III. CORRELATIONS BETWEEN ENVIRONMENT, PHYSIOLOGY, AND ACTIVITY AND THE EFFECTS ON THERMOREGULATION IN SKIPJACK TUNA

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A. *Introduction*

Anyone who is familiar with live tunas must surely be impressed with the tremendous morphological investment in adaptations for high speed swimming. And anyone who is conversant with engineering principles must be aware of the extra energy required for even small increases in swim speed. Because of these high costs involved in the evolution and maintenance of a high velocity life style, the ability to swim rapidly must be critical to survival and success of the family in terms of range as well as numbers. Thus, an understanding of the tunas' performance, responses, and physiological mechanisms of swimming should illuminate their habitat requirements. This is essential for efficient management of this valuable resource.

In the main, behavior for a tuna consists of going fast at some times and slow at others. Every aspect of the tunas' behavioral repertoire should have a characteristic optimized velocity associated with it. Food search, feeding, and migration must be tuned for optimum efficiency to enable survival in the patchy and unproductive areas that are characteristic of the tuna environment. It is possible through direct experimentation, hypothesizing with mechanistic models, and through correlation studies in conjunction with fishery oceanographers, to come to an understanding of the interrelation between environment, activity behavior, and physiology of the tuna.

Four recent experimental models form the framework for much of our recent work at the Tuna Research Facility at Kewalo Basin. Two models, one mostly empirical and the other mostly theoretical, can be used to predict core temperature, given water temperature and velocity. The third deals with aspects of growth and energy requirements and their interrelation with activity levels. The last model uses physiological data from experimentation on captive fish and maps a hypothet-

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ical habitat in the central Pacific Ocean; in doing so, some peculiar aspects of skipjack tuna distribution are clarified.

We will first briefly summarize the models' important features and then describe the body temperature models in greater mathematical detail later in this report.

The "empirical" model has its genesis in the work of Neill, Chang, and Dizon (1976) in which rates of core temperature change were measured in restrained fish subjected to abrupt ambient temperature shifts. Rates at which new equilibrium temperatures were achieved were measured and appropriate constants determined. These constants were tissue- and weight-specific, and they describe rates of temperature change as a function of an integrated driving gradient; that is, the difference between actual body temperature and equilibrium temperature. Equilibrium temperature is defined as that body temperature achieved after thermal equilibrium is reached, always a positive value with respect to the ambient. The coefficient of temperature change is thus a measure of thermal inertia. Equilibrium body temperature is that temperature at which the rate of temperature decrease estimated by the coefficient of temperature change is equal to the rate of temperature increase of that point in the tissue warmed by metabolic processes. The amount of energy liberated during swimming can be estimated from respiration studies on free-swimming fish. Oxygen consumption can be converted to caloric values and point respiration values assumed (more about that later). Heat production can be translated to temperature terms using the heat capacity of muscle. Thus, respiration rate of a whole fish is a function of swim speed and, via machinations to be described, a determiner of rate of temperature increase of a point of tissue within the core of the animal.

The weakness of this approach is the coefficient of temperature change; we have no theoretical reason to assume that it stays constant under conditions of varying activity. (However, experimental results would indicate that it might.) The model formulated by Sharp and Vlymen (this volume) circumvents the problem by considering whole body rates of heat loss. The relationship of thermogenesis to metabolism and swimming energetics was developed to estimate heat production rates, and subsequently a heat dissipation model was formulated for a generalized tuna form, and with estimated heat production rates, used to predict core temperature at specific activity and size levels.

Kitchell, Neill, Dizon, and Magnuson (this volume) use fish bioenergetic principles and respiration and feeding data collected at Kewalo Basin to develop a comprehensive spectrum of energy needs as a function of body weight for various life processes. Results indicate that growth in small (less than

7 kg) skipjack tuna is limited by food consumption rates, whereas growth in larger fish is curtailed by physiological constraints on activity and metabolic demand. However, we know nearly nothing about distribution of activity of wild fish in nature. We are confident that an energetic cost could be placed on various levels of activity, but more work must be done to measure actual distribution of swim speeds in real fish as a function of size. In this report we will present estimates of activity distributions.

Perhaps the reason for live studies, at least in terms of fishery science, is exemplified in the hypothetical habitat model of Barkley, Neill, and Gooding (ms). Using laboratory findings on temperature and oxygen requirements of skipjack tuna, these authors explain why large tuna are probably excluded from regions of the eastern tropical Pacific Ocean and that while skipjack tuna in the tropics are known to be abundant they are seldom observed. Because of size-related and activity-related upper temperature limits and a restrictive oxygen tolerance, larger-sized fish cannot find areas that are sufficiently cool and still have adequate amounts of dissolved oxygen. Their work also suggests that the habitat of adult skipjack tuna is the upper thermocline and not the mixed layer. Our report will deal with the ability of skipjack tuna to maintain activity at various temperatures.

We have organized this presentation into three broad topics; data from the various experiments will overlap the topics. The first will deal with "real world" estimations of tuna performance based on data from free-swimming fish carrying depth-sensitive ultrasonic transmitters. These data also provide some idea of the limits of preferred habitat within those available to the fish in the tracking area. The second topic is organized from those experiments relating behavioral responses to alterations of the environment. Experiments will be described relating skipjack tuna responses to variations in light, salinity, oxygen, and temperature. In some cases, data on the responses of yellowfin tuna will be drawn upon for comparison. The third topic is the interrelation of environment, behavior, and physiology. We will limit our discussion to water temperature and activity effects on core temperature. The efficiency of both models in predicting core temperature will be examined and the topic of thermoregulation in skipjack tuna discussed.

Before proceeding with the topic of tracking, we would like to put the concept of swimming speed into energetic terms. Throughout this report, we will be using specific swim speeds to report results. As Webb (1975) puts it, "specific swimming speeds remain the simplest and most useful method of comparison [p. 51]." However, performance-size effects are neglected and we have to remind ourselves continually of what changes in swim speed must really mean to the animal. If specific swim speed is scaled against size and energy consumption (Fig. 1), the high cost of fast swimming becomes apparent. A 50-cm skipjack tuna requires about 1 cal sec^{-1} to swim at its minimum hydrostatic equilibrium speed; at 10 lengths sec^{-1}, 100 cal sec^{-1} are required (or 418 watts). And we have observed skipjack tuna swimming more than 20 lengths sec^{-1}. In terms of heat dissipation and energy reserves, fast swimming is indeed costly.

B. *Performance of Tracked Skipjack Tuna*

The power required to propel an object through the water is related to its length, drag, and velocity; the relationship of these variables is known through much experimentation on animate and inanimate objects (see Webb, 1975, for review). However, notably lacking in the literature is data on real velocity levels partitioned on daily and maybe even lifetime intervals. This paucity of data is obviously due to the difficulty in experimental implementation in wild fish. Although we

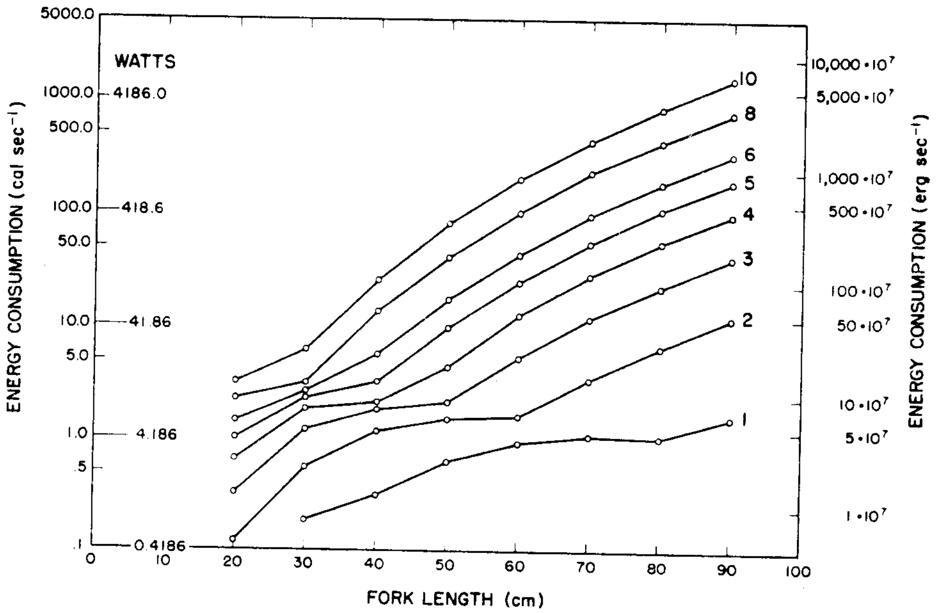

FIG. 1. Specific swimming speed (lengths sec^{-1}) is translated into energy consumption terms as a function of fish size. Swimming speed/power relationships are from Sharp and Francis (1976).

know approximately what energetic costs might accrue for a hypothetical distribution of activities, we need data on real activity levels.

