

THERMOREGULATION IN YELLOWFIN TUNA,
THUNNUS ALBACARES¹

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To determine their capacity for thermoregulation, yellowfin tuna, *Thunnus albacares*, were subjected to a series of 12-h periods at T_a 's of 20, 25, and 30 C. Muscle temperature, measured with an ultrasonic transmitter attached to the fish, and swim speed were simultaneously monitored. No relationship was found between speed and muscle temperature, although metabolic heat production is inexorably linked to the former. Because both direct and inverse muscle temperature/heat production relationships were observed, and because physical (as opposed to physiological) explanations for our data can be discounted, we hypothesize yellowfin tuna are capable of some type of central nervous system (CNS)-mediated physiological thermoregulation.

INTRODUCTION

Although it is undisputed that tunas and lamnid sharks are warm bodied, no consensus has been reached on whether their muscle temperature can be regulated. Can these fish modify internal temperature without seeking more favorable external temperatures? Behavioral thermoregulation in the lower vertebrates is well documented, and indeed teleosts and reptiles possess a thermoregulatory center now considered homologous to that in the anterior fore-brain of birds and mammals (Crawshaw 1977; Kluger 1978). Physiological ther-

moregulation is conceivable in tunas and lamnid sharks because they can maintain muscle temperatures significantly above T_a (Barrett and Hester 1964; Carey et al. 1971; Graham 1975; Stevens and Neill 1978).

Sustained elevated muscle temperatures are possible due to the presence of vascular heat exchangers and the internal position of the red-muscle-fiber portion of the myotomes (hereafter referred to as red muscle) (Carey et al. 1971; Erskine and Spotila 1977). Venous blood, warmed by metabolic heat, transfers this heat to the arterial blood in five plexi, formed from the dorsal aorta and posterior vena cava; from the epaxial, lateral cutaneous artery and vein; and from the hypaxial, lateral cutaneous artery and vein (Kishinouye 1923; Godsil and Byers 1944; Stevens, Lam, and Kendall 1974; Graham 1975); thus heat is retained within the red muscle.

Vascular heat exchangers are the anatomical characteristics which distinguish the tunas (Thunnini) from the other members of the family Scombridae, which include the mackerels (Scombrini),

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the Spanish mackerels (*Scomberom-rini*), and the bonitos (*Sardini*) (Collette 1978). All the true tunas maintain muscle temperature significantly above T_a .

Elevated muscle temperatures are thought to provide greater muscle power (Binkhorst, Hoofd, and Vissers 1977) and permit higher maximum swim speeds (Wardle 1975, 1977; Brill 1978). Also, heat exchangers give tunas a so-called thermal inertia far in excess of other teleosts of equal size (Neill and Stevens 1974; Neill, Chang, and Dizon 1976). Yet the advantages conferred by the specialized circulatory system and internal red muscle are still a matter of speculation (Stevens and Neill 1978).

There may be a disadvantage. At low activity, the excess temperature of the red muscle may be beneficial, but, because heat production is roughly proportional to the cube of swim velocity (Ware 1978; Wu and Yates 1978), at high activity muscle temperature could theoretically rise to deleterious levels (Sharp and Vlymen 1978). Thus, it is likely that tunas have the ability to control their thermoconserving mechanisms. Yet documentation of this ability is lacking.

Carey and Teal (1969) demonstrated that the difference between red-muscle temperature and water temperature (excess temperature or T_x) of recently captured bluefin tuna, *Thunnus thynnus*, was inversely proportional to sea-surface temperature. Red-muscle T_x of this fish varied only 5 C over a sea-surface temperature range of 10–30 C. Barrett and Hester (1964) showed the T_x of skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *T. albacares*, were maintained at approximately a fixed level above T_a . Carey et al. (1971) assumed the latter two species to be less adept at thermoregulation than bluefin tuna.

We feel data from recently captured fish are not compelling evidence for or against thermoregulatory ability for the following reasons. (1) The fish experienced an unknown thermal history prior to capture. Conceivably, tropical fish could have swum at greater depths, experiencing cooler temperatures than their more temperate conspecifics. Estimation of T_x based on sea-surface temperature would give a false impression of the ability to control muscle T_x . (2) The fish had an unknown activity history. Perhaps tropical tunas are less active prior to and during capture. Since metabolic heat production is almost a cubic function of velocity (Ware 1978; Wu and Yates 1978), activity level could be a prime determinant of muscle temperature. (3) Once boated, the reduced rate of heat transfer in air, effects of water evaporation, radiant heat exchange, and circulatory-pattern modifications may have an influence on muscle temperature.

