NOTES

EFFECT OF SWIMMING SPEED ON THE EXCESS TEMPERATURES AND ACTIVITIES OF HEART AND RED AND WHITE MUSCLES IN THE MACKEREL, *SCOMBER JAPONICUS*

Body temperatures of most fish typically are about the same as the water in which they swim for much of the heat generated by muscular activity is ducted away via the circulating blood and lost by convection at the gills and body surface.

Some scombrids and lamnid sharks conserve muscle heat using countercurrent vascular heat exchangers (retia mirabilia) so that temperatures are maintained significantly above ambient in the brain, eyes, red and white swimming muscles, and viscera (Carey et al. 1971; Stevens and Fry 1971; Linthicum and Carey 1972; Graham 1973). In other fishes lacking these heat conserving devices, only small temperature excesses above ambient have been recorded, but rarely more than 1°C (Stevens and Fry 1974). Since heat production must depend primarily on work output by the locomotor musculature, we have examined effects of swimming speed on the magnitude of the small temperature excesses in a "cool" scombrid not equipped with the retia exchangers, the mackerel, *Scomber japonicus* (locally the Pacific mackerel = chub mackerel).

Another important question concerning scombrid locomotion is how contractions of red and white muscle fibers are staged as swimming speed increases. It is generally thought that red muscle provides power for cruise swimming and that white muscle functions in "burst" swimming (Rayner and Keenan 1967). Red muscle is predominately aerobic and utilizes fatty acids as the major energy source whereas white muscle (which uses glycogen) usually functions anerobically (Gordon 1968; Bilinski 1974). The second objective of our study was to determine how heart rate and red and white muscle activity of *S. japonicus* are affected by swimming speed. For this purpose, electrodes were implanted into the pericardial space and in swimming muscles of fish so that simultaneous records of electrocardiograms (ECG's) and red and white electromyographs (EMG's) could be obtained.

The genus *Scomber* is a primitive member of the family Scombridae (Kishinouye 1923). It has a fusiform shape, is less heavily bodied than the skipjack tuna, *Katsuwonus pelamis*, and other tunas, but shares several characteristics with warm-bodied species; they swim continuously (swim bladders are reduced or absent), have high rates of oxygen consumption (Baldwin 1923; Hall 1930), and have high blood hemoglobin levels (Greer-Walker and Pull 1975). They are also obligatorily dependent upon ram gill ventilation as adults (Roberts 1975) and have large gill surface areas with a high diffusion efficiency (Hughes 1966; Steen and Berg 1966).

Materials and Methods

Surgical Procedures and Swimming Experiments

The general procedure was to implant either thermocouples or cardiac (ECG) and muscle (EMG) electrodes into mackerel which were then placed in a Blažka-Fry tunnel respirometer (12 cm i.d.) to swim at controlled velocities. Fifteen specimens (35-40 cm fork length (FL); 0.38-0.62 kg) were obtained from regularly replenished and maintained mackerel stocks at the Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA. After netting, each fish was anesthetized in a large basin of oxygenated seawater containing 0.2 g/l of tricaine methanesulfonate (Crescent Research Chemical, Inc.)[1] and placed on an operating table where its gills were perfused continuously with a fast flow of oxygenated seawater containing a small amount of the same anesthetic (0.08 g/l). Thermocouples (0.127 mm in diameter copper constantan, polyvinyl chloride insulation) or electrode pairs (hooked, 0.07 mm in diameter stainless-steel, epoxy insulated) were implanted within the pericardial cavity just posterior to the ventricle, and in red and white muscles just under the leading edge of the second dorsal fin.

The white muscle thermocouple tip was placed midway between the vertebral column and the lateral edge of the body at the level of the horizontal midline. Preliminary dissections confirmed that red muscle in *S. japonicus* occurs in bands

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

that are concentrated below the skin along the lateral midline and become thicker posteriorly (see also Kishinouye 1923, fig. 16; Braekkan 1959, fig. 1). To ensure that the tip of the red muscle thermocouple would remain in place, the wire was passed from near the second dorsal fin obliquely through white muscle and then into the thin red muscle band. Once inserted, its position was easily verified by gentle fingertip probing.

