

## Physiological thermoregulation in bigeye tuna, *Thunnus obesus*\*

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### Synopsis

Although a growing body of evidence has indicated that tuna can thermoregulate and have body temperatures that are decoupled from immediate changes in ambient temperature, demonstrating the extent and time-course of body temperature changes in tuna moving through their natural environments has proved to be elusive. Here we use body temperature data telemetered from free-ranging fish to demonstrate short-latency physiological thermoregulation in bigeye tuna. We used a recently developed modeling system to determine the magnitude and time-course of the whole-body thermal conductivity changes that would result in the body temperature changes observed in fish in the wild. The results indicate rapid, 100 to 1000-fold changes in whole-body thermal conductivity that occur in response to quickly changing ambient temperatures. Coupling this physiological response with behavioral thermoregulation expands the foraging space of these animals by permitting activity in wide ranges of water temperatures and depths.

### Introduction

For several decades, there has been increasing evidence that the true tunas can thermoregulate by passing oxygenated arterial blood through counter-current vascular retia containing warm venous blood returning to the heart from the swimming muscles. The evidence comes from variety of approaches, including morphological analysis of the vascular structures that comprise the counter-current heat exchangers (Carey 1973, 1975, Graham & Diener 1978), measurements of body temperatures of freshly caught tunas (Barret & Hester 1964), and from observations of the body temperatures ( $T_b$ ) of

captive tuna exposed to different ambient water temperatures ( $T_a$ ) or when swimming at different speeds (Dizon & Brill 1979, Graham & Dickson 1981). Although Carey & Lawson (1973) almost certainly observed thermoregulation occurring in bluefin tuna, *Thunnus thynnus*, the nature of their data was such that the  $T_b$  they observed could not be unequivocally separated from the effects of simple thermal inertia in these large animals (Neill & Stevens 1974). Changes in swimming speed, which impact the rate of endogenous heat production ( $T_o$  – Stevens & Neill 1978, Graham 1983), or small-scale irregularities in  $T_a$  can obscure physiologically induced changes in the whole-body heat-transfer

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coefficient ( $k$ ). Increased swimming speeds also result in altered cardiac output, which in turn changes the dwell time of blood in the retina. As a result, heat exchanger efficiency could be passively altered without any physiological manipulation of the vasculature (Graham 1983). It is activity-independent changes in  $k$  that indicate that true physiological thermoregulation is occurring.

Holland et al. (1992) recently demonstrated activity-independent changes in  $k$  in a single, free-ranging bigeye tuna, *T. obesus*. Here we present data from an additional animal and utilize a mathematical model to predict the  $T_b$  that would be observed in these fish under the same ambient water conditions if the tuna were unable to physiologically regulate  $k$ .

## Methods

The behavior of juvenile bigeye tuna (FL 65 to 80 cm, 7.0 to 12 kg) in Hawaiian waters is ideal for testing for the occurrence of physiological thermoregulation. During daylight hours, and when not influenced by the presence of natural or man-made floating objects (which cause the fish to swim significantly closer to the surface), bigeye tuna select water temperatures between 14° and 17° C which, in Hawaii, are found at depths around 250 m. However, while at these depths, the tuna make periodic, rapid excursions up into warmer waters. These vertical excursions are separated by 30 to 60 min and last about 12 min, with very similar rates of climbing and diving (Holland et al. 1990). During these excursions, the fish experience first increasing and then decreasing  $T_a$  changing at up to 12° C min<sup>-1</sup>. The comparatively small size of these fish reduces the influence of simple thermal inertia on  $T_b$ .

## Data acquisition

Acoustic telemetry techniques (Holland et al. 1985) were used to simultaneously monitor swimming depth and  $T_b$  of free ranging bigeye tuna. Body temperatures were measured by a thermistor in the tip of a 6.0 cm by 0.3 cm hypodermic needle inserted from the dorsal surface into the red swimming muscle, so that thermistor placement was very similar to that used by Dizon & Brill (1979). The temperature data were relayed through an 80 kHz sonic transmitter which, together with the 50 kHz depth transmitter, was attached with two nylon sutures to the dorsal surface of the fish (Holland et al. 1985). Water temperature strata were determined by frequent deployment of expendable bathythermographs (XBTs). The ambient water temperatures experienced by each fish were calculated from water temperature profiles (derived by interpolating between sequential XBT deployments), and knowing the swimming depth of the fish. On the tracking vessel, temperature and depth signals were recorded on separate channels of stereo audio tape, thereby preserving the synchrony of the depth/temperature relationships for analysis ashore. Horizontal position was determined by LORAN-C and visual fixes.

