Magnitude and ecological implications of thermal inertia in skipjack tuna, Katsuwonus pelamis (Linnaeus)

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Synopsis

Heat exchange experiments with sedated and free-swimming skipjack tuna, *Katsuwonus pelamis* (Linnaeus), yielded the following results: For fish between 0.4 and 3.5 kg in weight (W),

1) inertial resistance to cooling and warming were virtually equal over the same span of temperature (18° to 30° C);

2) thermal inertia of red muscle, white muscle, and brain (in intact, living animals) was proportional to $W^{0.45}$ (i.e., coefficient of temperature change, k, $\infty W^{-0.45}$ for each tissue);

3) white muscle, brain, and ventricular blood equilibrated with a changed environmental temperature about 1.1, 3.3, and 20 times as rapidly as red muscle;

4) the countercurrent heat exchanger was about 95% efficient as a thermal barrier between gills and red muscle; consequently, only about half (30%–80%, depending on W) the total heat transfer between the red muscle and the environment occurred across the gills;

5) under conditions of thermal equilibrium, the red muscle and white muscle of sedated fish were warmer than the environment by amounts independent of environmental temperature but proportional to $W^{0.58}$ and $W^{0.61}$, respectively; in contrast, the excess temperature of the brain was independent of fish weight but bore a weak, positive relation to environmental temperature; and,

6) in two free-swimming fish stimulated to violent activity by chasing, the red muscle warmed at rates up to 0.3° C min^{-1}, ultimately attaining temperatures 1.5° and 3.4° C above pre-chasing equilibrium levels.

Comparison of our results with those of other researchers indicated that skipjack tuna exchange core heat with the environment only about 60% as rapidly as do typical teleosts and even somewhat more slowly than do air-breathing aquatic reptiles. Results 1) and 5) were taken to imply no short-term physiological thermoregulation in skipjack tuna; problematic evidence for physiological thermoregulation in other tunas and in aquatic reptiles is discussed. Calculations based on thermal inertia, excess temperature, and rate of warming indicated that minimum and maximum rates of metabolism in the red muscle of skipjack tuna are about 4 and 25 cal g^{-1}hr^{-1}, respectively. Similar considerations suggested that large thermal inertia and high rates of metabolism may pose an ecological problem for skipjack tuna as they grow in body mass: excess core temperatures may become so large that the muscle of the fish overheats, especially during periods of greatest activity in warm waters; speculative upper temperature limits are offered for skipjack tuna as a function of body size and activity level. Two potential benefits of large thermal inertia are discussed and illustrated with simulation models; these are 1) substantial independence from rapid fluctuations of environmental temperature as the fish move between the upper mixed layer and the thermocline, and 2) inertial 'memory' of thermal history to permit or enhance perception of weak temperature gradients.

* For present address, see p. 80.

Introduction

A remarkable feature of the tunas (Scombridae) is their tendency to be warmer by several Celsius degrees than the water in which they swim (Barrett & Hester 1964; Carey & Teal 1966 and 1969b; Carey et al. 1971; Stevens & Fry 1971; Linthicum & Carey 1972; and earlier references in Carey & Teal 1966). Such elevated body temperatures are probably unique among teleosts, lamnid sharks (Lamnidae) being the only other group of fishes now characterized as 'warm-bodied' (Carey & Teal 1969a). Both tunas and lamnid sharks are continuously swimming, highly active, pelagic fishes; and, both possess countercurrent heat exchangers in their blood-vascular systems (Carey et al. 1971).

Anatomical descriptions of fishes' heat exchange systems have been provided by Carey & Teal (1969a) for lamnid sharks; by Carey & Teal (1966), by Linthicum & Carey (1972), and by Graham (1975) for tunas of the genus *Thunnus*; by Graham (1973) for the black skipjack, *Euthynnus lineatus* Kishinouye; and, by Stevens, Lam & Kendall (1974) and by Graham (1975) for the skipjack tuna, *Katsuwonus pelamis* (Linnaeus). The essential components of these fishes' heat exchange systems are *retia mirabilia* that retard the transport of blood-borne heat between the gills and core tissues, especially the muscle. Thus, heat generated as a by-product of metabolism is retained, causing elevated temperatures in the muscle mass and nearby tissues. The heat exchanger also damps the influence of changes in water temperature on core temperature. The latter effect has received only a fraction of the attention given to metabolic heat retention, but the two are of course complementary aspects of the same thing—large thermal inertia.

High metabolic rates (Gordon 1968) and large thermal inertia suggest the potential for physiological thermoregulation in tunas. In fact, the work of Carey and his associates (Carey & Teal 1966, 1969b; Carey et al. 1971; Linthicum & Carey 1972; Carey & Lawson 1973) has led to an apparent consensus that at least the larger tunas, such as the bluefin, *Thunnus thynnus* (Linnaeus), do physiologically thermoregulate over broad ranges of environmental temperature. However, Neill & Stevens (1974) have questioned the certainty of rapid physiological thermoregulation in bluefin tuna on grounds that existing data do not offer evidence of short-term variation (controlled or

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otherwise) in the magnitude of the bluefin's thermal inertia.

The purpose of this paper is to report the results of first experiments on heat exchange processes in a scombrid and to explore the role of large thermal inertia in tuna ecology. The skipjack tuna, physiologically and behaviorally the best known of the tunas, served both as the experimental animal and as the model for several conjectural probes into the thermal biology of scombrids.

Materials and methods

Source and maintenance of experimental subjects

Skipjack tuna, weighing 0.4 to 3.5 kg, were caught on barbless hooks from Hawaiian waters and transported in 2,500 liter shipboard tanks to the National Marine Fisheries Service's Kewalo Research Facility in Honolulu. There, the fish were transferred into 40,000 to 700,000 liter outdoor tanks open to the sky. Both transport and holding tanks were supplied with flowing seawater at 23° to 25° C; in addition, oxygen was bubbled through the water in the transport tanks.

Once each day, skipjack tuna in the holding tanks were offered as much thawed smelt or anchovies as they would eat; most fish fed vigorously by the fifth day in captivity. Every third or fourth day, each skipjack tuna was fed a multiple vitamin, in tablet form, to supplement its diet.

Nakamura (1972) has provided other details of the capture and transport of live tunas and their maintenance at the Kewalo Research Facility.

Cooling and warming experiments

Skipjack tuna were subjected to abrupt 4° to 6° C increases or decreases of water temperature which were maintained until tissue temperatures stabilized. Temperatures of red muscle, of venous blood, or of red muscle, white muscle, and brain simultaneously, were monitored throughout each experiment. From these records, excess temperatures and coefficients of temperature change were determined for each tissue; these parameters were then related to each other, to fish weight, and to other experimental variables.

Experiments were conducted both with sedated, restrained fish and with non-drugged, free-swimming fish. The two experiments with each of two

ee-swimming fish were performed to validate the
:ore efficient but previously untried procedure
.volving restrained fish, from which the majority
f data was obtained.

rocedure with restrained fish

or each set of experiments, one skipjack tuna
as removed from a holding tank either by angling
ith a barbless hook or by dipnetting. Within 10
:c. of capture, the fish was given a 0.2 to 0.6 ml
$_3^{-1}$ intramuscular injection of sodium pento-
arbital (in aqueous solution, 60 mg ml^{-1}) and
:turned to the holding tank. When, after 10 to 30
iin., the sedative caused deterioration of swim-
iing equilibrium, the fish was dipnetted from the
ink and secured in a perfusion trough.

The trough was U-shaped in cross-section and
iade from inert plastics. Seawater, for respiration
id heat exchange, flowed through a plastic pipe
iat penetrated the trough's incurrent endplate;
ist through the plate, the pipe ended in a foam-
lastic mouthpiece about which the fish's jaws
ere firmly secured. At the opposite end of the
ough, a movable excurrent end-plate was posi-
oned to make the effective length of the trough
ist exceed that of the fish; an overflow outlet in the
icurrent end-plate then was adjusted so that the
ough's water level just covered the fish's upper
irface. Thus, with proper adjustment of length
id water depth, the trough's effective volume was
iade to conform with body size of individual fish.

Further accomodation for fish size was achieved
y using two troughs of different widths. One, for
ih weighing less than 3 kg, was 15 cm wide, giving
o overall (fish plus water) operating volume that
veraged 7 liters per kg of fish. For larger fish, a
·ough 22 cm wide was used; its overall operating
olume was about 8 liters per kg of fish. At least
.5 cm of water separated each fish from the nearest
iner surface of its trough.

Gill perfusion rates were also varied to accomo-
ate fish of the two size groups: 6 liters min^{-1} for
ih weighing less than 3 kg; 10 liters min^{-1} for
irger fish.

In addition to binding the fish's jaws around the
erfusion mouthpiece, we also secured the fish with
vo 3 cm wide straps of knotless nylon netting
i mm bar mesh) that passed around the animal's
·unk, one just posterior to the pectoral fin inser-
ons and the other just anterior to the vent. The
nds of each strap passed from an anchor at the

trough's bottom, then around the body, crossing
over the animal's dorsum to anchor points on op-
posite sides of the trough's rim. The amount of
tension in the straps permitted a pencil to be slipped
between strap and fish.