To facilitate positioning of the two muscle thermocouples, 3-4 cm deep holes were tapped with a 20-gage hypodermic needle. The heart thermocouple was passed into the pericardial cavity through a 17-gage needle that was subsequently withdrawn. All wires were anchored in place by skin sutures. Wire leads (1 m long) to the recorder were lap wound together, passed posteriorly, and sutured to the dorsal midline near the finlets to prevent tangling around the tail. Implanting required about 15 min after which the fish was transferred to the respirometer swimming tube where aerated water was circulated over the gills by the driving impeller at a slow speed.

Two hours recovery from anesthesia and a brief period of swim training was required before a fish could maintain station in the tube and regulate swimming speed in response to water flow. This time delay also allowed stabilization of tissue temperature at ambient conditions following surgery.

Adaptation to the swimming chamber was carried out at a basal swimming speed which is 1.5 BL/s (body lengths per second) for *S. japonicus* (Magnuson 1973). This speed is also just above the velocity required for sustained ram gill ventilation (Roberts 1975). Flow rates in the respirometer were calibrated with a ducted flowmeter (Marine Advisors, Inc. model B-7C) and controlled by altering the applied armature voltage to the impeller pump motor. Eight fish were used for excess temperature measurements and seven were used to monitor EMG (4) and ECG (3) patterns.

Calibration Procedures

Thermocouples were made by soldering together the twisted bared tips of the copper and constantan wires and sealing them with epoxy cement. The three tissue thermocouples and a reference thermocouple (for respirometer water temperature) were each connected in series (constantan leads) to an ice-bath reference couple (0°C) and to an RS Beckman Dynograph (copper leads) through a high-quality, shorting rotary-switch. This arrangement permitted rapid switching between thermocouples without opening the recorder circuit. Thermocouples were standardized in a water bath at 20°±0.05°C before and after each trial.

Paired electrodes for recording ECG's and EMG's were prepared and implanted (in the same sites used for thermocouples) as described by Roberts (1975). The ECG and EMG signals were preamplified using high impedence, probe amplifiers (Grass, P511DR) to improve the frequency response of the RS Dynograph.

Seawater was kept continuously flowing through the respirometer tube and ambient temperature was maintained within 2.0°C in each experiment by mixing warm and cold seawater at the outlet taps of the laboratory seawater system. Over the 2-mo course of experiments, respirometer temperatures ranged from 16° to 22°C.

Results

Changes in excess tissue temperatures that accompany increased swimming speed in the mackerel are best seen in a particularly successful trial with fish number 6 (Figure 1). Similar, but somewhat variable records of heart, and red and white muscle temperatures were obtained for all fish (Table 1).

While cruising at low speeds, excess temperatures reached a maximum of about 0.3°C in the red and white muscles, but doubled within 3 min swimming at enforced higher speeds (3.2-4.5 BL/s). Excess temperatures recorded in the heart averaged about one-half of the excess developed in muscles at all swimming velocities. When swimming speeds were reduced once again to slow cruising, excess temperatures returned to preburst levels within 8-15 min.

During bouts of prolonged high-speed swimming (5-6 min), water in the swimming tunnel was warmed about 1°C due to frictional heating even though a continuous exchange of seawater was maintained from the supply tap (about 15 l/min). This thermal error was minimized by rapidly accelerating the fish from slow cruising to its predetermined, burst-swimming velocity. In Figure 1 for example, the fish was accelerated from 1.4 to 3.9 BL/s in about 5 s followed by sustained swimming for 3 min, and then rapidly decelerated to 1.4 BL/s. Equilibration of tissue thermal excess (i.e., generation minus dissipation) occurred in most