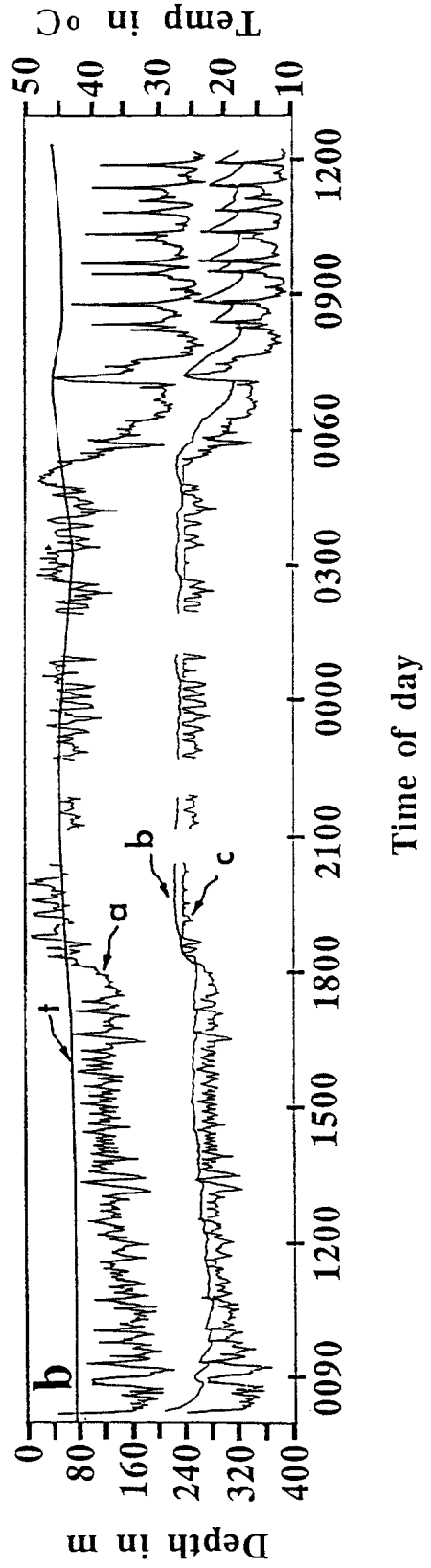
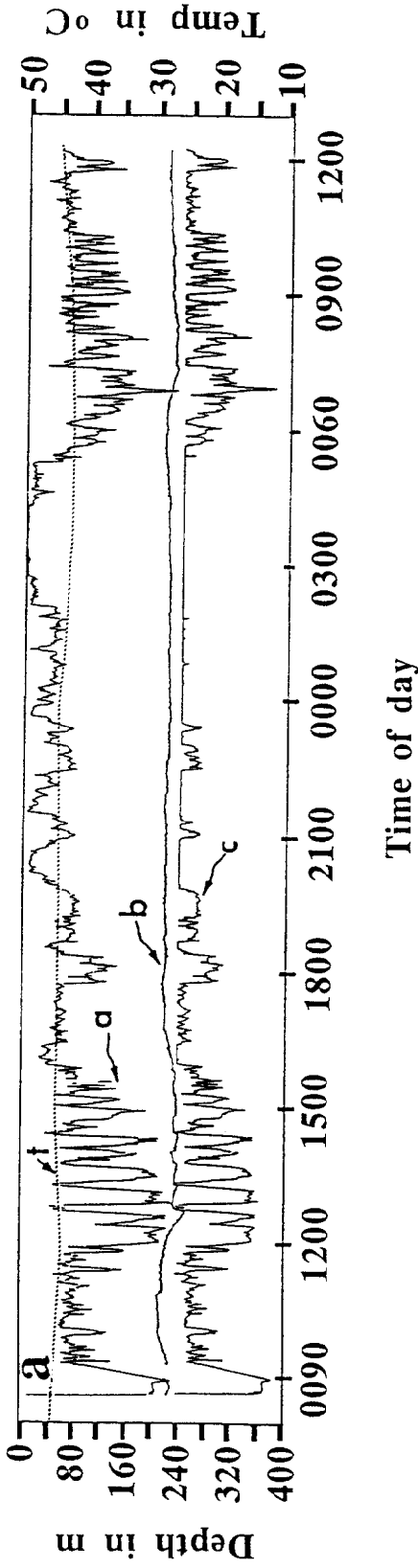
## Data analysis

