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Thermoregulation in Tunas

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SYNOPSIS. Because tunas possess countercurrent vascular pathways serving the trunk musculature, metabolic heat is retained, and muscle temperatures can considerably exceed that of the surrounding water (+1° to +21°C). And because tunas have this excess, it is reasonable to suppose they have some means of controlling its magnitude. Tunas must contend with two exigencies which can perturb body temperature: changes in water temperature and, in contrast to non-thermoconserving fish, changes in activity. Both can be met by adaptive change in excess muscle temperature. If this could be accomplished in the absence of changes in environmental temperature or activity level, this would constitute physiological thermoregulation. If excess muscle temperature cannot be altered sufficiently to acceptable levels, more favorable environmental temperatures must be sought or activity levels changed. We would consider this behavioral thermoregulation. High sustained swim speeds, characteristic of the continuously swimming tunas, require special consideration. Heat production is proportional to approximately the cube of swim speed. In order to maintain a slight temperature excess at basal swim speeds (1-2 lengths/sec), and yet not overheat during sustained high speed swimming (>4 lengths/sec), mechanisms are required to conserve heat under the former conditions and to dissipate it effectively under the latter. In this report, we review published observations other investigators have interpreted as physiological thermoregulation in tunas, describe recent findings in our laboratory, and suggest some possible thermoregulatory mechanisms.

INTRODUCTION

Tunas cannot be strictly classified as either poikilotherms or homeotherms. They are "thermoconserving" fish which can maintain muscle temperatures (T_b) several degrees above ambient (T_a). The thermoconserving mechanism, the countercurrent rete in the vascular system serving the trunk musculature (reviewed recently by Stevens and Neill, 1978), taxonomically distinguishes the 13 species of true tunas (tribe Thunnini) from other members of the family Scombridae, *e.g.*, the bonitos, seerfishes, and mackerels (Klawe, 1977; Collette, 1978). All true tunas have heat exchangers and all get hot (Carey *et al.*, 1971). There are seven species within the genus *Thunnus*, three in *Euthynnus*, two in *Auxis*, and one monotypic genus, *Katsuwonus*. As adults, the *Thunnus* spp. and *Katsuwonus pelamis* are pelagic fish that are distributed more or less continuously across the oceans; the others seldom occur more than a few hundred miles from land (Blackburn, 1965).

Because of the countercurrent rete, metabolic heat is retained and muscle temperatures range from 1° to 21°C above ambient (Barrett and Hester, 1964; Carey *et al.*, 1971; Stevens and Fry, 1971;

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Graham, 1975; Dizon *et al.*, 1978; Stevens and Neill, 1978). Because tunas are fast, continuous swimmers, and are the most highly adapted members of their family for life in the resource-poor pelagic oceans (Magnuson, 1973, 1978), elevated muscle temperatures have been hypothesized to increase muscle power (Carey *et al.*, 1971), maximum swim speed (Graham, 1975), thermal inertia (Neill and Stevens, 1974; Neill *et al.*, 1976), maximum sustained swim speed (George and Stevens, 1978), and muscle efficiency, *i.e.*, getting more kilometers per calorie. Stevens and Neill (1978) have outlined the arguments suggested above.

Aside from the fact of warm-bodiedness, investigators do not agree on why tunas maintain an excess muscle temperature (T_x, where: $T_x = T_b - T_a$) or if they can control T_x in response to thermoregulatory needs. For the purpose of this essay, we will assume that it is of significant benefit to maintain muscle temperatures above ambient. We will, however, establish that 1) control of T_x is demonstrable in at least 2 of the 13 species of tunas, 2) because of the fast sustained swim speeds in tunas, control is theoretically necessary, and 3) physiological control is possible.

THERMOREGULATORY OPTIONS FOR TUNAS

Before proceeding, we wish to clarify how we conceptualize the process of thermoregulation in tunas; we intend it to do no more than facilitate subsequent discussion. We define thermoregulatory options open to tunas as follows:

Behavioral thermoregulation

We subdivide behavioral thermoregulation into two types: a) by environmental selection (Reynolds, 1977), and b) by control of activity-dependent heat production. The first subdivision is open to all fish living in heterothermal environments. We know tunas have sensors to perceive ambient temperature changes (Dizon *et al.*, 1974, 1976; Steffel *et al.*, 1976), and they are mobile and live in a heterothermal environment. Their ranges, except for bluefin tuna (*Thunnus thynnus*), are narrowly circumscribed by temperature. Bluefin tuna have been observed in waters where surface temperatures range from 6° to 30°C (Carey and Teal, 1969; Sharp, 1978) but commercial concentrations occur between 14° and 21°C (Laevastu and Rosa, 1963). Like bluefin tuna, albacore (*T. alalunga*) are considered a temperate species and are found in fishable concentrations between 16° and 19°C (Laurs and Lynn, 1977). Tropical yellowfin tuna (*T. albacares*) are fished between 23° and 32°C (Sharp, 1978) and skipjack tuna (*Katsuwonus pelamis*), the other so-called tropical tuna, are fished between 19° and 23°C but observed between 17° and 28°C (Laevastu and Rosa, 1963). Little is known about the other less commercially important species. If these data, based on sea-surface temperatures, reflect actual temperature preference, tunas can behaviorally thermoregulate.

Because tunas are thermoconserving fish, they have a behavioral thermoregulatory option not open to other teleosts. They can presumably alter heat production simply by altering their activity levels. Approximately 80% of the free energy liberated by the propulsive musculature appears as heat (Webb, 1975). Heat production is related to approximately the cube of swim velocity (a fundamental relationship; see collected papers in Wu *et al.*, 1975). T_b is a function of heat production and heat dissipation. Alterations of T_b by changes of activity-related heat production would represent the second type of behavioral thermoregulation.

Passive thermoregulation

Here, we include any process that tends to stabilize T_b and which requires no CNS intervention:

a) Water temperature-related and swim velocity-related heat production. Temperature changes affect the viscosity and density of seawater and therefore alter the energetic requirements of a swimming animal (Ware, 1978). Also, as velocity increases, the coefficient of drag decreases slightly; some energy is saved here (Webb, 1975). Although the effects of temperature, swim speed, viscosity, and density are somewhat compensatory in terms of drag and, thus, heat production, their effects cannot be ignored and must be taken into account in any heat production-dissipation models. Otherwise these effects, in concert with others, could be responsible for observed thermoregulatory ability of tunas.

b) Thermal inertia. Thermal inertia may explain the observed stability of muscle and stomach temperatures in the giant bluefin tuna (Carey *et al.*, 1971; Carey and Lawson, 1973). Because of the countercurrent heat exchangers possessed by tunas, heat is exchanged with the environment at a much reduced rate when compared with other similar-sized teleosts (Neill and Stevens, 1974). Therefore, T_b can lag significantly behind abrupt changes in T_a. Neill and his colleagues (Neill and Stevens, 1974; Neill *et al.*, 1976) have quantified these effects.

c) Swim velocity-related heat dissipation. Under specified circumstances swim speed changes alter surface heat dissipation rate (Tracy, 1972; Erskine and Spotila, 1977; Brill *et al.*, 1978). Increased velocity can cause increased body surface heat loss (mathematical relationship generated for tunas by Sharp and Vlymen, 1978). Later we will discuss whether this increased convective-enhanced surface conductance (Strunk, 1973) could compensate for increased heat production in tunas.

