STUDIES OF TROPICAL TUNA SWIMMING PERFORMANCE IN A LARGE WATER TUNNEL

II. THERMOREGULATION

HEIDI DEWAR, JEFFREY B. GRAHAM* AND RICHARD W. BRILL†

Center for Marine Biotechnology and Biomedicine and the Marine Biology Research Division, Scripps Institution of Oceanography, 0204 La Jolla, CA 92093-0204, USA

Summary

The body temperatures (T_b) of nine yellowfin tuna (*Thunnus albacares*) were monitored while fish swam in a large water tunnel at controlled velocities (U) and ambient temperatures (T_a). Monitoring T_b during step changes in T_a at constant U permitted estimation of the thermal rate coefficient (k), an index of heat transfer. In the yellowfin, k is dependent on both T_a and the direction of the thermal gradient (i.e. whether T_a is greater or less than T_b). Modulation of k in response to T_a was further demonstrated during tests in which U was varied; the elevation of T_b in response to equal increases in U was 3–4 times less at 30 °C than at 25 and 20 °C. These experiments demonstrate that the yellowfin tuna can modulate heat transfer. This ability could prevent overheating during intense activity, retard heat loss during a descent into cool water and permit increased heat gain upon returning to warm surface waters (i.e. when $T_b < T_a$).

Introduction

This paper reports experiments, conducted in a large water tunnel, testing the capacity of yellowfin tuna (*Thunnus albacares*) to control rates of heat gain and loss in response to changes in ambient water temperature (T_a) and swimming velocity (U). Tunas swim continuously in search of prey and depend upon locomotion to ventilate their gills (Brown and Muir, 1970; Roberts, 1978) and to maintain hydrostatic equilibrium (Magnuson, 1973, 1978). Tuna aerobic locomotor (red) muscle, which powers sustained swimming, is unique among teleosts in that the supporting vasculature forms counter-current heat exchangers (retia mirabilia) that conserve metabolic heat. Large bluefin tuna can elevate body temperature (T_b, red muscle temperature) to as much as 20 °C above T_a (Carey and Lawson, 1973).

As in mammals and birds, the elevated T_b of tunas enhances physiological and biochemical functions (Graham, 1975; Stevens and Neill, 1978; Dizon and Brill, 1979;

Stevens and Carey, 1981). Endothermy also affords tunas a level of independence from the effects of acute changes in T_a such as those encountered during feeding sojourns into deeper, cooler water (Carey and Lawson, 1973; Neill and Stevens, 1974; Neill *et al.* 1976; Stevens and Neill, 1978; Dizon and Brill, 1979; Graham, 1983; Holland *et al.* 1992).

Although many endotherms (i.e. birds and mammals) maintain a nearly constant T_b by precisely balancing rates of heat gain and loss, the T_b and T_x ($=T_b-T_a$) of tunas is variable and is affected by both T_a and by U (Stevens and Fry, 1971; Carey and Lawson, 1973; Stevens and Neill, 1978; Dizon and Brill, 1979; Graham, 1983). This has raised questions about the potential for T_b control (Carey and Teal, 1966; Stevens and Fry, 1971; Carey and Lawson, 1973). Do tuna have thermoregulatory capabilities similar to, but less precise than, those of birds and mammals or is heat balance unregulated with the T_x values of the tuna being the consequence of a constant, though elevated, thermal inertia (Neill and Stevens, 1974; Stevens and Neill, 1978)?

Because there are circumstances in which an elevated T_b and thermal inertia may be a disadvantage, the ability to modulate thermoconservation would be useful. At high activity levels or in warm T_a, a tuna may risk overheating and thus would need to curtail heat retention to avoid thermal limits to activity and distribution (Neill *et al.* 1976; Stevens and Neill, 1978; Dizon and Brill, 1979). Also, a fish ascending to the surface following a period of foraging at depth, may have a T_b less than T_a and would be able to gain heat faster by increasing heat transfer (Dizon and Brill, 1979; Holland *et al.* 1992; Brill *et al.* 1994).