A statistical procedure was developed to estimate the changes in  $k$  necessary to account for the observed rates of body warming and cooling. Tuna body temperature is a function of heat exchange with the environment and internal heat production. Heat loss (or gain) is proportional to the difference between the tuna's body temperature and the water in which it is swimming:

$$\frac{dT_b}{dt} = K(T_a - T_b) + \dot{T}_o \quad (1)$$

→

*Fig. 1.* Simultaneous swimming depth, body temperature ( $T_b$ ), and ambient water temperature ( $T_a$ ) of two bigeye tuna: a – fish 8808 (FL=79.0cm, approx. 11.7kg); b – fish 8810 (FL=67 cm, approx. 7.3kg). In both panels, a = swimming depth (left axis), b =  $T_b$  (right axis), c =  $T_a$  (right axis), t = interface between the essentially uniform temperatures of the upper mixed layer and top of the thermocline. Both fish show the typical diel pattern of swimming closer to the surface at night.



where  $k$  = whole-body heat transfer coefficient, and  $T_o$  the rate of temperature change due to internal heat production - principally from the swimming muscles. Because the rates of ascent and descent in the vertical excursions were similar, and because speed over ground was uniform,  $T_o$  was assumed to be constant during course of these observations. Because these equations are applied to individual fish, which we assume were not changing mass during the period of observation, the changes in temperature directly reflect heat gain or loss.

Because preliminary inspection of the results indicated that large fluctuations in  $k$  might be occurring, three different possibilities for the value of  $k$  were examined:

$$k = \text{a constant}, \quad (2.1)$$

$$k = \begin{cases} k_1, & \text{if } T_a < T_b \\ k_2, & \text{if } T_a \geq T_b, \end{cases} \quad (2.2)$$

$$k = \begin{cases} k_1, & \text{if } T_a - T_b < \Delta T_{crit} \\ k_2, & \text{if } T_a - T_b \geq \Delta T_{crit}, \end{cases} \quad (2.3)$$

where  $k_1$  and  $k_2$  are two values for the whole body thermal conductivity coefficient such that  $k_1 \ll k_2$  and  $\Delta T_{crit}$  is some threshold value for the difference between  $T_b$  and  $T_a$ . Model (2.1) assumes that the heat exchange system is always engaged and there is no ability on the part of the fish to alter  $k$ . Model (2.2) assumes that the heat exchanger is engaged when the fish is in water cooler than  $T_b$ , and is disengaged when the fish is in water warmer than  $T_b$ . Model (2.3) assumes that the heat exchanger is engaged in water  $\Delta T_{crit}$  cooler than  $T_b$  and disengaged when in water  $\Delta T_{crit}$  warmer than  $T_b$ . Models

(2.2) and (2.3) are equivalent when  $\Delta T_{crit} = 0$ . For models (2.2) and (2.3),  $k = k_1$  when the fish is in heat retention mode and  $k = k_2$  when in heat absorption mode.

The parameters for each model were estimated using a numerical procedure which minimizes the squared difference between observed and predicted  $T_b$ . The differential equation (1) was solved for  $T_b$  at each time step using a fully implicit finite difference approximation. The time step was the interval between successive field measurements, usually 1 to 3 sec. A quasi-Newton numerical function minimizer was used to minimize the residual sum of squares between observed and predicted  $T_b$ :

$$S = \sum_{i=1}^n (T_{b,i} - \hat{T}_{b,i})^2, \quad (3)$$

where  $T_{b,i}$  is the body  $i^{\text{th}}$  temperature measurement,  $\hat{T}_{b,i}$  the body temperature estimated by the model for the  $i^{\text{th}}$  temperature measurement and  $n$  the number of body temperature measurements.