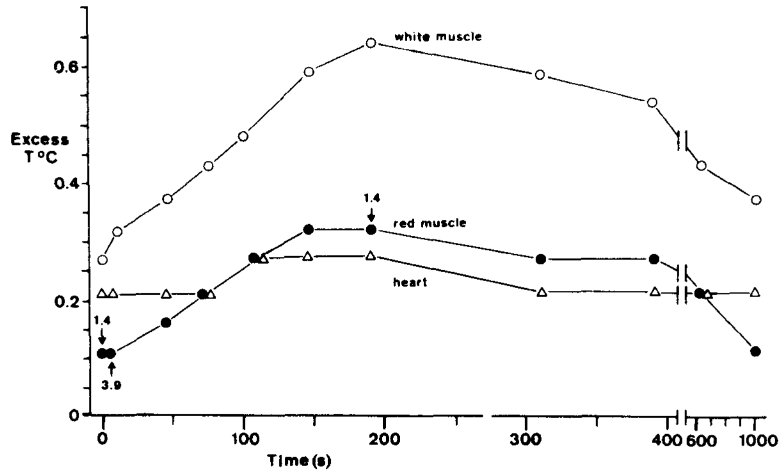

FIGURE 1.—Temperature excess in the heart and in red and white muscles recorded from *Scomber japonicus* no. 6 (35 cm FL, 0.45 kg) swimming at speeds from 1.4 to 3.9 BL/s. Arrows indicate timing and direction of speed changes. Ambient temperature, 19.5°-19.6°C.

TABLE 1.—Temperature excesses as ΔT (°C) recorded for seven *Scomber japonicus* swimming at basal and moderately fast speeds in body lengths per second (BL/s).[1]

Item	Fish number							Mean
	1	2	3	4	6	7	8	
Fork length (cm)	35.6	39.2	38.9	38.1	35.0	36.3	34.3	36.8
Weight (kg)	0.54	0.62	0.59	0.55	0.45	0.58	0.39	0.53
Highest ΔT at basal speed (1.3-1.9 BL/s) in:								
Red muscle	0.2	0.1	0.2	0.2	0.2	0.3	0.5	0.24
White muscle	0.2	0.3	0.3	0.2	0.4	0.3	0.3	0.29
Heart	0.0	0.3	0.1	0.1	0.2	0.2	(2)	0.15
Highest ΔT and swimming speeds (BL/s) in:								
Red muscle	0.9	0.75	0.55	0.85	0.3	0.5	0.8	0.66
	(4.2)	(3.2)	(3.7)	(4.2)	(3.9)	(3.8)	(4.3)	(3.9)
White muscle	0.75	0.8	0.65	0.6	0.65	0.3	0.7	0.64
	(4.2)	(3.2)	(3.7)	(3.9)	(3.9)	(3.8)	(4.3)	(3.9)
Heart	0.45	(2)	(2)	0.4	0.25	0.25	(2)	0.34
	(4.2)			(4.5)	(3.9)	(3.8)		(4.1)
Maximum trial speed (BL/s)	4.2	3.2	3.7	4.5	3.9	3.8	4.3	3.9
Water temperature, range (°C)[3]	16.1-17.0	16.5-17.0	16.8-17.8	17.1-17.5	19.5-19.6	20.5-21.0	21.1-21.8	

[1]Fish no. 5 omitted because it would not swim in the respirometer tube.
[2]Thermocouple malfunction.
[3]Starting temperature is that of the seawater supply from mid-June to mid-July.

cases within the 3-min swimming bouts. Although the thermal excess was greater in white muscle of fish number 6 (Figure 1), mean maximum temperature excesses recorded in red and white muscles of the seven mackerel were about the same (Table 1).

Variability observed in excess temperature measurements seems attributable to different performances of individual fish. Some specimens had more body fat than others and did not swim steadily. Others were affected by the trailing thermocouple cable as evidenced by their tail-beat patterns. The cable also added drag which reduced speed but probably increased total heat production at a specific speed. None of the fish trailing thermocouple cables could swim steadily above 5 BL/s, whereas fish trailing the thinner ECG and EMG cables could maintain a speed of 6 BL/s. Some of the variability in recorded thermal excesses may have also been due to the slightly differing locations of thermocouples in each fish. In addition, trauma due to thermocouple insertion, which probably interrupts normal blood flow locally may have been a factor influencing thermal convection. In a few cases, thermocouple signals changed abruptly possibly because of insulation failure at the tip due to rapid body flexing of fishes at higher swimming speeds.

A wide range was found in heart rates of mackerel cruising at 1-1.5 BL/s (mean, 106; range, 80-140 beats/min). With acceleration to 4-5 BL/s, the mean heart rate increased by 54%, (mean, 130; range, 112-150), but rapidly returned to the resting rate within a few minutes of deceleration.