Equipping wild (freely ranging) fish with ultrasonic transmitters and following their movements in the ocean over several days is the most practical method so far developed; presently it has serious shortcomings. Resolution of small-scale movements is poor. These movements might contribute strongly to the total energy consumption. Effects of the transmitter on drag coefficients and of handling on behavior could be a problem. Long-term collection is impractical because of ship costs and lack of endurance of personnel. Nevertheless, tracking has provided first-cut estimates of performance, preferences, and activities and is worthwhile for such purposes.

Six skipjack tuna have been tracked to date; Yuen (1970) tracked two small "bank" fish (approximately 45 cm) in the late 1960's. Behavior of these fish was remarkable; days were spent on the banks, nights off the bank. Distribution of estimated swimming speeds was strongly weighted toward speeds below hydrostatic minimums, implying that small-scale movements were very important. No data on temperature or depth could be collected.

In May of 1977 we tracked three larger "season" fish (approximately 70 cm) and in October tracked another small (approximately 45 cm) bank fish. Behavior of the small fish was virtually identical to that of Yuen's fishes. Behavior of the larger fish, however, seemed independent of the banks, and data collection was improved using depth-telemetering tags.

Skipjack tuna were tagged by a technician aboard a commercial pole-and-line vessel. During scouting operations prior to fishing the RV *Townsend Cromwell* (the tracking vessel) shadowed the fishing boat in readiness. Tags employed were cylindrical (16 mm dia. by 92 mm long) and transmitted on a frequency of 48 khz. Pulse rates were determined by depth and varied from 60 at the surface to about 150 at 300 m. The tags had a useful life of approximately 3 days and a range of less than 2 km.

Five season fish were actually tagged on separate occasions; tags were force fed to the tunas. Two of the five regurgitated their tags before any useful information was obtained; one immediately after release, the other after 2 h. The remaining three were tracked for 24, 11, and 10 h (Table I). We had visual confirmation that at least two of the fish rejoined their schools after release; we sighted large skipjack tuna schools at the range and bearing of our tagged fish. Relative to small tuna tracked previously, these larger tunas proved difficult to track since their occasional bursts of speed moved them rapidly out of tracking range and

TABLE I. Summary of Ultrasonic Tracking Data

	Fish (skipjack tuna, 70 cm FL)		
	A	B	C
Time tagged (l.s.t.)	1230	1030	1600
Tracking period (h)	24	11	10
Termination	lost	lost	died
Total distance swum (km)	141.6	50.2	24.8
Mean velocity (m sec^{-1})	1.64	1.27	0.72
Mezn velocity (lengths sec^{-1})	2.30	1.75	1.03
Mean depth (m)	68.6	143.1	231.7
Mean temperature (°C)	22.4	20.1	14.9

were responsible for the eventual termination of two of the tracks. The third fish apparently died since he began to slowly sink into very cold water about 10 h after tagging. The sinking rate was too slow to indicate a free-falling regurgitated tag and we had the impression of a gradually weakening tuna maintaining positional equilibrium but swimming too slowly to maintain hydrostatic equilibrium (Magnuson, 1973). In about 30 min, the fish glided from 120 m to 450 m (7.5°C) when we terminated the track.

Since depth information was available, we were able to improve our estimates of swim speed by accounting for small-scale vertical movements. Behavior of our fish was characterized by many rapid vertical migrations superimposed on a fairly consistent northwesterly migration. Horizontal positions were determined every half hour; vertical positions, approximately every 3 min. Movement was then assumed to be from depth position to depth position along the hypotenuse of a triangle whose horizontal leg was determined from half-hour position information. The vertical leg was determined by the difference in two adjacent depth measurements. Thus, our swimming speed estimates are better than those obtained with only the horizontal component of velocity but are still underestimates of what the fish was actually doing. The estimates were most accurate during periods of relatively fast horizontal movement on a steady course. During periods when the fish was feeding and circling, our estimates fell below the minimum hydrostatic equilibrium speed.

Skipjack tuna A, tracked for 24 h, traveled 141.6 km horizontally and vertically (Table I). All three fish resolved about 10% of their total movement into vertical migrations. Mean velocities ranged from as high as 2.30 lengths sec^{-1} (164 cm sec^{-1}) to less than hydrostatic equilibrium speeds in the case of the fish that died. Mean depths and temperature varied considerably among the three fish (Table I). Skipjack tuna C's swimming depth is deeper, and the temperature encountered is colder than the others because of its gliding descent. If the glide is excluded from data set, mean depth is 87.8 m and temperature is 21.4°C, both of which are intermediate between Fish A and B.

All three fish remained in water above 20°C during 85% of the track periods although all fish did dive to cold water which would ultimately prove lethal if they remained indefinitely at these temperatures (Dizon, Neill, and Magnuson, 1977). Figure 2 is a frequency distribution of temperature observations; fish C only includes data prior to glide to depths. No thermocline was evident during the tracking periods (Fig. 3) so no observations of fish position relative to the thermocline can be made. (It is interesting to note that these fish do not violate activity-size boundaries hypothesized by Neill, Chang, and Dizon, 1976); fish of this size at activity levels equivalent

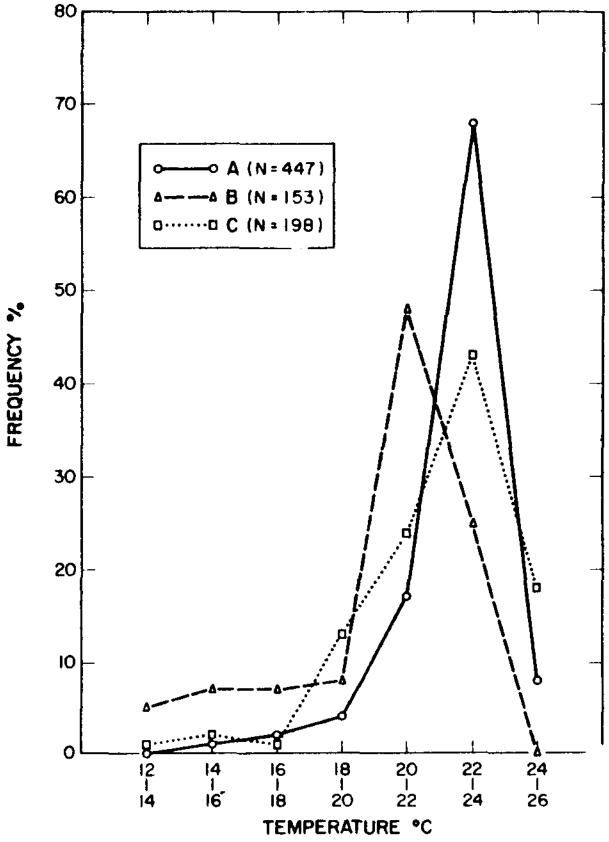

FIG. 2. Distribution of temperatures encountered by three fish tracked with ultrasonic transmitters.