After the fish had been secured in the trough and
perfusion flow rate and trough volume had been
adjusted, sensors for monitoring temperatures of
gill-perfusion water, red muscle, white muscle, and
brain were placed. Each sensor was a thermistor
mounted in the tip of a hypodermic needle, 18
gauge, except 20 gauge for brain. The tip of the
water-temperature probe was located in the gill-
perfusion flow, just upstream from the incurrent
end-plate of the trough. Muscle temperatures
were monitored in the region of maximum fish
girth. The red-muscle probe was inserted vertically
into the deep red muscle, 1 to 2 cm lateral to the
12th or 13th vertebra. White-muscle temperatures
were measured in the epaxial mass, at a point in the
longitudinal plane 45° above the vertebral-frontal
plane and half way between the 14th vertebra and
the overlying skin surface. The brain probe was
pushed through the pineal window, between the
optic lobes, and to a point in or near the dien-
cephalon. Each tissue-temperature probe was se-
curely positioned by first pushing the needle
through a 4 mm thick, 20 mm square of Neoprene[1]
glued to a 20 mm wide strap of Velcro that passed
snugly around the fish's body.

The thermistors were electrically connected to
separate channels of an electronic thermometer.
Temperature measurements were accurate to
0.1° C, with an operating time constant of about
5 seconds.

Experiments began with each tissue at thermal
equilibrium with the perfusion water. Then, the
perfusion temperature was abruptly increased or
decreased by 4° to 6° C. When all tissues had
equilibrated with the new perfusion temperature,
the experiment ended. With 8 of the 15 subjects, a
second experiment was then performed; this ex-
periment usually involved a perfusion-temperature
change opposite in direction but equal in magni-
tude to that of the first. With four subjects, a third
experiment replicated the temperature treatment
applied in the first experiment. All experiments
were performed within the perfusion-temperature
range, 18.3°–29.4° C.

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

After conclusion of the last experiment in the sequences described above, other experiments were performed on some subjects. In a pair of such experiments with each of three skipjack tuna, we monitored venuous blood temperature as the perfusion water temperature first was increased abruptly from 19° to 23.5° C and then, after the blood equilibrated at 23.5° C, was decreased to 19° C. Each subject began the first experiment of the pair at equilibrium with 19° C water. The probe that had been used to monitor brain temperature was removed, the fish was turned on its side, and the tip of the probe was inserted through the gular isthmus into the bulbus arteriosus of the heart. The fish remained on its side, with the probe tip in the bulbus arteriosus, until both experiments of the pair had been completed.

Procedure with free-swimming fish

For each of two sets of experiments, one skipjack tuna was removed from a holding tank by angling with a barbless hook. The fish was then quickly transferred, in a polyethylene bag with a few liters of seawater, to an experimental tank. The experimental tank was made of fiberglass-reinforced polyester resin, circular in shape with a diameter of 2.4 m, and filled to a depth of 0.6 m with circulating seawater at 24° C.

One or three days later, the fish was caught from the experimental tank and provided with a transducer of red-muscle temperature. The temperature sensor was a thermistor sealed in the tip of a 3 cm long barbed dart made of 12 gauge stainless steel tubing. To implant the sensor, we held the fish by its lower jaw while a stream of 24° C seawater irrigated the gills; the dart was inserted to approximately the same location in the red muscle as that monitored in restrained fish. A 2 mm diameter cord of braided nylon was drawn with a needle (in the manner of a spaghetti tag) through the dorsal white musculature just posterior to the dart's insertion; the ends of the cord then were united above the fish's dorsal midline and connected by another length of cord to a swivel 1.5 m above the tank's water surface. Electrical leads from the thermistor were slackly taped to the cord, from fish to overhead swivel; this arrangement prevented undue strain on the sensor. A mercury-ring connector in the swivel afforded a continuous electrical circuit between the thermistor and the electronic thermo-

meter, despite the circular path the fish would swim upon its release.

Installation of the sensor and related harnessing required 1.5 min. in one case and 2.5 min. in the other; when these were completed, the fish was released into a second experimental tank. This tank was immediately adjacent to the first and identical to it, except 5° C cooler. A lever, on which the swivel-had been mounted, was positioned so that the swivel was above the center of the second tank; length of the line between fish and swivel was sufficient to allow the fish access to all parts of the tank.

Activity of the fish, red-muscle temperature, and water temperature were monitored until muscle temperature reached equilibrium. Then a warming experiment was performed. The fish was carefully dipnetted from the 19° C tank and put back into the 24° C tank; simultaneously, the swivel-lever was swung into position above the 24° C tank. Again, fish activity, red-muscle temperature, and water temperature were observed until muscle temperature stabilized.

When the warming experiment was completed, the fish was vigorously chased with a dipnet for several minutes to determine the effect of heightened activity on red-muscle temperature. Afterwards, the fish was removed from the tank, weighed, and measured for fork length.

Estimation of heat-exchange parameters

Time series of tissue and water temperatures comprised the primary data from experiments both with restrained and free-swimming fish. From graphical plots of these series (Fig. 1A), an excess temperature and a coefficient of temperature change were estimated for each tissue.

Excess temperature (Stevens & Fry 1970; Neill & Stevens 1974), T_x, was estimated by the difference between tissue and water temperatures at thermal equilibrium. Thermal equilibrium was defined by lack of tissue-temperature change exceeding 0.1° C in a period of at least 10 min. for muscle and brain or 1 min. for blood.

To quantify the rate of each tissue's approach to thermal equilibrium, we calculated the coefficient of temperature change, k. The rate of tissue-temperature change was assumed to be directly proportional to the difference between equilibrium and actual tissue temperatures (Neill & Stevens

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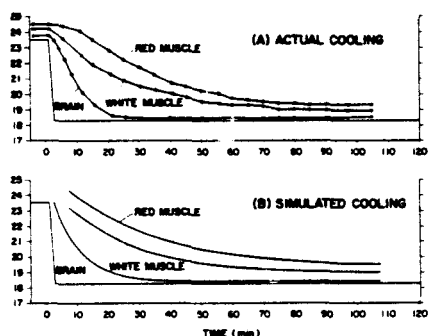
Fig. 1. Actual (A) and simulated (B) time series of tissue temperatures in a 1.60 kg skipjack tuna subjected to an abrupt decrease in water temperature, from 23.5° to 18.3° C. Parameters estimated from the actual series and used in the simulations were as follows:

Tissue	T_x (°C)	k (°C min^{-1} °C^{-1})
Red muscle	1.0	0.034
White muscle	0.6	0.043
Brain	0.1	0.117

1974), the former being a constant function of water temperature and, therefore, itself constant within experiments:

$$\frac{dT_b}{dt} = k[T_e - T_b(t)] \tag{1}$$

or, integrating with respect to t,

$$\frac{T_e - T_b(t)}{T_e - T_b(o)} = e^{-kt} \tag{2}$$

which gives, after transforming and rearranging,

$$k = -\frac{1}{t}\log_e\left[\frac{T_e - T_b(t)}{T_e - T_b(o)}\right] \tag{3}$$

where k = coefficient of temperature change, °C min^{-1} °C^{-1}; $T_b(o)$ = tissue temperature, °C, at some initial time; $T_b(t)$ = tissue temperature, °C, t minutes after the initial time; T_e = equilibrium tissue temperature, °C; and t = time, min., for tissue temperature to change from $T_b(o)$ to $T_b(t)$.

In experiments with restrained fish, $T_b(o)$ for muscle was taken 5 min. after the perfusion water

reached the temperature to be maintained for the duration of the experiment. The 5 min. delay assured complete flushing of the trough by water at the new perfusion temperature and still permitted calculation of k's to be based on temperature differences [i.e., $T_e - T_b(t)$; $T_e - T_b(o)$] at least an order of magnitude larger than experimental noise ($\pm 0.1°$ C). Brain and venous blood changed temperature more rapidly than muscle, making it necessary to take $T_b(o)$ for these tissues as soon as the perfusion temperature reached its experimental level. Complete flushing of the entire trough was not as critical for accurate estimation of brain and blood k's as for muscle k's. The brain exchanged heat primarily with water in the incurrent one-third of the trough, throughout which part flushing was complete within 30 sec. Heat exchange between blood and water occurred primarily at the gills, where water temperature lagged perfusion temperature changes by less than 5 sec.

To maximize comparability of data from restrained and free-swimming fish, we took $T_b(o)$ for red muscle in free-swimming fish at 5 min. after the fish was put into the experimental tank.

After $T_b(o)$ and T_e had been read from a given time-series plot, k was then calculated from equation (3) by finding $T_b(t)$ at $t = \lambda$ such that $[T_e - T_b(t)]/[T_e - T_b(o)]$ was 0.37:

$$k = -\frac{1}{\lambda}\log_e(0.37) \simeq \frac{1}{\lambda}. \tag{4}$$

Evaluation of heat-transfer pathways: gills versus outer body surface

To assess the relative contribution of gills versus outer body surface to heat exchange in skipjack tuna, we estimated for red muscle, white muscle, and brain the proportion of total heat transfer via the gills. These data were collected from each of seven restrained fish immediately after it had served in the cooling/warming experiments described above.