The EMG's demonstrate that both red and white muscle fibers contract synchronously while the mackerel swims at 2 BL/s (Figure 2). At slower velocities, even below basal speed, both red and white fibers were active during each tail-beat cycle. With acceleration to velocities above cruising, rates and amplitudes of both red and white EMG's showed proportionate increases; red muscle EMG'S reached maximal amplitude between 3 and 4 BL/s. White muscle EMG's of the first mackerel tested appeared to increase in amplitude more than red muscle, and in proportion to velocity up to the highest speed at which the fish could swim steadily (about 6 BL/s). However, subsequent records obtained from three other fish did not confirm a consistent pattern of amplitude development with swimming velocity in the two fiber types. Variations in EMG amplitudes of single tail-beat cycles were commonly found in the recordings of all the fish from both red and white muscles at all swimming speeds. This is evident in the 1-s records for the fish in Figure 2. In this case, amplitude variability was more apparent at 5.9 BL/s because the fish's swimming became erratic—characterized by asymmetrical tail beats (unsteady or dart swimming). High-speed bilateral recording as used by Hudson (1973) would have aided the analysis. Figure 2 also shows that large bursts in white muscle sometimes accompany small bursts in red muscle, but confirmation of interactive contractile events in red and white muscles was not attempted.

Discussion

Body Temperatures

This study shows that *Scomber japonicus*, a strong continuous swimmer, does not develop large temperature excesses in its tissues while swimming at basal (1.3-1.9 BL/s) or sustainable (3-5 BL/s) speeds. Temperature excesses measured in the heart and in red and white muscles of this fish never exceeded 1°C and thus are not different from values typically found in species without specialized heat-conserving retia mirabilia (Lindsay 1968; Carey et al. 1971; Stevens and Fry 1974).

At high speeds, the lowest thermal excesses measured for the mackerel were in the heart. It was not possible to discriminate between heat actually produced by increased cardiac activity and that transported to the heart either via the blood (i.e., convectively) or by conduction. Some heat production must occur in the heart, but its mass is small compared with the volume of blood pumped per unit of time. Thus much of the muscle heat is either dissipated at the body surface or is conducted very slowly to other tissues before it reaches the heart and gills. There are several reasons why muscle heat may not reach the heart in venous blood. First, blood warmed in active muscles would be cooled as it mixes with blood returning from metabolically less active tissues. Also some countercurrent heat transfer (i.e., from

