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Physiological and behavioural thermoregulation in bigeye tuna (*Thunnus obesus*)

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TUNA are unique among teleost fishes in being thermoconserving. Vascular counter-current heat exchangers maintain body temperatures above ambient water temperature, thereby improving locomotor muscle efficiency, especially at burst speeds and when pursuing prey below the thermocline[1–6]. Because tuna also occasionally swim rapidly in warm surface waters, it has been hypothesized that tuna thermoregulate to accommodate changing activity levels or ambient temperatures[7]. But previous field experiments have been unable to demonstrate definitively short-latency, mammalian-type physiological thermoregulation[8,9]. Here we show using telemetered data that free-ranging bigeye tuna (*Thunnus obesus*) can rapidly alter whole-body thermal conductivity by two orders of magnitude. The heat exchangers are disengaged to allow rapid warming as the tuna ascend from cold water into warmer surface waters, and are reactivated to conserve heat when they return into the depths. Combining physiological and behavioural thermoregulation expands the foraging space of bigeye tuna into otherwise prohibitively cold, deep water.

In all fish, oxygenated arterial blood leaves the gills essentially equilibrated to ambient water temperature (T_a). But in tunas, arterial blood passes through dense retia of interdigitated veins carrying warm blood away from the swimming muscles. The whole-body heat-transfer coefficient (k) is thereby reduced and heat is returned into the tissues[1-3]. Although elevated body temperature (T_b) improves locomotor muscle power for these obligate swimmers when they are at high speeds or below the thermocline[4,5], a permamently engaged heat retention system could be counterproductive for tuna swimming rapidly (fleeing, or chasing prey) in warm surface waters, because T_b may rise to injurious levels. Thus, it has been postulated that tuna can modify thermoconservation efficiency to fit the immediate demands of activity level and thermal environment[7].

Studies with captive tuna have been suggestive of an ability to regulate k by a few per cent (probably through altered cardiac output which changes the dwell time of blood in the retia)[7,1] . but data from field experiments with bluefin tuna (*T. thynnus*), are ambiguous[8,9], and a transmitter placed in a bigeye tuna stomach failed to demonstrate thermoregulation[8]. Hysteresis in the warming and cooling rates of swordfish, *Xiphias gladius*, occurs over periods of hours[11] and is associated with irregular diving patterns, making it difficult to separate the effects of changes in activity level, cardiac output and thermal inertia imparted by simple heat exchangers[3,11-13]. Tuna, however, experience very rapid changes in T_a, which would require fast thermoregulatory adjustments. Thus, the question remained: can tuna perform physiological thermoregulation, or are the reti simply passive devices sensitive to blood flow rate?

The behaviour of subadult bigeye tuna in Hawaiian waters is ideal for testing for the occurrence of physiological thermoregulation. During daytime, they select temperatures between 14 and 17 °C (at depths around 250 m), from which they make regular periodic, rapid vertical excursions up into warmer waters[14]. During these excursions, the fish experience first increasing and then decreasing T_a, changing at up to 12 °C min^{-1}. The comparatively small size of these tuna (65 to 80 cm; 7.0 to 12 kg), reduces the influence of simple thermal inertia on T_b.

In open-ocean tracking experiments, we telemetered swimming depth and T_b data from two bigeye tuna, one of which exhibited typical bigeye distribution and behaviour (Fig. 1). The radically different rates of body warming and cooling observed during the vertical excursions were modelled with a numerical parameter estimation procedure[15] which minimizes the squared differences between observed and estimated T_b.

Tuna body temperature is a function of heat exchange with

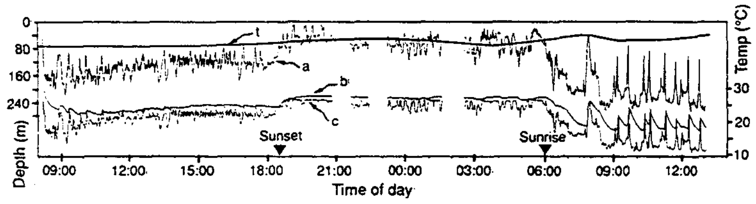

FIG. 1 Simultaneous swimming depth (a; left axis), T_b (b; right axis) and T_a (c; right axis) of bigeye tuna number 2 (length, 79 cm; weight ~11.7 kg). Acoustic telemetry techniques[18] were used to monitor simultaneously swimming depth and T_b of a free-ranging bigeye tuna for 29 h. T_b was measured by a thermister in the tip of a 6.0 × 0.25 cm hypodermic needle inserted from the dorsal surface. Thermister probe length was pre-set to reach swimming muscles 2 to 3 cm dorso-lateral to the spine; angling the probe caudally prevented it from moving during swimming (as confirmed with captive fish). T_a was derived by interpolating between sequential expendable bathythermograph deployments and knowing the depth of the fish. T_b and depth data were recorded on tape on the tracking vessel. This fish demonstrated the typical diel pattern of swimming closer to the surface at night and, on the second morning, the deep distribution and vertical excursions regularly observed in previous bigeye tracks[14]. T_b were buffered against changes in T_a resulting from brief movements up and down through the water column. Solid horizontal line (t) represents the interface between the bottom of the surface mixed layer and the top of the thermocline.