The minimization algorithm depends on the partial derivatives  $\partial S/\partial k_1$ ,  $\partial S/\partial k_2$ ,  $\partial S/\partial T_o$ , and  $\partial S/\partial \Delta T_{crit}$  which were calculated by an automatic differentiation system (Griewank & Corliss 1991). This system, and the quasi-Newton function minimizer, are components of AUTODIF, a general purpose modelling package (Anon.)<sup>2</sup> The model parameters were estimated in a stepwise fashion. The first step was to estimate  $k$  and  $\hat{T}_o$  in equation (1). Next,  $k_1$  and  $k_2$  of equation (2.2) and, finally,  $\Delta T_{crit}$  of equation (2.3). The switch between  $k_1$  and

<sup>2</sup> Anon. 1991. AUTODIF: A c++ array language extension with automatic differentiation for use in non-linear modelling and statistics. Otter Research, Nanaimo. 102 pp.

Table 1. Results of parameter estimation steps.

| Model                     | $k_1$                 | $k_2$                 | $T_o$                 | $\Delta T_{crit}$ | $S$      |
|---------------------------|-----------------------|-----------------------|-----------------------|-------------------|----------|
| Track 8810 (Entire track) |                       |                       |                       |                   |          |
| 2.1                       | $2.38 \times 10^{-4}$ |                       | $6.50 \times 10^{-4}$ |                   | 11966.73 |
| 2.2                       | $5.45 \times 10^{-4}$ | $8.96 \times 10^{-2}$ | $1.21 \times 10^{-4}$ |                   | 2345.56  |
| 2.3                       | $5.22 \times 10^{-4}$ | $4.01 \times 10^{-2}$ | $1.12 \times 10^{-4}$ | 0.0349            | 1775.86  |
| Track 8808 (1140-1445 h)  |                       |                       |                       |                   |          |
| 2.1                       | $2.45 \times 10^{-4}$ |                       | $1.81 \times 10^{-3}$ |                   | 169.00   |
| 2.2                       | $2.65 \times 10^{-4}$ | $2.60 \times 10^{-1}$ | $1.96 \times 10^{-3}$ |                   | 136.85   |
| 2.3                       | $2.61 \times 10^{-4}$ | $3.72 \times 10^{-1}$ | $1.94 \times 10^{-3}$ | 0.0669            | 133.77   |