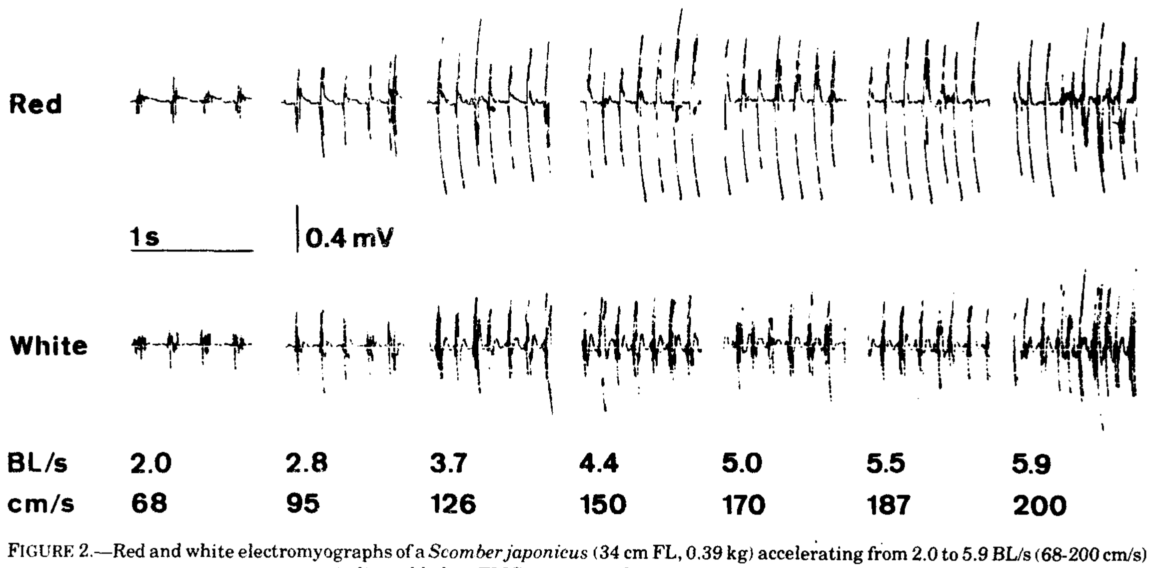

FIGURE 2.—Red and white electromyographs of a *Scomber japonicus* (34 cm FL, 0.39 kg) accelerating from 2.0 to 5.9 BL/s (68-200 cm/s) as indicated below EMG traces. Ambient temperature, 17°C.

a warm vein to an artery) between parallel and closely positioned arteries and veins (either segmental vessels or postcardinal vein and dorsal aorta) could reduce convective heat transport. For example, Stevens and Sutterlin (1976) demonstrated a mechanism of this type that transferred heat directly from afferent to efferent gill arteries in the sea raven, *Hemitripterus americanus*.

Fish body temperatures are not uniform. In most species, including the warm-bodied forms, the highest thermal excesses occur in deep muscles (both red and white) where body thickness is maximum (Lindsey 1968; Carey et al. 1971; Graham 1975). For this reason white muscle temperatures in the mackerel might be higher in more anterior regions of the body (i.e., at the first dorsal fin) where the white muscle mass and body thickness are greater. By contrast, higher temperatures in red muscle would not be expected because in *Scomber* this tissue is a thin band along the side of the body, only reaching maximum thickness as the body tapers toward the caudal peduncle (see figures in Kishinouye 1923 and Braekkan 1959).

Red and White Muscle Activity at Different Swimming Speeds

We were unable to determine a specific velocity where white muscle is recruited for swimming in the mackerel. At very low speeds, tail beats often became erratic or excessively strong. This may have been due to the added cable drag. Also, the basal speeds for fish in this study coincide with their minimum velocity needs for ram gill ventilation (Roberts 1975) which may have elicited struggling at slow speeds. Our EMG's do show low amplitude, synchronous potentials in both red and white muscles that were correlated with tail beats from very slow speeds up to about 2 BL/s. Amplitudes of EMG's in both muscle types seemed to reach a maximum for steady swimming at 3-4 BL/s, demonstrating that white fibers are active well within the range of sustainable cruising velocities for this species and that red muscle remains active at high speeds.

Neither patterns of motor innervation of red and white muscle fibers (focal or distributed) of scombrid myotomes nor the nature of their electrical responses seem to be known. Whether the compound potentials we recorded represent all-or-none spikes, abortive spikes, or rapid drifts in membrane potentials (local potentials) following excitation, also is unknown.

We suggest that the amplitude changes recorded from both the red and white fibers as the fish accelerated represent fiber recruitment. White muscle electrodes were located close to the vertebral column, probably not closer than 1 cm to the lateral strips of red muscle, so detection of conducted red fiber potentials was unlikely. Amplitude variations detected in both muscle types during single tail-beat cycles was considerable. These variations were attributed to movement artifacts and possible drop-out of motor units nearby the electrodes.

A nearly completed dissertation study in one of our laboratories has demonstrated clearly that EMG's of red muscle in striped bass, *Morone saxatilis*, and in bluefish, *Pomatomus saltatrix*, also grade in amplitude with increasing swimming speed up to about 3 BL/s (M. A. Freadman, Graduate Student, Department of Zoology, University of Massachusetts, Amherst, MA 01003. Pers. commun., September 1977). But unlike *S. japonicus*, white muscle activity in these species does not appear until they reach burst-swimming velocities—a pattern of red and white muscle activation that resembles the herring (Bone 1975).