Carey and Lawson (1973) presented what appeared to be direct evidence of a mammalian type of thermoregulation. They observed a free-swimming bluefin tuna that maintained a relatively constant stomach temperature during an 11 C change in water temperature. This fish, equipped with an ultrasonic telemetry device, dove from 19 C surface water into 5 C water, remained for 4 h, then returned to 13–14 C water. Stomach temperature did not change more than 2 C over the 4-h period spent in 5 C water. The authors concluded physiological thermoregulation. Subsequently, Neill and Stevens (1974) showed that no thermoregulatory ability need be postulated to explain the above data. Employing a constant coefficient of temperature change commensurate with the size of the animal and constant heat production, the temperature of the blue-

fin tuna was successfully modeled. Because no physiological processes influencing the rate of heat exchange needed to be included in the model, thermal inertia rather than thermoregulation was sufficient to explain Carey and Lawson's data.

Our current study is an extension of the efforts of Carey and his co-workers but is distinguished by a continuous record of swim speed and muscle temperature recorded under controlled environmental temperatures. In this report we demonstrate that swimming activity and red-muscle temperature are not inexorably coupled. This observation provides evidence that a mechanism exists for regulating metabolic heat dissipation. We elaborate these findings to suggest a conceptual model of physiological thermoregulation in tunas.

MATERIAL AND METHODS

Our experimental design employed equipment to determine swim speed and muscle temperature and to control seawater temperature. Fish were tested in a tank system consisting of an annular swim chamber equipped with photocells to determine fish position (and ultimately swim speed) and a heat exchanger that controlled water temperature, at either 20, 25, or 30 C. Red-muscle temperature of the fish was telemetered by a temperature-sensitive ultrasonic transmitter. Fish were tested individually using five consecutive 12-h temperature treatments (25, 20, 30, 20, and 25 C, or 25, 30, 20, 30, and 25 C), then killed, weighed, measured, and autopsied to verify thermistor position.

Yellowfin tuna (45.0–66.4 cm, fork length) were chosen from stocks maintained at 24 C in outdoor pools (7.3-m diameter \times 1.2-m deep) at the Kewalo Research Facility of the Honolulu Laboratory of the National Marine Fisheries

Service. Nakamura (1972) has outlined details on capture, transportation, and maintenance of tuna stocks at this facility. We removed fish by angling with a barbless hook and transported them to the test tank in a plastic bag cushioned with a little seawater.

After transfer, the fish were rested for 2 h and then outfitted with the temperature-sensitive ultrasonic transmitter (generously supplied by Charles Coutant and James Rochelle, Oak Ridge National Laboratory). The transmitters (1.7-cm diameter \times 3.4-cm length, 12 g in air) have a 10-cm long \times 0.3-cm diameter probe containing the thermistor. The probe was inserted into the red muscle about 2 cm laterad to the origin of the first dorsal fin (fig. 1). The final thermistor position, later verified by dissection, was immediately adjacent to the vertebral column. Dart tags were inserted into the corselet and tied to the probe to secure the transmitter. After attachment of the transmitter, the fish was returned to the test tank; data collection began 2 h later.

The ultrasonic transmitter was designed for extended temperature monitoring from small fish (Rochelle and Coutant 1974). Temperature is telemetered by pulse-interval modulation, with the interval varying between 1,400 and 300 ms over a temperature range of 5–35 C. The transmitter was calibrated before deployment. Significantly, the calibration is not affected by a transmitter-thermistor temperature differential.

Transmitter output was received on a receiver-hydrophone system specially designed for underwater telemetry (CR-40, Communication Associates, Inc.).³ Pulse intervals were measured with a

³ Mention of trade names does not imply endorsement by the National Marine Fisheries Service, National Oceanic and Atmospheric Administration.