This study reports on several aspects of yellowfin thermoregulation determined with an experimental design that permitted calculation of the thermal rate coefficient (k) and determination of its dependence on T_a. Because k quantifies the internal and external conductive and convective properties influencing heat transfer, any modulation of heat flux by the fish should be reflected in changes in k (Dizon and Brill, 1979; Holland *et al.* 1992; Brill *et al.* 1994). By monitoring T_b during controlled changes in T_a, it was possible to calculate k [measured as $°C \, min^{-1}$ ($°C$ thermal gradient)$^{-1}$ and therefore with units of min^{-1}; Graham, 1983; Weller *et al.* 1984; Brill *et al.* 1994] in relation to other variables in the heat transfer equation:

$$\mathrm{d}T_b/\mathrm{d}t = k(T_a - T_b) + Hp, \tag{1}$$

where $\mathrm{d}T_b/\mathrm{d}t$ ($°C \, min^{-1}$) is the rate of change of T_b and Hp ($°C \, min^{-1}$), or heat production, is the rate at which T_b would increase (as a by-product of metabolic processes occurring in the red muscle) in the absence of heat transfer ($k=0$). Because red muscle powers sustained swimming, Hp, although not directly measured, was regulated in our studies by controlling U.

Materials and methods

The water tunnel and the protocols for maintaining tuna in captivity and during an experiment are described in Dewar and Graham (1994). An important feature for thermoregulation studies was the ability to bring about rapid ($1 \, °C \, min^{-1}$) thermal changes by the admixture of large reservoirs (3000 l each) of hot and cold water.

Yellowfin selected for study were dip-netted from the holding tank, placed immediately in a plastic cradle filled with hyperoxic water, and quickly fitted with a 30 gauge copper–constantan thermocouple that penetrated the red muscle (Fig. 1A,B). To facilitate implantation and prevent thermocouple damage during insertion, the wire was housed in a 17 gauge hypodermic needle and its tip bent to form a hook. The needle and thermocouple were inserted through a preformed hole in the corselet (at the leading edge of the first dorsal fin, approximately 1.5 cm from the dorsal mid-line; Fig. 1A) and directed ventro-posteriorly. The thermocouple was connected to a Physi-Temp digital thermometer (model BAT 12) and, during insertion, the temperature readout was used to position the thermocouple tip in the warmest sector of red muscle. Once the thermocouple position had been set, the 17 gauge needle was carefully withdrawn while T_b was monitored to ensure patent thermocouple position. The wire was then disconnected from the thermometer and secured in place by 'self-tying' loops through the corselet. Thermocouple implantation generally required less than 2 min, following which the fish was placed into the water tunnel. Thermocouple position was verified *post mortem*.

Immediately after placing the fish in the water tunnel's working section, the lid was secured and the thermocouple wire was fed out and reconnected to the digital thermometer. For the first 2 h, U and illumination were adjusted to induce stable swimming as detailed by Dewar and Graham (1994). Throughout the experiment T_b, T_a, O_2 concentration and U were monitored continuously.

Effect of T_a on T_b

The response of T_b to rapidly implemented cyclic changes in T_a was monitored while the fish swam at a constant U. Fig. 2 illustrates the sequence of temperature changes used in all tests. Once the fish had been swimming stably in the water tunnel for at least 2 h, T_a was rapidly cooled from initial, ambient levels (23–25 °C) to 18 °C. After T_b had fallen to at least 22 °C the first cyclic T_a change was initiated; T_a was increased by 7 °C then, once T_b had risen to just 0.5 °C below T_a, T_a was rapidly reduced by 4 °C. The same sequence and timing were repeated two more times, but each subsequent thermal cycle was shifted upward by 3 °C. Thus, the complete experiment consisted of three thermal cycles staggered by 3 °C (Figs 2, 3 and 4).

Velocity effects on T_b

After the final cyclic change in T_a, the influence of increased U on heat balance was examined by monitoring the response of T_b to two incremental increases in U at T_a values of 30, 25 and 20 °C (see Fig. 5). At each T_a, the yellowfin was first held at a U of $0.9\,L\,s^{-1}$ (where L is fork length) and T_b was recorded. Then U was increased to $1.5\,L\,s^{-1}$ and held there for 10 min while changes in T_b were recorded. Following this, U was returned to $0.9\,L\,s^{-1}$. After T_b had cooled to control levels, U was elevated to $2\,L\,s^{-1}$ for 5 min, and T_b records were obtained. Then U was returned to $0.9\,L\,s^{-1}$ while cooling was again monitored.