Red and white muscle fibers have different anatomical, physiological, and biochemical characteristics that relate directly to their roles in the swimming of different fishes (George 1962; Bone 1966; Bilinksi 1974; Johnston et al. 1977). In some species red muscle functions over a wide range of speeds whereas white muscle is used only in burst swimming (Bone 1966). Staging in the activity of red and white muscles, that is the recruitment of white (mosaic red and white mixed as in salmonids; pink and white as in some carp) as velocity increases, has been observed in many species (viz., dogfish, Bone 1966; skipjack tuna, Rayner and Keenan 1967; rainbow trout, Webb 1971, Hudson 1973; coalfish, Greer Walker 1971; and carp, Johnston et al. 1977). The relative contribution of these muscle types to swimming no doubt relates to species-specific locomotory requirements for cruise swimming and maneuverability. However, more recently acquired data on this point show, as in *S. japonicus*, that white muscle fibers do often function at low, sustainable swimming speeds (e.g., in coalfish and carp) and thus are not exclusively reserved for high-speed burst swimming (Johnston et al. 1977).

For scombrids, which swim continuously and rely upon forward motion to ventilate their gills, the existence of a relatively high speed for the division of labor between red and white muscles, has been assumed primarily on the basis of work done by Rayner and Keenan (1967). These investigators concluded that in the skipjack tuna, red muscle alone powered cruise swimming and white muscle only became active at burst velocities. The initial objective of Rayner and Keenan's study was to demonstrate contractile properties of red muscle, and to this end they blocked white muscle activity (pentobarbital) and worked exclusively with tranquilized (propriopromazine) or sedated fish. Moreover, their specimens were restrained in a fixed position and artificially ventilated by perfusion tubes in the mouth. Thus the movements by these skipjack tunas that were identified as "low frequency swimming," were in fact only casually related to the swimming requirements for gill ventilation and hydrostatic equilibrium; both are controlling factors in normal swimming (Magnuson 1973; Roberts 1975).

Our results with *S. japonicus* contrast in that they show both red and white muscles function in low-speed swimming. Also, Dizon and Brill (A. E. Dizon, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812. Pers. commun., September 1977) recorded red and white EMG's from yellowfin tuna, *Thunnus albacares,* and found that white muscle activity begins at swimming velocities of <3 BL/s—a speed only slightly above the minimum for hydrostatic equilibrium and well below maximal burst capabilities (Magnuson 1973). These observations indicate that in fast-swimming scombrids, patterned staging of red and white muscle activity may differ in that activity begins in white fibers at very low speeds, and that both red and white muscle remain active throughout a wide range of sustainable speeds as well as at burst velocities. Implicit in this idea is the presence of a high scope for aerobic activity in scombrid white muscle which has been recently demonstrated for the skipjack tuna (Guppy et al. in press). Also required by the hypothesis are specializations in red muscle for high-speed contraction which is supported by the findings of Johnston and Tota (1974) that high levels of myofibrillar ATPase occur in the red muscle of bluefin tuna, *T. thynnus*.

What physiological advantage might be gained by a 1°C thermal excess during fast swimming? Assuming a Q_{10} of 2 then a 10% increase in metabolism would afford about a 2-3% rise in swimming speed, but an insignificant change in overall swimming efficiency (Webb 1971). An interesting speculation is that the extensive heat-exchanging vascular network used for endothermy in the scombrids may have initially evolved to meet the high oxygen requirements of red and white myotomal muscle. More metabolic heat is produced during aerobic respiration and natural selection may have proceeded toward a vascular design that maximized oxygen delivery, yet augmented muscle function by conserving heat and insulating the swimming musculature from ambient conditions.

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Literature Cited

BALDWIN, F. M.
1923. Comparative rates of oxygen consumption in marine forms. Proc. Iowa Acad. Sci. 30:173-180.

BILINSKI, E.
1974. Biochemical aspects of fish swimming. *In* D. C. Malins and J. R. Sargent (editors), Biochemical and biophysical perspectives in marine biology, Vol. 1, p. 239-288. Academic Press, N.Y.

BONE, Q.
1966. On the function of the two types of myotomal muscle fibre in elasmobranch fish. J. Mar. Biol. Assoc. U.K. 46:321-349.
1975. Muscular and energetic aspects of fish swimming. *In* T. Y.-T. Wu, C. J. Brokaw, and C. Brennen (editors), Swimming and flying in nature, Vol. 2, p. 493-528. Plenum Press, N.Y.

BRAEKKAN, O. R.
1959. A comparative study of vitamins in the trunk muscles of fishes. Fiskeridir. Skr. Ser. Teknol. Unders. 3(8):1-42.