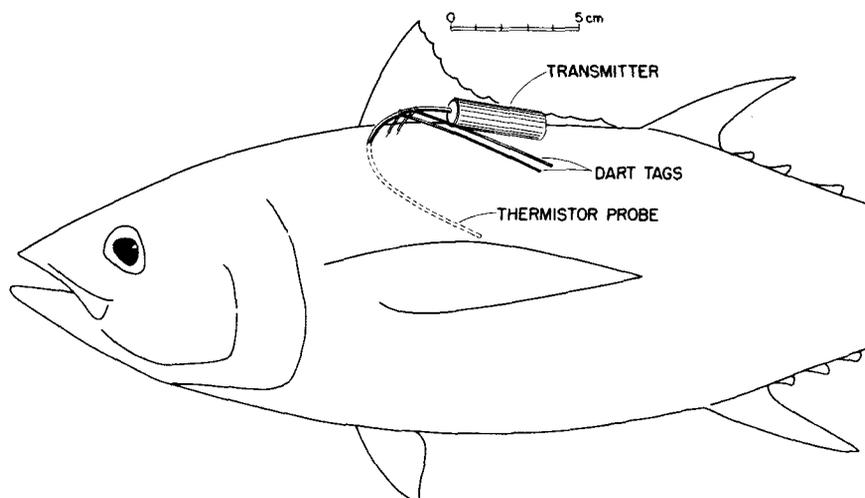


FIG. 1.—Tuna equipped with a temperature-sensitive ultrasonic transmitter for telemetering muscle temperature. The temperature-sensitive element lies immediately adjacent to the vertebral column.

frequency counter (HP 5300B/5308, Hewlett-Packard) and printed on paper tape (HP 5150) for later analysis. Precision of the telemetry system was approximately 0.05 C.

The fiberglass test tank (6.1-m diameter \times 0.6-m deep) was fitted with a concentric inner wall so that the fish was constrained to swim in a 0.75-m wide \times 0.61-m deep swim channel around the periphery. Six laps are equal to 100 m swum; swim speed was determined by lap times sensed with banks of photocells in each of the four tank quadrants. Water was introduced (and removed) from the swim chamber via two pairs of concentric polyvinyl chloride pipes positioned on the floor of the swim chamber. Entering (and exiting) water was divided into the paired pipes so that distribution of the temperature-controlled water to all parts of the tank was equal and no longitudinal temperature gradients developed. The seawater was recirculated at 1,136 liters/min through an outside stainless steel heat exchanger, and new seawater was added at about 38 liters/min. Temperature was generally regu-

lated within 0.05 C by 12 7.5-kW heaters and a 36.5-kW chiller. Maximum rate of seawater temperature change approached 0.1 C/min.

RESULTS

Six yellowfin tuna (fish 1–6) were individually subjected to consecutive 12-h temperature treatments: 25, 20, 30, 20, and 25 C. Fish 4 refused to swim laps after the first 30 C test period. Its data are incomplete since translation of position information into swim speed requires complete laps. Six other fish (7–12) experienced an altered temperature sequence (25, 30, 20, 30, and 25 C); four fish died (fish 9–12) during the second temperature period (30 C) and one (fish 8) during the third period (20 C). Data from fish 9–12 were discarded. The reason for mortality with the later test temperature sequence is not known.

Swim speed and water temperature were printed on paper tape every time the fish completed a lap (approximately every 20–30 s). For fish 1–6, red-muscle temperature was recorded every 10 min. Then, acquisition of a HP 9825A com-

puter allowed red-muscle temperature and water temperature to be recorded approximately every 30 s for fish 7 and 8.

Figure 2 presents a time series of the consecutive temperature treatments and swim speeds for fish 5, the largest fish tested. Note that, during water-temperature changes (approximately 0.1 C/min), red-muscle temperature changed also, but not as fast. This reflects the significant thermal inertia of tunas (Neill and Stevens 1974; Neill et al. 1976). Thermal inertia is also responsible for the periods during tank heating when body temperature was actually cooler than water temperature. The 30 C test period is most interesting. Here, the fish swam significantly faster than at 20 or 25 C, but red-muscle temperature decreased relative to water temperature. As noted, heat production is proportional to approximately the cube of swim speed (Ware 1978; Wu and Yates 1978). Therefore, if the fish could not adjust their thermoconserving mechanisms, muscle temperature should have increased.

We calculated the mean and standard deviation for swim speed (and red-muscle temperature for fish 7 and 8) for each 10-min period. Table 1 lists the

grand means for each temperature treatment (and 95% confidence limits) based on the 10-min means (single 10-min red-muscle-temperature readings for fish 1-6). Means are based only on data recorded during the final 8 h of the 12-h temperature treatment, in order to minimize the effects of previous temperature levels. Four hours is sufficient time for tunas of these sizes to reach thermal equilibrium (Neill et al. 1976).