Calculation of the thermal rate coefficient

Values of k were determined for both the increases and decreases in T_b occurring in

each of the successive thermal steps. k is the time constant of the integral of equation 1 after removal of the *Hp* term:

$$T_b(t) = T_e - [T_e - T_b(t = 0)]e^{-kt} ,\qquad (2)$$

where t is the elapsed time, T_e is the equilibrium T_b at the new T_a [in fish that maintain a thermal excess, T_a (equation 1) is replaced by T_e], and the other variables are as defined above (Neill *et al.* 1976; Stevens and Neill, 1978; Weller *et al.* 1984; Brill *et al.* 1994).

Using equation 2 and a MATLAB curve-fitting program, k was calculated from the $T_b(t)$ curves associated with each change in T_a. The program was applied after the latency, or lag time, when T_b began to change exponentially (Fechhelm and Neill, 1982; Weller *et al.* 1984; Brill *et al.* 1994). To remove the latency period from each data set, successive points were eliminated from the beginning of the data set until the predicted values closely approximated the actual data over the region where T_b changed most rapidly [minimizing the square root of the mean of the sum of the squared residuals (RMS error)]. The T_e (equation 2) was estimated from the T_x measured at the end of the initial 2 h recovery period and was then adjusted for each estimation of k to minimize the RMS error.

Results

Effects of T_a *on* T_b

The effects of cyclic T_a changes on the T_b of three yellowfin tuna are shown in Figs 2, 3 and 4 and the k values for the warming and cooling phases are summarized for nine fish in Table 1. The high k for cooling during cycle 3 (Fig. 2) occurred in all fish (Table 1) and this value is significantly higher [$P<0.05$; non-parametric *a posteriori*, multiple-comparison test (Nemenyi, 1963)] than k values in cycles 1 and 2, which do not differ from one another. No significant differences exist between the k values for warming.

The thermal latency (the time interval between the reversal of the thermal gradient and the onset of the exponential decline in T_b) provides another indication of the yellowfin's capacity to regulate heat transfer. Fig. 3 illustrates the effect of T_a on the latency for yellowfin no. 5. The reduction in cooling latency between cycles was observed for all yellowfin and the values in cycle 3 (mean 2.9 min) are significantly less ($P<0.05$; statistics as above) than in both cycles 1 and 2 (mean values 6.0 and 6.4 min). Latencies during heating were brief (1.5–4 min) and did not differ among cycles. This pattern of thermal dependence is the same as that observed for k.

Thermal notches

The T_b traces for yellowfin no. 8 (Fig. 4) are distinguished by the 'thermal notches' that

