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# Red and white muscle fibre activity in swimming skipjack tuna, *Katsuwonus pelamis* (L.)

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To test the hypothesis that white muscle fibre portions of the myotomes are used at sustainable swimming speeds, skipjack tuna, *Katsuwonus pelamis*, were forced to swim against various current velocities in a water tunnel while electrical activity of the red and white muscle fibres was simultaneously recorded. Eight fish were tested, five fish graded white muscle fibres into activity at swimming speeds above their minimum hydrostatic equilibrium speed, but well below the estimated maximum sustainable swimming speed of skipjack tuna. Three other fish showed white muscle fibre activity at minimum swimming speeds, a possibly abnormal condition.

## I. INTRODUCTION

Like most teleosts, the myotomes of tuna (family Scombridae, tribe Thunnini) contain red and white muscle fibres grouped into distinct areas (Bone, 1975). However, tuna are unique because the red muscle fibre portions of the myotomes (hereafter referred to as ' red muscle fibres ') are internal and make little or no contact with the body surface (Stevens *et al.*, 1974). Because of their internal position and the presence of vascular countercurrent heat exchangers, red muscle fibres in tuna are maintained significantly warmer than ambient temperature (Carey & Teal, 1966; Graham, 1975; Dizon *et al.*, 1978).

Rayner & Keenan (1967) recorded the electrical activity from the red and white muscle fibres of restrained and sedated skipjack tuna, *Katsuwonus pelamis*, and showed that red muscle fibres alone were active during low frequency swimming movements. White muscle fibres showed activity only at the higher tail beat frequencies caused by tactile stimulation of the head and operculum. Based on their results, Rayner & Keenan (1967) implied that skipjack tuna use red muscle fibres at sustainable swimming speeds and white muscle fibres only at unsustainable burst speeds. However, because Rayner & Keenan (1967) used restrained skipjack tuna, red and white muscle fibre activity could not be correlated with specific swimming speeds. A growing body of evidence now indicates that

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numerous teleost species employ their white muscle fibres at sustainable speeds. This has been demonstrated by: (a) direct electromyographic recording (Hudson, 1973; Davison *et al.*, 1976; Johnston *et al.*, 1977; Bone *et al.*, 1978), (b) hypertrophy of each muscle fibre type (Greer-Walker, 1970; Greer-Walker & Pull, 1973), (c) metabolite depletion (Pritchard *et al.*, 1971; Johnston & Goldspink, 1973a, 1973b), and (d) apparent increases in swimming efficiency (Smit, 1965; Smit *et al.*, 1971). Hochachka *et al.* (1978) have shown that the white muscle fibres in skipjack tuna have the enzymatic capacity to sustain significant levels of aerobic metabolism. It is possible (as suggested by Bone *et al.*, 1978) that skipjack tuna may also employ white muscle fibres at sustainable swimming speeds. Furthermore, this may have a thermoregulatory function in tuna (Dizon & Brill, 1979). Our study was therefore undertaken to find at what swimming speeds the white muscle fibres of skipjack tuna become active, by forcing fish to swim against various current velocities in a water tunnel.

## II. MATERIALS AND METHODS

The water tunnel was a 20-cm diameter polyvinyl chloride (PVC) pipe fitted with a curved plexiglass access hatch. Stainless steel screens constrained the fish within a 1-m long test section. The upstream end of the tunnel was attached to a port approximately 1 m below the surface of a 120 000-l oceanarium. Water flow through the tunnel was due to gravity and was controlled by a butterfly valve located downstream of the test section. Maximum water velocity was approximately 160 cm $s^{-1}$.

Water velocity was measured with a ducted impeller current meter (Marine Advisors Inc.*). The ducted impeller was mounted behind the test section rear screen, but upstream of the butterfly valve.

Red and white muscle fibre activity was simultaneously recorded using two pairs of bipolar electrodes consisting of the bared tips of four strands of insulated 30 AWG silver plated copper wire. The wires were inserted in a 6 cm length of 2 mm diameter polyethylene (PE) tube. The red muscle electrodes protruded from the end of the tube, and the white muscle electrodes 4 cm distally.