Table 1 presents the summarized data on individual fish. In most cases, the pattern is similar to that of fish 5. During the 30 C test period, the tunas swam faster but had lower excess red-muscle temperatures. Fish 6 is an exception. Perhaps this fish was not thermoregulating, because muscle temperature and swim speed appear correlated.

The data from fish 7 (tested under the 25, 30, 20, 30, and 25 C temperature sequence) were also significantly different from those for the other fish. During the first 30 C test period mean swim speed was 62.70 cm/s, and mean excess red-muscle temperature was 0.54 C. During the single 20 C test period mean swim speed decreased to 43.16 cm/s, but mean red-muscle excess temperature remained at 0.51 C. During the second

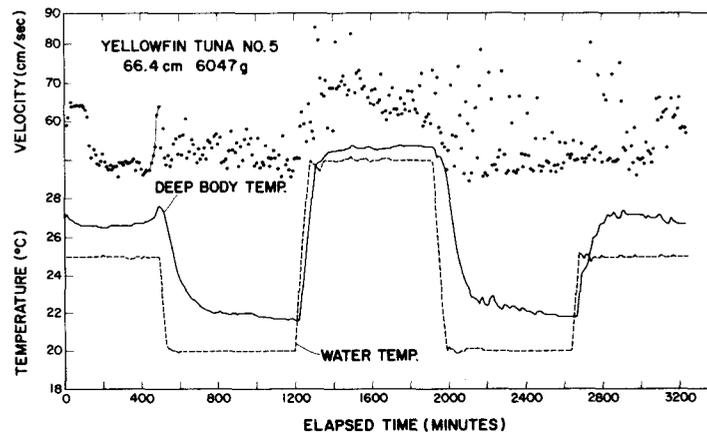


FIG. 2.—Time series of muscle temperature, water temperature, and swim speed of a yellowfin tuna

TABLE 1
SUMMARY OF EXPERIMENTAL RESULTS

FISH	FORK LENGTH (cm)	WEIGHT (g)	TEST TEMPERATURES (°C)					
			25	20	30	20	25	
Fish 1	45.9	1,853	55.00 ± 1.06	45.55 ± .36	65.61 ± 1.30	43.68 ± 1.16	50.47 ± 1.34	
Swim speed (cm s ⁻¹)	1.34 ± .03	1.07 ± .02	.94 ± .01	1.55 ± .05	1.24 ± .06	
Temperature excess (C)	2.72	2.53	2.98	2.50	2.61	
Estimated heat production (W)	47.8	2,219	67.88 ± 1.56	67.34 ± 1.27	84.82 ± 2.56	61.32 ± 1.77
Fish 2	47.8	2,219	67.88 ± 1.56	67.34 ± 1.27	84.82 ± 2.56	61.32 ± 1.77	73.70 ± 1.37	
Swim speed (cm s ⁻¹)	1.47 ± .02	1.28 ± .03	.62 ± .01	1.15 ± .04	1.48 ± .03	
Temperature excess (C)	3.40	3.43	4.04	3.22	3.63	
Estimated heat production (W)	45.5	2,677	51.70 ± 1.32	51.13 ± .28	77.48 ± 1.65	54.17 ± .21
Fish 3	45.5	2,677	51.70 ± 1.32	51.13 ± .28	77.48 ± 1.65	54.17 ± .21	55.10 ± 1.48	
Swim speed (cm s ⁻¹)	1.30 ± .09	1.38 ± .01	1.05 ± .04	1.24 ± .04	1.42 ± .04	
Temperature excess (C)	3.13	3.15	3.88	3.22	3.21	
Estimated heat production (W)	48.3	1,942	55.67 ± .89	46.54 ± 1.28	57.91 ± 2.72	...
Fish 4	48.3	1,942	55.67 ± .89	46.54 ± 1.28	57.91 ± 2.72	
Swim speed (cm s ⁻¹)	1.75 ± .05	1.43 ± .04	.90 ± .02	
Temperature excess (C)	2.84	2.64	2.86	
Estimated heat production (W)	66.4	6,047	52.38 ± 1.54	51.17 ± .96	66.89 ± 1.55	52.28 ± 2.24
Fish 5	66.4	6,047	52.38 ± 1.54	51.17 ± .96	66.89 ± 1.55	52.28 ± 2.24	57.79 ± 2.41	
Swim speed (cm s ⁻¹)	1.72 ± .06	1.87 ± .05	.63 ± .02	2.16 ± .09	1.85 ± .10	
Temperature excess (C)	5.07	5.07	5.70	5.11	5.30	
Estimated heat production (W)	45.0	1,491	67.52 ± .61	47.88 ± 1.81	61.52 ± 1.07	44.11 ± .76
Fish 6	45.0	1,491	67.52 ± .61	47.88 ± 1.81	61.52 ± 1.07	44.11 ± .76	49.72 ± 1.02	
Swim speed (cm s ⁻¹)99 ± .13	.27 ± .06	.64 ± .02	.43 ± .01	.76 ± .01	
Temperature excess (C)	2.82	2.32	2.59	2.24	2.34	
Estimated heat production (W)	53.0	2,237	67.08 ± 1.27	62.70 ± .77	43.16 ± .34	56.37 ± .53
Fish 7	53.0	2,237	67.08 ± 1.27	62.70 ± .77	43.16 ± .34	56.37 ± .53	58.35 ± 1.38	
Swim speed (cm s ⁻¹)64 ± .09	.54 ± .02	.51 ± .03	.74 ± .04	.76 ± .02	
Temperature excess (C)	3.91	3.66	3.14	3.44	3.56	
Estimated heat production (W)	65.0	3,797	42.83 ± .55	83.39 ± 4.13
Fish 8	65.0	3,797	42.83 ± .55	83.39 ± 4.13	
Swim speed (cm s ⁻¹)81 ± .02	.66 ± .04	
Temperature excess (C)	3.74	5.74	
Estimated heat production (W)	