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Fig. 1. (A) Illustration of the point of thermocouple insertion in a yellowfin (adapted from Collette and Nauen, 1983). (B) Transverse sections of three tuna species showing the features related to endothermy. Indicated are the central rete (CR), the lateral retia (LR), the internal position of the aerobic locomotor (red) muscle, the dorsal aorta (DA) and post-cardinal vein (PCV) (adapted from Graham, 1975). Note that *Thunnus thynnus* has no PCV.
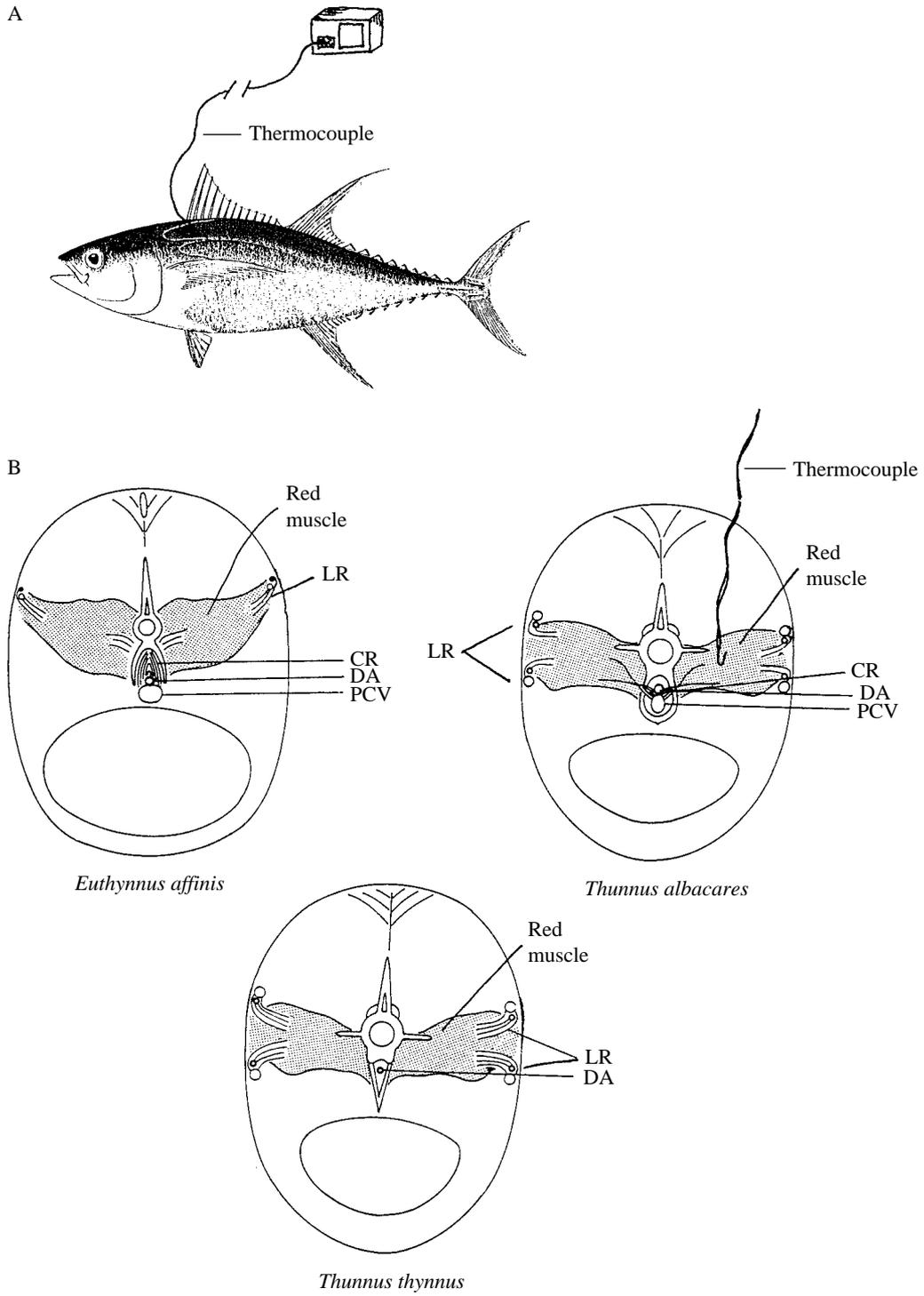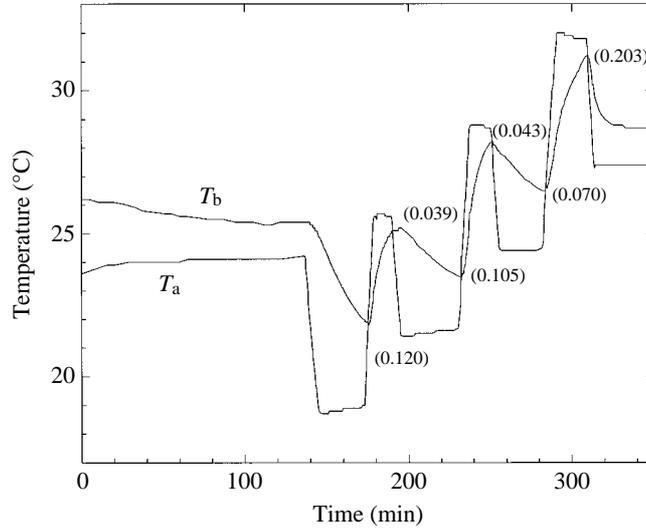
A