The gills and mouth of each fish were perfused with seawater different in temperature from that which bathed the general skin surface. This was accomplished by maintaining the usual gill-perfusion flow at 28° to 29° C (variation less than 0.2° C within experiments) while water at 23.5 ± 0.1° C flowed directly into the incurrent end of the

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trough at 30 liters min.$^{-1}$. Mixture of the two flows provided a bath surrounding the fish that varied less than 0.2° C throughout the trough and was about 4° C cooler than water perfusing the gills. Dual-temperature perfusion continued until tissue temperatures equilibrated.

The proportion of heat transferred via the gills was estimated by considering for each tissue the measured equilibrium temperature relative to the equilibrium temperatures that hypothetically would have obtained had the entire fish been bathed in water at either gill-perfusion temperature or at trough temperature:

$$T_e = \alpha(T_{ag} + T_x) + (1 - \alpha)(T_{ab} + T_x) \qquad (5)$$

which gives, after rearranging and simplifying,

$$\alpha = \frac{T_e - T_{ab} - T_x}{T_{ag} - T_{ab}} \qquad (6)$$

where α = proportion of heat transferred via gills (and mouth); T_e = measured equilibrium temperature, °C; T_{ag} = gill-perfusion temperature, °C; T_{ab} = trough temperature, °C; and, T_x = excess temperature, °C, measured in preceding series of cooling/warming experiments.

Results

Activity and behavioral responsiveness of fish (steady state)

Even sedated fish exhibited swimming activity and were responsive to touch throughout the major part of each experimental set. Characteristically, violent bursts of activity gave way to strong, rhythmic swimming at 2 to 4 tail beats sec.$^{-1}$ after fish had been in the trough 10 to 30 min. Thereafter, both the amplitude and frequency of tail beats gradually decreased until, after a few hours, swimming motions generally were weak or ceased entirely. Occasionally, tail beating resumed or became stronger for periods lasting up to an hour during the course of an experimental set. Throughout all experiments reported in this paper, fish that had become immobile still 'gasped' in response to a finger's touch on the opercular margin.

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Free-swimming skipjack tuna swam continuously at 1.5 to 3 body lengths sec.$^{-1}$, with 2 to 4 tail beats sec.$^{-1}$, except during the terminal experiments in which they were chased. Chasing caused fish to swim at speeds in excess of 10 body lengths sec.$^{-1}$, decreas .g to 5 body lengths sec.$^{-1}$ as the fish tired. Only brief (less than 5 min.) increases in swimming speed followed transfer between experimental tanks.

Neither restrained nor free-swimming fish varied activity in a way detectably related to temperature.

Excess tissue temperatures (steady state)

Excess temperatures ranged from 2.6° C in the red muscle of one free-swimming and one restrained fish to 0.0° C in the brain of several restrained fish.

For restrained fish, potential dependence of red muscle, white muscle, and brain excess temperatures on several independent variables was evaluated by step-wise linear regression analysis (Dixon 1967). The following full model was assumed:

$$\log T_x' = \beta_0 + \beta_1 \log W + \beta_2 T_a + \beta_3 t + \beta_4 d + \epsilon \qquad (7)$$

where $T_x' = \begin{cases} T_x, °C, \text{ for red and white muscle;} \\ T_x + 1, °C, \text{ for brain;} \end{cases}$ W = fish weight, kg; T_a = perfusion temperature, °C; t = time, min., in the trough; d = sedative dosage, ml kg^{-1}; β_i = regression parameters; and, ϵ = random experimental error. The analysis yielded the following set of reduced regression equations [P ≤ 0.05; (a ± b)$_{95°}$ indicates 95% parametric confidence interval on a]: for red muscle,

$$\log T_x = 0.1608 + (0.5800 \pm 0.3350)_{95°} \log W$$
$$- (0.0009 \pm 0.0006)_{95°} t,$$
$$R = 0.62** (n = 26); \qquad (8)$$

for white muscle,

$$\log T_x = 0.1110 + (0.6067 \pm 0.3883)_{95°} \log W$$
$$- (0.0009 \pm 0.0008)_{95°} t,$$
$$R = 0.57* (n = 25); \text{ and} \qquad (9)$$

for brain,

$$\log (T_x + 1) = -0.1724$$
$$+ (0.0105 \pm 0.0045)_{95°} T_a,$$
$$R = 0.69** (n = 26). \qquad (10)$$

Thus, excess temperature relations of red and white muscle were similar to each other but markedly different from that of brain. Sedative dosage done among the independent variables failed to affect significantly excess temperature of any tissue among the three.

Variation in fish weight and time in the trough significantly affected excess temperatures of both red and white muscle. Excess temperatures of the two muscle tissues differed only in their means; both responded, with almost identical slopes, positively to increases in fish weight and negatively to increases in trough-time. For a given fish weight and trough-time, excess white muscle temperature was about half the corresponding excess red muscle temperature; consideration of paired red and white muscle T_x's (Fig. 2) confirmed this result. Point solutions of equations 8 and 9 for T_x at $t = 300$ min. ($\simeq \bar{t}$) are $0.46°$ and $1.61°$ C for red muscle, and $0.24°$ and $0.89°$ C for white muscle of restrained fish weighing 0.4 and 3.5 kg, respectively.

Two observations were made on excess red muscle temperature of each free-swimming skipjack tuna; these were $1.2°$ and $1.5°$C for the 1.21 kg fish, and $1.7°$ and $2.6°$C for the 1.78 kg fish. Solving equation 8 for point estimates of T_x at $t = 0$ min. gives $1.62°$ and $2.02°$C for restrained skipjack tuna weighing 1.21 and 1.78 kg, respectively.

In contrast to muscle, brain excess temperature depended only on perfusion temperature; increase in brain T_x was associated with increase in T_a. Point solutions of equation 10 for T_x are $0.04°$ C for minimum T_a, $18°$ C, and $0.39°$ C for maximum T_a, $30°$ C.

Fig. 3. Relation between fish weight and the coefficient of temperature change (k) in the red muscle of skipjack tuna. Point symbols indicate values determined by cooling restrained fish (v), by warming restrained fish(∧),by cooling free-swimming fish (◆), and by warming free-swimming fish (◆). The heavy middle line is the regression of k on weight for both cooling and warming experiments with restrained fish; the inner and outer pairs of lighter lines indicate $95%$ confidence intervals (about the regression line) for expected k given weight and for a single observation on k given weight, respectively.

Excess temperatures of venous blood were too small to be reliably measured when the entire fish was at thermal equilibrium. However, the relatively slow rate of temperature change in the muscle mass permitted indirect estimation of blood excess temperatures from the ratio, $(T_a - T_{bl})/(T_a - T_{rm})$, where T_{bl} was blood temperature when its rate of change just slowed to approximate the rate of change in non-equilibrium red muscle temperature, T_{rm}. Values of the ratio from two experiments with each of three skipjack tuna (weighing 1.55 to 1.61 kg) ranged from 0.075 to 0.285 with a median of 0.11. This implies that excess temperature of venous blood was about $11%$ of the corresponding red muscle T_x.

Coefficients of tissue-temperature change

Red muscle, white muscle, and brain of restrained skipjack tuna cooled and warmed at rates inversely proportional to fish weight (Figs. 3–5). Double logarithmic plots of the coefficient of temperature change, k, against fish weight appeared linear, with slopes for all three tissues identically equal -0.45 to two decimal places. Red and white muscle yielded k versus W relations not only alike in slope
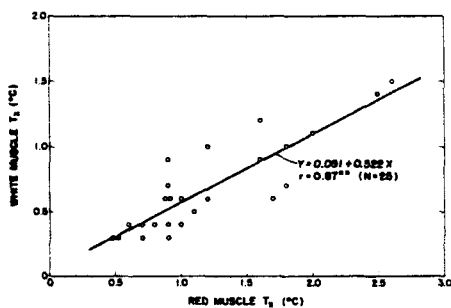
Fig. 2. Relation between excess temperatures of red and white muscle in skipjack tuna. Each point indicates one of 25 paired observations; data were collected from 15 sedated fish.
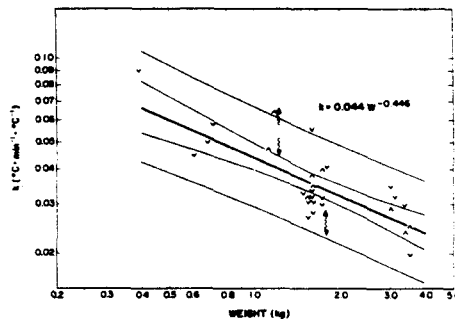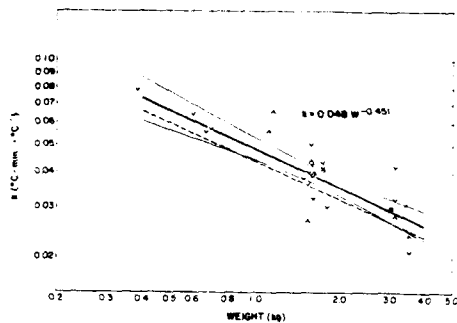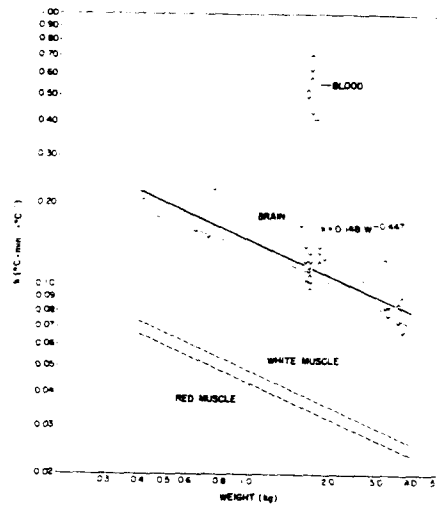
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Fig. 4 Relation between fish weight and the coefficient of temperature change (k) in the white muscle of skipjack tuna. Point symbols indicate values determined by cooling (v) and warming (⊆) restrained fish. The heavy solid line is the regression of k on weight for both cooling and warming experiments: the pair of lighter solid lines indicates the 95% confidence interval (about the regression line) for expected k given weight. The dashed line gives the regression of red muscle k on weight (from Fig. 3) for comparison.