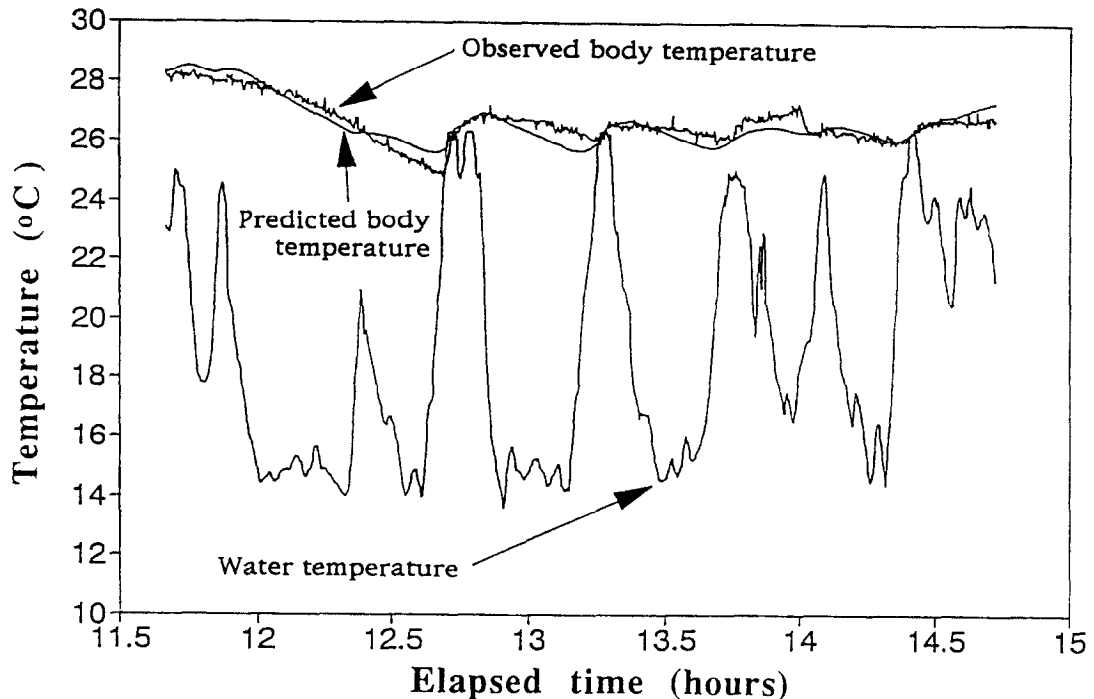


Fig. 2. Ambient water temperature ( $T_a$ ), and observed and estimated body temperatures ( $T_b$ ) of fish 8808, 1145 to 1445. Modelled  $T_b$  curve was generated by  $k_1 = 2.61 \times 10^{-4}$ ,  $k_2 = 3.72 \times 10^{-1}$ , and  $\Delta T_{crit} = 0.0669$  of model (2.3) from Table 1.

$k_2$  was accomplished using the continuous inverse tangent function to approximate the discontinuous step function. The improvement of fit at each step was tested using a simple F test on the decrease in the residual sum of squares.

## Results

Three bigeye tuna (8808, 8809 and 8810) were caught with baited handlines at fish aggregating device (FAD) 'F' off the Kona coast of Hawaii. They were tagged with the transmitters, released, and tracked for 23 h, 28 h and 29 h, respectively. Fish 8808 and 8809 remained in the vicinity of the FAD for the entirety of their respective tracks, and made comparatively few prolonged excursions down into deep cold water (Fig. 1a). However, fish 8810 moved away from the FAD and, on the second day, exhibited the deep daytime distribution and associated upward excursions observed during previous bigeye tracks (Fig. 1b, Holland et al. 1990).

The interaction between depth,  $T_a$ , and  $T_b$  during the tracks revealed several aspects of tuna thermo-

regulation. First, when swimming in the uniform temperatures of the mixed layer (e.g., portions of the nighttime behavior),  $T_b$  of all three fish were elevated above  $T_a$  by 2.0 to 3.0°C (Fig. 1a, b). Second, the fish were able to buffer  $T_b$  during short-lived changes in  $T_a$ , such that  $T_b$  decreased only slightly during brief forays below the thermocline. Third, and most remarkable, was the contrast between this thermal inertia and the rapid, short-latency increases in body temperature observed during the rapid upward excursions. This contrast was particularly evident on the second day of track 8810 (Fig. 1b), although similar disparate rates of warming and cooling were also observed during a section of behavior on day 1 (1145 to 1445) of fish 8808. Consequently, that section of 8808, and the entire track of 8810, were analyzed with the numerical system for estimating  $k$ .

The parameter estimates and residual sum of squares for each model are presented in Table 1. The decrease in the residual sum of squares was significant at the 1% level for each iteration of the model, leading to the selection of model (2.3) as the closest approximation of the observed data. The