Muscle fibre electrical activity was amplified by two Tectronix 122 low level differential preamplifiers, displayed on a Tectronix 502A dual beam oscilloscope and recorded on a Beckman R421 Dynograph recorder.

Skipjack tuna were selected from stocks maintained at the Kewalo Research Facility of the National Marine Fisheries Service. Nakamura (1972) provides details on handling of tuna at this facility. An animal was removed from its holding tank, transferred to the water tunnel, and immediately outfitted with muscle activity electrodes. The PE tube, containing the electrodes, was pushed into a puncture wound made about 1 cm laterad and slightly posterior to the origin of the first dorsal fin. The fish was then rested for 20–30 min at water velocities at or below its estimated minimum hydrostatic equilibrium speed (Magnuson, 1978). To determine at what speed white muscle fibres become active, current velocity was slowly increased until maximum water velocity was reached, and then decreased until the fish was again swimming at its minimum swimming speed. Periods of elevated water velocity were alternated with 15–30 min rest periods, as long as a fish showed good stamina.

At the end of each experiment, the fish was killed. The exact electrode position was then confirmed by dissection. White muscle electrodes were generally found 0·5–1 cm below the dorsal body surface, and the red muscle electrodes immediately lateral to the vertebral column.

*Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Because the effective cross sectional area of the tunnel is reduced due to solid blocking by the fish, the measured water velocity ($U_m$) is less than the velocity of the water as it passes the fish. This velocity ($U_c$, assumed equal to the fish's swimming speed) was calculated by

$$U_c = \frac{S_t}{S_t - S_b} \cdot U_m \qquad \text{(Webb, 1975)}$$

where: $S_t$ = cross sectional area of the tunnel, $S_b$ = maximum cross sectional area of the fish. Velocity correction factors are listed in Tables I and II.

TABLE I. Swimming speeds at which white muscle fibres become active (during increasing speed) and inactive (during decreasing speed)

| Fish No. | Fork length (cm) | Velocity correction factor | Test No. | Swimming speed at which white muscle fibres become active | | Swimming speed at which white muscle fibres become inactive | |
|---|---|---|---|---|---|---|---|
| | | | | cm $s^{-1}$ | bl $s^{-1}$ | cm $s^{-1}$ | bl $s^{-1}$ |
| 1 | 50·6 | 1·37 | 1 | 187 | 3·69 | 172 | 3·40 |
| | | | 2 | 151 | 2·99 | 190 | 3·75 |
| | | | 3 | 187 | 3·69 | 193 | 3·82 |
| | | | 4 | 197 | 3·89 | 200 | 3·96 |
| | | | 5 | 190 | 3·75 | 187 | 3·70 |
| | | | 6 | 207 | 4·10 | 204 | 4·03 |
| 2 | 49·0 | 1·34 | 1 | 210 | 4·29 | 175 | 3·58 |
| 3 | 48·5 | 1·33 | 1 | 174 | 3·59 | 205 | 4·23 |
| | | | 2 | 219 | 4·51 | 212 | 4·38 |
| | | | 3 | 202 | 4·16 | 202 | 4·16 |
| | | | 4 | 212 | 4·38 | 205 | 4·23 |
| | | | 5 | 266 | 5·49 | stopped swimming | |
| 4 | 38·2 | 1·13 | 1 | 148 | 3·88 | 64 | 1·67 |
| 5 | 40·1 | 1·17 | 1 | 150 | 3·74 | 123 | 3·08 |
| | | | 2 | 162 | 4·05 | 204 | 5·10 |
| | | | 3 | 190 | 4·73 | 168 | 4·20 |

TABLE II. Range of swimming speed at which red and white muscle fibres were active in Fish 6–8

| Fish No. | Fork length (cm) | Velocity correction factor | Range of swimming speeds at which white muscle fibres were active | |
|---|---|---|---|---|
| | | | cm $s^{-1}$ | bl $s^{-1}$ |
| 6 | 39·2 | 1·15 | 59– 86 | 1·51–2·19 |
| 7 | 40·1 | 1·17 | 78– 81 | 1·95–2·12 |
| 8 | 50·0 | 1·36 | 77–113 | 1·54–2·26 |