Fig. 5 Relation between fish weight and the coefficients of temperature change (k) in the brain and venous blood of skipjack tuna. Point symbols indicate values determined by cooling (v) and warming (Λ) restrained fish. The heavy solid line is the regression of brain k on weight for both cooling and warming experiments: the pair of lighter solid lines indicates the 95% confidence interval (about the regression line) for expected brain k given weight. The dashed lines give the regressions of red and white muscle k on weight (from Figs. 3 and 4) for comparison.

but also in mean (P ≤ 0.05: Fig. 5). Brain cooled and warmed about 3.3 times as rapidly as muscle of the same fish, over the fish-weight range 0.4 to 3.5 kg. For fish weighing 1.6 kg, at least, venous blood changed temperature about 20 times faster than muscle (Fig. 5).

The above relations were developed without distinction between warming and cooling experiments, because we found no evidence for a systematic difference between warming and cooling k's. Both warming and cooling k's were available from each of seven restrained skipjack tuna ranging in weight between 1.55 and 3.53 kg. Geometric means of the quotient, warming k/cooling k, were 1.07, 0.99, and 0.96 for red muscle, white muscle, and brain, respectively. For each tissue, the quotient 1.0 fell well within the 95% parametric confidence interval on the geometric mean. Thus, none of the tissues/warmed at a rate significantly different from the rate at which it cooled.

Red muscle k's from free-swimming fish were similar to those obtained from restrained fish. One free-swimming fish yielded k's larger, and the other k's that were smaller than those of similarly-sized restrained fish. Only one of the four values from free-swimming fish fell outside the 95% parametric confidence interval on red muscle k, given weight, for restrained fish (Fig. 3).

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Red muscle temperatures of highly active (chased) fish

Red muscle temperatures of free-swimming skipjack tuna increased from their equilibrium values at rates of about 0.3° C min.⁻¹ during the first few minutes of chasing (Fig. 6). Maximum temperature attained by red muscle of the larger fish was 29.6° C – 3.4° C over the equilibrium temperature and 5.7° C greater than water temperature. This temperature was reached after 15 min. of chasing, when the fish stopped swimming and lost attitudinal equilibrium: the fish did not resume swimming and had no detectable heart beat 15 min. after chasing ended. The smaller fish was chased 4.5 min. until the onset of exhaustion became evident. After an 18.5 min. 'rest' period, chasing was resumed for 2 min.; the fish then stopped swim-
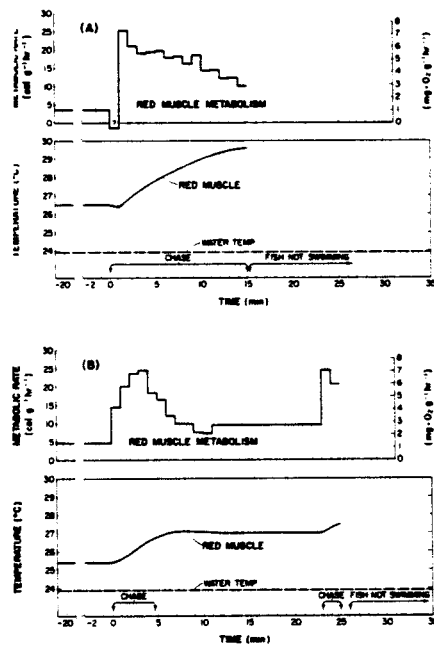
Fig. 6. Time-course of red muscle temperature and metabolic rate in two free-swimming skipjack tuna before and during violent swimming activity (stimulated by chasing). A. 1.78 kg skipjack tuna; red muscle k (measured) = 0.028° C min^{-1} ° C^{-1}.
B. 1.21 kg skipjack tuna; red muscle k (measured) = 0.065° C min^{-1} ° C^{-1}.

ming and died. Red muscle temperature of the smaller fish reached 27.1° C (1.5°C above equilibrium temperature and 3.2° C above water temperature) shortly after the first period of chasing ended, remained almost constant at 27.0° C during the rest period, and had increased to 27.5° C when swimming stopped following the resumption of chasing.

Proportion of heat transfer via gills

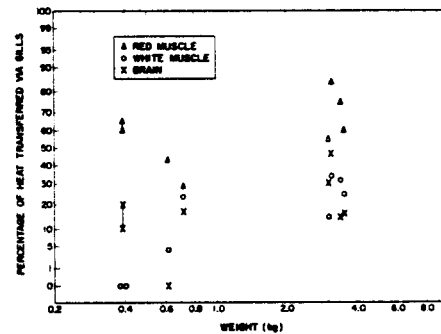The gills accounted for a larger fraction of heat transfer between the environment and red muscle

Fig. 7. Relation between skipjack tuna weight and the fraction of heat transfer accomplished by way of the gills. Two replicate observations (symbols connected by a line) were made for each tissue in the 0.4 kg fish; single observations were made for each tissue in each of the other six fish.

than between the environment and white muscle or brain (Fig. 7). Deep, well vascularized red muscle effected 27% to 84% of its heat exchange via the gills. Percentages of gill heat-transfer were similar for white muscle and brain, ranging from 0% to 35% and from 0% to 46%, respectively.

A part of the inter-fish variation in gill heat-transfer seemed to be associated with variation in fish size. Red muscle, white muscle, and brain of larger skipjack tuna tended to exchange more heat via the gills than did respective tissues of smaller skipjack tuna (Fig. 7).

Discussion

Adequacy of exponential model for rates of tissue-temperature change

We, like other students of heat exchange in aquatic poikilotherms (Bartholomew & Lasiewski 1965; Stevens & Fry 1970; Weathers & White 1971; Spray & May 1972), adopted an exponential model to describe rates of temperature change. The basic model has been called 'Newton's law of cooling' (Kleiber 1972, among many others) and, more appropriately, 'Newton's law of excess temperature' (Fry 1967). In conformity with the reasoning of Neill & Stevens (1974), we used T_e instead of the more conventional value, T_a, in equation 1 and in its descendants.

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Temperature change in one tissue of skipjack tuna could not have been wholly independent of simultaneous temperature changes in other tissues. The effective driving gradient of temperature at each anatomical point was the difference, $T_e - T_b$. Although T_a was constant, T_e must have continuously changed as temperatures of surrounding tissues changed and as (if) metabolism at the point varied. Therefore, the model specified by equation 1 could not have been strictly appropriate, because absolute constancy in T_e was not achieved.

Despite weakness of the model on theoretical grounds, we accepted it as adequately descriptive of the process of concurrent temperature change in the various tissues of living skipjack tuna. Grounds for the model's acceptance included the lack of significant differences between k's determined by cooling and warming experiments and the close agreement between actual cooling/warming curves and those simulated by application of equation 2 with empirically derived parameters (e.g., Fig. 1, cf. panels A and B).

Physiological thermoregulation in skipjack tuna and other aquatic poikilotherms

Countercurrent heat exchangers in the circulatory systems of tunas (Carey & Teal 1966; Linthicum & Carey 1972; Graham 1973, 1975; Stevens, Lam & Kendall 1974) and lamnid sharks (Carey & Teal 1969a) provide these fishes with one essential ingredient of physiological thermoregulation — large thermal inertia that retards the loss of metabolic heat, resulting in large excess body temperatures. However, realization of physiological thermoregulation must also involve a second essential ingredient, the ability to *control* excess body temperature so that it varies inversely with environmental temperature. Such control could be achieved either by decreasing metabolic rate or, more logically, by increasing k as environmental temperature increases.

Large bluefin tuna, *Thunnus thynnus* (Linnaeus), and shortfin mako, *Isurus oxyrinchus* Rafinesque, have smaller excess body temperatures when caught in warm waters than when they are taken in cold waters (tuna: Carey & Teal 1969b; Linthicum & Carey 1972; shark: Cary & Teal 1969a). Thus, these fishes would appear to be capable of considerable physiological thermoregulation, at least when exposure to a given environmental temperature

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persists for the days or weeks necessary for acclimatory adjustments. On the basis of telemetry experiments, Carey and his associates (Carey et al. 1971; Carey 1973; Carey & Lawson 1973) have carried the case for physiological thermoregulation in the bluefin tuna further by suggesting that large bluefin are capable of rapid physiological thermoregulation in the same sense as mammals. Neill & Stevens (1974) have offered a different interpretation of these telemetry data — i.e., that the observed responses of body temperature to changes in water temperature could simply reflect constant but small k coupled with constant heat production to produce a constant T_b (large thermal inertia, but no physiological thermoregulation).