NOTE.—95% confidence limits are provided for mean swim speeds and temperature excess. To insure the fish were in thermal steady state, mean excess temperatures are based on readings from the last 8 h of each test period. Heat production is estimated using biological parameters of swim speed, weight, length, and muscle efficiency as well as temperature-dependent properties of viscosity and density of the seawater.

30 C period, mean swim speed increased to 56.37 cm/s, and mean excess red-muscle temperature increased to 0.74 C.

From the data, it is clear that red-muscle temperature is not inexorably linked to swim speed (as suggested by Sharp and Vlymen 1978). Previous work with skipjack tuna under identical conditions demonstrated a similar independence, rather than a direct or inverse relationship, of muscle temperature and swim speed (Dizon, Brill, and Yuen 1978).

WHOLE-BODY THERMAL CONDUCTANCE

To quantify thermoregulatory ability, mammalian physiologists (e.g., Kleiber 1972) often employ an index of whole-body thermal conductance. The concept is based on the equation:

$$H_L = K \cdot (T_c - T_a) \quad (1)$$

where H_L = steady-state heat loss (i.e., T_c is not changing, therefore H_L must equal heat production) (W), T_c = the temperature of the isothermal core (C), T_a = ambient temperature (C), and K = whole-body thermal conductance (W/C). The K is a lumped parameter which reflects properties of both the animal and the environment (Strunk 1971, 1973; Tracy 1972). In an aquatic environment, heat transfer due to radiation and evaporation can be ignored (Erksine and Spotila 1977). Thermal conditions are, therefore, adequately defined by water temperature and the velocity of the animal relative to the water. In addition, since comparisons are made between temperature treatments, not fish, we are not concerned with the absolute value of K but, rather, with how this parameter varies with changes in T_a .

We measured steady-state red-muscle and water temperatures. Therefore, by estimating heat production, we can use

the concept of K (eq. [1]) to quantify the thermoregulatory ability of our yellowfin tuna. To estimate the heat production of the fish, we proceeded as follows: metabolic energy required for propulsion is related to swim velocity by the following fundamental equation (see Webb 1975; Sharp and Francis 1976; Ware 1978; Wu and Yates 1978 for a more detailed development):

$$\eta \cdot P_1 = 0.5 \rho \cdot V^3 \cdot S \cdot C_d \cdot 10^{-7}, \quad (2)$$

where P_1 = rate of free energy liberation by the swimming muscles (W); ρ = density of seawater (g/cm³); V = mean swim velocity (cm/s); S = surface area ($\sim 0.4 L^2$) (cm²); L = fork length (cm); C_d = coefficient of drag, a dimensionless number (this parameter takes into account the effect of temperature on seawater viscosity); and η = muscle efficiency, assumed equal to 0.20 (Webb 1975).