## III. RESULTS

### ELECTROMYOGRAPHIC RECORDINGS

Plate I presents the complete electromyographic recording made from Fish 1, during test 5 (Table I). Red muscle fibre activity is shown in the upper trace,

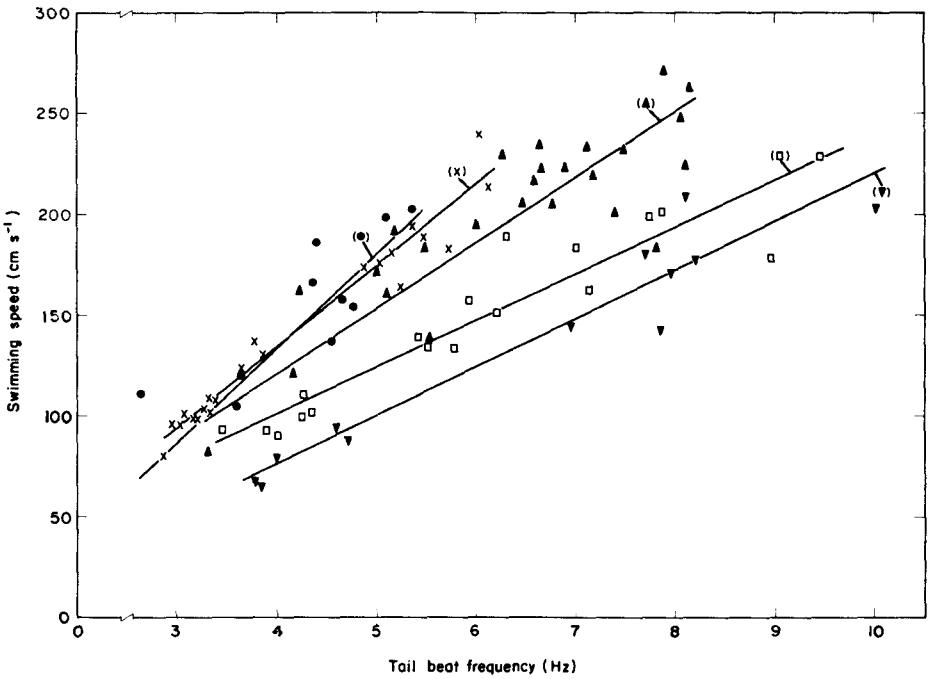


FIG. 1. A plot of tail beat frequency (Hz) versus swimming speed (cm $s^{-1}$), for fish 1–5 (×, ●, ▲, ▼, and □, respectively). The lines were fitted by a linear least squares regression.

white muscle fibre activity in the lower trace. The increasing amplitude of the upper trace, with increasing speed, is assumed to be due to red muscle fibre recruitment (Grillner & Kashin, 1976). The smaller spikes in the lower trace, seen at slower swimming speeds, are also assumed to reflect red muscle fibre activity. White muscle fibre action potentials begin at a swimming speed of 190 cm $s^{-1}$ (arrow, Plate I). White muscle fibre use clearly increases and decreases with water velocity. At swimming speeds below 187 cm $s^{-1}$ (arrow, Plate I), white muscle fibre activity ceases.

The four other fish that were tested at higher water velocities demonstrated red and white muscle fibre activity patterns similar to Plate I. The swimming speeds at which white muscle fibres commenced and ceased activity are listed in Table I.

In contrast, three skipjack tuna (Fish 6, 7, and 8) demonstrated white muscle fibre activity at swimming speeds near their minimum hydrostatic equilibrium speeds (Table II). Fish 7, shown in Plate II, employed its white muscle fibres at swimming speeds as low as 78 cm $s^{-1}$. Neither Fish 6, 7, nor 8 had good stamina. They could not maintain their position in the water tunnel against current velocities above approximately 113 cm $s^{-1}$.