The effectiveness of countercurrent heat exchangers are dependent upon length of the channels, velocity of the fluids within the channels, and the thermal transfer characteristics of the fluids and the channel walls (Mitchell and Myers, 1968). Because the effectiveness of tuna's vascular countercurrent system is inversely related to blood flow, increases in cardiac output, required by increases in swim velocity, could decrease the heat exchanger's effectiveness so that increased heat production could be dissipated without appreciably increasing T_x. Carey and Teal (1969) observed that violent struggles of fish caught on hook and line do indeed reduce, rather than increase, T_b of large bluefin tuna.

Physiological thermoregulation

Here, we wish to be more restrictive in our definition. Activity-independent (*i.e.*, physiological) thermoregulation requires that the CNS has the ability to alter the effectiveness of the thermoconserving mechanisms. Presumably, these changes are mediated by a thermoregulatory center homologous to that in the anterior forebrain of birds and mammals (Crawshaw, 1977; Kluger, 1978). Proof of physiological thermoregulation will be alterations in T_x independent of or opposite to activity-related changes in heat production, when passive thermoregulatory effects are discounted. The remainder of the essay will deal with this topic.

Although our definition of physiological thermoregulation focuses on CNS-mediated changes in heat dissipation, biochemical control of heat production may exist. However, our data only allows us to distinguish behavioral from physiological thermoregulation, not physiological from biochemical. In addition, use of basic hydrodynamic principles allows us to distinguish physiological thermoregulation from what we term passive thermoregulation. Investigation into biochemical solutions by tunas to acute or chronic temperature challenges have yet to be initiated.

FIELD EVIDENCE FOR TUNA THERMOREGULATION

Can field evidence be used to demonstrate thermoregulatory abilities of tuna? If so, what types? Presumably, if T_b's were relatively constant and independent of T_a, considerable thermoregulatory ability could be assumed (Bligh and Johnson, 1973).

Figure 1 summarizes the existing field observations concerning the abilities of tunas to defend a relatively fixed T_b. Barrett and Hester (1964) determined the following linear least squares regression relationships between muscle temperatures and sea-surface temperatures for skipjack and yellowfin tunas:

$T_b = 0.81\ T_a + 7.47$ (yellowfin tuna) and
$T_b = 0.58\ T_a + 16.39$ (skipjack tuna).

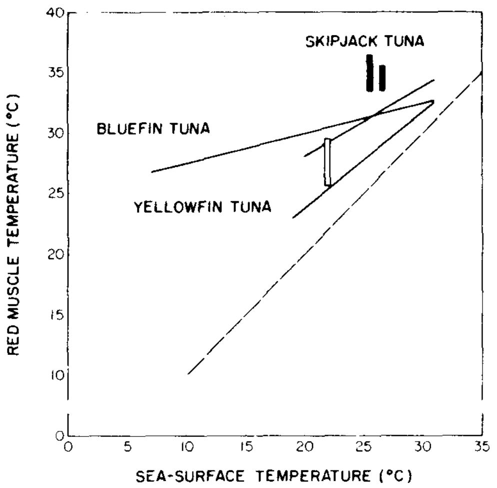

FIG. 1. Linear regression of red muscle temperature (T_b) on sea-surface temperature for skipjack and yellowfin tunas (SJ and YF, respectively, from Barrett and Hester, 1964) and bluefin tuna (BF, from Carey and Teal, 1969). Solid bars are ranges of red muscle temperatures from skipjack tuna (from Stevens and Fry, 1971—right-hand bar from 9 fish averaging 73.5 cm FL, left-hand bar from 20 fish averaging 44.5 cm FL). Open bar is range of red muscle temperatures from skipjack tuna (from Carey and Teal, 1969).

The results were significantly different in slope and level. Over the range tested, size was an unimportant determinant of body temperature in yellowfin tuna. However, larger skipjack tuna tended to be slightly warmer:

$$T_b = 0.59\,T_a + 0.015\,L + 8.63$$

where L = fork length, mm.

The slopes were significantly different from unity, therefore fish from cooler waters tended to have greater T_x's, a first indication of a thermoregulatory response.

By the test of "slope," (Fig. 1) bluefin tuna are quite adept at temperature regulation (Carey and Teal, 1969):

$$T_b = 0.25\,T_a + 24.94.$$

Bluefin tuna apparently maintain greater independence of T_b from T_a and are also relatively warmer than either skipjack or yellowfin tunas (at least at the center of their ambient temperature range. Their T_b's varied only 5°C over a range of sea-surface temperature from 7° to 30°C. The greatest T_x observed was 21.5°C in areas of 7.3°C surface-water temperature.

At least for skipjack tuna, the regression relationship presented by Barrett and Hester (1964) is confounded by additional information from Carey and Teal (1969) and Stevens and Fry (1971). The former observed excess muscle temperatures below (Fig. 1, open bar) and the latter, above (Fig. 1, solid bars) values predicted by Barrett and Hester (1964). The excess red muscle temperatures observed by Stevens and Fry (1971) are almost double those observed by Barrett and Hester (1964) although the fish were taken from areas with the same surface-water temperatures; thus it appears that body temperatures of tunas, at least skipjack, are quite labile.

Nevertheless, as a result of their own and Barrett and Hester's (1964) observations, Carey and Teal (1969) concluded that bluefin tuna were more adept at temperature control than skipjack or yellowfin tunas. Stevens and Fry (1971) concluded that skipjack tuna could also maintain a fixed T_b in waters of 25° to 34°C. Carey and Teal (1969, p. 212) implied that a physiological thermoregulatory mechanism might be employed by the bluefin tuna: "Modifications of the rete under the fish's (bluefin tuna) control maintain temperatures at a constant level." Stevens and Fry (1971) simply state that skipjack tuna regulate muscle temperature; they do not suggest a mechanism.

However, does this field data justify the conclusion that tunas control their muscle temperatures? We do not think so. Evidence from just captured fish is difficult to interpret because:

1) The fish have experienced an unknown thermal history. The open ocean is a heterothermal environment. Very cool water is available at depths easily reached by tunas because all but the largest species lack swim bladders, or have swim bladders which are reduced in size or atrophied (Godsil and Byers, 1944; Gibbs and Collette, 1971). Dizon *et al.* (1978) show that extensive vertical migrations (surface to 273 m) are continuous features of the day-

light activity pattern of skipjack tuna (70 cm), in areas where T_a ranged from 25°C at the surface to less than 12°C at 270 m depth. Because all tunas possess a degree of thermal inertia, their characteristic T_b would be a function of the sequence of ambient temperatures experienced prior to capture, and not just the sea-surface temperature used by Barrett and Hester (1964), Carey and Teal (1969), and Stevens and Fry (1971). Looking for thermoregulatory ability by relating T_b to T_a is meaningful only if T_a has been constant long enough for the fish to reach thermal steady state (Neill and Stevens 1974; Neill *et al.*, 1976). This time period is size-related, and is thus especially important for larger tuna.