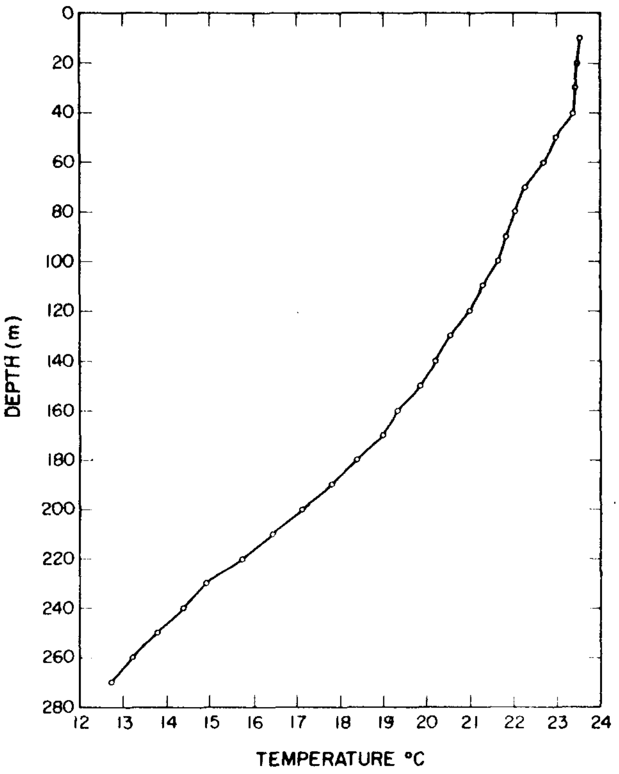

FIG. 3. Typical temperature profile occurring during tracking period.

to 3 mg O_2 $g^{-1}h^{-1}$--suggested as the average metabolic rate in red muscle of normally active tuna--must remain in water below 23.5°C. Water above this temperature was not available during the tracking period.)

Distribution of measured swim speeds varied considerably among the three fish (Table II). Speeds below minimum hydrostatic equilibrium speeds were observed; obviously small-scale movements were occurring during those sampling periods. As speed increases, the accuracy of our measurements did also since the fish was more likely to swim a straight course. Fish A was the best performer and demonstrates remarkable abilities (Table III). The intervals in this table are continuous observations of swim speed without rest and seem to be periods when the fish was moving rapidly, perhaps from one feeding area to another. The high velocities and relatively warm temperatures indicate to us that the fish must have some mechanism to rid themselves of the terrific amount of heat generated; at the highest velocity (6 lengths sec^{-1}) approxi-

TABLE II. Distribution of Swim Speeds (Sampled at 30-Min Intervals)[a]

	Fish (skipjack tuna, 70 cm FL)		
	A	B	C
Below 1.33 (lengths sec^{-1})	27	45	58
1.34 to 2.33	29	41	37
2.34 to 3.33	21	0	5
3.34 to 4.33	15	14	0
Above 4.34	8	0	0
Number of observations	48	22	19

[a] *Minimum hydrostatic equilibrium speeds for fish of this size is 1.33 lengths sec^{-1} (Magnuson, 1973).*

TABLE III. Maximum Swim Speeds Achieved by Skipjack Tuna A (70 cm FL)[a]

Interval (min)	Swim speed		Depth (m)			Temperature at depth (°C)		
	Lengths sec^{-1}	m sec^{-1}	Min.	Med.	Max.	At min.	At med.	At max.
30	6.08	4.33	6	53	85	23.5	22.9	21.9
60	4.89	3.48	2	6	38	23.5	23.5	23.4
120	3.85	2.74	2	15	56	23.5	23.5	22.8
240	3.10	2.21	54	143	262	22.9	20.1	13.1

[a] *Speeds are continuous for periods indicated with no resting periods intervening.*

mately 100 cal sec^{-1} are being consumed. (We will discuss this more in a later section dealing with thermoregulation.)

C. *Responses of Tunas to Environmental Parameters*

Before introducing the topic of thermoregulation, we would like to describe briefly some recent work with captive tunas responding to artificial environments. Our methods are simple; captive tunas were acclimated to a tank situation, their activity measured, and then some environmental parameter changed (oxygen, temperature, or salinity). Significant alterations in swim speed or swimming direction constituted a response. We observed two types of responses: "automatic" and "behavioral." Although there is no real evidence to support the distinction, it seems appropriate at least for the moment. Automatic responses were characterized by a gradual change in swim speed which follows the changing treatment level; a characteristic Q_{10} can be applied. Behavioral responses, in contrast, seem to be triggered responses and occur rather abruptly, presumably when a tolerance level or sensory level was reached. Of course, we did also observe intermediate-type responses.

For most of the work we have been using a tank system in which swim speed, direction, and temperature are automatically collected (Fig. 4). The swimming channel is equipped with photocells to record movement and has reasonably restricted dimensions (0.75 by 0.75 m) so that environmental changes can be made rapidly and economically. Intakes and discharges into the tank are made through countercurrent pipe systems so that spatial gradients are eliminated. The system will accommodate oxygen, salinity, or temperature changes.

Tuna--skipjack or yellowfin--did not seem to make any responses to salinity changes; when salinity was reduced from normal concentrations to below $20^{o}/_{oo}$, no alterations in swim speed were observed (Dizon, 1977, Table IV). Although our sample size was small, we are confident small salinity changes (of a magnitude that a tuna would experience) are not very important behavioral regulators.

Oxygen, in contrast, produces dramatic behavioral changes in skipjack tuna (Dizon, 1977). Skipjack tuna responded by increasing their swim speed abruptly when dissolved oxygen levels were reduced from saturated to 4 ppm; yellowfin tuna made no responses to 2 ppm, which was the lowest attainable in the system (Fig. 5). Eight skipjack tuna and three yellowfin tuna were tested; median swim speed changed from 1.6 lengths sec^{-1} at above 4.5 ppm to 2.0 lengths sec^{-1} at 3.5 ppm and 2.3 lengths sec^{-1} at 2.5 ppm (Fig. 6). These responses did not appear to be related to increasing ram jet ventilation because adequate oxygen could

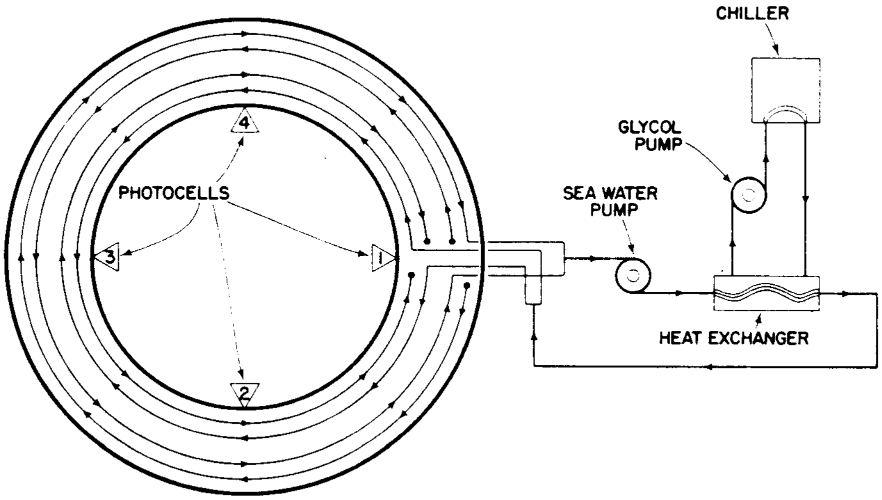

FIG. 4. Tank system for examining activity responses of tunas to spatial gradient-free alterations of oxygen, salinity, or temperature levels.