## TAIL BEAT FREQUENCY VERSUS SWIMMING SPEED

Above a minimum swimming speed, most teleosts show a linear relationship between tail beat frequency and swimming speed (Bainbridge, 1958; Hunter & Zweifel, 1971; Hudson, 1973). As a rough indication of the normal pattern of the

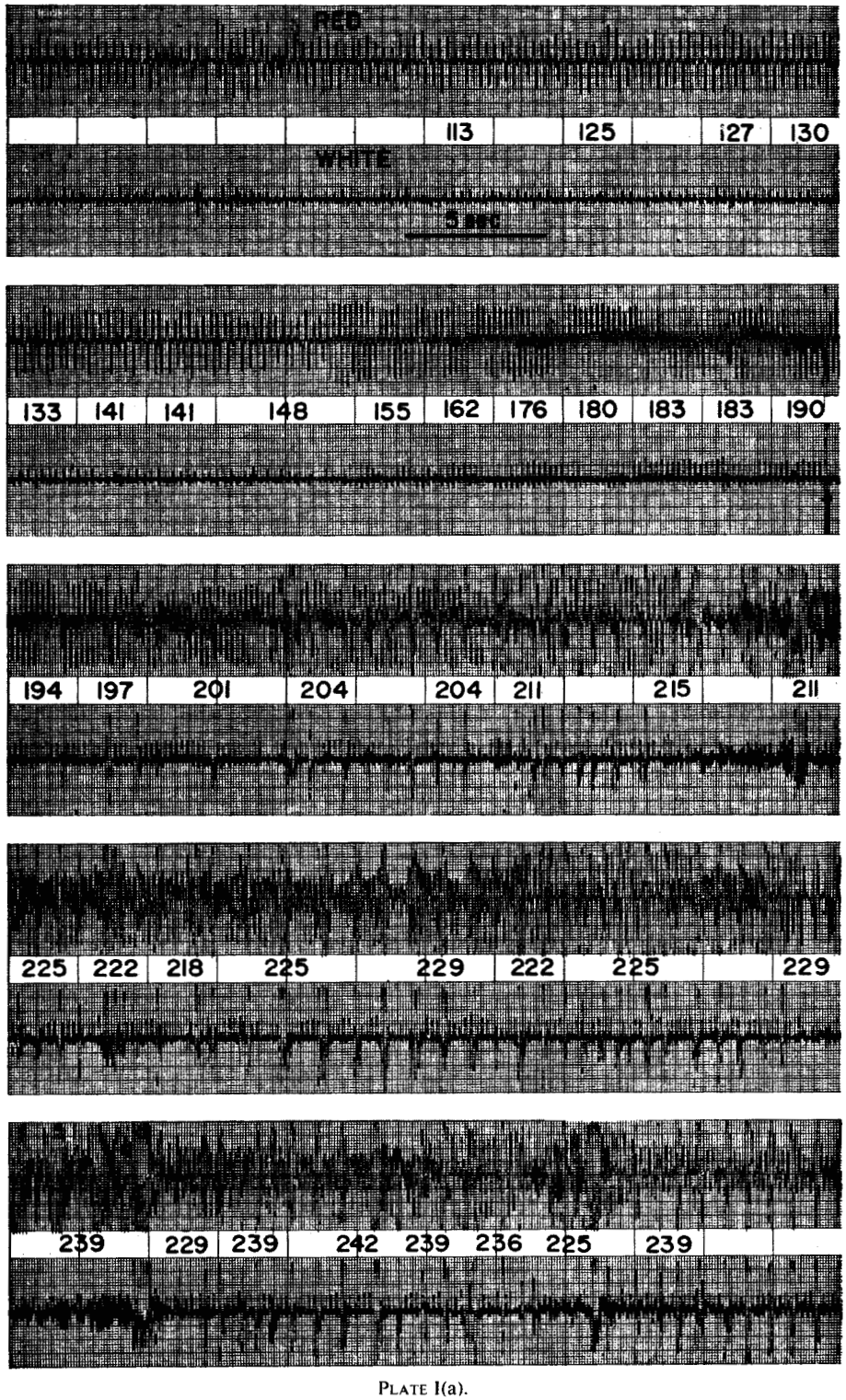
RED
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PLATE I(a).