2) As described earlier, there is a fundamental relationship between activity and heat production, but field evidence is contradictory on the effect of activity on T_b. Carey and Teal (1966) show that "lively" bigeye tuna (*Thunnus obesus*) have higher body temperatures than "weak" ones. Also, Stevens and Fry (1971) unequivocally demonstrate that skipjack tuna T_x's increase by one-third when strenuously exercised, but Carey and Teal (1969) show that hook-and-line caught fish have lower muscle temperatures than trap-caught ones. Even though hook-and-line fish presumably have fought harder and longer than trap-caught fish, they are cooler.

3) Perhaps, fish measured at different surface-water temperatures, in widely divergent geographical areas, are members of different stocks (Sharp, 1978). T_x differences might result from acclimation processes spanning days to generations (Hazel and Prosser, 1974).

To alleviate uncertainties outlined above, Carey and Lawson (1973) proposed an experiment involving long-term monitoring of T_b in response to controlled changes in T_a. They designed a field experiment using the naturally occurring heterothermal conditions around Nova Scotia, the northernmost range of giant bluefin tuna. Ultrasonic transmitters were used to simultaneously monitor stomach or muscle temperature and water temperature. (Heat exchangers also service the visceral structures of the more phylogenetically advanced bluefin tuna group, *cf.*, Kishinouye, 1923; Godsil and Byers, 1944; Gibbs and Collette, 1967.)

Transmitters were placed on 14 bluefin tuna. Because several fish exhibited muscle and stomach temperatures that were independent of T_a's, Carey and Lawson (1973) concluded that bluefin tuna can thermoregulate in the mammalian sense (*i.e.*, maintain relatively constant body temperatures even though subjected to prolonged changes in T_a) by altering the effectiveness of their vascular heat exchange system.

There is, however, an alternate explanation. Using a purely empirical approach, Neill and Stevens (1974) successfully mathematically modeled the bluefin tuna telemetry data assuming a constant rate of heat dissipation and heat production (Fig. 2). No physiological thermoregulatory mechanisms dependent upon T_a were postulated, and yet the model could explain the observed muscle and stomach temperature stability observed by Carey and Lawson (1973).

Although the Neill and Stevens' (1974) analysis does not prove or disprove the possibility that bluefin tuna are capable of rapid physiological thermoregulation, thermal inertia (passive thermoregulation) of these large tunas may well have accounted for the observed stability of T_b.

LABORATORY EVIDENCE FOR TUNA THERMOREGULATION

To differentiate between behavioral, passive, or physiological thermoregulation requires an experiment that monitors activity levels at constant T_a for long periods of time. We designed equipment to control T_a precisely in a tank sufficiently large to accommodate small yellowfin and skipjack tunas, which are routinely maintained in captivity at the Kewalo Research Facility in Honolulu (Nakamura, 1972). To monitor muscle temperature, we employed a small, ultrasonic transmitter (Fig. 3; Rochelle and Coutant, 1974). A photocell system monitored activity, and T_a was generally maintained within 0.05°C in the annular-shaped test tank (6.1 m major diam × 5.3 m minor diam × 0.6 m deep, Fig. 3).

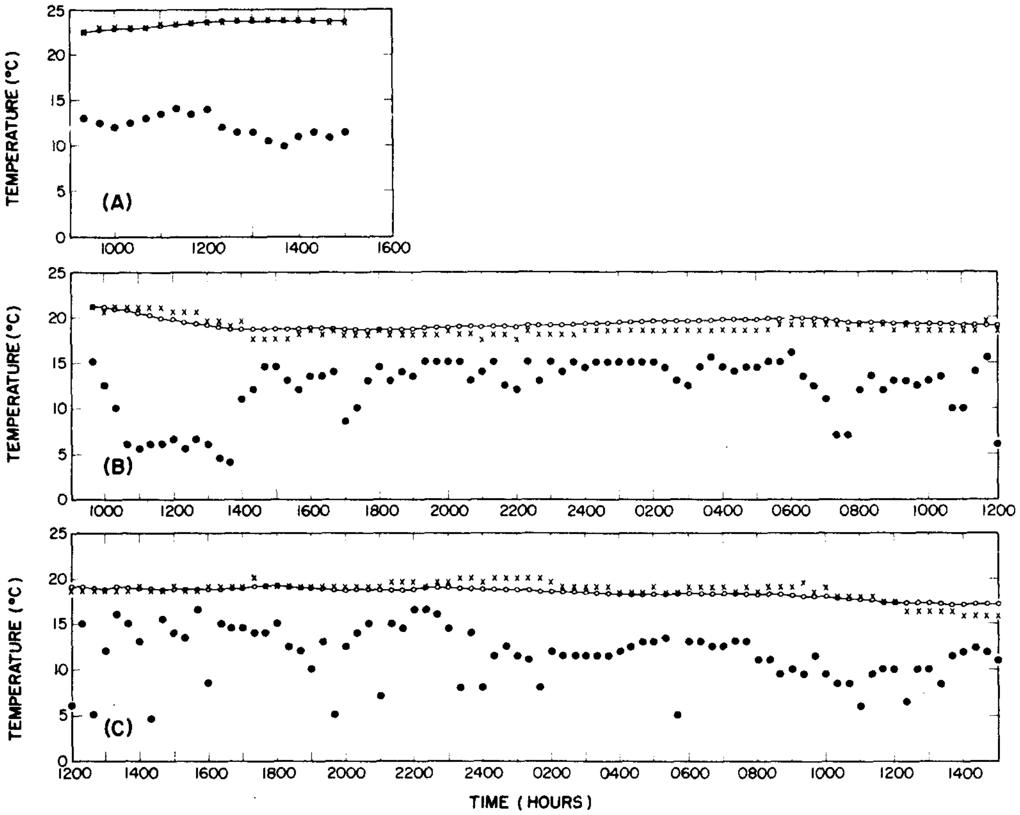

FIG. 2. Actual T_b (x) and modeled T_b (o) of two free-swimming bluefin tuna (Carey and Lawson, 1973) encountering abrupt changes in T_a (●) (from Neill and Stevens, 1974). No assumption of physiological thermoregulation is used in constructing the model, yet the fit is remarkably good. Panel A shows muscle temperatures from bluefin tuna No. 8, B and C show temperatures from bluefin tuna No. 14.