TABLE IV. *Effect of Decreasing Salinity on Swimming Speed in Tunas*

	n	$\bar{X}$	SD
Skipjack tuna			
Fish No. 1 (38.3 cm, 925 g)			
Before salinity change	28	2.10	0.40
During salinity change	22	1.82	0.40
Fish No. 2 (37.7 cm, 882 g)			
Before salinity change	44	2.03	0.26
During salinity change	12	2.37	0.19
Fish No. 3 (42.0 cm, 1.352 g)			
Before salinity change	30	1.21	0.07
During salinity change	15	1.16	0.06
Yellowfin tuna			
Fish No. 1 (45.3 cm, 1,491 g)			
Before salinity change	39	1.54	0.30
During salinity change	31	1.81	0.26

be had by increasing gape slightly. Increasing oxygen requirements of faster swimming offsets any increased ventilation. It did seem to be an appropriate behavioral response for a fish to remove itself from a suboptimal environment. However, in our tank it was maladaptive since no appropriate environment was available.

An example of the automatic response was the skipjack tuna's response to temperature. In this experiment fish were held for long periods of time at one of three treatment temperatures (20°, 25°, and 30°C). Swim speeds were measured for every lap over the 2- to 3-day experiment, 10 min averages were made and used for analysis. (Note that 6 laps equal 100 m swum.) Although reported earlier that temperature changes had no effects upon swim speed in skipjack tuna (Dizon *et al.*, 1977; Stevens and Fry, 1971) a slight effect was noted when extensive observations were made (Fig. 7). Yellowfin tuna, in contrast, had a swim speed/temperature Q_{10} equal to about 2 (Dizon *et al.*, 1977).

Behavioral type responses to temperature were also observed with captive fish. Some fish were noted to cease lap swimming when water cooled to 20°C and to initiate a characteristic reversal behavior consisting of swimming elongated figure eights extending about 4 m. We interpreted this behavior to be a response to stress, since it was observed at the low temperatures and also when a fish was initially introduced into the tank system.

If distance swum in 50 min is plotted against a time series of temperature, it is apparent that skipjack tuna were either exhibiting a stress response or were reluctant to swim

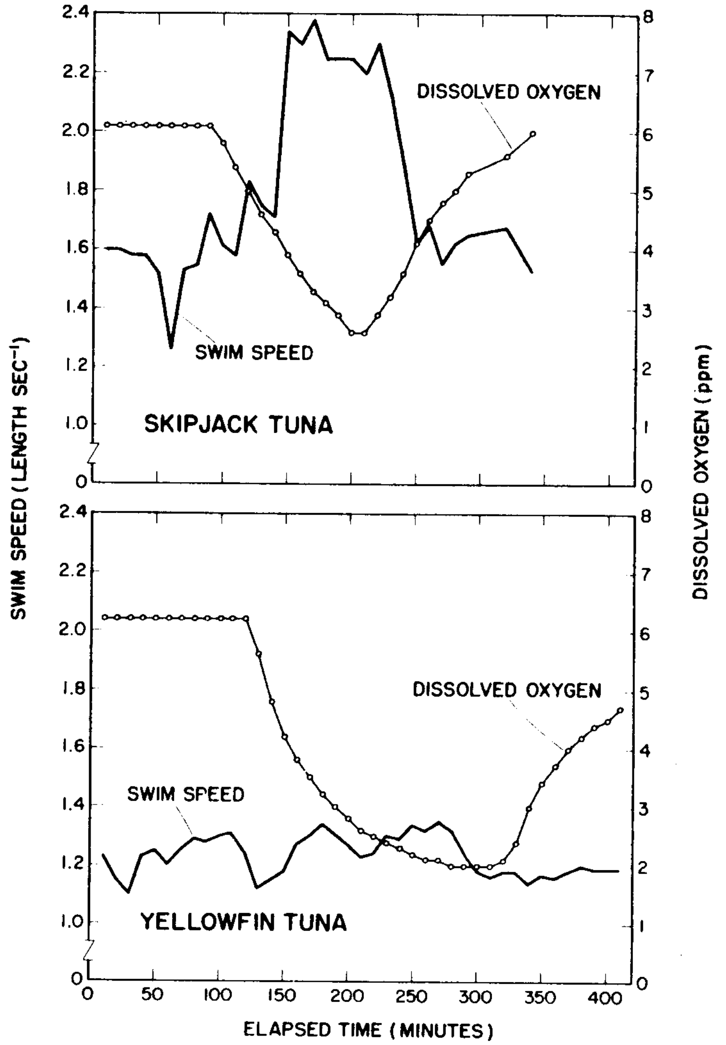

FIG. 5. Effect of dissolved oxygen level on swim speed in skipjack and yellowfin tunas. Swim speeds are median values sampled for 10 min periods (Dizon, 1977).

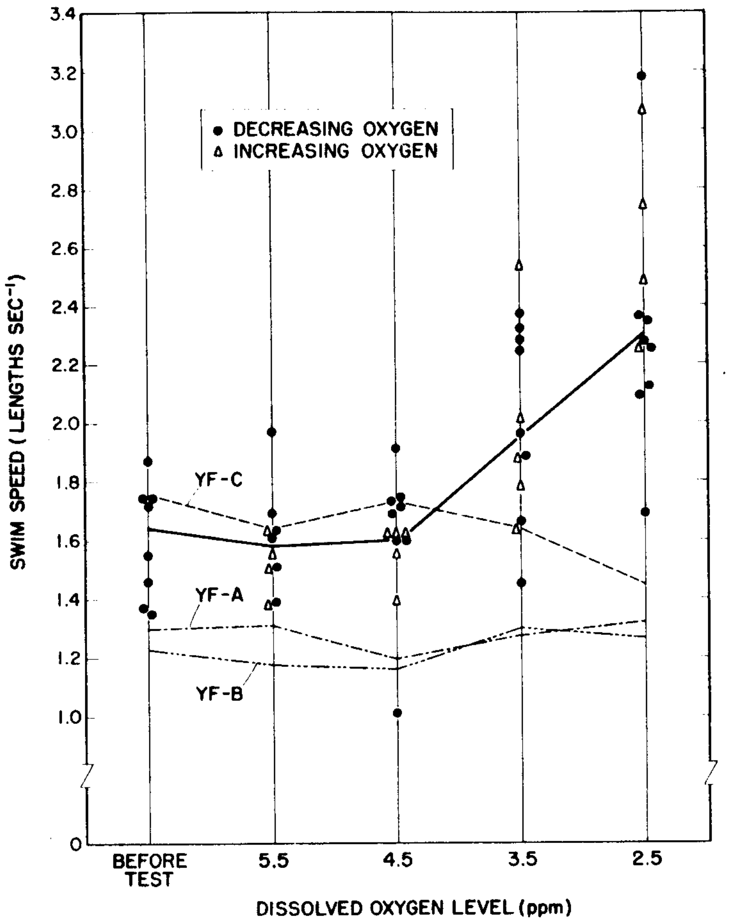

FIG. 6. Summary of data from responses of eight skipjack and yellowfin tunas. Solid dots--decreasing oxygen levels, median swim speeds grouped by 1 ppm intervals, and "before" test observations. Open triangles--increasing oxygen levels, median swim speeds grouped by 1 ppm intervals. Solid lines--grand median for skipjack tuna. Broken lines--individual medians for each of the three yellowfin tuna, decreasing oxygen levels only (Dizon et al., 1977).