Brill (1979) determined the standard metabolic rate (i.e., metabolic rate associated with nonswimming physiological functions, such as osmoregulation and cardiac work) by measuring the oxygen consumption of skipjack tuna (at 24–26 C) with no overt muscular activity. The relationship, converted to power units, is:

$$P_2 = 1.53 W^{0.563}, \quad (3)$$

where P_2 = standard metabolic rate (W) and W = fish weight (kg).

Because no data for the yellowfin tuna standard metabolic rate are yet available, we assume this relationship to be a suitable approximation. Furthermore, we rejected use of a temperature correction to P_2 ; i.e., we assumed P_2 , the standard metabolic rate, to have a $Q_{10} = 1$. We realize that this is unlikely, but we have no data on the effect of temperature on tuna standard metabolic rate. Assuming that the $Q_{10} > 1$ results

in proportionally greater heat production at higher test temperatures and, consequently, higher estimated K . Use of a P_2 which is independent of temperature is conservative with respect to our hypothesis.

Heat production within the fish (H_p) can be estimated by adding the standard metabolic rate to the muscular heat production due to swimming. The latter quantity is determined by assuming the caudal propeller is 100% efficient and the swimming muscles 20% efficient (i.e., $\eta = 0.20$). The H_p is therefore approximated by the sum of the two power-producing processes, less the power dissipated as thrust:

$$H_p = P_2 + (1 - \eta)P_1. \quad (4)$$

We substituted estimated H_p (based on V), mean red-muscle temperature, and water temperature into equation (1). Results are presented in figure 3. In fish 1-5 and 8, increased thermal conductance was observed at the 30 C test temperature. This temperature is close to the upper limit of occurrence of the species (31 C [Blackburn 1965]). Also, for fish 1-5, K was reasonably constant at 20 and 25 C. Fish 6 and 7 showed no apparent pattern. These results indicate

that faster swimming (which must increase H_p) does not necessarily increase red-muscle temperature because some mechanism intervenes to alter the pattern of thermal transfer, which is reflected by changes in K .

DISCUSSION

We have no reliable method for experimental control of swim speed. Because the fish were swimming near their minimum hydrostatic equilibrium speeds (Magnuson 1973), excess red-muscle temperatures are low when compared with wild fish (Barrett and Hester 1964; Stevens and Fry 1971; Graham 1975). However, the differences in swim speeds and excess muscle temperatures between temperature treatments are statistically significant. Presumably, if our yellowfin tuna were forced to swim at elevated speeds, the reductions of the resultant higher excess muscle temperature would have been more dramatic as test temperatures rose. We have already shown this to occur in skipjack tuna, *Katsuwonus pelamis*, forced to maintain elevated swim speeds at 25 and 30 C (Dizon and Brill 1979).

At least four mechanisms could account for the apparent increase in K

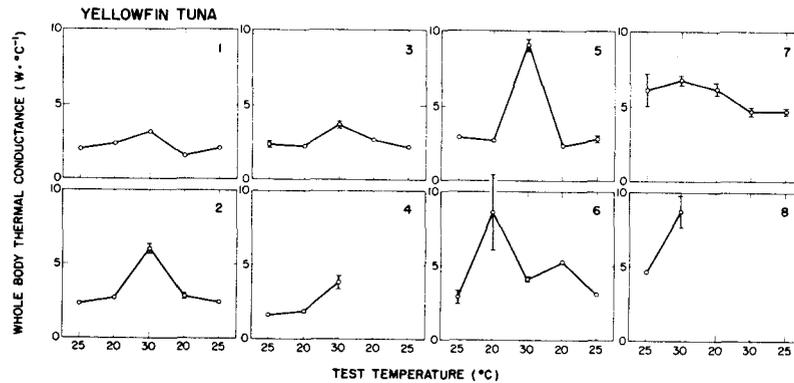


FIG. 3.—The effect of T_a on whole-body thermal conductance (K). The K was determined by dividing estimated heat production by excess muscle temperature (T_x). Vertical lines represent extreme values of K based upon the 95% confidence limits of mean swim speed and T_x .

that would not constitute physiological thermoregulation per se. Each is considered below and can be discounted.