Nine skipjack tuna (SJ 1-9) were individually subjected to consecutive temperature treatments: 4-8 hr at 25°C, 12 hr at 20°C, 12 hr at 30°C, 12 hr at 20°C, and 12 hr at 25°C (Table 1). Six yellowfin tuna (YF 1-6) were subjected to consecutive 12-hr temperature treatments: 25°, 20°, 30°C, 20°C, and 25°C (Table 2). Six other yellowfin tuna (YF 6-12) were subjected to an altered sequence of 12-hr temperature treatments: 25°, 30°, and 25°C (Table 2). To eliminate any effects of thermal inertia, we analyzed only data collected after T_b stabilized following ambient temperature changes. Some sets of data are incomplete because the fish died prematurely or because it would not swim complete laps which are required for the logic equipment to translate position information from the photocells into swim speed.

Does a simple plot of T_b versus T_a reveal if yellowfin and skipjack tunas are compensating for increasing T_a by reducing T_x, as bluefin tuna seem to do (Carey and Teal, 1969; Carey *et al.*, 1971)? That is, are the slopes of the regression of T_b on T_a significantly different from one? No such compensations occurred (Fig. 4); T_x was independent of T_a. The regression relationships are:

$T_b = 2.12 + 0.95\,T_a$ (yellowfin tuna)
$T_b = 3.14 + 0.97\,T_a$ (skipjack tuna)

T_b is clearly highly dependent on T_a and skipjack tuna are warmer than yellowfin tuna. At 25°C, the fish in our experiments are 1.5°C cooler than those measured by Barrett and Hester (1964) (27.7°C com-

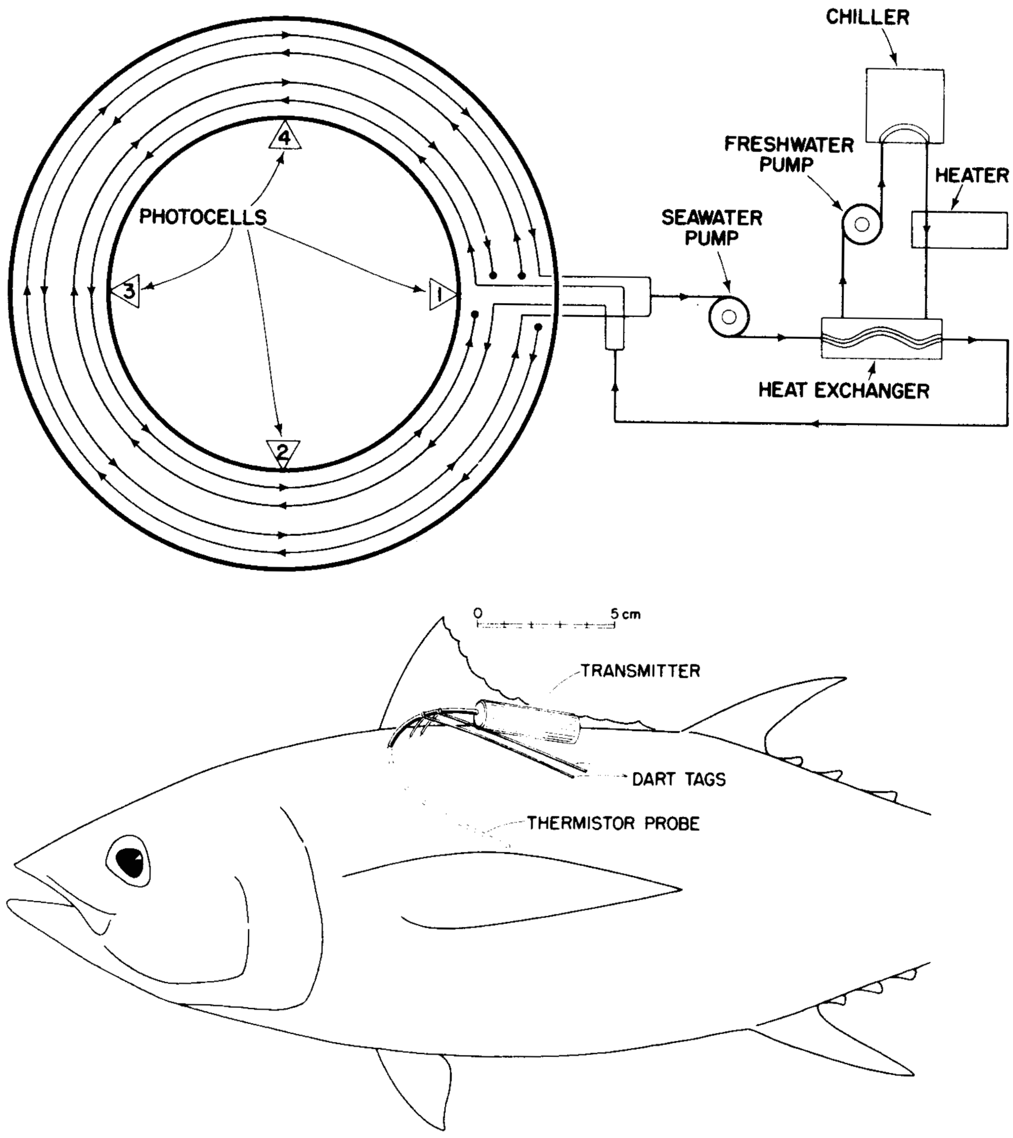

FIG. 3. Schematic diagram of the annular test tank system and of deployment of temperature-sensitive ultrasonic transmitter on a yellowfin tuna. Seawater is delivered to and removed from the swim channel through countercurrent perforated pipes, so that longitudinal temperature gradients do not develop.

pared to 26.2°C for the yellowfin tuna and 30.9°C compared to 27.2°C for skipjack tuna), probably reflecting the higher states of activity prior to capture of the wild fish. The differences in slope (0.98 *vs.* 0.81 and 0.95 *vs.* 0.58, respectively) are perhaps due either to the unknown past thermal and activity histories, or to long-term acclimatory adjustments of the fish caught by Barrett and Hester (1964).

The T_x of skipjack tuna exceed those of yellowfin tuna (Tables 1 and 2), but we do not know whether this is due to activity differences or heat exchanger efficiency differences. To resolve this, heat production (Fig. 5, estimated by the following proce-

TABLE 1. *Grand mean swim speeds and T_x's (±95% confidence limits) for skipjack tuna.*[a]