Thermocouple

B

Euthynnus affinis

Thunnus albacares

Thunnus thynnus

Fig. 1

Fig. 2. Traces of T_a and T_b *versus* time for yellowfin no. 1 at a constant swimming speed $(0.83 L s^{-1})$ show the typical experimental design used for all fish. The 120 min handling–recovery period and the initial drop in T_a set the stage for the subsequent cyclic changes in T_a. The k value for each T_a step change is given in parentheses.

occurred immediately after the thermal gradient reversal during cycles 1 and 2 but not during cycle 3. The thermal notch is characterized by an abrupt reduction and then rise in T_b, followed by a more gradual decline. The same pattern of notches was observed for yellowfin no. 9 and a notch is also seen in Fig. 5.
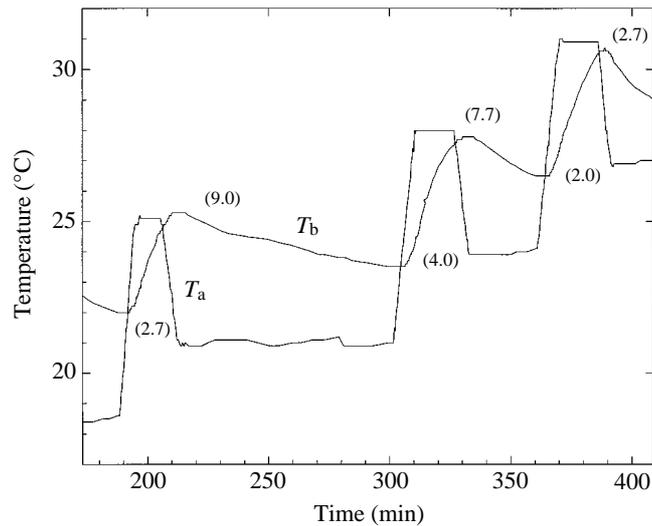

Fig. 3. Traces of T_a and T_b for yellowfin no. 5 (U=1.12 $L s^{-1}$). The latency period (min) for each T_a step change is indicated in parentheses.
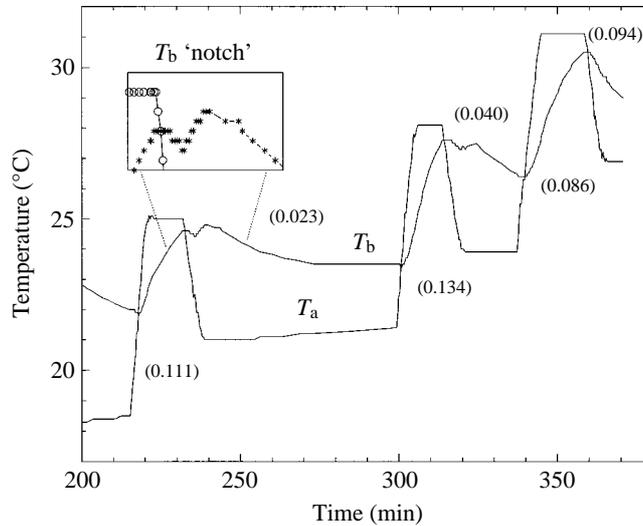
Fig. 4. Traces of T_a and T_b for yellowfin no. 8 (U=0.93 Ls^{-1}). Note that the first and second step reductions in T_a (230 and 310 min) led to a 'notch' (inset, T_a=○; T_b=*) followed by a more gradual decline in T_b.

Activity effects

The effect of increased U on T_b at three T_a values is shown in Fig. 5. At 30 °C, the initial steady-state T_x is low (0.7 °C) and the two step changes in U have a minimal effect
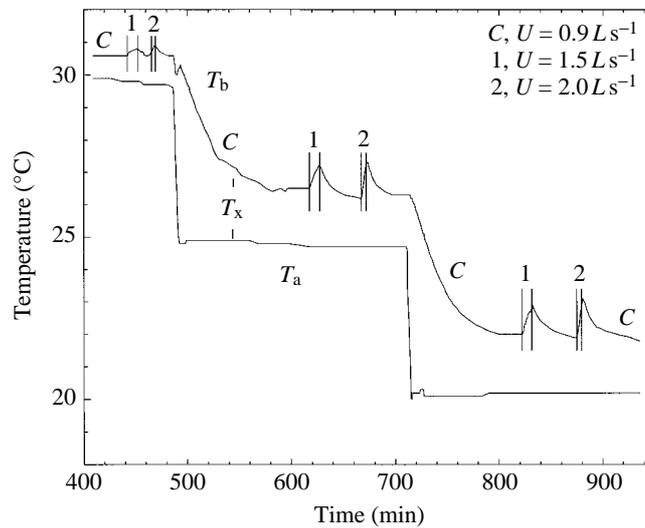