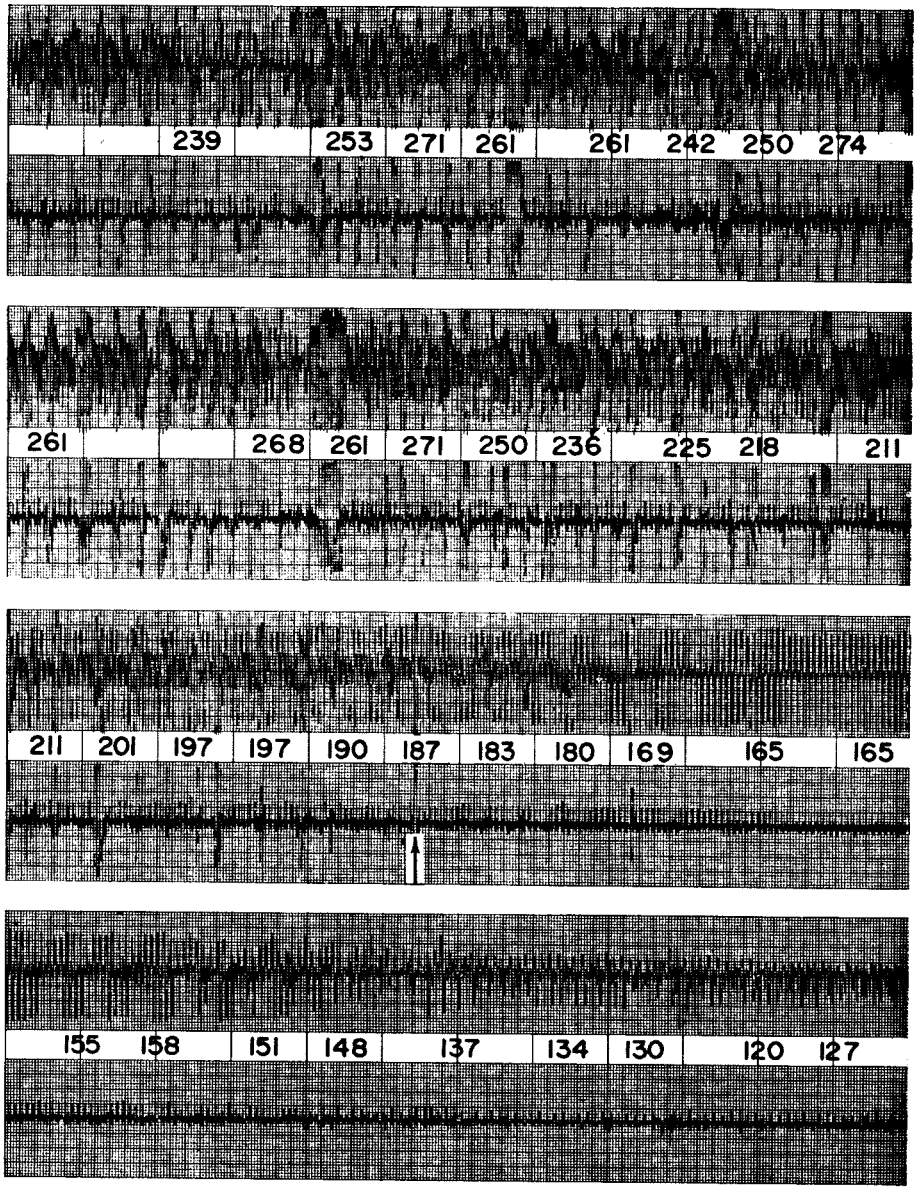


PLATE I(b).

PLATE I. The complete electromyographic record for Fish 1, during test 5. Red muscle activity is shown in the upper trace, white muscle activity in the lower. The numbers indicate swimming speed (cm $s^{-1}$). The activity seen in the lower trace, at the slower swimming speeds, is assumed to represent red muscle activity. White muscle activity (large amplitude traces) begins at 190 cm $s^{-1}$ (arrow) and ceases at 187 cm $s^{-1}$ (arrow). Chart speed is shown by a horizontal line at the start of the record.