	Fork length *(cm)*	Weight *(g)*	Test temperatures (C)				
			25°	20°	30°	20°	25°
Skipjack tuna 1	43.3	1,343					
Swim speed (cm/sec)			77.82±4.77	64.31±1.24	93.09±2.22	—	—
Temperature excess (°C)			3.11±0.14	3.06±0.06	3.59±0.08	—	—
Estimated heat production (watts)			3.02	2.60	3.59	—	—
Skipjack tuna 2	46.5	1,673					
Swim speed (cm/sec)			75.29±1.62	68.06±0.55	76.54±1.71	67.60±3.35	—
Temperature excess (°C)			2.44±0.25	2.02±0.04	1.62±0.07	2.60±0.10	—
Estimated heat production (watts)			3.29	3.07	3.26	3.05	—
Skipjack tuna 3	46.1	1,758					
Swim speed (cm/sec)			61.47±0.99	44.24±1.77	62.43±0.86	62.97±2.98	72.16±0.68
Temperature excess (°C)			1.97±0.10	3.13±0.07	1.71±0.02	2.40±0.14	1.86±0.09
Estimated heat production (watts)			2.84	2.45	2.82	2.93	3.21
[b]***Skipjack tuna 4***	46.3	1,826					
Swim speed (cm/sec)			75.70±1.01	68.43±0.73	75.91±1.80	—	68.60±1.19
Temperature excess (°C)			1.37±0.10	1.17±0.03	1.44±0.04	—	1.47±0.04
Estimated heat production (watts)			3.40	3.18	3.33	—	3.13
[b]***Skipjack tuna 5***	47.6	1,918					
Swim speed (cm/sec)			67.76±1.04	68.43±1.09	81.48±0.99	68.94±1.10	72.54±1.41
Temperature excess (°C)			1.27±0.03	1.30±0.03	1.52±0.08	1.55±0.03	1.55±0.04
Estimated heat production (watts)			3.20	3.28	3.68	3.30	3.38
Skipjack tuna 6	43.4	1,154					
Swim speed (cm/sec)			79.84±3.54	74.85±2.38	—	—	—
Temperature excess (°C)			1.84±0.16	3.31±0.09	—	—	—
Estimated heat production (watts)			2.96	2.83	—	—	—
Skipjack tuna 7	48.6	1,708					
Swim speed (cm/sec)			87.37±2.45	77.82±0.61	75.51±1.36	60.79±3.75	—
Temperature excess (°C)			1.77±0.08	1.45±0.01	2.26±0.14	2.83±0.17	—
Estimated heat production (watts)			4.00	3.60	3.33	2.89	—
Skipjack tuna 8	47.9	1,640					
Swim speed (cm/sec)			61.83±1.54	57.82±3.05	—	—	—
Temperature excess (°C)			1.98±0.04	1.68±0.09	—	—	—
Estimated heat production (watts)			2.82	2.73	—	—	—
Skipjack tuna 9	45.4	1,405					
Swim speed (cm/sec)			59.11±1.20	58.61±0.51	63.08±1.17	54.08±0.57	—
Temperature excess (°C)			3.81±0.08	3.61±0.07	2.90±0.08	2.93±0.10	—
Estimated heat production (watts)			2.51	2.53	2.58	2.41	—

[a] Heat production is based on swim speed, muscle efficiency, and standard metabolic rate.

[b] SJ 4 and 5 had the thermistor probe in their white muscle.

TABLE 2. *Grand mean swim speeds and T_x's (±95% confidence limits) for yellowfin tuna.*[a]

	Fork length (cm)	Weight (g)	Test temperatures (C)				
			25°	20°	30°	20°	25°
Yellowfin tuna 1	45.9	1,853					
Swim speed (cm/sec)			55.00±1.06	45.55±0.36	65.61±1.30	43.68±1.16	50.47±1.34
Temperature excess (°C)			1.34±0.03	1.07±0.02	0.94±0.01	1.55±0.05	1.24±0.06
Estimated heat production (watts)			2.72	2.53	2.98	2.50	2.61
Yellowfin tuna 2	47.8	2,219					
Swim speed (cm/sec)			67.88±1.56	67.34±1.27	84.82±2.56	61.32±1.77	73.70±1.37
Temperature excess (°C)			1.47±0.02	1.28±0.03	0.62±0.01	1.15±0.04	1.48±0.03
Estimated heat production (watts)			3.40	3.43	4.04	3.22	3.63
Yellowfin tuna 3	45.5	2,677					
Swim speed (cm/sec)			51.70±1.32	51.13±0.28	77.48±1.65	54.17±0.21	55.10±1.48
Temperature excess (°C)			1.30±0.09	1.38±0.01	1.05±0.04	1.24±0.04	1.42±0.04
Estimated heat production (watts)			3.13	3.15	3.88	3.22	3.21
Yellowfin tuna 4	48.3	1,942					
Swim speed (cm/sec)			55.67±0.89	46.54±1.28	57.91±2.72	—	—
Temperature excess (°C)			1.75±0.05	1.43±0.04	0.90±0.02	—	—
Estimated heat production (watts)			2.84	2.64	2.86	—	—
Yellowfin tuna 5	66.4	6,035					
Swim speed (cm/sec)			52.38±1.54	51.17±0.96	66.89±1.55	52.28±2.24	57.79±2.41
Temperature excess (°C)			1.72±0.06	1.87±0.05	0.63±0.02	2.16±0.09	1.85±0.10
Estimated heat production (watts)			5.07	5.07	5.70	5.11	5.30
Yellowfin tuna 6	45.0	1,491					
Swim speed (cm/sec)			67.52±0.61	47.88±1.81	61.52±1.07	44.11±0.76	49.72±1.02
Temperature excess (°C)			0.99±0.13	0.27±0.06	0.64±0.02	0.43±0.01	0.76±0.01
Estimated heat production (watts)			2.82	2.32	2.59	2.24	2.34

			Test temperatures (C)				
			25°	30°	20°	30°	25°
Yellowfin tuna 7	54.5	2,784					
Swim speed (cm/sec)			67.08±1.27	62.70±0.77	43.16±0.34	56.37±0.53	58.35±1.38
Temperature excess (°C)			0.64±0.09	0.54±0.02	0.51±0.03	0.74±0.04	0.76±0.02
Estimated heat production (watts)			3.91	3.66	3.14	3.44	3.56
Yellowfin tuna 8	65.0	3,797					
Swim speed (cm/sec)			42.83±0.55	83.39±4.13	—	—	—
Temperature excess (°C)			0.81±0.02	0.66±0.04	—	—	—
Estimated heat production (watts)			3.74	5.74	—	—	—

[a] Heat production is based on swim speed, muscle efficiency, and standard metabolic rate.

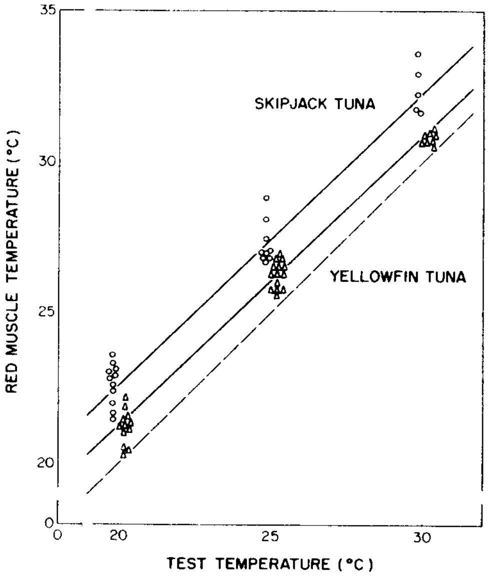

FIG. 4. Linear regression of red muscle temperature (T_b) on ambient temperature (T_a). Relationships are: $T_b = 2.12 + 0.95\ T_a$ (yellowfin tuna) and $T_b = 3.14 + 0.97\ T_a$ (skipjack tuna). The dotted line is $T_b = T_a$.

dures, see also Webb, 1975; Sharp and Francis, 1976; Sharp and Vlymen, 1978; Ware, 1978; and Wu and Yates, 1978) was used as a covariate because it accounts for swim velocity, fish size, and the temperature-dependent properties (viscosity and density) of seawater.