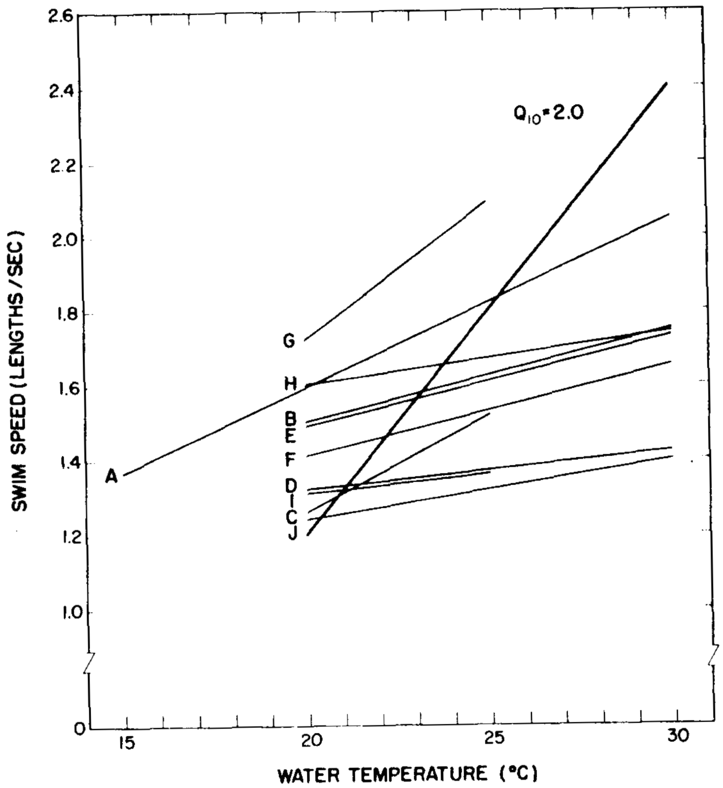

FIG. 7. *Effect of temperature upon swim speed in 10 skipjack tuna. Lines fitted by linear regression analysis; all, save fish I, are significant at the 0.01 level. The median swim speed-temperature relationship of three yellowfin tuna (tested three times each) is also plotted,* $Q_{10} = 2$.

any further into cold water (Fig. 8). Note how the response was not exhibited until many minutes of exposure to cold water. Body temperature had equilibrated long before responses were made. It was, however, difficult to quantify this behavior further since not all fish would respond in this manner (Table V). If the number of 10 min sample periods containing reversal are compared at 20°C and at 30°C, only two or three of the seven fish tested at 30°C respond. But we have repeatedly observed this response to cold water in other experiments and assume it manifests itself in wild fish in the reluctance of the sonic-tracked fish to spend more than an insignificant amount of time at temperatures lower than 20°C.

A curious response observed during the tracking study is

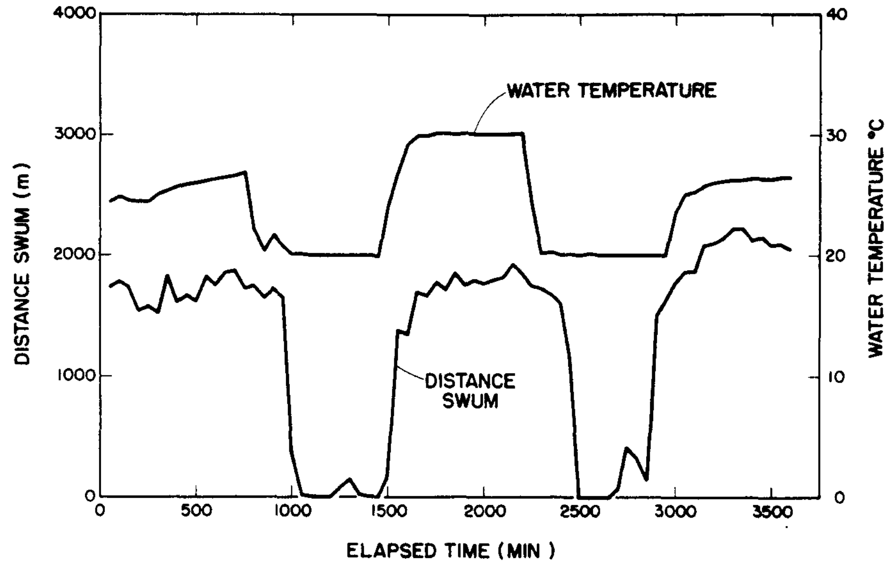

FIG. 8. Effect of temperature on willingness of a single skipjack tuna to swim laps in test tank. Distance swum is number of laps in 50 min multiplied by 16.67 (6 laps = 100 m swum).

TABLE V. *Fraction of 10-Min Sample Periods That Contain Reversals*

	Fish						
	A	B	D	E	F	H	J
20°C	0	.07	.78	.18	.60	.01	.05
30°C	0	.01	0	.02	.09	0	0

evident in Fig. 9; this fish ranged throughout the water column during the day. Time was spent at the surface and at depths as great as 263 m. However, at the end of twilight the fish rose into shallow water and remained there until dawn when an abrupt dive to 210 m was made. All three fish demonstrated evening ascents but data are missing for fish B and C for times comparable to the morning descent of fish A. Fish A swam at a mean depth of 58 m during the day, 14 m during the night; Fish B, 46 m versus 32 m; and Fish C, 70 m versus 19 m. We have no idea whether this was a response to food, light level, or some sort of endogenous rhythm. More work is planned in which we hope to examine these questions.

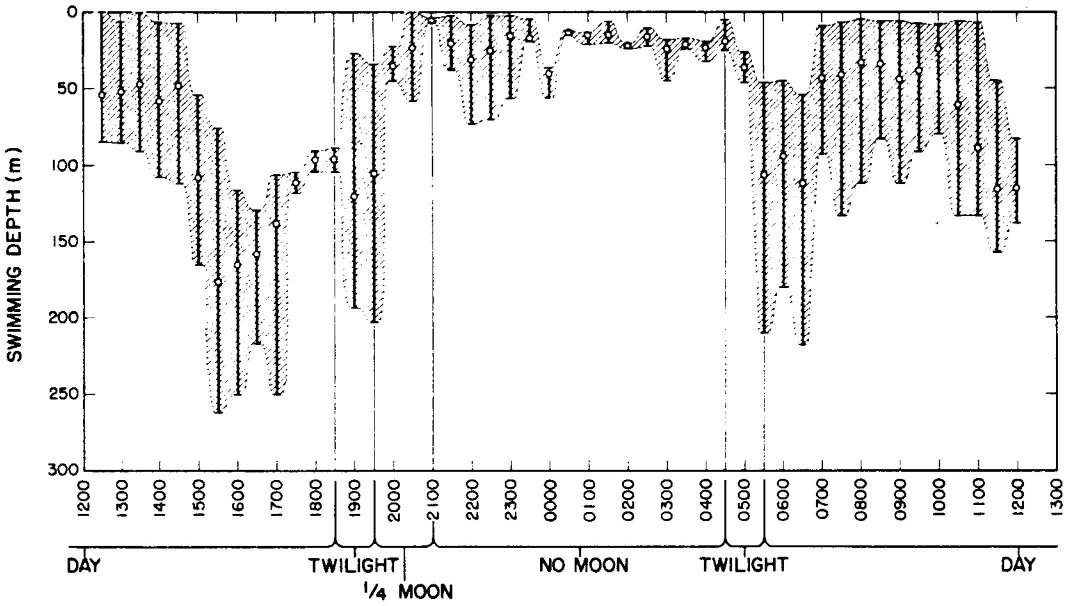

FIG. 9. Depth range (and median depths) plotted as a function of chronological time at 30 min intervals for skipjack tuna A. Depth measurements made on 3 min intervals.

D. *Activity and Water/Body Temperature*

Prediction of body temperature given swim speed and water temperature is very important for three reasons: (a) Predicting such a complex phenomenon usually means understanding it and statements can be made as to its importance. (b) Body temperature is a readily telemetered parameter whereas the related respiration rate is not; knowledge of daily respiration rates is essential to any growth and energy models. (c) Two circumstances occur in which high levels of activity are a problem. In areas of high water temperature activity might need to be curtailed to avoid excessive body temperature, and the fishes' efficiency at prey capture might be seriously reduced. Or during capture, frantic escape efforts might cause muscle damage and consequent reduction of market value--the so-called burnt tuna problem.

Interpretation of measurements of body temperature in wild fish suffer from unknown influences of past activity and temperature history. Most tracking work only measures location of fish and depth or temperature of the water. Accurate measures of activity, body temperature, and experimentally controlled environmental temperatures are necessary to formulate and test models predicting body temperature and to measure thermoregulating abilities in free-swimming tunas (Brill, Guernsey, and Stevens; Sharp and Vlymen, this volume).