Fig. 5. Data for yellowfin no. 1 showing the effects of two incremental increases in U on T_b at 30, 25 and 20 °C. At each T_a the control U was 0.9 Ls^{-1} (C), where L is fork length. Velocity increments were to 1.5 Ls^{-1} (1) for 10 min and 2.0 Ls^{-1} (2) for 5 min. Each increase and decrease in U is marked by a vertical line. T_b was allowed to return to control levels after each test. The thermal excess (T_x) is also indicated.

Table 1. *Summary of the body mass,* U *and* k *values at each* T_a *step change in the three thermal cycles for nine yellowfin tuna*

Fish no.	Mass (kg)	U ($L s^{-1}$)	k (min^{-1})					
			Heating, $T_a > T_b$			Cooling, $T_a < T_b$		
			1	2	3	1	2	3
1	1.83	0.83	0.120	0.105	0.070	0.039	0.043	0.203
2	0.97	0.72	0.105	0.078	0.111	0.085	0.058	0.196
3	2.18	1.20	0.127	0.122	0.080	0.055	0.047	0.111
4	1.28	1.17	0.088	0.081	0.108	0.040	0.034	0.137
5	1.78	1.12	0.075	0.065	0.055	0.015	0.050	0.071
6	1.63	1.03	–	0.156	0.152	0.099	0.096	0.159
7	1.75	0.75	0.065	0.062	0.062	0.057	0.060	0.070
8	2.03	0.93	0.111	0.134	0.086	0.023	0.040	0.094
9	1.83	1.13	0.113	0.029	0.090	0.021	0.034	0.097
Mean			0.101	0.092	0.093	0.048	0.051	0.126
S.D.			0.022	0.040	0.030	0.029	0.019	0.050

(1,+0.2 °C; 2,+0.3 °C). The steady-state T_x at both 25 °C (1.7 °C) and 20 °C (1.8 °C) is greater than that at 30 °C, and the elevation of T_b associated with increases in U is three-to fourfold higher at 25 °C (1,+0.7 °C; 2,+1.1 °C) and 20 °C (1,+0.9 °C; 2,+1.2 °C) than at 30 °C. It is also noteworthy that a thermal notch occurred with the reduction of T_a from 30–25 °C.

Discussion

Several previous studies examined the potential of tunas to control heat retention physiologically. Long-term ocean tracks by Carey and Lawson (1973) showed that large bluefin tuna can maintain stomach temperature within 5 °C during 15 °C changes in T_a. Holland *et al.* (1992) analyzed T_b/T_a relationships for a bigeye tuna tracked at sea: they determined that it could adjust k to retard heat loss during excursions into cool water and to allow rapid heat gain upon its return to warmer surface waters (when $T_a > T_b$). Modulation of k was also inferred during laboratory studies by Dizon and Brill (1979), where long-term changes in T_a from 20 to 30 °C, while increasing swimming speed and consequently Hp, had a negligible effect on the steady-state T_x of yellowfin tuna.

While all of these findings support the hypothesis that tuna can regulate heat balance physiologically, each study is problematic in that swimming speed and consequently Hp (equation 1) were either unknown or uncontrolled (Brill *et al.* 1994). Hp will influence both steady-state and non-steady-state T_b and therefore estimated k values (Graham, 1983; Brill *et al.* 1994). In addition, inferences about physiological regulation based solely on comparisons of rates of heating and cooling (Holland *et al.* 1992) are complicated by the absence of Hp data. Because Hp can retard cooling and increase the rate of heating (Graham, 1983; Brill *et al.* 1994), it may produce results similar to those

expected through the physiological regulation of heat balance. The differential influences of *Hp* on heating and cooling may be further confounded by the increased swimming effort associated with swimming upward as opposed to downward.