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

where

P_1 = input metabolic power to the swimming muscles (watts)

η = muscle efficiency, in this instance the efficiency of converting chemical energy into propulsive power (dimensionless), ~0.2 (Brown and Muir, 1970; Webb, 1975). Note, the caudal fin is assumed to be 100% efficient;

ρ = seawater density (g/cm) a temperature-dependent parameter;

V = swim velocity (cm/sec);

S = surface area, which is approximately equal to 0.4 L^2 where L is fork length in centimeters (Webb, 1975);

C_d = drag coefficient (dimensionless), a temperature, velocity, and length dependent empirical constant equal to:

$$C_d \cong 10\ R_L^{-0.5} \quad (2)$$

where

$R_L = \rho \cdot V \cdot L \cdot \mu^{-1}$ (3)

R_L = Reynolds number

μ = seawater viscosity (poise), a temperature-dependent property.

Brill (1979) estimated standard metabolic rate (SMR) for skipjack tuna as:

$$P_2 = 1.53\ W^{0.563}, \quad (4)$$

where

P_2 = SMR (watts),

W = weight (Kg).

We hope this is similar for yellowfin tuna.

Heat production within the muscle of the fish is assumed to be approximately equal to P_1 (the input metabolic power)

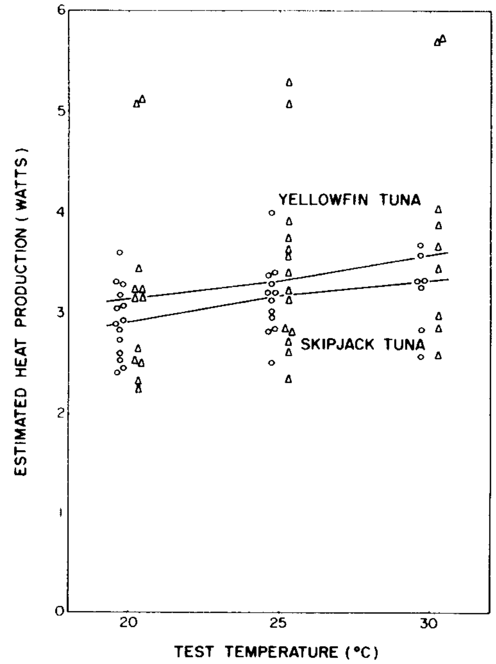

FIG. 5. Estimated heat production (based on swim speed, muscle efficiency, and standard metabolic rate) at each test temperature. The lines are drawn through the median heat production estimates. ○—skipjack tuna, △—yellowfin tuna.

minus the output power dissipated as thrust, plus P_2 (the SMR),

$$H_p = (1 - \eta) P_1 + P_2 \qquad (5)$$

It thus appears (Fig. 5), that although the T_x values of skipjack tuna are above those of yellowfin tuna, heat production in yellowfin tuna is generally higher. For both fish, heat production increases with T_a.

Yet, here we have a contradiction. Figure 4 indicates no thermoregulatory ability, T_x remains virtually constant over the 10° range of test temperatures. Because heat production also increases at 30°C (especially in yellowfin tuna, Fig. 5), heat dissipation rate per degree of driving gradient must be greater at higher test temperatures. The ability to maintain a constant T_x at various levels of heat production suggests that heat dissipation per degree of driving gradient is variable, and possibly controllable.

Mammalian physiologists (Kleiber, 1972) often employ an index of whole-body thermal conductance to quantify thermoregulatory ability:

$$H_L = K \cdot (T_b - T_a), \qquad (6)$$

where

H_L = steady state heat loss (T_b is not changing, therefore $H_L = H_P$) (watts), and

K = whole body thermal conductance (watts/°C).

Whole body thermal conductance (K) includes thermal conditions within the animal and the environment (Tracy, 1972). Comparisons will be made only between temperature treatments, not fish; we are concerned only with how K changes with T_a and not its absolute value. For this reason, absolute values of heat production are less important and the use of K is justified.

Yellowfin tuna seem the most adept at thermal regulation (Fig. 6). YF 1-5 and YF 8 seem to have controlled their heat dissipation rate appropriately; K was greatest at 30°C (close to upper preferred ambient temperature, 32°C, Sharp, 1978), reduced at 25°C, and reduced still further at 20°C in some fish. YF 6 and 7 show no apparent pattern, T_a and K were uncorrelated.

In contrast to yellowfin tuna, skipjack tuna exhibited great variability in whole body thermal conductance over the three test temperatures (Fig. 6). SJ 1, 2, 5, and 9 showed a significant increase in K during the 30°C test treatment. For the other fish, large changes in K were the only commonality. In some cases, the alteration in T_x was appropriate, decreasing in the face of increasing T_a and the heat load imposed by faster swimming; in other cases it was not. However, the significance of these data are that alterations in swim speed, and consequently, heat production were not accompanied by expected changes in T_x (Tables 1 and 2), even though heat production is inexorably linked to swim speed. Clearly, some mechanism intervenes to alter the pattern of heat loss, heat generation, or both.

In our experiment, the changes in K were appropriate for thermoregulation in six of the eight yellowfin tuna but in only a few of the skipjack tuna. Exceptions were not unexpected, because we are dealing with very small temperature changes within the thermal zones of tolerance for both species. We have also stressed these fish by confinement, and by application of the telemetry device. Under these conditions, appropriate thermoregulatory responses may have been impossible for some of the fish, or simply not necessary.

When a tuna is forced to swim at greater speeds (and hence has higher internal heat production) in water temperatures close to its upper lethal temperature, thermoregulation is more critical. We increased swim speed in 23 skipjack tuna by increasing their density which demands faster swimming in order to maintain hydrostatic equilibrium. These fish have no swim bladder. Only three survived long enough to give meaningful data after force-feeding the plastic-coated weights and attaching the ultrasonic transmitter. Data were collected for 12 hr at 25°C and subsequently 12 hr at 30°C (Table 3). SJ 1 responded to the increase in ambient temperature by reducing both swim speed and muscle temperature (Table 3), perhaps a behavioral thermoregulatory response. Because of the weights, SJ 2 and 3 apparently could