1. Propulsive musculature of yellowfin tuna may be more thermally efficient (i.e., produce less heat per unit energy provided to the caudal propeller) at higher T_a 's. If so, we would be overestimating H_p at 30 C and inflating the value of K . Using fish 5 as an example, the following calculations show η would have to be unreasonably increased for the values of K determined at 25 and 30 C to be equal. Here we will even ignore the heat production from nonswimming physiological functions (SMR):

$$K = H_p \cdot T_x^{-1}, \quad (5)$$

$$H_p = (1 - \eta) \cdot P_1, \quad (6)$$

$$\therefore K = (1 - \eta) \cdot P_1 \cdot T_x^{-1}, \quad (7)$$

and

$$P_1 = (0.5 \cdot \rho \cdot V^3 \cdot S \cdot C_d \cdot 10^{-7}) \cdot \eta^{-1}. \quad (8)$$

Substituting equation (8) into (7) yields:

$$K = (1 - \eta) \cdot (0.5 \cdot \rho \cdot V^3 \cdot S \cdot C_d \cdot 10^{-7}) \cdot (\eta \cdot T_x)^{-1}. \quad (9)$$

Substituting the average velocity (66.89 cm s⁻¹) and excess muscle temperature (0.63 C) for yellowfin 5 at 30 C and the K value at 25 C (0.458 W C⁻¹, when the SMR is not included) into equation (9) shows η would have had to increase from 20% at 25 C to 55% at 30 C. This is unlikely, especially since the SMR contribution to H_p is considerable.

2. Any effects of seawater viscosity or density changes are taken into account in equation (2). The H_p would not be over- or underestimated due to temperature-induced changes in these parameters.

3. If the main resistance to heat flow occurred at the body surface-water interface, increased swim speed could

result in lower excess red-muscle temperature because a higher rate of water flow over the body surface would cause increased surface heat loss (Tracy 1972; Erskine and Spotila 1977; Brill, Guernsey, and Stevens 1978). In other words, increased swim speed would cause increased convective-enhanced surface conductance (Strunk 1973), and, at higher swim speeds, the requisite increase in heat loss could then be accomplished with a lower temperature driving gradient (i.e., lower excess red-muscle temperature).

However, as we have stated, H_p is roughly proportional to velocity cubed, whereas surface heat loss at best increases only as the square root of velocity (Erskine and Spotila 1977; Sharp and Vlymen 1978). Therefore, increased convective-enhanced surface conductance could not account for our data. If water velocity was the main determinant of K , a direct and nonlinear relationship between swim speed and excess muscle temperature would be predicted. We, however, observed a direct relationship in only one of eight fish.

Furthermore, a mathematical model developed by Sharp and Vlymen (1978) describing the relationship of excess muscle temperature and swim speed in yellowfin and skipjack tunas predicts that these fish will develop lethal muscle temperature at upper sustainable swim speeds unless the effectiveness of their thermoconserving mechanisms can be reduced.

4. Because increased swim speed requires increased cardiac output and the effectiveness of a countercurrent heat exchanger is inversely proportional to flow (Mitchell and Myers 1968), tuna then should show an inverse relationship between excess muscle temperatures and swim speeds. This concept does seem to fit some of our data (e.g., fish 4, 5, and

8) and, since no central nervous system (CNS)-mediated conductance changes are required, we may have no proof of activity-independent thermoregulation. However, the data presented here (see also Dizon et al. 1978; Dizon and Brill 1979) clearly show swim speed and excess red-muscle temperature have no fixed relationship, either direct or inverse.

POSSIBLE MECHANISMS OF PHYSIOLOGICAL
THERMOREGULATION

The lack of any predictable relationship between red-muscle temperature and swim speed strongly suggests that we are dealing with physiologically labile processes, presumably under CNS control. Tunas face two situations where changes in the patterns of heat transfer are required: (1) excess red-muscle temperatures must be reduced in response to increases in seawater temperatures; and (2) increased H_p , due to increased swim speed, must be effectively dissipated to prevent development of potentially lethal T_b 's. We hypothesize that these two exigencies could be met either with changes in circulatory patterns, alterations in the relative contributions of the red- and white-muscle fibers to propulsion, or both.