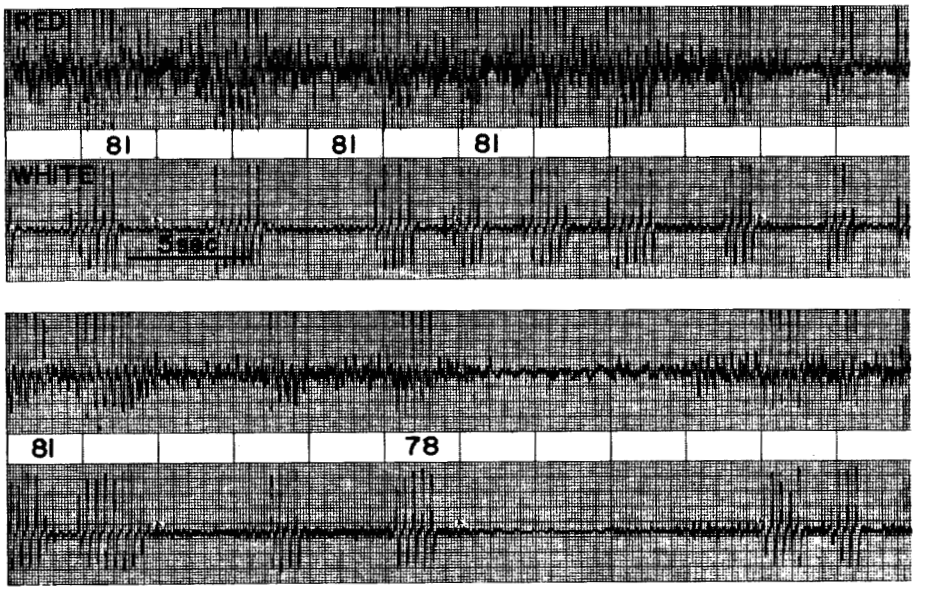


PLATE II. An electromyographic record from Fish 7. Note the use of white muscle fibres (lower trace) at slow swimming speeds. The numbers indicate swimming speed (cm $s^{-1}$); chart speed is indicated by a horizontal line.

TABLE III. Linear regression parameters for swimming speed (cm $s^{-1}$) and tail beat frequency (Hz), the means and ranges of stride length coefficients are also given

| Fish No. | *n* | Intercept | Slope (± 95% confidence limits) | Coefficient of determination | Mean stride length coefficient | Range |
|---|---|---|---|---|---|---|
| 1 | 25 | −26·98 | 40·20 ± 3·56 | 0·96 | 0·66 | 0·56–0·78 |
| 2 | 11 | −13·85 | 38·85 ± 15·77 | 0·78 | 0·72 | 0·61–0·86 |
| 3 | 25 | 8·39 | 30·45 ± 6·06 | 0·82 | 0·65 | 0·50–0·77 |
| 4 | 12 | −20·39 | 24·22 ± 4·99 | 0·92 | 0·54 | 0·45–0·67 |
| 5 | 18 | 10·10 | 22·85 ± 4·27 | 0·89 | 0·61 | 0·50–0·74 |

swimming of the fish in our water tunnel, we regressed tail beat frequency on swimming speed, based on the electromyographic records from fish 1–5. Each upward pen deflection was considered one tail beat. The number of tail beats within 2–10 s were sampled from those portions of the records where tail beat frequency was more distinct. In all cases, the slope of the regression line was significantly different from zero (Fig. 1, Table III). The regression of swimming speed on tail beat frequency was able to account for 78% to 96% of the observed variation of swimming speed (coefficient of determination, Table III). Furthermore, only fish 4 (Table III) had a mean stride length coefficient (i.e. the fraction of body length travelled per complete tail beat cycle) that fell outside the range of stride length coefficients found for other teleosts (0·6–0·8, Bainbridge, 1958). These data imply that the water tunnel used in this study is suitable, because the tail beat frequency—swimming speed relationship—remained normal.

## IV. DISCUSSION

The data clearly show that white muscle fibres of skipjack tuna are graded into activity far below maximum swimming speed (15–20 bl $s^{-1}$ at the water temperatures used in this study, Brill & Dizon, 1979), and are also used at speeds below the estimated maximum sustainable speed for this species (6 bl $s^{-1}$, Dizon *et al.*, 1978). Also, the white muscle fibres function in such a way that when they do become active they do not change the linear relationship of tail beat frequency and swimming speed (Fig. 1) during either periods of increasing or decreasing swimming speed.