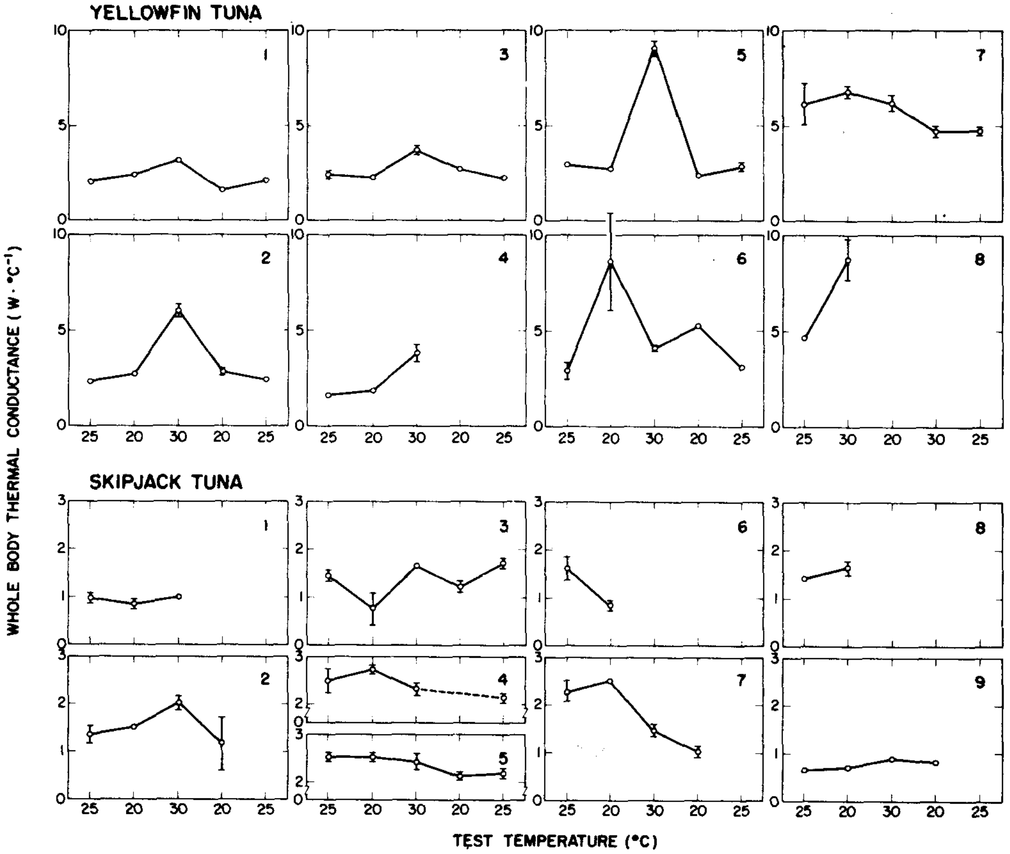

FIG. 6. The effect of ambient temperature on whole body thermal conductance (K). K was determined by dividing estimated heat production by excess muscle temperature (T_x). Vertical lines represent extreme values of K based upon the 95% confidence limits of mean swim speed and T_x. Note: The K values for SJ 4 and 5 are based upon T_x of white muscle.

not reduce speed significantly, but T_x decreased nonetheless. Mean T_x for SJ 3 at 30°C was 40% less than at 25°C, and we estimated that heat dissipation rate increased 38%. This occurred with no change in swim velocity.

POSSIBLE THERMOREGULATORY MECHANISMS

Our data show that T_x can change directly, inversely, or independently of swim velocity and heat production (Tables 1, 2, and 3), consequently whole body thermal conductance (K) changes quite dramatically (Fig. 6). In addition, yellowfin tuna and weighted skipjack tuna seem to alter their whole body thermal conductance in an appropriate manner to reduce T_x at high ambient temperatures. But is a conclusion of physiological thermoregulation appropriate? As suggested in the introduction, several processes could serve to stabilize or alter T_x when a fish is confronted with changes in T_a or increased metabolic heat production.

As swim speed increases, increased heat production may be dissipated at a lower T_x because increased blood flow through the countercurrent heat exchangers may reduce their effectiveness (Mitchell and Myers, 1968), thus allowing more heat to be dissipated via the gills. In addition, increased heat production may be more effectively dissipated at the body surface due

TABLE 3. *Grand mean swim speeds and* T_x*'s (95% confidence limits) for skipjack tuna weighted with plastic-coated lead to increase swim speed.*

	Fork length (cm)	Weight (g)	Weight carried (g)	Test temperatures (C)	
				25°	30°
Skipjack tuna 1	42.4	1,262	67.5		
Swim speed (cm/sec)				93.82±1.31	89.18±1.10
Temperature excess (°C)				2.79±0.05	2.58±0.04
Estimated heat production (watts)				3.62	3.30
K (watts/°C)				1.30±0.05	1.28±0.07
Skipjack tuna 2	44.7	1,405	86.7		
Swim speed (cm/sec)				87.05±1.50	84.44±1.81
Temperature excess (°C)				3.15±0.06	2.28±0.08
Estimated heat production (watts)				3.54	3.20
K (watts/°C)				1.12±0.05	1.46±0.08
Skipjack tuna 3	41.6	1,174	211.5		
Swim speed (cm/sec)				96.27±1.21	95.88±0.83
Temperature excess (°C)				4.96±0.21	2.95±0.05
Estimated heat production (watts)				3.62	3.48
K (watts/°C)				0.73±0.05	1.18±0.03

to enhancement of surface conduction due to faster water velocity over the body (Tracy, 1972; Strunk, 1973; Erskine and Spotila, 1977; and Brill *et al.*, 1978). Both processes must occur, but they cannot be the sole explanation for our data because we show T_x and swim speed bear no fixed relationship.

Furthermore, the effectiveness of the heat conservation system must drastically decrease with increasing swim speed. A significant T_x is generated at slow speeds but the subsequent cubic increases in heat production are effectively dissipated at reasonable temperature driving gradients. Enhanced surface conduction due to water velocity increases will not compensate for the increased heat production caused by faster swimming. If no physiological thermoregulatory mechanisms are assumed to be operating, T_x will rise approximately as the square of swim speed, since heat production rate is roughly proportional to $V^{2.5}$ and surface conduction is proportional to $V^{0.5}$ (Sharp and Vlymen, 1978). Figure 7 is the T_x velocity relationships of a hypothetical, non-thermoregulating yellowfin tuna (the same size as YF 5); the independent variable in this mathematical model (created by Sharp and Vlymen, 1978) is swim speed, no changes in internal thermal conductivity or gill heat loss are assumed. In the absence of any effective thermoregulatory mechanisms, T_x obtains absurd levels at the sustainable speed of 4 lengths/sec, even if the heat exchanger is only 25% efficient (*i.e.*, 75% of the estimated heat production is dissipated via the gills). Clearly, in a real tuna, some mechanism must intervene to increase thermal conductivity as swim speed increases, and this mechanism must have a greater dynamic range than convective-enhanced surface conduction or the reduction in effectiveness of the heat exchanger due to faster blood flow through its vessels. For these reasons and the lack of any predictable relationship between swim speed and body temperature, we feel tunas are capable of some degree of physiological thermoregulation.