Our studies with stably swimming yellowfin are the first investigations of tuna thermoregulation in which the key variables influencing T_b (T_a and *U*) could be controlled. The ability to work with fish several hours after handling and to implement cyclic changes in T_a, approximating those experienced during foraging excursions (Holland *et al.* 1990), enabled us to mimic natural conditions and thereby to increase the probability of triggering 'normal' thermoregulatory responses.

The water tunnel, in conjunction with our experimental design, also enabled us to factor out effects that changes in T_a may exert on *Hp* (controlled in our tests) and cardiac output, both of which affect *k*. Cardiac performance affects tuna heat balance because retial heat transfer is inversely related to blood velocity (Dizon and Brill, 1979; Graham, 1983). Thus, alterations in cardiac output, in response to changes in either *U* or T_a, could affect heat exchange and produce results that mask or mimic physiological thermoregulation. The heart-rate reduction caused by cooler water would retard heat flux whereas warmer water would increase it.

Our experimental design allowed for separate comparisons of the *k* values estimated for heating and cooling during each of the thermal steps. This eliminated the need to correct for the influences of *Hp* and cardiac output within one thermal cycle. Also, the potential contribution of *Hp* and cardiac output between cycles can be estimated. If only thermally induced changes in *Hp* and cardiac output were responsible for the observed patterns, we would have expected a gradual increase in *k* with the rise in T_a from cycle 1 to cycle 3. Also, *k* should have changed maximally during the heating phases when both *Hp* and cardiac output would synergistically augment warming. Thus, because the *k* values for heating in cycle 2 are not intermediate to those of cycles 1 and 3, and because the most dramatic effects are observed during cooling (when *Hp* and cardiac output act in opposition, Figs 2, 3, 4 and Table 1), changes in *k* are due to the active modulation of heat flux.

Thermal notches

We interpret the thermal notches as evidence for the active regulation of heat transfer. Fig. 4 suggests that during the warming phase (i.e. $T_b < T_a$, and T_x is negative), heat transfer was increased to allow the influx of ambient heat to augment warming. Then, when T_a was dropped (T_x became positive), the fish was momentarily trapped in a 'high-*k* mode' which led to the rapid but short-lived fall in T_b. To prevent continued heat loss at the lower T_a in cycles 1 and 2, heat flux was abruptly curtailed, leading to the levelling off and subsequent increase in T_b. The absence of a notch in cycle 3 indicates that thermoconservation was not increased after T_a was reduced and that heat transfer is maximized at high T_a.

Given the constraints of equation 1, and because *Hp* should be constant over this short time span, the best explanation for the 'notch' is the active modulation of heat transfer. If this is the case, how can the subsequent rise in T_b be explained? The most parsimonious

explanation for the rise in T_b is that the rapid induction of thermoconservation curtailed convective heat loss sufficiently to elevate T_b. Also, with the heat exchangers 'turned off' during the warming phase, the abrupt onset of cool water may have channelled unheated blood directly into the yellowfin's red muscle to cause localized convective cooling. Because the adjacent white muscle is also warm but less vascularized (Carey, 1973; Bone, 1978; Dickson, 1988), its temperature would not decline as rapidly. Thus, conductive heat flux from the white to the red muscle may have also contributed to the elevation of T_b.

The dramatic reversal of dT_b/dt suggests that tuna can control heat transfer to permit the influx of ambient heat if $T_a > T_b$. This confirms the contention of Holland *et al.* (1992), who reported that the heating and cooling k values, calculated during rapid vertical excursions of a bigeye tuna, were different.

Thermal dependence of velocity effects on T_b

Fig. 5 demonstrates that while changes in U can affect T_b, the magnitude of the change is dependent on T_a. The extent that an increase in U (=Hp) affects T_b is determined by the level of counter-current heat exchange. Thus, the slight increase in T_b at 30 °C in comparison with that at 20 and 25 °C verifies that thermoconservation is reduced at 30 °C. That heat transfer is increased at high T_a is also indicated by the elevated T_x at both 25 and 20 °C and by the 'thermal notch' that occurred when T_a was dropped from 30 °C to 25 °C. These findings corroborate earlier conclusions that heat is lost more rapidly at high T_a and show that the risk of overheating during high activity can be alleviated.