Our warming and cooling experiments yielded no evidence for physiological thermoregulation in skipjack tuna. Excess temperatures of red and white muscle were statistically unrelated to environmental temperature. Brain excess temperatures not only were small but also varied directly with environmental temperature (presumably an Arrhenius effect), whereas physiological thermoregulation requires an inverse relationship between T_x and T_a. Moreover, there was no indication that tissue k's varied systematically with either the level of T_a or direction of change in T_b. Therefore, our experiments offer no support to the hypothesis of Stevens & Fry (1971) that '... skipjack tuna [physiologically] regulate their body temperature over an ambient temperature range of about 25° – 34° C.'

Many investigators of reptilian thermobiology (Bartholomew & Tucker 1963, 1964; Bartholomew & Lasiewski 1965; Bartholomew, Tucker & Lee 1965; Weathers & White 1971; Spray & May 1972) have construed dissimilar rates of warming and cooling to indicate physiological thermoregulation. In fact, several circulatory mechanisms whereby reptilian k's may change in response to temperature have now been demonstrated (Heath, Gasdorf & Northcutt 1967; Baker & White 1970; Weathers & White 1971). However, the fact that reported rates of warming exceed those of cooling for the majority of lizards and turtles (see compilation of data by Spray & May 1972) may be attributed in part to the convention of calculating rates of temperature change as if dT_b/dt were a linear function of $T_a - T_b$. Neill & Stevens (1974) have argued that such cannot be the case for animals that maintain excess body temperatures. Whenever $T_x > 0$ ($T_e - T_a > 0$), $|T_a - T_b|$ will exceed
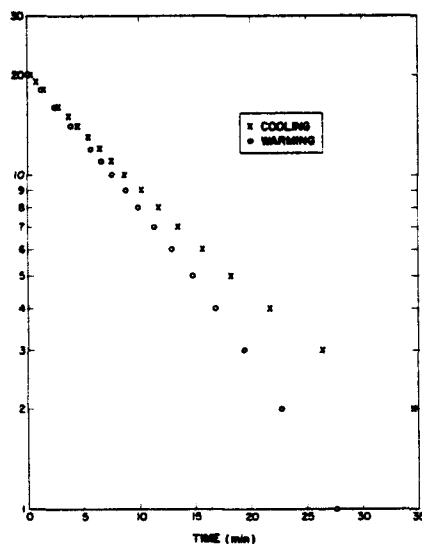
g. 8. Simulation of cooling and warming curves for a point
the body of an aquatic poikilotherm that has constant
$_t$ = 1.0° C and constant k = 0.0856°C min^{-1}°C^{-1}(for both
)oling and warming). |ΔT|is the absolute difference between
)dy temperature and water temperature. Note that the curves
'e, in fact, curves rather than straight lines and that the
ite of cooling is less than that of warming even though the
s are identical.

$T_c - T_b$| when the animal is cooling and will be
ess than $|T_c - T_b|$ when the animal is warming
given the same $|T_a - T_b|$ and T_x in the two experi-
nents); this relation leads automatically to the
esult that $d|T_a - T_b|/dt$ is greater for warming
han for cooling when k is the same for warming
md cooling (Fig. 8). (For terrestrial poikilotherms
inder conditions of low relative humidity, T_x may
)e negative owing to evaporative cooling [e.g.,
Whitfield & Livezey 1973]; then, $d|T_a - T_b|/dt$ is
;reater for cooling than for warming, given con-
;tant k.) Moreover, k's calculated from the rela-
ion

$$k' = -\frac{1}{t} \log_e \left[\frac{T_a - T_b(t)}{T_a - T_b(o)} \right] \qquad (11)$$

ire in error by an amount that increases as $T_b(t) -$
T_a approaches T_x; i.e., 'k' approaches zero as
$T_b(t) - T_a$ approaches T_x (because t approaches ∞).

Bartholomew & Tucker (1963), recognizing the
flaw inherent in calculations of k based on $d|T_a -$
$T_b|/dt$, corrected their apparent k's for the effects of
metabolism; heart rate was monitored in bearded
dragon, *Amphibolurus barbatus*, undergoing tem-
perature change and then indexed to equivalent
heat production according to heart-rate/O_2 con-
sumption relations determined from separate ex-
periments at consta..t temperatures. Spray & Belkin
(1972) have since pointed out that heart rate in
Iguana iguana is linearly related to temperature of
blood flowing through the heart, which, in iguana
(Spray & Belkin 1973) as in skipjack tuna, has less
thermal inertia than the body 'core.' Thus, heart
rate in a lizard or fish whose body temperature is
changing would appear a poor indicator of meta-
bolic heat production.

Spray & May (1972) used oxygen consumption
data from the literature to correct their apparent
k's for several turtles. They concluded that resting
metabolism alone was not enough to account for
differences between observed heating and cooling
rates, suggesting that turtles are capable of chang-
ing k by altering blood flow to the periphery of the
body in response to changes in temperature.

Rates of heat exchange in skipjack tuna and other aquatic poikilotherms compared

Stevens & Fry (1974) have compiled coefficients of
core-temperature change for fishes and aquatic
reptiles. Comparing cores of animals with equal
weight, our skipjack tuna equilibrated with a new
water temperature only about 60% as rapidly as
typical teleosts (Catostomidae) and even some-
what more slowly than aquatic reptiles (turtles of
the genera *Pseudemys* and *Chelydra*, and the
Galápagos marine iguana, *Amblyrhynchus crista-
tus*). Considering that fishes must achieve respira-
tory exchange with water (which has much greater
heat capacity and much less oxygen per unit volume
than air), the observation that skipjack tuna ex-
change heat more slowly than aquatic lung-
breathers is evidence of high efficiency in the
skipjack's countercurrent heat exchanger.

Red muscle, white muscle, and brain of skip-
jack tuna —despite marked differences in vascular-
ization and distance from the skin surface—yielded
k's related to body weight by almost identical
exponents of weight: -0.446, -0.451, and -0.447.
We know of no other published study in which
rates of temperature change were monitored simul-

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taneously at several locations within a fish. Spray & Belkin (1973) observed that the cloaca and head of terrestrial lizards have greater thermal inertia than the heart and lungs, but these authors presented no information on the relation between thermal lag of lizard tissues and body weight.

It seems to us that k's measured very near the skin surface ought to be weight-independent ($\propto W^0$), whereas the relation between core k and body weight should be similar to that between the inverse of mean blood circulation time (between tissue and heat sink/source) and body weight. That weight exponents for red muscle, white muscle, and brain k's of skipjack tuna were virtually identical, non-zero values suggests that the heat exchange process of overwhelming predominance in all three tissues was convection, especially forced convection via blood circulation.

Efficiency of skipjack tuna heat exchanger as a thermal barrier

Present data permit coarse estimation of the efficiency with which the countercurrent heat exchanger of skipjack tuna acts as a thermal barrier. The estimate is provided by considering the median temperature excess — 0.11 times that of red muscle — carried by venous blood just before it reached the gills (T_{xbl}). Calculation of efficiency is based on the following estimates and assumptions:

1) Of venous blood in the bulbus arteriosus, 60% has passed through the countercurrent heat exchanger and 40% has not (Stevens, Lam & Kendall 1974).

2) Arterial blood entering the heat exchanger has no temperature excess.

3) Venous blood entering the heat exchanger has a temperature excess equal that of red muscle (T_{xrm}).

4) Venous blood not passing through the heat exchanger has a temperature excess (T_{xvo}) equal that of the body average excluding red muscle; we assume $T_{xvo} \simeq 0.2\,T_{xrm}$.

5) Changes of blood temperature in the veins are negligibly small.

6) Venous blood from all tissues has mixed thoroughly by the time it reaches the bulbus arteriosus.

If all the above statements are correct, then the temperature excess of venous blood leaving the heat exchanger (T_{xvhe}) may be calculated as

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follows:

$$0.6\,T_{xvhe} + 0.4\,T_{xvo} \simeq T_{xbl}; \qquad (12)$$

$$0.6\,T_{xvhe} + 0.4\,(0.2\,T_{xrm}) \simeq 0.11\,T_{xrm}; \qquad (13)$$

thus,

$$T_{xvhe} \simeq 0.05\,T_{xrm}. \qquad (14)$$

This calculation implies that the heat exchanger's efficiency as a thermal barrier is about 95%.

Another way of examining thermal efficiency of the skipjack tuna's heat exchanger is by comparison, with non-scombrid teleosts, of the gill's relative importance as an avenue of heat transfer. Unfortunately, relative contributions of gills and other pathways to core heat exchange are not empirically known for typical fishes (Stevens & Fry 1970). However, the predominant opinion among fish physiologists seems to be that expressed by Fry (1967, p. 308): '... the overwhelming fraction of heat transfer [in typical gill-breathers] probably takes place at the respiratory surface. . . .' Thus, typical fishes weighing 0.5 kg may achieve 95% of core heat transfer via the gills as opposed to only 50% in skipjack tuna of the same weight. If resistance to heat exchange by other routes is the same in the two types of fishes, the difference between the above percentages suggests that the heat exchanger of skipjack tuna provides at least 20 times the resistance of typical teleosts to core heat transfer via the gills.

