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 scom-
brid 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 pre-
dominately 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
(EGC'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 ob-
ligatorily 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 lead-
ing 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 hori-
zontal midline. Preliminary dissections confirmed
that red muscle in S. japonicus occurs in bands

1Reference 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 BLs (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.

Cali brat ion 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°C ±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 impedance, 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°C 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 pre-burst 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
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 ∆T (°C) recorded for seven *Scomber japonicus* swimming at basal and moderately fast speeds in body lengths per second (BL/s).  

<table>
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<th>Item</th>
<th>Fish number</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>Mean</th>
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<tr>
<td>Red muscle</td>
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<td>0.2</td>
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<td>White muscle</td>
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<td>Highest ∆T and swimming</td>
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<tr>
<td>Red muscle</td>
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<td>(4.2)</td>
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<td>White muscle</td>
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<td>0.8</td>
<td>0.65</td>
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<td>0.65</td>
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<td>(4.3)</td>
<td>(3.9)</td>
<td></td>
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<tr>
<td>Heart</td>
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<td>(1)</td>
<td>(1)</td>
<td>0.4</td>
<td>0.25</td>
<td>0.25</td>
<td>(1)</td>
<td>0.34</td>
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<td>(4.5)</td>
<td>(3.9)</td>
<td>(3.8)</td>
<td>(4.3)</td>
<td>(4.1)</td>
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<tr>
<td>Maximum trial speed (BL/s)</td>
<td></td>
<td>4.2</td>
<td>3.2</td>
<td>3.7</td>
<td>4.5</td>
<td>3.9</td>
<td>3.6</td>
<td>4.3</td>
<td>3.9</td>
<td></td>
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<tr>
<td>Water temperature, range (°C)</td>
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<td>16.5-17.0</td>
<td>16.8-17.8</td>
<td>17.1-17.5</td>
<td>19.5-19.6</td>
<td>20.5-21.0</td>
<td>21.1-21.8</td>
<td>19.1-20.1</td>
<td></td>
</tr>
</tbody>
</table>

*Fish no. 5 omitted because it would not swim in the respirometer tube.*

*Thermocouple malfunction.*

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 EMGs 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 EMGs showed proportionate increases; red muscle EMGs reached maximal amplitude between 3 and 4 BL/\(s\). White muscle EMGs 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...
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, *Hemithrapterus americana*.

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 Braeckkan 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 scorpionid 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; Bilinksy 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 to demonstrate contractile properties of red muscle only. They showed 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.

A notable physiological advantage that might be gained by a 1°C thermal excess during fast swimming is the increase in oxygen consumption. Assuming a \(Q_{10}\) of 2 then a 10% increase in metabolism would account for 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.

Acknowledgments

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