Comparative aspects of tuna thermoregulation

Our results warrant consideration of the possible mechanisms used by yellowfin to modulate heat transfer. Among the factors affecting k (i.e. internal and external conductive and convective processes), conductive heat loss is dependent upon fixed variables (surface area, tissue properties affecting molecular heat diffusion) and is thus not subject to short-term regulation. Convective heat loss is, by contrast, affected by blood flow, and rapid circulatory modifications are employed by many animals to alter heat flux. Also, changes in latency, which in this study show the same thermal dependence as the k values, are suggested to reflect variations in blood flow (Fechhelm and Neill, 1982). Thus, it is likely that alterations in blood flow to or through the retia are used to regulate heat transfer. There is presently no anatomical evidence for vascular shunts that affect tuna heat transfer. It is, nevertheless, possible to obtain insight into this question by comparing the general circulation patterns of tuna heat exchangers.

In addition to the yellowfin, there are 12 other endothermic tuna species in the scombrid tribe Thunnini. It is therefore useful to consider how factors such as retial configuration (which varies considerably) may influence both T_b and thermoregulatory capabilities. Among the Thunnini, there is a range of reliance on the central and lateral retia (Fig. 1B; Graham, 1975). At one extreme, *Auxis* and *Euthynnus* rely primarily on a central rete and have only one small pair of lateral retia. At the other extreme, the three species comprising the 'bluefin group' of *Thunnus* (*T. thynnus, T. alalunga* and *T. maccoyii*), as well as the bigeye tuna (*T. obesus*), have two pairs of lateral retia and

have completely lost the central rete (Graham, 1975; Stevens and Neill, 1978). The yellowfin tuna is intermediate in this morphology, having a central rete and two pairs of well-developed lateral retia. It has been speculated that the frequent occurrence of the bluefin-group species and the bigeye tuna in cool waters at high latitude and below the thermocline relates to their sole reliance on the lateral retia (Graham, 1975; Stevens and Neill, 1978).

The results of preliminary studies with kawakawa (*Euthynnus affinis*) support the hypothesis that the lateral heat exchangers enhance thermoregulatory capabilities. In experiments similar to those described for yellowfin, we found the mean k for warming for three kawakawa to be $0.04\,\text{min}^{-1}$ ($N=7$), which is less than half that for the yellowfin (Table 1). This reduced capacity for regulating heat flux may be attributable to a primary dependence on blood flow through the dorsal aorta and post-cardinal vein and the adjacent central rete.

Three facts demonstrate the ability of yellowfin tuna to regulate heat transfer in response to changes in T_a and the thermal gradient. First, the abrupt increase in heat loss between cycles 1 and 2 and cycle 3, and the maximal changes during cooling (Figs 2, 3, 4 and Table 1), are indicative of active control of heat flux rather than passive changes in Hp and cardiac output. Second, the thermal notches (Figs 4 and 5) indicate that both T_a and the direction of the thermal gradient trigger a thermoregulatory response. Finally, the ability to regulate k is confirmed by the differential effects of U (Hp) and T_a on steady-state and non-steady-state T_x (Fig. 5).

Tuna, like homeothermic vertebrates, affect T_b through alterations of both k and Hp. However, while Hp can be altered independently of locomotion in birds and mammals, it is logical to assume that Hp cannot be controlled independently of swimming speed in tunas. Thus, the physiological, energetic and hydrodynamic constraints on tuna swimming limit the contribution of Hp to the control of T_b. Consequently, regulating heat balance is dependent on altering heat transfer, most probably through changes in retial blood flow. The physiological modulation of heat retention is thus a powerful complement to behavioural thermoregulation in tunas. Enhanced warming during an ascent in concert with reduced cooling during the subsequent descent will augment foraging time at depth. An elevated heat flux will also reduce the risk of overheating. Although tunas have variable T_b and are only regionally endothermic, physiological thermoregulation reduces potential limitations to distribution and activity and thus facilitates the effective exploitation of cooler waters.

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