Excess tissue temperatures of skipjack tuna

For a fish to have tissue temperatures much different from ambient temperature, one or both of two circumstances must obtain: (1) the fish encounters rapidly changing environmental temperatures and is not, therefore, continuously in equilibrium with environmental temperature, or (2) the fish has a high metabolic rate and large thermal inertia. Large thermal inertia is important in (1) as well as in (2), in that the time required to reach thermal equilibrium depends directly on thermal inertia.

Both circumstances apply in the case of tunas. The magnitude and cause of tunas' large thermal inertia have been discussed above. It remains to develop the evidence that tunas voluntarily subject themselves to rapid changes of environmental tem-

erature and that tunas have unusually high meta-olic rates.

Yuen (1967)[2] used CTFM sonar to observe hort-term vertical movements of tuna schools in lawaiian waters. Skipjack tuna, observed while ıey fed at the surface, moved vertically at speeds p to 3.3 m sec^{-1} and sounded to depths of 195 m; ırface and 195 m temperatures were 26.4° and 6.2° C, respectively. Skipjack tuna and kawa-awa, *Euthynnus affinis* (Cantor), have been ob-:rved visually from a submarine at depths as reat as 150 m, where water temperature was 7.8° C (Strasburg, Jones & Iversen 1968). We ave trained captive skipjack tuna to swim repeat-dly between connected tanks whose temperatures ere 24° and 18° C, respectively.

Metabolism of free-swimming skipjack tuna ⁄eighing 0.4 to 3 kg is minimally 0.5–0.6 mg)₂ g^{-1} hr^{-1} and exceeds 2 mg O_2 g^{-1} hr^{-1} under onditions of moderate swimming activity (R. M. Jooding and W. H. Neill, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Ionolulu, HI 96812, unpublished data). These alues are 3 to 5 times larger than those for non-combrid teleosts of similar size (cf. Brett 1972). .tevens (1972) has pointed out several features of irculatory and respiratory physiology that cor-elate with the skipjack tuna's high metabolic rate; .g., the effectiveness with which skipjack remove ıxygen from water is 90%, a value 3 to 9 times ıgher than for non-scombrid fishes.

Stevens & Fry (1971) measured excess tissue :mperatures of skipjack tuna immediately after apture at sea and after various periods of time in aptivity. One sample of 20 just-caught fish, averag-ng 1.64 kg in weight, had excess red muscle, white ıuscle, and brain temperatures averaging 9.1°, :.6°, and 4.5° C, respectively. After 10 days in aptivity, fish from the same school had excess emperatures about one-third those of just-caught ısh; 35 more days in captivity resulted in no further lecreases in excess tissue temperatures.

Stevens & Fry (1971), like other workers who Jso have measured large excess temperatures in ust-caught skipjack tuna (Barrett & Hester 1964; Jarey & Teal 1969b), made their observations on ish that were in a state of 'feeding frenzy' (Stras-

Yuen, H. S. H., 1967. Short term vertical movements of skip-ıck tuna. Report presented at 18th Pacific Tuna Conference, ⌐ke Arrowhead, November 1967. Report on file Southwest ⁻isheries Center, National Marine Fisheries Service, NOAA, ⌐onolulu, HI 96812.

burg & Yuen 1960) when caught. Neither Stevens & Fry (1971) nor we were able to generate compar-able excesses in captive skipjack tuna, even through violent chasing.

We doubt that wild skipjack tuna have excess body temperatures much different from those of equally active captive fish. Moreover, the obser-vation that schools of skipjack tuna are highly variable in the extent to which frenzy feeding develops upon live-bait chumming (Yuen 1959, 1966) suggests that variation in excess red muscle temperature may be as much a function of activ-ity and feeding motivation as of ambient tem-perature. Stevens & Fry (1971) supposed that relatively small excess red muscle temperatures in skipjack tuna caught from 28° to 30° C waters reflected physiological thermoregulation at am-bient temperatures above 25° C.

Heat production by red muscle of skipjack tuna

Gordon (1968) found that unstimulated, minced preparations of red muscle from skipjack tuna metabolize at about 2.1 mg O_2 g^{-1} hr^{-1}. Our ex-periments with intact skipjack tuna yielded data on red muscle metabolism that can be compared with Gordon's (1968) measurements from excised tissue.

To arrive at estimates of red muscle metabolism we reasoned that the rate of heat production, r, at a point in the red muscle is proportional to the rate of potential temperature decrease, $k(T_{rm} - T_x)$, plus the rate of any actual change in red muscle temperature, dT_{rm}/dt, given constancy in T_x:

$$r \propto k(T_{rm} - T_x) + dT_{rm}/dt. \tag{15}$$

Under conditions of thermal equilibrium and con-stancy in r, this proportionality reduces to

$$r \propto k \cdot T_x, \tag{16}$$

and, finally, to the equations,

$$r(\text{cal g}^{-1} \text{ min}^{-1}) = 0.8 \, k \cdot T_x, \tag{17}$$

given that the heat capacity of fish muscle is about 0.8 cal g^{-1}°C^{-1} (Slavin 1964; Charm & Moody 1966), and

$$r(\text{mg } O_2 \text{ g}^{-1} \text{ hr}^{-1}) = \frac{60 \cdot 0.8}{3.42} k \cdot T_x = 14.0 \cdot k \cdot T_x, \tag{18}$$

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given that the oxycaloric equivalent for fish is about 3.42 cal mg O_2^{-1} (Warren & Davis 1967).

For red muscle of skipjack tuna weighing W kg and restrained for t min., we estimated that

$$\log k = -1.356 - 0.446 \log W \qquad (19)$$

and

$$\log T_x = 0.161 + 0.580 \log W - 0.0009 \, t. \qquad (20)$$

Logarithmically transforming equation 18 and then substituting into it the above relations with $t = 0$, we have

$$\log r = \log 14.0 + \log k + \log T_x \qquad (21)$$

and

$$\log r(mg \, O_2 \, g^{-1} \, hr^{-1}) = -0.049 + 0.134 \log W. \qquad (22)$$

Solutions of equation 22 at $W = 0.4$ kg and $W = 3.5$ kg are 0.79 and 1.06 mg $O_2 \, g^{-1} \, hr^{-1}$, respectively. [We note that equation 22 implies an increasing rate of red muscle metabolism for increasing size of sedated skipjack tuna. In most fishes, whole-body routine metabolic rate decreases as size increases (whole-body rate $\propto W^{-0.2}$; Beamish & Dickie 1967); however, whole-body routine metabolic rate of skipjack tuna appears independent of fish weight, at least over the range 0.3–5.0 kg (R. M. Gooding, National Marine Fisheries Service, NOAA, Honolulu, HI 96812, unpublished data).]

We attribute the difference between Gordon's (1968) and our estimates of metabolic rate in skipjack red muscle primarily to the vast difference between the methods of respirometry *in vitro* and direct calorimetry *in situ*. Gordon (1972, p. 249) has cautioned that his measurements were '...from substrate saturated, non-contracting preparations ... [and, therefore,] give no information as to the properties of active, functioning muscle exposed to physiologically more normal substrate supplies.' Our data, we believe, are the first for any fish to provide the sort of information to which Gordon referred.

Recourse to the basic calorimetric proportionality, together with the constants assumed above, allowed us to estimate heat production rates in the red muscle of two skipjack tuna that were forced to high levels of activity by chasing (Fig. 6). T_{rm}

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and dT_{rm}/dt were estimated for 1 min. intervals; tank temperature, T_a, was constant. The values of k used were those estimated earlier from temperature-change experiments with the same fish and probe placement. Heat production rates prior to chasing were about 4.7 cal $g^{-1} \, hr^{-1}$ (1.4 mg O_2 $g^{-1} \, hr^{-1}$) in the 1.21 kg fish and 3.5 cal $g^{-1} \, hr^{-1}$ (1.0 mg $O_2 \, g^{-1} \, hr^{-1}$) in the 1.78 kg fish; maximum rates of heat production were about 25 cal $g^{-1} \, hr^{-1}$ in each fish (Fig. 6). The maximum rates of heat production corresponded to a rate of oxygen demand exceeding 7 mg $O_2 \, g^{-1} \, hr^{-1}$. It is unlikely that such a large demand could be met aerobically (see Brett 1972); the result of continued forced activity, then, was a lethal oxygen debt.

Inferred upper environmental temperature limits for skipjack tuna

Considerations like those of the previous section suggest that large thermal inertia and high rates of metabolism may pose an ecological problem for skipjack tuna as they grow in body mass: excess core temperatures may become so large that the muscle of the fish overheats, especially during periods of greatest activity in warm waters.