the environment and internal (metabolic) heat production ($\dot{T}_m$). In this case, the symmetry of the rates of ascent and descent, combined with constant horizontal speed over ground, indicated that locomotor output, and hence $\dot{T}_m$, was constant during the observed periods of warming and cooling. Heat loss (or gain) is proportional to the difference between body temperature and the surrounding water:

$$\frac{dT_b}{dt} = k(T_a - T_b) + \dot{T}_m \tag{1}$$

The estimated values of k for warming and cooling which best fit the observed data (Fig. 2) are: $k_1 = 5.22 \times 10^{-4}$ (cooling), and $k_2 = 4.01 \times 10^{-2}$ (warming). These values indicate that the fish was rapidly varying the rate of instantaneous heat transfer by over two orders of magnitude. Examination of the onset of changes in T_b indicates that the conductivity switches were implemented in about 45 s.

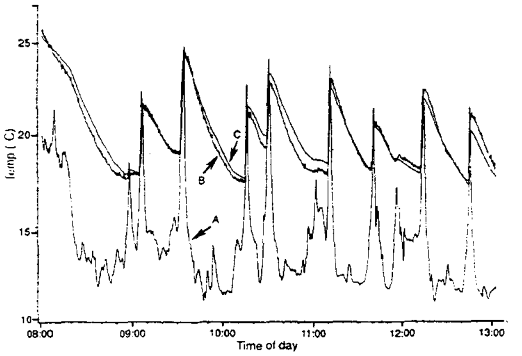

FIG. 2 Relationship between ambient temperature (A), observed body temperature (B), and estimated body temperature (C) for fish number 2, day 2. Using equation (1), and a switching function (equation (2)), automatic differentiation[15,19] was used to fit two possible values of k to the observed data from fish 2

$$k = \begin{cases} k_1, & \text{if } T_a - T_b \leq \Delta T_{crit} \\ k_2, & \text{if } T_a - T_b > \Delta T_{crit} \end{cases} \tag{2}$$

where k_1 and k_2 are different values for whole-body heat-transfer coefficient such that $k_1 \ll k_2$, and $k = k_1$ when the fish is in heat-retention mode and $k = k_2$ when in heat-absorption mode. ΔT_{crit} is some threshold value for the difference between T_b and T_a, such that the heat exchanger is engaged when the fish is in water that is ΔT_{crit} cooler than T_b and disengaged when in water that is ΔT_{crit} degrees warmer than T_b. The model parameters were estimated in a stepwise fashion; first $\dot{T}_m$, then k_1 and k_2 and finally ΔT_{crit}. Improvement in fit at each step was tested using a simple F test on the decrease in the residual sum of squares. The T_b curves resulting from the modelled k_1 and k_2 values closely match the rapid warming and slow cooling observed during the vertical excursions. These excursions were consistently initiated when T_b declined to ~17.5 °C, possibly indicating a minimum tolerable T_b, even though still 6 °C above T_a. The estimated value for $\dot{T}_m$ was 1.12×10^{-4} °C s^{-1} and estimated value of ΔT_{crit} was 0.03 °C, within the range of temperature detection thresholds observed experimentally with captive fish[20,21].

The tunas have progressively evolved away from the typical teleost vasculature; blood supplying the swimming muscles is delivered and retrieved less through central blood vessels running through the haemal arch, and more through sub-dermal retia and cutaneous arteries and veins[1-3,5]. In the comparatively primitive skipjack tuna (*Katsuwonus pelamis*), there are both central and lateral heat exchangers, whereas the most highly evolved (and most temperate in distribution) bluefin tuna no longer has a complete central blood supply to the musculature, but a complex lateral rete system. This progressive lateralization of blood supply may be a response to the radiation of tuna away from tropical environments; supplying the muscles entirely through lateral heat exchangers most effectively insulates the fish and limits the flow of cold arterial blood into the core[5].

Bigeye tuna are intermediate in both their vascular design and distribution; they have well developed lateral heat exchangers, and retain a modest central blood supply, but it does not pass through a countercurrent rete[2,5]. Routing arterial 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). The latency of onset of warming is consistent with adrenergic neural control of vascular dilation[16]; in skipjack tuna at least, heat exchanger arteries have smooth muscle in their walls[17].

Although inhabiting semitropical latitudes, bigeye tuna have expanded their range by invading the cooler depths below the surface mixed layer and evolving a behavioural repertoire and circulatory system that take advantage of the vertical proximity of warm water. Their vascular anatomy provides a capacity for short-latency physiological thermoregulation which, when coupled with behavioural thermoregulation expressed as the brief vertical excursions, allows them to forage in deep waters and still maintain the advantages of high muscle temperatures derived from their tropical lineage. □

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