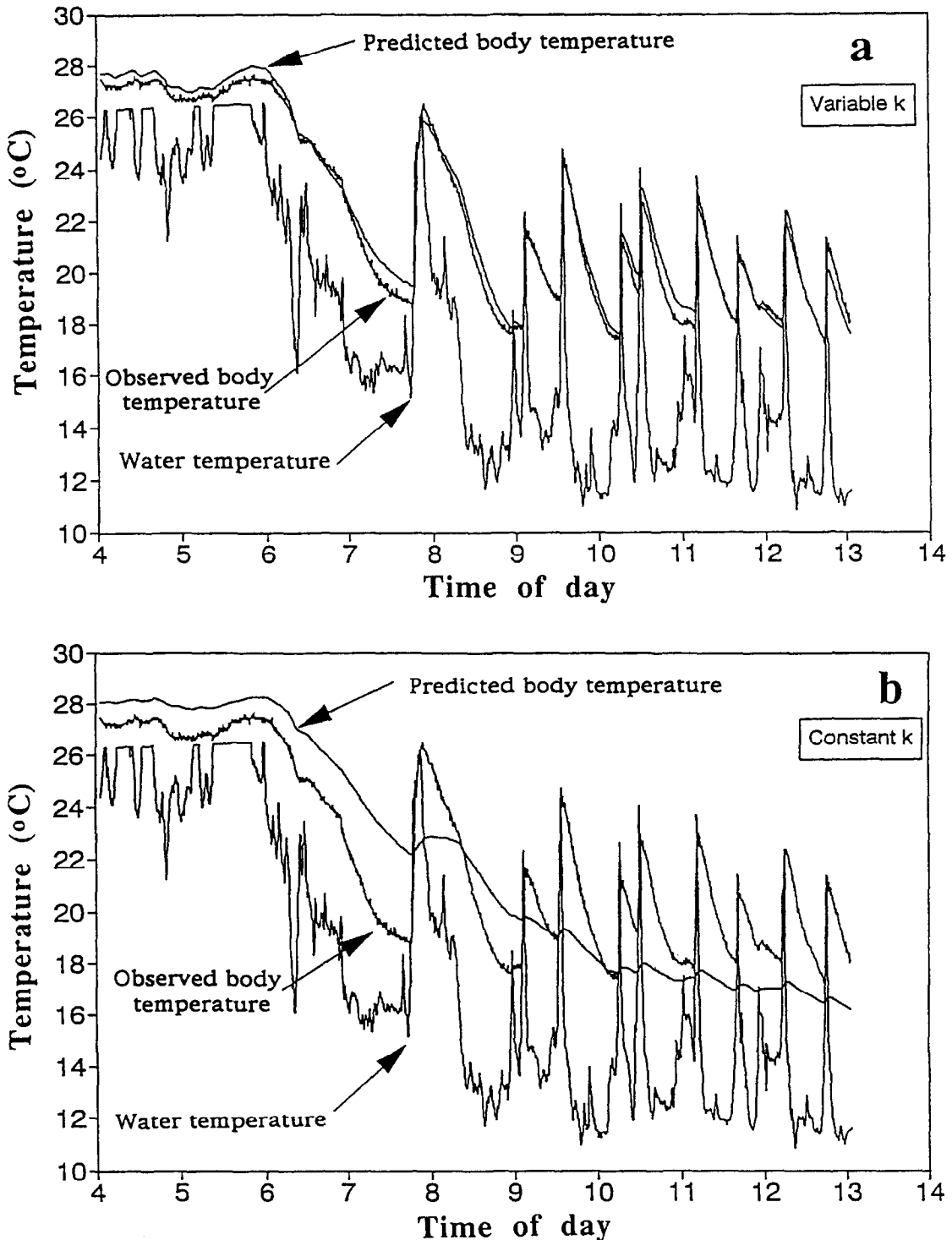


Fig. 3. a – Ambient water temperature ( $T_a$ ), observed and modelled body temperature ( $T_b$ ) for fish 8810, day 2 0400 to 1315h. The modelled  $T_b$  curve was generated by  $k_1 = 5.22 \times 10^{-4}$ ,  $k_2 = 4.01 \times 10^{-2}$  and  $\Delta T_{crit} = 0.0349$  of model (2.3) from Table 1. b – Modelled  $T_b$  curve for the same section of track of fish 8810 using a single, constant value of  $k = 2.38 \times 10^{-4}$  of model (2.1) from Table 1. This was the best fitting modelled curve using a single value for  $k$ .