As mentioned in the introduction, two approaches have been made to predict body temperature; the first is an empirical approach outlined in Neill and Stevens (1974) and Neill *et al.* (1976) and used to predict red muscle temperature in Dizon *et al.* (1977). Given the rate at which a tissue mass loses or gains heat (k) and the rate of heat production, the temperature of a tissue can be estimated as a function of any time series of temperatures encountered by the fish. From respiration studies by Gooding and Neill (ms), swim speed and fish weight were significant determiners of oxygen uptake:

$$\log r = -1.2012 + 0.2131\, s + 0.1911 \log w \qquad (1)$$

where

r = respiration rate, mg O_2 g^{-1} h^{-1};

s = swim speed, lengths sec^{-1};

w = fish weight, g.

Since the concern is red muscle temperature, we need an estimate of respiration rate of this tissue and for the moment we will estimate it to be about twice that of the whole fish on a per weight basis (Neill *et al.*, 1976). Thus

$r_{rm} = 2\ r$ and substituting into equation (1) (2)

$$\log r_{rm} = -0.9002 + 0.2131\ s + 0.1911 \log w \quad (3)$$

where

r_{rm} = red muscle respiration rate, mg $O_2\ g^{-1}\ h^{-1}$.

Respiration rate can be converted into an estimation of the rate of temperature change using the heat capacity of fish muscle (0.8 cal g^{-1} °C^{-1}) and the oxycaloric equivalent for fish (3.42 cal mg O_2^{-1}) (Neill *et al.*, 1976).

$$r'_{rm} = r_{rm}\ 3.42\ (0.8)^{-1}\ (60)^{-1} \quad (4)$$

where

r'_{rm} = red muscle respiration rate, °C min^{-1} and substituting into equation (3)

$$\log r'_{rm} = -2.0474 + 0.2131\ s + 0.1911 \log w. \quad (5)$$

Now, if the fish is in thermal equilibrium, body temperature is constant and heat production rate (r'_{rm}) must equal rate of heat loss. The tendency for the tissue temperature to increase must be balanced by temperature decrease through conduction and convection. Thus

$$r'_{rm} = k\ (T_{rm} - T_a) \quad (6)$$

where

k = coefficient of temperature change, °C min^{-1} °C^{-1};

T_{rm} = red muscle temperature, °C;

T_a = ambient water temperature, °C.

Excess temperature (T_x) is the difference between the temperature of the tissue and the water temperature

$T_x = T_{rm} - T_a$, substituting and rearranging equation (6)

$T_x = r'_{rm}\ k^{-1}$ which can be combined with equation (5) to give

$$T_x = \frac{10^{(-2.0474 + 0.2131\ s + 0.1911 \log w)}}{k} \quad (7)$$

The coefficient of temperature change (k) is dependent upon weight for the various tissues studied in skipjack tuna (Neill *et al.*, 1976):

$$k_{rm} = 0.044w^{-0.446} \quad (8)$$

where

k_{rm} = red muscle coefficient of temperature change, rate of temperature change per degree (°C) of driving gradient, °C min^{-1} $°C^{-1}$.

Rather than approaching prediction of body temperature from the empirically derived functions of respiration and rate of temperature change, the theoretical model of Sharp and Francis (1976) and Sharp and Vlymen (this volume) has its beginnings in the power equation from hydrodynamic theory. In this equation, power, which can be converted to respiration terms, is a function of the coefficient of total drag, length squared, velocity cubed, and water density. Stasis respiration is added to respiration due to swimming, and the total is the caloric expenditure required for swimming at specific activity levels. The coefficient of total drag is obtained from literature values of Reynolds number (Re) which are functions of speed and organism size (Sharp and Francis, 1976); this value is assumed to approach a constant, 0.01, as Re approaches 6.8×10^{-5}.

Heat loss is based upon a forced convection model at the lateral surface of a tuna-sized cylinder. The entire metabolic surface is assumed to be located in this middle cylinder and conduction to the head and tail sections considered to be negligible. For a fish at equilibrium, heat loss (q_t) is again assumed to equal heat production (C_v) reduced by a muscle-propulsion efficiency term (M_e) so that

$$q_t = (1 - M_e)\ C_v. \qquad (9)$$

The relationship is then a complex function of the physical dimensions of the midsection cylinder, velocity, density of the fish and the medium, viscosity of the medium, thermal conductivity of the fish, heat capacity of the medium, metabolic mass of the fish, and magnitude of the driving gradient--T_x. The model also includes a term for the properties of heat lost via the gills (Q_g) which we have examined empirically.

Thus, two models are available that predict body temperature as a function of velocity and water temperature. Other values are available as accepted constants or are measurable parameters of the fish itself (length, weight, etc.). Problems, of course, occur in the estimation of total drag which is a sensitive parameter in determining T_x and stasis metabolic rate. The theoretical model thus requires some assumptions about drag, muscle efficiency, and stasis metabolic rate but is more soundly based than the empirical. Muscle efficiency terms are ignored in the empirical model, or are implied in the estimation of red muscle metabolism. Nevertheless both models form a starting point for the investigations of thermoregulatory performance in our captive fishes.

Activity under conditions of constant and variable temperatures was measured again in the ring tank system. Fish were equipped with ultrasonic transmitters with long probes that could be inserted into the muscle core (Fig. 10). Fish were captured from our outdoor tanks and placed in the channel for 4 h to allow recovery time from the effects of the capture and transport struggle. After that, the subject was persuaded to swim into a plastic bag and was removed from the channel. We held the fish by the jaw on an inclined plastic sheet; water was played over the gills, and the fish blinded with a dark rag over the eyes. The tag thermistor probe was inserted into the red muscle from the dorsal side just lateral of the forward edge of the dorsal fin. The tag body itself was secured to the corselet with two Floy dart tags or later with a Peterson-type button. The latter was faster and more secure. The procedure took less than a minute and the fish was then returned to the swimming channel.

The ultrasonic transmitter was developed at the Oak Ridge National Laboratory and generously loaned by Drs. Charles Coutant and James Rochelle. The tag was designed for telemetry of the body temperature of a small fish or the water temperature. The tag is 17 mm OD, 34 mm long, and weighs less than 14 g in water. Temperature is encoded by pulse interval modu-

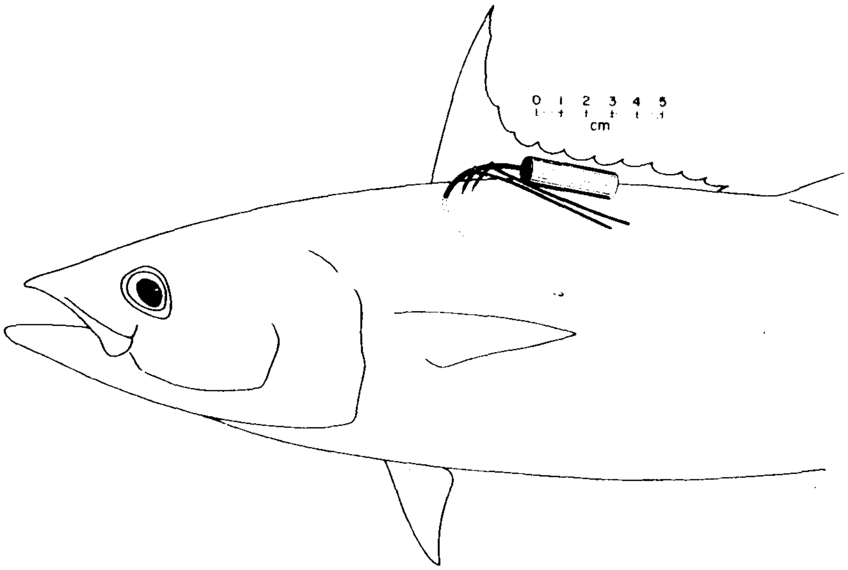

FIG. 10. Method of securing ultrasonic transmitter. Temperature sensitive element is located at distal end of the probe embedded in red muscle.

lation, with the interval varying from 1400 to 300 msec over a range from 5° to 35°C. This calibration shifts less than ±0.2°C throughout the expected life of 21 weeks and is not significantly affected by a thermistor-tag temperature differential (Rochelle and Coutant, 1974:1).