Hudson (1973), Bone (1975), and Bone *et al.* (1978) have suggested that in certain teleosts the polyneuronally innervated white muscle fibres may function even at very slow swimming speeds, through local contractions initiated by junctional potentials which are below the threshold for initiation of spike potentials. We interpret the electrical activity appearing in the white muscle trace (Plate I) at slow swimming speeds to be an overlap of electrical activity from the red muscle fibres. Conceivably, our recording techniques may have failed to detect local contractions of white muscle fibres. Still, we feel our data support the hypothesis of Rayner & Keenan (1967), that white muscle fibres are not normally used at very slow swimming speeds.

Plate II shows a skipjack tuna displaying white muscle fibre activity at very slow swimming speeds. We believe these data represent an abnormal condition, based on the following line of reasoning: the efficiency (i.e. work output per quantity of ATP hydrolyzed) of isolated muscles has been shown to be maximized at a given speed of shortening. Muscle efficiency falls away sharply at speeds other than the maximally efficient speed (Goldspink, 1975). The speed of shortening of an unloaded muscle has been shown to be proportional to its myofibrillar ATPase level (Barany, 1967). Therefore, the speed of contraction at which a muscle is most efficient is also linked to its myofibrillar ATPase level. Because the myofibrillar ATPase level in skipjack tuna white muscle is likely to be about twice that in the red muscle fibres (Johnston & Tota, 1974), white muscle fibres must be inefficient if they are used at very slow swimming speeds. Thus we suspect that white muscle fibres are not normally active at very slow swimming speeds, as in Fish 6–8. However, our data do show that, like other teleosts, skipjack tuna grade their white muscle fibres into activity at apparently sustainable swimming speeds.

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## References

Bainbridge, R. (1958). The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. *J. exp. Biol.* **35**, 109–133.

Barany, M. (1967). ATPase activity of myosin correlated with speed of shortening. *J. gen. Physiol.* **50**, 197–219.

Bone, Q. (1975). Muscular and energetic aspects of fish swimming. In *Swimming and Flying in Nature* (T. Y. Wu, C. J. Brokaw & C. Brennen, eds), pp. 493–528. Proceeding of the Symposium on Swimming and Flying in Nature Held at California Institute of Technology, Pasadena, Calif., 8–12 July 1974. New York: Plenum Publishing Corporation.

Bone, Q., Kiceniuk, J. & Jones, D. R. (1978). On the role of the different fibre types in fish myotomes at intermediate swimming speeds. *Fishery Bull. U.S.* **76**, 691–699.

Brill, R. W. & Dizon, A. E. (1979). Effect of temperature on isotonic twitch of white muscle and predicted maximum swimming speeds of skipjack tuna, *Katuswonus pelamis*. *Env. Biol. Fish.* **4**, 199–205.

Carey, F. G. & Teal, J. M. (1966). Heat conservation in tuna fish muscle *Proc. Natl. Acad. Sci. U.S.A.* **56**, 1464–1469.

Davison, W., Goldspink, G. & Johnston, I. A. (1976). The division of labour between fish myotomal muscles during swimming. *J. Physiol. Lond.* **263**, 185–186.

Dizon, A. E. & Brill, R. W. (1979). Thermoregulation in tuna. *Am. Zool.* **19**, 249–265.

Dizon, A. E., Brill, R. W. & Yuen, H. S. H. (1978). Correlations between environment, physiology, and activity and its effects on thermoregulation in skipjack tuna, *Katsuwonus pelamis*. In *The Physiological Ecology of Tunas* (G. D. Sharp & A. E. Dizon, eds), pp. 233–259. New York: Academic Press.

Goldspink, G. (1975). Biochemical energetics of fast and slow muscles. In *Comparative Physiology—Functional Aspects of Structural Materials* (L. Bolis, S. H. P. Maddrell & K. Schmidt-Nielson, eds), pp. 173–185. Amsterdam: North Holland Publishing Company.

Graham, J. B. (1975). Heat exchange in the yellowfin tuna, *Thunnus albacares*, and skipjack tuna, *Katsuwonus pelamis*, and the adaptive significance of elevated body temperatures in scombrid fishes. *Fishery Bull. U.S.* **73**, 219–229.