Maximum red muscle temperatures observed from skipjack tuna cluster about 35° C (Stevens & Fry 1971). Suppose that the red muscle of this fish cannot function on a sustained basis at temperatures higher than 35° C. (In reality, the limiting upper temperature for red muscle operation may be subject to acclimatory adjustment.) Then, the maximum environmental temperature, max T_a, at which skipjack tuna can live indefinitely is a function of metabolic rate and thermal inertia, the latter depending on body size:

$$\max T_a = 35. - T_x \qquad (23)$$

$$= 35. - \left(\frac{3.42}{60 \cdot 0.8} \cdot \frac{r}{k} \right) \qquad (24)$$

$$= 35. - \frac{0.071 \, r}{k}. \qquad (25)$$

From equation 19,

$$k = 0.044 W^{-0.446}. \qquad (26)$$

Therefore,

$$\max T_a = 35. - (1.614 \cdot r \cdot W^{0.446}) \qquad (27)$$

here

$\text{ax } T_a$ = maximum environmental temperature, °C;

r = metabolic rate of red muscle, mg O_2 g^{-1} hr^{-1}; and

W = fish weight, kg.

he above relation implies that r in free-swimming dpjack tuna is independent of W, a proposition pported by unpublished data collected by R. M. rooding (National Marine Fisheries Service, iOAA, Honolulu, HI 96812). Mc⁻eover, we sug-est that the equation in present form is equally pplicable to skipjack tuna of all sizes, up to the iaximum attained — 22 kg, according to Collette : Gibbs (1963).

From the analysis presented in the last section, iinimum r for skipjack tuna red muscle would rem to be about 1.0 mg O_2 g^{-1} hr^{-1}. Solving equa-on 27 with r = 1 gives max T_a = 33.4° C at W = . kg, max T_a = 30.5° C at W = 10 kg, and max $_a$ = 28.6° C at W = 22 kg (Fig. 9). In the sense that ven minimal activity could not be sustained at mperatures above max T_a for r = 1, these tem-eratures are equivalent to typical fishes' incipient pper lethal temperatures (Fry, Hart & Walker 946). (Of course, if some other tissue, such as eural tissue, ceases to function above a tempera-re less than 35° C, then that temperature rather
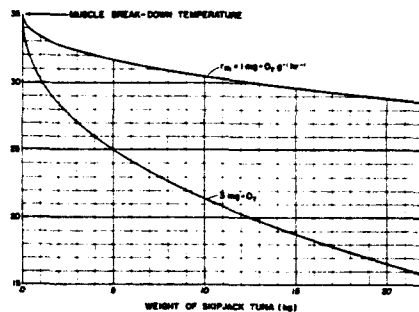

1g. 9. Speculative limits of upper environmental tempera-re for skipjack tuna as a function of body weight and wimming activity. Minimal activity is equated with a red uscle metabolic rate of 1 mg · $O_2g^{-1}hr^{-1}$; normal activity equated with a red muscle metabolic rate of 3 mg·$O_2g^{-1}hr^{-1}$.

than max T_a becomes limiting for fish smaller than some particular size.)

While r = 1 mg O_2 g^{-1} hr^{-1} may be the physio-logical minimum for red muscle metabolism in skipjack tuna, the ecological minimum must be higher if the fish is to feed successfully, escape predators, and migrate. In the absence of data, we offer r = r mgO_2g^{-1} hr^{-1} as the average metabolic rate in the red muscle of normally active skipjack tuna. Limiting upper environmental temperatures then become 30.2° C at W = 1 kg, 21.5° C at W = 10 kg, and 15.8° C at W = 22 kg (Fig. 9).

These calculations imply that large skipjack tuna must occupy cooler waters if they are to be as active as smaller fish. This could be achieved by large fish living at higher latitudes or at greater depths than smaller fish. Low rates of heat ex-change in large skipjack tuna would permit forays of several minutes' duration into surface waters warmer than max T_a if the fish were initially at thermal equilibrium with deeper, cooler water.

Simulated tissue temperatures in a school of skipjack tuna at sea

Simulation of body temperatures in time series is a useful adjunct in grasping how effectively large thermal inertia can damp fluctuations of environ-mental temperature. Such an illustration has been provided for a very large scombrid, the bluefin tuna (Neill & Stevens 1974), but not for smaller fish.

For the skipjack tuna simulation, we chose an environmental temperature series derived from actual observations by Yuen (1967) (see footnote [2]) on the movements of a skipjack tuna school in waters off Oahu, Hawaii. Vertical position of this school of 1.8 kg fish was estimated at 30 sec. inter-vals from CTFM sonar data (contact distance and tilt angle); target identification as to species and estimated fish size was made visually when the school was near the surface.

From the position estimates and from a con-commitant bathythermograph record, we estim-ated T_a experienced by these fish at 1 min. intervals for the entire 54 min. period during which the school was observed (Fig. 10). Then, assuming appropriate and constant values of k and T_x for 1.8 kg skipjack tuna, we simulated thermal responses of red muscle, white muscle, brain, and venous blood by exponentially filter-
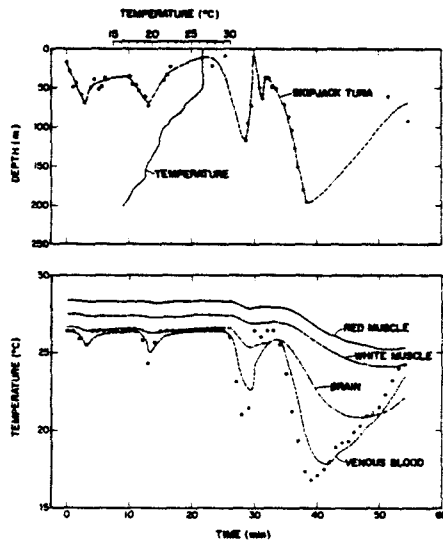
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Fig. 10. Vertical movements and simulated tissue temperatures in a school of 1.8 kg skipjack tuna tracked by sonar off the Waianae coast of Oahu, Hawaii. The upper panel gives individual and smoothed sonar 'fixes' on the school's depth position and the concomitant vertical distribution of sea temperature. The lower panel gives estimated environmental temperature at one minute intervals and the time-course of simulated red muscle, white muscle, brain, and venous blood temperatures. The fish were assumed to be in thermal equilibrium with the water at the onset of observation. Parameters of heat exchange used in the simulations were as follows:

Tissue	$T_x(^\circ C)$	$k(^\circ C\,min^{-1}\,^\circ C^{-1})$
Red muscle	2.0	0.034
White muscle	1.1	0.038
Brain	0.3	0.114
Venous blood	0.0	0.500

ing the $T_e(= T_a + T_x)$ series:

$$T_{b_i} = T_{e_i} - (T_{e_i} - T_{b_{i-1}})e^{-kl} \qquad (28)$$

where $l = 1$ min.

The effect of differences in thermal inertia (varied k) among tissues was clearly illustrated by the varying magnitude and phase lag of response to T_a decreases that occurred when the fish sounded

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into the thermocline (Fig. 10). During the deepest dive, T_a decreased to 16.8° C at 39 min.; this 9.6° C decrease in T_a caused hypothetical maximum decreases of 2.5°, 2.9°, 5.0°, and 7.0° C in temperature of red muscle, white muscle, brain, and venous blood, respectively. Whereas minimum venous blood temperature occurred 3 min. after minimum T_a, the equivalent lag was about 11 min. for red muscle, by which time T_a had increased to 23° C.

Thus skipjack tuna even as small as 1.8 kg achieve substantial independence from rapid fluctuations of environmental temperature. In the case of small fish sounding into the cool waters of the thermocline, the musculature would remain relatively warm and, therefore, presumably more efficient for swimming than it would otherwise be. Larger skipjack tuna are potentially able to regulate body temperature within narrow limits by low-frequency vertical movements within the thermocline or between the upper mixed layer and the thermocline.

Inertial storage of thermal information: a hypothesized mechanism for perception of weak temperature gradients

It now appears that tunas as a group are no more responsive to abrupt changes of temperature than are other fishes (Dizon et al. 1974; Steffel et al., MS.[3]). Smallest discrimination thresholds for temperature change in a scombrid were those obtained by Steffel et al. (MS.[3]) for free-swimming kawakawa; two instrumentally conditioned fish responded to abrupt temperature increases as small as 0.10° and 0.125° C, respectively. Thresholds no smaller than 0.1° C preclude directed orientation (klinotaxis or tropotaxis; see Fraenkel & Gunn 1961) to even the more steep horizontal gradients of the open sea (0.0001 to 0.001° C m⁻¹).

Yet, the evidence for a cause-effect relationship between temperature and tuna distribution is convincing (Howard 1963; Laevastu & Rosa 1963; Broadhead & Barrett 1964; Blackburn 1965). How do tunas, with only ordinary sensitivity to abrupt changes of temperature, behaviorally thermoregulate in an environment whose temperature-

ange signals are much weaker than those avail-
le to freshwater and inshore marine fishes? The
swer to this question may involve tuna's rela-
ely large thermal inertia, in the role of a simple
mperature 'memory' mechanism.