There are two situations arising for tunas in which changes in heat dissipation rate per degree of driving gradient would be beneficial; 1) T_x may be increased or decreased when ambient temperatures approach lethal limits and 2) increased heat production, brought on by fast swimming, must be effectively dissipated to prevent generation of lethal muscle temperatures. We hypothesize that these two exigencies may be met by physiological processes involving changes in circulatory patterns that alter the effectiveness of the heat exchangers or changes in the relative contributions of the red and white muscle

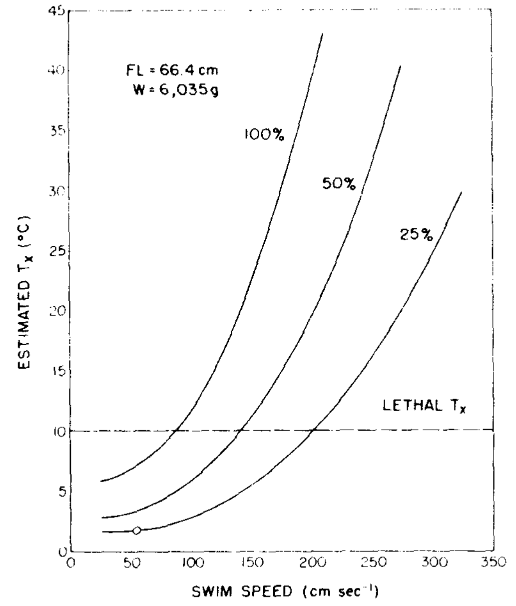

FIG. 7. Predicted excess red muscle temperature (T_x) of a nonthermoregulating tuna similar in size to YF 5 (66.4 cm FL, 6,035 g body weight) as a function of swim speed. Calculation of T_x is based on a model of convective-enhanced surface conductance (Sharp and Vlymen, 1978). The 100% function requires that all metabolic heat be dissipated at the body surface; the other two functions assume 50% and 25% of the estimated heat production is dissipated through the body surface. The latter presumably represent situations where the heat exchangers allow a greater proportion of metabolic heat to be dissipated via the gills. The open dot is the measured mean swim speed and mean T_x of YF 5 at 25°.

fiber systems to propulsion.

The second exigency, prevention of overheating, presents no conceptual problem. However, the notion that white muscle fibers are only used at high, unsustainable swim speeds (only used anaerobically) must be discarded. White muscle fibers of skipjack tuna have the enzymatic capacity to function aerobically (Hochachka *et al.*, 1978), and become active at velocities below maximum sustainable swim speed (Brill and Dizon, unpublished data). Other fish have been shown to use their white muscle fibers at sustainable speeds (Pritchard *et al.*, 1971; Bone, 1975; Bone *et al.*, 1978). White muscle fibers of tunas are supplied by circulatory pathways that bypass the vascular heat exchangers (Kishinouye, 1923; Godsil and Byers, 1944), therefore heat generated aerobically by this muscle is not retained but dissipated in the same manner as nonthermoconserving fish, via the gills and body surface (Stevens and Sutterlin, 1976; Erskine and Spotila, 1977). We suspect that the contribution of red muscle fibers to propulsion may be limited to slow swim speeds.

Control of the relative contribution of the red and white muscle fibers to propulsion may also serve in fine control of T_x in response to changing T_a. At high ambient temperatures white muscle, which contributes significantly less to the temperature burden of the fish, may be used to a greater extent than red. Alternatively, circulatory modifications within the heat exchangers may alter their effectiveness as thermal barriers. In fish, changes in water temperature and activity significantly affect cardiovascular dynamics by altering the concentrations of circulating catecholamines (Randall, 1970; Stevens *et al.*, 1972; Watters and Smith, 1973). Stevens *et al.* (1974) show that the arterial vessels of the central heat exchanger have thick muscular walls, although apparently not innervated. However, circulating catecholamines could modify circulatory patterns within the central and lateral heat exchangers and thereby alter their effectiveness.

The latter mechanism may be more important in skipjack and yellowfin tunas, because the lateral cutaneous vessels, which supply blood to the white muscle and bypass the heat exchangers, are much smaller than the dorsal aorta and postcardinal vein (Godsil and Byers, 1944), although the cutaneous vessels may be highly distensible. In the other *Thunnus* spp., these vessels are well developed.

SUMMARY

Tunas are thermoconserving fish that sometimes adjust their T_x in an appropriate manner—lower in warm waters, higher in cool. Yet, investigators do not agree whether tunas can regulate T_x, or even the biological advantage of having a T_x. Three thermoregulatory options are theoretically

open to tunas: 1) Behavioral thermoregulation, 2) passive thermoregulation, and 3) physiological thermoregulation, in which heat dissipation rates per degree of driving gradient can be controlled.

Maximum muscle temperatures of recently landed skipjack and yellowfin tunas suggested that as T_a increased, T_b slightly decreased. Is this physiological temperature regulation or the result of interaction of the effects of thermal inertia and past temperature and activity history?

Telemetry measurements from large, free-swimming bluefin tuna have been used to build a case for rapid physiological thermoregulation; subsequent analysis of the same data demonstrated that the thermal inertia characteristic (passive thermoregulation) of tunas is sufficient to explain the observed temperature constancy.

To differentiate between the three forms of thermoregulation, we devised an experiment to monitor T_b and swim speed and maintain T_a for a time sufficiently long so that only steady state T_b's were used for analysis. Yellowfin and skipjack tunas demonstrated alterations in swim speed that were *not* accompanied by expected changes in T_x. Clearly, skipjack and yellowfin tunas are not prisoners of their own thermoconserving mechanisms. Most of the yellowfin tuna and about half of the skipjack tuna showed appropriate thermal conductance changes (K)—conductance rates rose with increasing T_a. Skipjack tuna forced to swim fast at temperatures close to their upper lethal temperature, were able to reduce T_x without reducing swim speed. Significant is the lack of any predictable relationship because here is where thermoregulatory control may be exerted.

To maintain a significant T_x at slow swim speeds, and yet not overheat during bouts of sustainable high speed swimming requires tuna be able to control heat dissipation. Altering the proportion of red and white muscle power to the caudal propeller might serve the above function. White muscle does not add to the temperature burden because its circulation has no heat exchangers. For basal rate swimming, sufficient temperature excess may be built up through red muscle supplying the necessary power. As speeds increase, temperature could be kept within acceptable limits by proportionally grading more white muscle fibers into activity. White muscle has been shown to have significant aerobic capacity and to become active at sustainable swim speeds. In addition, circulatory pattern alterations within the heat exchangers may serve to reduce their effectiveness or to shunt proportionally more blood around the heat exchangers.

Thus, tunas have the capacity to control T_b's by behavioral means, such as seeking more favorable environments or altering swim speeds to change heat production. In addition, passive thermoregulation is possible due to significant thermal inertia. Thermal sequestering of the muscle by the vascular heat exchangers allows tunas to develop a significant T_x and to maintain a temperature constancy extending from minutes to several hours depending upon size. Physiological thermoregulatory mechanisms seem indicated because of the labile and independent nature of T_x and accommodation of very high heat production during fast sustainable swim speeds. These adaptations, as well as acclimatory processes, provide tunas with potent thermoregulatory mechanisms for dealing with their thermally heterogeneous habitats.

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