The second exigency, prevention of overheating during bouts of fast swimming, presents no conceptual problem if one discards the notion that the white muscle is only used at high unsustainable speeds (only used anaerobically). White muscle of skipjack tuna has the enzymatic capacity to function aerobically (Hochachka, French, and Guppy 1978) and apparently becomes active at sustainable swimming velocities (3–5 lengths/s, based on electromyographic evidence [Brill and Dizon, in preparation]). Other teleosts have also been shown to use white muscle at sustainable

swim speeds (Pritchard, Hunter, and Lasker 1971; Bone 1975). White muscle of *Thunnus* sp. is supplied by circulatory pathways which bypass the heat exchangers (Godsil and Byers 1944); therefore, metabolic heat generated aerobically by the white muscle is not retained but dissipated in the same manner as in nonthermoconserving fish, via the gills and the body surface (Stevens and Sutterlin 1976; Erskine and Spotila 1977).

Unless heat-exchanger efficiency could be reduced, the contribution of red muscle to propulsion would probably be limited to power-production levels which will not generate damaging temperatures. Small tunas do not appear to overheat; in tests of chased fish either carrying telemetry equipment or dragging thermistor wires, muscle temperatures were never observed above 32°C (Neill et al. 1976; Hulbert and Guppy, personal communication, 1978).

Control of excess muscle temperature extends beyond prevention of overheating; observations have been made here and in other reports (Barrett and Hester 1964; Carey and Teal 1969) that tunas reduce their muscle temperatures in response to increasing water temperatures (the first exigency). We imagine two mechanisms that the fish might employ. (1) Modification of the circulatory pattern in the central or lateral heat exchangers may reduce their effectiveness as thermal barriers. Changes in water temperature and activity levels have been shown to affect teleost cardiovascular dynamics by simultaneously increasing the level of vagal activity and circulating catecholamines (Randall 1970; Stevens et al. 1972; Watters and Smith 1973). Furthermore, Stevens et al. (1974) show the arterial vessels of the central heat exchanger in skipjack tuna have thick walls containing smooth muscle. If moderate in-

creases in T_a or swim speed cause a sympathetically controlled release of catecholamines, change in vagal activity, or both, a modification of the circulatory pattern within the central or lateral heat exchangers could result, diminishing their effectiveness. (2) The relative contribution of red and white muscle to propulsion at slow speeds might be under the control of the thermoregulatory center. At high T_a 's white muscle, which does not contribute to the temperature burden, may become active at slower swim speeds than it would at low T_a 's.

The former thermoregulatory mechanism would presumably be more important in skipjack tuna and kawakawa, *Euthynnus affinis*, because, in these species, the lateral cutaneous blood vessels are much smaller than the dorsal aorta and postcardinal vein. Unless the lateral cutaneous vessels are extremely distensible, it is unlikely that they could carry enough blood to the segmental vessels to maintain a significant level of aerobic metabolism in the white muscle.

SUMMARY

Tunas have developed a degree of independence between red-muscle temperature and swim speed even though H_p is inexorably linked to the latter. We have observed this independence in yellowfin tuna (this report) and skipjack tuna (Dizon et al. 1978). Furthermore, six of the eight yellowfin tuna used in this study showed significantly lower excess muscle temperatures at 30 C than at 20 or 25 C, although their mean swim speeds were significantly increased at the higher T_a .

Data exist demonstrating that white muscle has significant aerobic enzymatic capacity (Hochachka et al. 1978), is used at apparently sustainable swim speeds (Brill and Dizon, in preparation), and has a circulatory system which bypasses the vascular countercurrent heat exchangers (at least in *Thunnus* sp. [Godsil and Byers 1944]). Excess muscle temperatures observed in tuna must be wholly due to heat produced and retained in the red muscle. Here, heat dissipation is limited by its internal position, surrounded by white-muscle fibers and by the five vascular heat exchangers interposed in the circulatory system serving the red-muscle fibers. Based on a mathematical model of H_p and surface heat dissipation in skipjack and yellowfin tunas (Sharp and Vlymen 1978), we hypothesize that, at sustained elevated swim speeds (3-6 body length s^{-1}), red-muscle fibers must contribute a relatively small fraction of the necessary power; otherwise, overheating could result.

Tunas therefore face two exigencies that require adjustment of their thermoconserving mechanisms. One, excess muscle temperature must be reduced at T_a 's near lethal limits. Two, the fraction of metabolic H_p lost via the gills must be significantly increased at the higher sustainable swim speeds. We suggest that tuna meet these two thermoregulatory exigencies either by: (1) using their white-muscle fibers at upper sustainable swim speeds and at low swim speeds when T_a 's approach lethal limits; or (2) using cardiovascular alterations that diminish or enhance their vascular heat exchanger's effectiveness; or both.

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