Inertial memory of the recent thermal environ-
ent is contingent on perception of the instan'a-
ous difference between body-core and ambient
mperatures. This difference will increase for
h swimming into cooler water and decrease for
h swimming into warmer water. The magni-
de of the difference depends on the coefficient
core-temperature change, the time-rate of
nbient temperature change (which in turn
pends on slope of the gradient and speed of
vimming: dT/ds·ds/dt = dT/dt), and the tem-
oral persistence of the particular time-rate of
ange. Largest differences will develop for
rge fish (which swim fast and have small k's)
vimming for long periods of time perpendicular
isotherms in steep temperature gradients. In
shes like tunas, which maintain excess core
mperatures, the difference consists of two com-
onents, one the equilibrium excess and the
ther a non-equilibrium difference attributable
thermal lag. In order that the temperature
ifference $T_b - T_a$ provide environmental in-
ormation, the fish must be able to separate the
omponents of difference; i.e., the fish must
now' the value of T_e to properly partition the
ifference, $T_b - T_a$:

$$b - T_a = (T_b - T_e) + (T_e - T_a),\qquad(29)$$

here
$b - T_e$ is the non-equilibrium difference, a func-
on of k and changing ambient temperature; and,
$e - T_a$ is the equilibrium excess temperature, T_x,
function of metabolic rate and k.

equisite 'knowledge' of T_e might be achieved
uite simply, through a neural transformation of
ome metabolic correlate, such as tail-beat rate
A):

$$e = T_a + f(A, k) = T_a + T_x.\qquad(30)$$

That fishes can make adjustments in behavior that
ompensate for variations in metabolism is con-
irmed by Rozin (1964), who showed that temporal
liscrimination in goldfish, *Carassius auratus* (Lin-
aeus), is independent of metabolic changes ac-
ompanying shifts in environmental temperature.

For linear gradients of temperature in which a
fish swims at constant speed with constant meta-
bolic rate, it follows from equation 1 that

$$T_b - T_e = -s \cdot G/k \cdot [1 - e^{-kt}]\qquad(31)$$

where

$T_b = T_e$ at $t = 0$;
s is swimming speed;
G is slope of the temperature gradient;
k is the coefficient of core-temperature change;
and, t is time.

By way of example, we have considered a skipjack
tuna, 47 cm long and weighing 2 kg, swimming at
1.77 bl sec.$^{-1}$ (50 m min.$^{-1}$) into a linear tempera-
ture gradient of $-0.001°$ C m^{-1} (Fig. 11). Red
muscle of the fish has k and T_x of $0.033°$ C
min.$^{-1}$ °C^{-1} and 2° C, respectively, both of which
are invariate. At $t = 0$, the fish enters the gradient in
thermal equilibrium. After 10 min. (0.5 km into the
gradient), $T_b - T_e$ is $+0.43°$ C; after 30 min.
(1.5 km), $T_b - T_e$ is $+0.95°$ C; and, after 100 min.
(5 km), $T_b - T_e$ is $+1.46°$ C, only $0.06°$ C short of
the asymptotic value of $+1.52°$ C.

We suggest that fishes may perceive the differ-
ence, $T_b - T_e$, and use it as the basis for klino-
kinetic (Fraenkel & Gunn 1961) orientation
responses that comprise behavioral thermoregula-
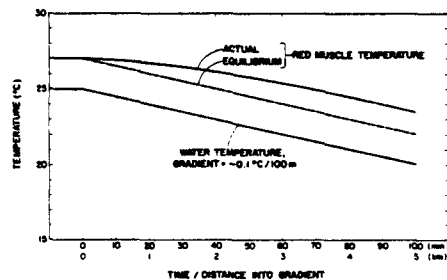tion. For typical fishes, $T_e \simeq T_a$; thus, the fish need

Fig. 11. Time-series simulation of red muscle temperature in
a 2 kg, 47 cm long skipjack tuna swimming at 50 m min^{-1}
(1.77 body lengths sec^{-1}) into a $-0.001°$ C m^{-1} temperature
gradient. Thermal inertia results in the development of a
difference between actual and equilibrium red muscle tempera-
tures; such a difference may constitute the basis for percep-
tion of weak temperature gradients in tunas and other fishes.
(Heat exchange parameters used in the simulation were
$T_x = 2.0°$ C and $k = 0.033°$ C min^{-1} °C^{-1}.)

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only make a simple comparison between temperatures sensed at the water-fish interface and somewhere in the body core. To obtain the same information, scombrids must have a mechanism such as that suggested above whereby $T_b - T_a$ is 'corrected' for the contribution of varying heat production; that is, their 'comparator' must be continuously offset by the variable amount, T_x. But, the heat exchanger of scombrids, in part responsible for this complication, also confers on these fishes a distinct advantage: Gradients so gentle as to be otherwise imperceptible are in effect amplified by a factor of about 2. Thus, the skipjack tuna considered in the above example could theoretically detect a temperature gradient as weak as $\pm 0.000066°$ C m^{-1} ($\pm 0.066°$ C km^{-1}) if it were sensitive to an instantaneous difference, $T_b - T_e$, as small as $\pm 0.1°$ C. A fish without the heat exchanger but otherwise the same could theoretically detect a temperature gradient only as weak as $\pm 0.00011°$ C m^{-1} ($\pm 0.11°$ C km^{-1}).

Another of the heat exchanger's possible benefits in thermo-perception is that thermal information derived from the difference $T_b - T_a$ is spatially condensed over the short distance separating the ends of the exchanger vessels — only about 10 mm in a 2 kg skipjack tuna (Stevens, Lam & Kendall 1974). Such sharp gradients cannot occur in fishes without specialized heat exchangers.

We can offer little evidence that body temperature differentials are in fact used by fishes in perception of gradients. Perhaps the most direct support for the hypothesis comes from observations by Peterson & Anderson (1969) on spontaneous activity of Atlantic salmon, *Salmo salar* Linnaeus, exposed to temperature changes. Activity peaks lagged initial changes of ambient temperature by several minutes. E. D. Stevens (University of Hawaii, Honolulu) and the senior author have simulated body temperatures of these fish by the methods described above; peaks of activity generally were simultaneous with estimated maximum values of $|T_b - T_e|$. Faster changes of water temperature over the same span of temperature produced larger values of $|T_b - T_e|$ and greater peak levels of activity.

There appear to be no published data contrary to the hypothesis. Certainly, the results of experiments on discrimination of temperature changes by fishes (e.g., Bull 1936; Bardach & Bjorklund 1957; Dizon et al. 1974; Steffel et al. MS.[3]) do not deny the possibility that discriminating subjects

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were perceiving abrupt increases in $|T_b - T_e|$ rather than temporal or spatial variation in T_a. Arctic sculpins of the genus *Myoxocephalus* exhibit overt escape behavior upon transfer to warm water only when the body core reaches a specific temperature (Hammel, Strømme & Myhre 1969), in apparent disregard for the difference $T_b - T_e$; however, there is nothing about these results to suggest that perception of the temperature step-change, minimally 7° C, did not occur the moment of transfer to warmer water. In similar experiments with two antarctic fishes, *Notothenia coriiceps* and *Chaenocephalus aceratus*, escape behavior appeared after a time lag inversely proportional to magnitude of the temperature change (Crawshaw & Hammel 1971).

Conclusion: ecological benefits and costs of large thermal inertia for skipjack tuna

Heat exchange between the core of skipjack tuna and the environment is retarded by a highly efficient countercurrent heat exchanger in the blood-vascular system. The resultant augmentation of thermal inertia, together with a high metabolic rate, makes skipjack tuna perhaps the warmest of 'warm-bodied' fishes on a per weight basis.

Our experiments provided no evidence that skipjack tuna regulate the efficiency of heat exchange, thereby achieving the capability for physiological thermoregulation. Rather than regulating body temperature as do mammals and birds or metabolically conforming to environmental temperature as do typical fishes, skipjack tuna apparently have adopted a third strategy of thermal adaptation — metabolic near-independence from temperature (Gordon 1968).

Why, then, have skipjack tuna made the evolutionary investment in a countercurrent heat exchanger, if not for use in rapid regulation of core temperature? One possibility is that the skipjack's heat exchanger functions only in long-term (weeks or months) physiological thermoregulation about which we have as yet no information. A second possibility is that the enzymatic systems compatible with high metabolic rates and evolutionarily available to the skipjack tuna are intrinsically more efficient at temperatures somewhat higher than those of the tropical seas; thus, because elevated body temperatures are adaptive, large thermal inertia is adaptive. Another is that the heat ex-

.nger protects the muscle mass from rapid .nges of temperature and from short-term ex-:ure to extreme temperatures, both of which ght damage the muscle or lessen its efficiency of :ration; in this sense, large thermal inertia .ances behavioral thermoregulation, both by reasing the effectiveness of correct responses .i by lessening the consequences of mistakes. .ally, increased thermal inertia may be im-rtant in perception of the weak horizontal gra-:nts of temperature that characterize the high-.s habitat of skipjack tuna.

Whatever the benefits of large thermal inertia skipjack tuna, they must be sufficient to offset .at we suggest is a major ecological cost—risk of erheating the muscle mass, especially during riods of high activity in warm water. Excess core uilibrium temperatures presumably increase th fish size; so, skipjack tuna must seek out oler and cooler water as they grow larger. In eas where surface waters are too warm for con-.uous occupancy by skipjack tuna of a given :e, the fish probably adopt a cyclical pattern of -pth distribution, alternately rising to the surface feed or navigate and sounding into the thermo-ine to cool.

cknowledgements

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