Test treatments consisted of 8 h treatments at three temperatures (4 h at 25°C, 12 h at 20°C, 12 h at 30°C, 12h at 20°C, and 8 h at 25°C and repeat). In one case 15°C was used, but it proved fatal and was discontinued. Body temperatures and activities were sampled at 10 min intervals for the former and were averaged at 10 min intervals for the latter. Swim speed was calculated for all laps swum during the course of the experiment. We attempted to test all ten fish at each of the three test temperatures; three fish did not survive the 20°C treatment.

Surprisingly, initial analysis of the results showed no correlation between swim speed and body temperature; as swim speed increased, body temperature sometimes decreased, sometimes increased, or sometimes stayed the same (Fig. 11). No pattern was evident in the ten fish and it was obvious that intercorrelations between swim speed, environmental temperatures, and body temperatures made any type of multiple regression analysis impossible.

Use of the two models and a smoothing function designed by Neill and Stevens (1974) proved effective in sorting out the interrelationships between the variables. The data set in turn provided a method of testing the effectiveness of the two models. But it was immediately clear from observations of the T_x's from the data that the theoretical model predicted body temperatures that were too high. From data collected by Brill, Guernsey, and Stevens (this volume), we learned that a significant amount of heat could be leaking from the central heat exchanger to be dissipated at the gills. Sharp and Vlymen (this volume) recognized the problem of fishes with central heat exchangers and suggested that one reduce the predicted body temperature by at least 50% to account for heat lost at the gills; but in most cases this is not enough.

The empirical model, in contrast, sometimes predicted too high and sometimes too low.

For comparison purposes it was decided to force each model to fit the mean T_x and the mean swim speed at 25°C before attempting to compare their effectiveness. We adjusted the amount of heat lost at the gills (heat exchanger effectiveness) to force the fit of the theoretical model. We adjusted the respiration multiplier (the degree to which muscle respiration exceeded whole fish respiration) to force the fit of the empirical model. The results are shown in Table VI. According to the theoretical model, skipjack tuna lose at the gills from 0.83 to 0.53 of the heat generated by muscle contraction,

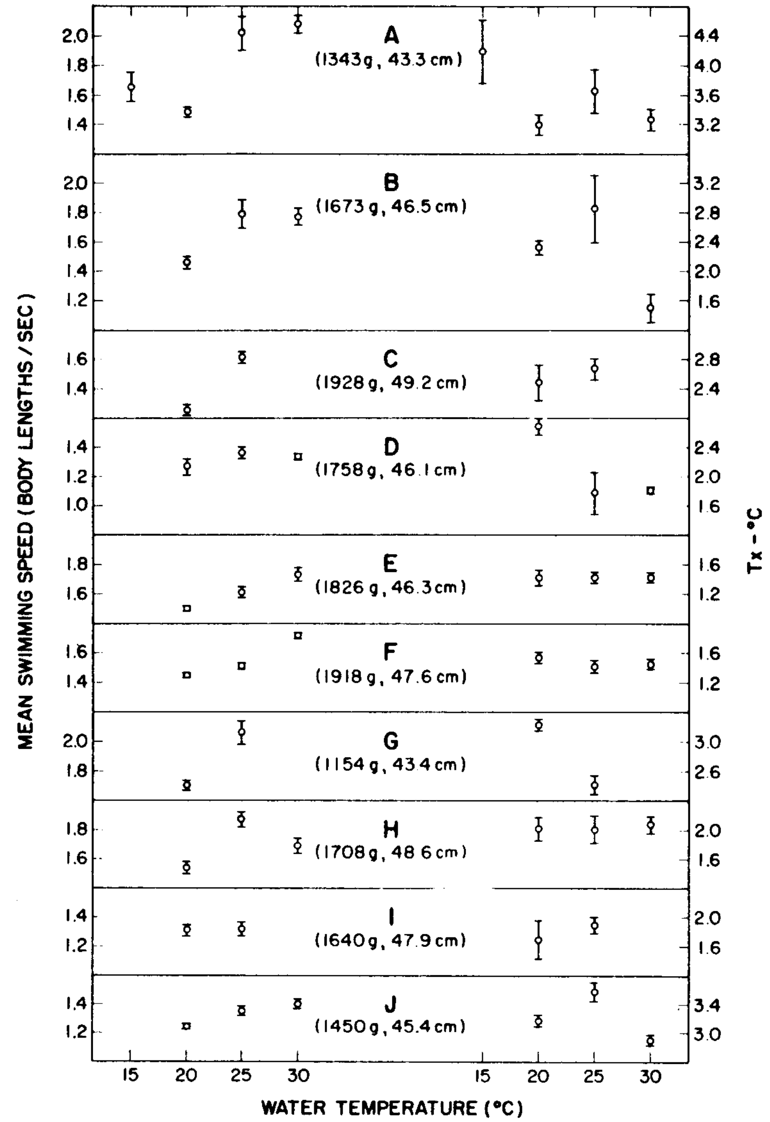

FIG. 11. Swim speed (±95% C.L.) and red and white muscle temperatures (±95% C.L.) sampled at 15°, 20°, 25°, and 30°C test temperatures. Note: fish E and F are white muscle rather than red muscle temperatures.

TABLE VI. Forcing Coefficients to Initiate Models[a]

			At 25°C test temperature			
Fish	FL (cm)	Weight (Kg)	Mean T_x (°C)	Mean speed (lengths sec^{-1})	Fraction heat loss at gills	Respiration multiplier
A	43.3	1.343	3.653	2.020	0.68	3.0X
B	46.5	1.673	2.852	1.789	0.73	2.2X
C	49.2	1.928	2.670	1.612	0.74	2.1X
D	46.7	1.758	1.766	1.355	0.76	1.7X
E (white)	46.3	1.826	1.420	1.610	0.83	1.3X
F (white)	47.6	1.918	1.409	1.510	0.83	1.3X
G	43.4	1.154	2.407	2.057	0.82	2.0X
H	48.6	1.708	2.023	1.874	0.84	1.6X
I	47.9	1.640	1.902	1.321	0.77	2.0X
J	45.4	1.450	3.576	1.348	0.53	3.8X

[a] *Theoretical model was forced to fit mean T_x and mean swim speed at 25°C by reducing the assumed 50% heat loss at the gills to appropriate levels. Empirical model was forced by adjusting the assumed respiration relationship (muscle respiration rate = 2 × whole body respiration rate) to appropriate levels.*

which would mean that the effectiveness of the heat exchanger varies from 0.47 to 0.17. According to the empirical model, muscle respiration rate varies from 1.3 times to 3.8 times that of whole fish respiration rate. Two fish carried probes in their white muscle; the T_x was predictably lower. Consequently more heat was indicated as lost via gills and lower multipliers found.

Use of these forced predictors of T_x and the exponential smoothing function (Neill and Stevens, 1974) enabled us to predict body temperatures from time series of water temperature and activity. Thus

$$T_{rm_i} = T_{e_i} - (T_{e_i} - T_{rm_{i-1}})\, e^{-k\Delta t}$$

where .

$T_e = T_a + T_x$;

Δt = time interval, sec.

A computer program was written to determine T_{rm_i} at 5 min intervals and to plot expected body temperature (T_{rm_i}), observed body temperature (telemetered), swim speed, and water temperature. Both the theoretical and the empirical models fit the observed data with surprising accuracy.