CAREY, F. G., J. M. TEAL, J. W. KANWISHER, K. D. LAWSON, AND J. S. BECKETT.
1971. Warm-bodied fish. Am. Zool. 11:137-145.

GEORGE, J. C.
1962. A histophysiological study of the red and white muscles of the mackerel. Am. Midl. Nat. 68:487-494.
GORDON, M. S.
1968. Oxygen consumption of red and white muscles from tuna fishes. Science (Wash., D.C.) 159:87-90.
GRAHAM, J. B.
1973. Heat exchange in the black skipjack, and the blood-gas relationship of warm-bodied fishes. Proc. Natl. Acad. Sci. U.S.A. 70:1964-1967.
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. Fish. Bull., U.S. 73:219-229.
GREER WALKER, M.
1971. Effect of starvation and exercise on the skeletal muscle fibres of the cod (*Gadus morhua* L.) and the coal fish (*Gadus virens* L.) respectively. J. Cons. 33:421-427.
GREER-WALKER, M., AND G. A. PULL.
1975. A survey of red and white muscle in marine fish. J. Fish Biol. 7:295-300.
GUPPY, M., W. C. HULBERT, AND P. W. HOCHACHKA.
In press. The tuna power plant and furnace. *In* G. D. Sharp and A. E. Dizon (editors), The physiological ecology of tunas. Academic Press, N.Y.
HALL, F. G.
1930. The ability of the common mackerel and certain other marine fishes to remove dissolved oxygen from sea water. Am. J. Physiol. 93:417-421.
HUDSON, R. C. L.
1973. On the function of the white muscles in teleosts at intermediate swimming speeds. J. Exp. Biol. 58:509-522.
HUGHES, G. M.
1966. The dimensions of fish gills in relation to their function. J. Exp. Biol. 45:177-195.
JOHNSTON, I. A., AND B. TOTA.
1974. Myofibrillar ATPase in the various red and white trunk muscles of the tunny (*Thunnus thynnus* L.) and the tub gurnard (*Trigla lucerna* L.). Comp. Biochem. Physiol. 49B:367-373.
JOHNSTON, I. A., W. DAVISON, AND G. GOLDSPINK.
1977. Energy metabolism of carp swimming muscles. J. Comp. Physiol. 114:203-216.
KISHINOUYE, K.
1923. Contributions to the comparative study of the so-called scombroid fishes. J. Coll. Agric., Imp. Univ. Tokyo 8:293-475.
LINDSEY, C. C.
1968. Temperatures of red and white muscle in recently caught marlin and other large tropical fish. J. Fish. Res. Board Can. 25:1987-1992.
LINTHICUM, D. S., AND F. G. CAREY.
1972. Regulation of brain and eye temperatures by the bluefin tuna. Comp. Biochem. Physiol. 43A:425-433.
MAGNUSON, J. J.
1973. Comparative study of adaptations for continuous swimming and hydrostatic equilibrium of scombroid and xiphoid fishes. Fish Bull., U.S. 71:337-356.
RAYNER, M. D., AND M. J. KEENAN.
1967. Role of red and white muscles in the swimming of the skipjack tuna. Nature (Lond.) 214:392-393.
ROBERTS, J. L.
1975. Active branchial and ram gill ventilation in fishes. Biol. Bull. (Woods Hole) 148:85-105.
STEEN, J. B., AND T. BERG.
1966. The gills of two species of haemoglobin-free fishes compared to those of other teleosts—with a note on severe anaemia in an eel. Comp. Biochem. Physiol. 18:517-526.
STEVENS, E. D., AND F. E. J. FRY.
1971. Brain and muscle temperatures in ocean caught and captive skipjack tuna. Comp. Biochem. Physiol. 38A:203-211.
1974. Heat transfer and body temperatures in non-thermoregulatory teleosts. Can. J. Zool. 52:1137-1143.
STEVENS, E. D., AND A. M. SUTTERLIN.
1976. Heat transfer between fish and ambient water. J. Exp. Biol. 65:131-145.
WEBB, P. W.
1971. The swimming energetics of trout. II. Oxygen consumption and swimming efficiency. J. Exp. Biol. 55:521-540.

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