Greer-Walker, M. (1970). Growth and development of the skeletal muscle fibres of the cod (*Gadus morhua* L.). *J. Cons. Perm. Int. explor. Mer.* **33,** 228–244.

Greer-Walker, M. & Pull, G. (1973). Skeletal muscle function and sustained swimming speeds in the coalfish, *Gadus virens* L. *Comp. Biochem. Physiol.* **44A,** 495–501.

Grillner, S. & Kashin, S. (1976). On the generation and performance of swimming in fish. In *Neural Control of Locomotion: Advances in Behavioral Biology* (R. M. Herman, S. Grillner & P. S. G. Stein, eds), pp. 181–201. New York: Plenum Press.

Hochachka, P. W., Hulbert, W. C. & Guppy, M. (1978). The tuna power plant and furnace. In *The Physiological Ecology of Tunas* (G. D. Sharp & A. E. Dizon, eds), pp. 153–174. New York: Academic Press.

Hudson, R. C. L. (1973). On the function of the white muscles in teleosts at intermediate swimming speeds. *J. exp. Biol.* **58,** 509–522.

Hunter, J. R. & Zweifel, J. R. (1971). Swimming speed, tail beat frequency, tail beat amplitude, and size in jack mackerel, *Trachurus symmetricus*, and other fishes. *Fishery Bull. U.S.* **69,** 253–266.

Johnston, I. A., Davison, W. & Goldspink, G. (1977). Energy metabolism of carp swimming muscles. *J. comp. Physiol.* **114,** 203–216.

Johnston, I. A. & Goldspink, G. (1973a). A study of glycogen and lactate in the myotomal muscles and liver of the coalfish (*Gadus virens* L.) during sustained swimming. *J. mar. biol. Ass. U.K.* **53,** 17–26.

Johnston, I. A. & Goldspink, G. (1973b). A study of the swimming performance of the Crucian carp *Carassius carassius* (L.) in relation to the effects of exercise and recovery on biochemical changes in the myotomal muscles and liver. *J. Fish Biol.* **5,** 249–260.

Johnston, I. A. & Tota, B. (1974). Myofibrillar ATPase in the various red and white trunk muscles of the tunny (*Thunnus thynnus* L.) and the tub gurnard (*Trigla lucerna*). *Comp. Biochem. Physiol.* **49B,** 367–373.

Magnuson, J. J. (1978). Locomotion by scombrid fishes—hydromechanics, morphology, and behaviour. In *Fish Physiology* Vol. VII (W. H. Hoar & D. J. Randall, eds), pp. 240–313. New York: Academic Press.

Nakamura, E. L. (1972). Development and uses of facilities for studying tuna behavior. In *Behavior of Marine Animals Current Perspectives in Research 2: Vertebrates* (H. E. Winn & B. L. Olla, eds), pp. 245–277. New York: Plenum Publishing Corporation.

Pritchard, A. W., Hunter, J. R. & Lasker, R. (1971). The relation between exercise and biochemical changes in red and white muscle and liver in the jack mackerel, *Trachurus symmetricus*. *Fishery Bull. U.S.* **69,** 379–386.

Rayner, M. D. & Keenan, M. J. (1967). Role of red and white muscles in the swimming of skipjack tuna. *Nature, Lond.* **214,** 392–393.

Smit, H. (1965). Some experiments on the oxygen consumption of goldfish (*Carassius auratus* L.) in relation to swimming speed. *Can. J. Zool.* **43,** 623–633.

Smit, H., Amelink-Koutstall, J. M., Vijverberg, J. & von Vaulpel-Klein, J. C. (1971). Oxygen consumption and efficiency of swimming goldfish. *Comp. Biochem. Physiol.* **39A,** 1–28.

Stevens, E. D., Lam, H. M. & Kendall, J. (1974). Vascular anatomy of the counter-current heat exchanger of skipjack tuna. *J. exp. Biol.* **61,** 145–153.

Webb, P. W. (1975). Hydrodynamics and energetics of fish propulsion. *Fish. Res. Bd Can., Bull.* **190,** 159 pp.