When both observed and expected temperatures were available (during periods of lap swimming) goodness-of-fit was compared by calculating mean squared residuals

$$\text{m.s.r.} = \frac{\Sigma\,(T_{rm_i} - T_{o_i})^2}{n-2}$$

where

m.s.r. = mean squared residuals, °C^2;

T_{o_i} = observed body temperature, i th interval, °C;

T_{rm_i} = expected body temperature, i th interval, °C;

n = number of observations.

There was little difference in the ability of both models to track observed body temperatures (Table VII). In some fish one model worked better than in others and no pattern was apparent. However, fit was noticeably better for both models in the two fish monitored for white muscle temperature. Perhaps small changes in activity affect temperature less in the white muscle. During the experimental series, we have no records of fish swimming over 2.5 lengths sec^{-1}; presumably no white muscle contribution and anaerobic metabolism were required. Goodness-of-fit was also markedly improved with larger fish. Again, the increased thermal inertia of large fish might have contributed to damp small changes in activity.

As noted earlier, both models were forced to fit the observations by setting constants so that the average swim speed and body temperature were predicted at 25°C; this assumed that no thermoregulatory changes occurred in model constants as a result of changes in environmental temperature. The theoretical model allowed a test of this assumption. If a thermoregulatory response was occurring, a simple mechanism would be to allow more heat to be lost via the gills when environmental temperatures increased. Although there are many other ways in

TABLE VII. Mean Squared Residuals to Compare Goodness of Fit of Each Model

	Mean squared residuals		
Fish	Empirical (°C^2)	Theoretical (°C^2)	Number of observations
A	0.2973	0.5505	328
B	0.8764	0.8036	490
C	0.1949	0.2231	100
D	0.1581	0.2014	584
E (white)	0.0611	0.0623	492
F (white)	0.0460	0.0478	668
G	1.0319	1.2154	228
H	0.3949	0.4660	464
I	0.3406	0.3117	174
J	0.3937	0.3374	492

which the fish may become more thermally efficient with increases in water temperature, for the moment we will assume that uncoupling of the heat exchanger represents the simplest solution. When the amount of heat lost via the gills necessary to fit mean activity and observed body temperature at each of the three treatment temperatures was calculated, the trend was for a greater predicted heat loss at higher temperatures (Table VIII). This trend was poorly defined in white muscle; this is not surprising since the theoretical model heat loss parameter is designed for heat loss from the center of the cylinder.

TABLE VIII. Fraction of Heat Loss at Gills as a Function of Water Temperature

Fish	15°C	20°C	25°C	30°C
A	0.53	0.58	0.68	0.72
B	--	0.72	0.73	0.86
C	--	0.66	0.74	--
D	--	0.66	0.76	0.75
E (white)	--	0.89	0.83	0.85
F (white)	--	0.81	0.83	0.85
G	--	0.70	0.82	--
H	--	0.80	0.84	0.87
I	--	0.73	0.77	--
J	--	0.53	0.53	0.64

E. Thermoregulation in Skipjack Tuna

Thermoregulation is supported by the work of Barrett and Hester (1964), Carey and Teal (1969), and Linthicum and Carey (1972). Furthermore, theoretical considerations alone suggest there must be some mechanism to sink heat at high activity rates and retain it at low. Some mechanism must be employed by the fish to increase thermal efficiency to get more thrust for less heat retained. If heat production is indeed proportional to a high exponent of velocity (and there is no reason to suppose that it is not considering abundant experimental work) forced convection at the lateral surface is insufficient to dissipate the heat produced at even aerobic activity levels. Using relationships formulated by Sharp and Vlymen (this volume) and Sharp and Francis (1976), excess temperatures can be calculated for a 70 cm FL skipjack tuna and plotted with swim speed as the dependent variable (Fig. 12). Using coefficients of total drag that approach 0.01, excessive temperatures are developed at speeds as low as 3 lengths sec^{-1}. A 10° excess is reached--which would limit fish to below 25°C water (Neill *et al.*, 1976)--even with a heat exchanger efficiency of only 25%. If the lowest conceivable coefficients of total drag are used (.001) damaging temperatures are reached at 6 lengths sec^{-1}

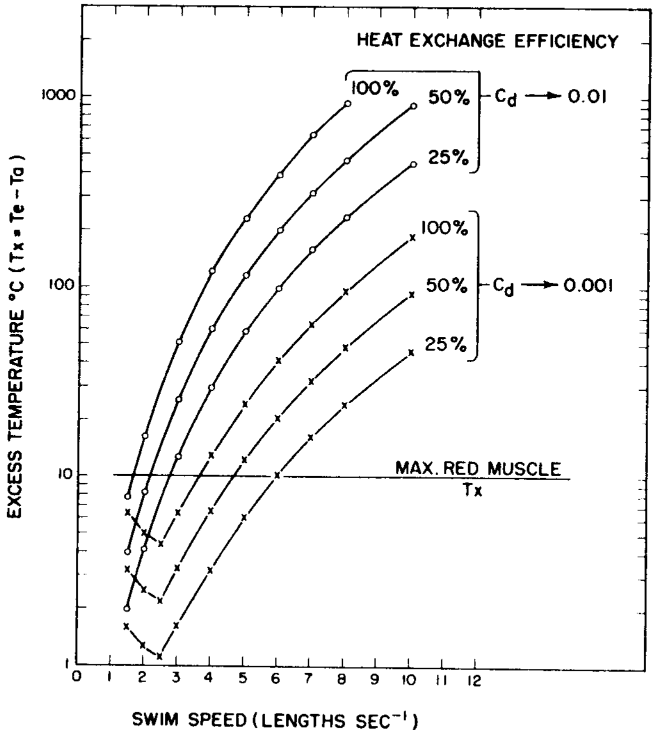

FIG. 12. Excess temperatures (T_x) calculated for a 70 cm skipjack tuna by methods of Sharp and Vlymen (this volume) at three levels of heat exchanger efficiencies and at two coefficient of drag minimums. T_x maximum of about 10°C is assumed for a fish swimming in 25°C water.

activity levels. We tracked a fish of this size swimming at this rate for more than 30 min.

Clearly then, skipjack tuna have a twofold problem; they must conserve heat during periods of low activity (or during their early life history) and they must dissipate excess heat during periods of moderate to high activity (or when they are larger) to avoid muscle temperatures in excess of 35°C (Neill *et al.*, 1976). We would like to suggest a mechanism.

As activity increases in a skipjack tuna, body temperature rises but it does not rise as fast as would be predicted by a model of forced convection at the lateral surface. Two mechanisms intervene: (a) swimming efficiency increases and (b) the heat exchanger allows proportionally more heat to escape to be dissipated at the gills. The latter would seem to be of a physiological process rather than a strictly mechanical one since at higher environmental temperatures more heat is also lost at the gills. These two mechanisms work to limit temperature during sustained, aerobic swimming. As swimming speed increases to levels where the white muscle must be called upon, anaerobic processes of energy production occur. Thermal efficiency may be much higher under these conditions; possibly lactate is excreted or at least retained until later recovery periods. During white muscle activity (perhaps now red muscle heat production has reached saturation) heat production may be less of a problem: (a) thermal efficiency may be greater; and (b) heat production occurs throughout a much greater (80%) muscle mass which is located closer to the lateral surface where forced convection removes heat more efficiently. The parabolic temperature profile used as a model for the Sharp and Vlymen forced convection simulation is replaced by the situation in which temperature is relatively homogeneous throughout the muscle mass. Upon capture, the animal is removed from the water and no heat is lost via the gills. But activity and thus heat production remain the same if not higher. The parabolic temperature profile reasserts itself due to the decreased central heat loss.

So for the moment, we suggest it would be safer to assume that skipjack tuna (and possibly other tunas with central exchangers) do physiologically thermoregulate; they have some mechanism to conserve heat during some periods of their life and to shunt heat to be dissipated at the gills during other periods and conditions. A central heat exchanger whose efficiency could be changed represents a simply implemented mechanism; so simple that it is hard to believe such an important evolutionary step has not been taken.