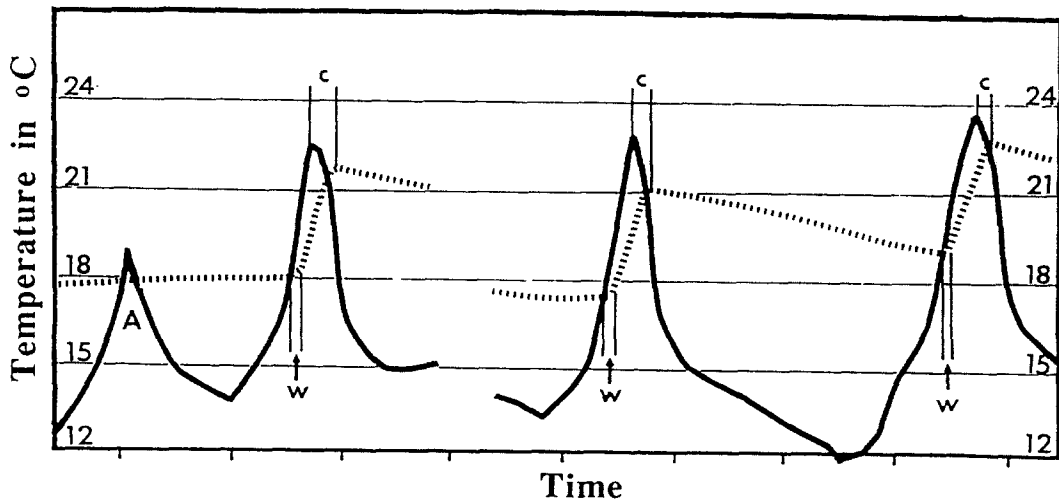


Fig. 4. Time course of  $T_b$  during four representative rapid vertical excursions from the track of fish 8810. Solid line =  $T_a$ , dashed line =  $T_b$ . Onset of warming (w) of  $T_b$  lags behind increases in  $T_a$  by 25–35 sec, whereas cooling (c) starts 45–60 sec after maximum  $T_a$ . Rapid body warming does not occur during the first vertical excursion (A), which peaked with  $T_a$  close to  $T_b$ . Time marks on the horizontal axis are 5 min intervals.

values of  $k_1$  and  $k_2$  produced by model (2.3) generate warming and cooling curves which closely match the observed changes in  $T_b$  for both 8808 and 8810 (Fig. 2, 3a). These  $k$  values, and the resultant estimated body temperature curves, indicate that these tuna were rapidly adjusting thermal conductivity over a range of two and three orders of magnitude (for 8810 and 8808, respectively). Changes in  $k$  of this size indicate that the observed rates of warming and cooling cannot be due simply to changes in the temperature gradient between  $T_a$  and  $T_b$ . This is clearly demonstrated when a constant value of  $k$  ( $k_1 = 2.38 \times 10^{-4}$ ), the best fitting single  $k_1$  value from model 2.1 (Table 1), is applied to the observed data from fish 8810. Under this constant  $k$  regime (i.e., a permanently engaged heat exchanger), the rate of warming of  $T_b$  is more than twice as fast as the cooling rate (approximately  $0.1^\circ \text{C min}^{-1}$  warming versus  $0.04^\circ \text{C min}^{-1}$  cooling), but the resultant long-term  $T_b$  inexorably declines because the fish can not warm up fast enough during the course of the upward excursions (Fig. 3b).

Fish 8810 consistently initiated upward excursions when  $T_b$  declined to approximately  $17.5^\circ \text{C}$ . Onset of body warming during these upward excursions lagged behind the increasing  $T_a$  by 25 to 30 sec, whereas  $T_b$  cooling started 40 to 60 sec after peak  $T_a$ . Increases in  $T_b$  did not occur during up-

ward excursions that were reversed prior to the fish entering ambient temperatures warmer than  $T_b$ , indicating that the increases in  $T_b$  observed in the large excursions resulted from heat absorbed from the surrounding water rather than from the endogenous heat produced by the act of swimming upward (Fig. 4).

## Discussion

The excess body temperatures ( $T_x$ , where  $T_x = T_b - T_a$ ) observed in fish moving within the essentially uniform temperatures of the mixed layer are consistent with  $T_b$  observed in captive fish exposed to constant tank temperatures. Also, the thermal inertia and transient  $T_x$  as large as  $10^\circ \text{C}$  which occurred during rapid, short-lived dives were predicted by results from captive fish (Dizon & Brill 1979, Graham & Dickson 1981), and by data from free-swimming bluefin tuna (Carey & Lawson 1973). This thermal inertia could be produced by a low, but constant  $k$  associated with a permanently engaged countercurrent heat exchange system (Neill & Stevens 1974).

Model (2.3) best fits the observed data and indicates that the animals are able to detect small differences between body and ambient temperatures. The  $\Delta T_{\text{crit}}$  values for fish 8808 and 8810 are quite

similar and are in agreement with temperature sensitivities determined experimentally with captive tuna (Dizon et al. 1976, Steffel et al. 1976). That fish 8810 consistently initiated upward excursions when  $T_b$  declined to between 17.5 and 18° C, suggests that this temperature, although 6° C above  $T_a$  in these circumstances, may represent a minimum tolerable body temperature for this species (Fig. 3a). If this is the case, and if bigeye tuna swimming in uniform water temperatures could maintain a stable  $T_x$  of perhaps 1 to 2° C, these data predict that ocean surface temperatures of 16 to 17° C would delineate the horizontal limits of bigeye tuna distribution and that bigeye tuna would be found at the surface at those locations.

