculoskeletal model of tuna in MATLAB (Figure 1). The model was based on a novel set of musculoskeletal measurements of 5 tuna (1 Pacific Bluefin, 2 Albacore, 2 Yellowfin), which included the 44 most distal individual red muscle segments

called myomeres, 44 corresponding tendon lengths, rib lengths, and spine insertion points of ribs and tendons. Measurements were made with calipers on freshly dissected specimens. Tuna were collected from the wild, acclimated to a tank at 20C and euthanized under Stanford APLAC-approved protocols. The 23 spine segment joints were modeled as pin joints, the 38 ribs were rigidly joined to the vertebrae, and the 38 musculotendon actuators were geometrically represented by a series of line segments.

We used our model to create a kinematic simulation of three tail beats of steady state cruising swimming at 2 tailbeats per second by animating the kinematic model to match tuna cruising kinematics [4]. To assess whether tendons stretch during this motion, we calculated the fiber strain assuming the tendons did not stretch (using a rigid-tendon muscle model [7]) and compared these results to in-vivo experimental observations of red muscle fiber strain during cruising. We used a rigid-tendon muscle model because it allows us to calculate fiber strain using only the muscle-tendon length, the muscle's activation and tendon's material properties are not required.

RESULTS AND DISCUSSION
The muscle fibers were strained by ±11.7% during the kinematic simulation of tuna cruising (Figure 2), which is more than double the fiber strain measured by in vivo sonomicrometry [8]. Our results suggest that during cruising the tendons stretch appreciably, keeping the muscle fibers at a favorable operating point. The stretching tendons may also be storing and releasing energy similar to humans and other terrestrial animals [1-3].

We also observe that the muscle-tendon strains and velocities increase. We hypothesize that the more caudal tendons may be slowly storing energy and then quickly releasing it as the tail changes directions. Such a quick release of energy would be quite metabolically expensive for muscle fibers alone, but is efficient if the muscle fibers contract isometrically while the tendon stretches and rapidly recoils [3].

The medial placement of tuna red muscle, unique among fish, may also reduce the fiber velocities required for cruising swimming. Medially placed red muscle has a shorter moment arm about spine bending than would laterally placed muscle. Similarly, the Achilles' tendons of elite human sprinters have shorter moment arms about the ankle than those of non-sprinters [6]. For the same rate of muscle-tendon unit shortening, the displacement speeds of the joint are shorter.

Future quantification of the kinematics, kinetics, and energetics of tuna musculoskeletal biomechanics will lend insight into how the musculoskeletal system of the tuna interacts with the water to create one of the most efficient cruising fish in the open ocean. These questions are of central importance to understanding whether biomechanics, heat conservation, or both were driving forces in the evolution of this unique structure [5].

Red Muscle Strain
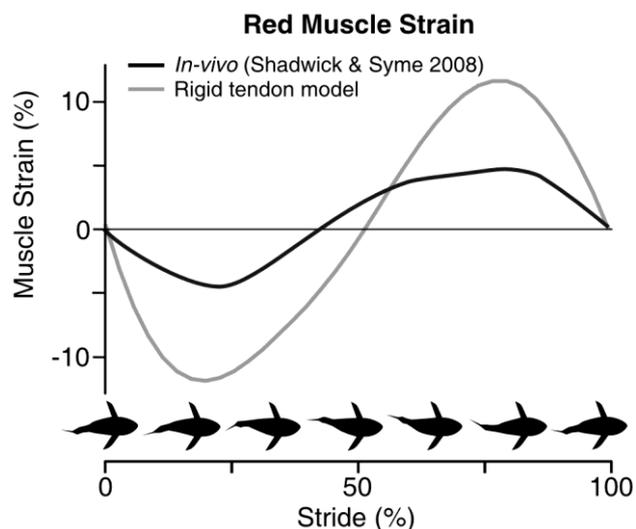
Figure 2: Fiber strains during one tail beat cycle from our simulation with rigid tendons (black) and from in vivo sonomicrometry (grey, [8]). With rigid tendons the fibers are required to strain three times the measured amount to maintain the observed kinematics. Simulated and measured strains are from muscle fibers at 50% of the anterior-posterior distance from head to tail.

CONCLUSIONS
This is the first musculoskeletal simulation of tuna swimming. In this first investigation, our results suggest the tendons allow the muscle fiber to operate at a more favorable length. Additionally the tendons may allow the tuna to slowly store elastic energy and then rapidly release it when the tail changes directions. These roles are central to understanding the processes that drove the evolution of this unique structure [5].

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