The closeness of fit of the estimated  $T_b$  curves generated by model (2.3) is noteworthy in that they were generated using only two values for  $k$ . This may be because the very large changes in  $k$  observed during the upward excursions represent switches between the extreme limits of thermal conductivity for these animals. That is, they are switching between maximum heat absorption and maximum insulation. Thus, under these circumstances, the fish were providing the model with extreme and consistent values of  $k$ . During less extreme patterns of behavior (for instance, when making medium sized vertical movements in waters of intermediate depth and temperature), the fish may frequently modulate heat exchanger efficiency along a continuum of  $k$  values. Therefore,  $k$  values can not be compared among different fish; each fish may be utilizing a different portion of the dynamic scope of its heat exchanger and have different activity rates. Thus, the principle value of the model is to show the ranges and time-courses of  $k$  within each individual animal. This was made much easier under the current circumstances because the rates of ascent and descent during the vertical excursions (and the speed of movement over ground) were constant, thereby eliminating possible influence of changes in  $T_o$  on the rates of warming and cooling.

As illustrated by the estimated  $T_b$  of Figure 3b, a simple difference in warming and cooling rates cannot be construed as evidence for physiological thermoregulation. This analysis showed that, even with a constant  $k$ , warming can be more than twice as fast

as cooling due simply to the physical thermal gradients between  $T_a$  and  $T_b$  extant during the ascending and descending parts of the excursions. The very large changes in  $k$  values exhibited by both 8808 and 8810 indicate that these fish must be changing blood flow through the tissues in ways other than simply changing the dwell time of blood in the retia and, anatomically, bigeye tuna appear to have a circulatory system capable of mediating these large and rapid changes in  $k$ .

With their adaptive radiation away from their tropical origins, and the concurrent development of countercurrent retia, the tunas have increasingly departed from the typical teleostean vascular design. Blood supplying the trunk swimming muscles is delivered and retrieved less and less through central arteries and veins running through the haemal arch, and more through subdermal vessels supplying the lateral retia located along the flanks (Carey 1973, Graham 1975, Graham & Diener 1978, Graham 1983). In the tropical, comparatively primitive skipjack tuna, *Katsuwonus pelamis*, there are both central and lateral heat exchangers; the central blood supply is still of considerable size, but it passes through a large central countercurrent rete before reaching the red swimming muscles. On the other end of the spectrum, the most highly evolved bluefin tuna, *T. thynnus*, which encounters temperate waters in at least parts of its range, has almost completely diverted the blood supply to lateral rete systems and no longer has a complete central blood supply to the trunk musculature (Graham 1975).

Bigeye tuna are intermediate in both vascular design and their distribution; they have well developed lateral heat exchangers, and also retain a modest central blood supply, but it does not pass through a countercurrent rete on its way to the swimming muscles (Carey 1973, Graham 1975). Thus, routing the blood through the lateral rete system would put the tuna into a thermoconserving mode ( $k_1$ ), passing the blood through the central system would result in an essentially poikilothermic fish ( $k_2$ ) and the rapid warming observed during the rising phases of the vertical excursions. The observed latency of onset of warming (Fig. 4) is consistent with a change in blood circulation mediated by adrenergic neural control of the degree of dilation



of the heat exchanger arteries. Adrenergic control of systemic resistance has been demonstrated in other teleosts (Axelsson & Nilsson 1986) and the central rete of skipjack tuna and the lateral rete of albacore tuna, *T. alalunga*, have smooth muscle in the arterial walls (Stevens et al. 1974, Dickson personal communication). The microanatomy of the retia of other tuna species has yet to be investigated.

Bigeye tuna have expanded their foraging space by invading the cooler depths below the upper mixed layer while retaining the ability to hunt in surface waters. Unlike poikilothermic fish, these tuna can routinely move unimpeded throughout a thermally heterogeneous habitat. They have evolved a circulatory system and behavioral repertoire (the regular vertical excursions) which take advantage of the vertical proximity of warm water and which buffers them from the immediate influences of the rapidly changing water temperatures to be found in the thermoclines of tropical oceans. It would be instructive to observe the behavior of larger bigeye tuna under the same ambient conditions to see if body size changed the rate of heat loss and the frequency or time-course of the upward excursions. Similarly, tracking bigeye tuna in locations where the ocean's thermal profile is very different from that of Hawaii would further elucidate behavioral thermoregulatory styles and allow differentiation between the role of thermal preference versus depth per se in determining the vertical distribution of this species.

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