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Differential heating and cooling rates in bigeye tuna (*Thunnus obesus* Lowe): a model of non-steady state heat exchange

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Summary

We analyzed water temperature, visceral cavity temperature and depth data from archival tags retrieved from bigeye tuna (Thunnus obesus) at liberty in the central Pacific for up to 57 days using a mathematical model of heat exchange. Our model took into account the transfer of heat between the portions of the myotomes comprising red muscle fibers adjacent to the spinal column and served by vascular counter current heat exchanges (henceforth referred to as 'red muscle') and the water, as well as between the red muscle and the temperature sensor of the archival tags in the visceral cavity. Our model successfully predicted the recorded visceral cavity temperatures during vertical excursions provided that the rate constants for heat transfer between the ambient water and the red muscle during cooling (k_{low}) and those during heating (k_{high}) were very dissimilar. Least-squares fitting of k_{low} and k_{high} for the entire period that the fish were at liberty yielded values

Introduction

Bigeye tuna (Thunnus obesus) occupy sub-tropical oceans where they spend the nighttime in the warm surface waters, but descend at dawn to depths where temperatures can be well below 10°C following the organisms comprising the Sound Scattering Layer (SSL) and apparently exploiting them as a food resource (Holland et al., 1990; Josse et al., 1998; Dagorn et al., 2000). During the day, bigeye tuna make regular (albeit brief) vertical excursions up through the thermocline. Upon entering the warm surface layer, red muscle temperature is rapidly elevated (Holland et al., 1992; Musyl et al., 2003). Increases in whole body thermal conductance, most likely accomplished through physiologically controlled reductions in the efficiency of vascular counter current heat exchangers, accelerate the rise of red muscle temperature (Holland and Sibert, 1994). Upon descending to cooler waters, bigeye tuna re-enter a thermo-conserving mode again by presumably increasing heat exchanger efficiency and thereby reducing generally in the ranges $0.02-0.04 \text{ min}^{-1}$ and $0.2-0.6 \text{ min}^{-1}$ (respectively), with an average ratio $k_{\text{high}}/k_{\text{low}}$ of ≈ 12 . Our results confirmed those from previous studies showing that bigeye tuna have extensive physiological thermoregulatory abilities probably exerted through changes of blood flow patterns that controlled the efficiency of vascular countercurrent heat exchanges. There was a small but significant negative correlation between k_{low} and size, whereas there was no correlation between k_{high} and size. The maximum swimming speeds during vertical excursions (calculated from the pressure data) occurred midway during ascents and averaged $\approx 2 FL \text{ s}^{-1}$ (where FL=fork length), although speeds as high $\approx 4-7 FL \text{ s}^{-1}$ were also noted.

Key words: archival tag, endothermy, Scombridae, swimming speed, temperature, thermoregulation, vertical movement.

whole body thermal conductance. Previous laboratory and field studies have shown that other tuna species also have control over the efficiency of vascular counter current heat exchangers (Dizon and Brill, 1979a; Dizon and Brill, 1979b; Graham and Dickson, 1981; Brill et al., 1994; Dewar et al., 1994; Graham and Dickson, 2001) although none apparently to the extent of that observed in bigeye tuna, with the possible exception of Atlantic and Pacific bluefin tunas (*Thunnus thynnus* and *T. orientalis*, respectively) (Block et al., 2001; Marcinek et al., 2001).

Previous estimates of the physiological thermoregulatory abilities of bigeye tuna based on the rate constants for warming and cooling were, however, based on short-term observations of swimming fish carrying ultrasonic telemetry devices (Holland et al., 1992). Electronic data recording (i.e. 'archival') tags have made it feasible to monitor fish movements, ambient and internal body temperatures for several months to years at a time (Block et al., 2001; Musyl et al., 2003; Sibert et al., 2003; Musyl et al., 2001; Schaefer and Fuller, 2002; Schaefer and Fuller, 2005). In this paper we take advantage of one of these large data sets (Musyl et al., 2003) and explore further the behavioral and physiological thermoregulatory abilities of bigeye tuna by modeling the events associated with their daily vertical movements. We thus provide a framework for analysis that can be applied to archival tag data sets from other tuna species, as well as for future studies of tunas in the wild. We have, however, specifically excluded any general discussion of the advantages conferred by elevated body temperatures as this subject has already received considerable attention (e.g. Block et al., 1993; Katz, 2002; Dickson and Graham, 2004; Graham and Dickson, 2004).

Materials and methods

Capture and tagging

A detailed account of the capture and tagging procedure, size of the fish, etc. have been reported elsewhere (Musyl et al., 2003) and only brief descriptions will be given here. Adult bigeye tuna *Thunnus obesus* Lowe were captured using conventional longline and recreational fishing gear. On board the ship, archival tags (Wildlife Computers, Redmond, Washington, USA) were placed into the visceral cavity through a 1–1.5 cm incision, which was closed with one or two sutures and veterinary surgical adhesive. The fish were then released. The tags recorded four channels of data: internal (i.e. visceral cavity) temperature, water temperature, ambient light and depth. All channels were sampled and data stored by the archival tags once every minute.

The tagged fish were captured in the central Pacific Ocean, near the main Hawaiian Island, at Cross Seamount (18°40'N, 158°17'W) or at NOAA weather buoy 51003 (19°11'N, 160°44'W, henceforth referred to as 'Buoy 3'). In the latter instance, the fish had very different behaviors when and when not immediately associated with the buoy. Bigeye tuna associated with floating objects tended to remain within the uniform-temperature surface layer both day and night. But after they moved away from the buoy they resumed their now welldescribed movement patterns (Holland et al., 1990; Musyl et al., 2003; Sibert et al., 2003; Schaefer and Fuller, 2005): descending at dawn, primarily remaining at depth during the day, making regular brief upward excursions, ascending at dusk, and remaining within the uniform-temperature surface layer at night. Likewise, the daily vertical movement patterns of bigeye tuna were different when and when not associated with the seamount (Musyl et al., 2003). While associated with Cross Seamount, daily vertical movements were constrained by bottom topography (Holland et al., 2001). The data recorded when the fish were in the open ocean were therefore separated from the data obtained when the fish were associated with Cross Seamount or Buoy 3.

Modeling

We analyzed the collected data using a simple twocompartment model. We found this to be the simplest possible model that could account satisfactorily for the observed data. In this model there are two first order ordinary differential equations, one for the actual red muscle temperature $(T_{\rm rm})$ and one for the temperature recorded by the sensor on the tag body (T_s) (i.e. the temperature in the visceral cavity):

$$dT_{\rm rm} / dt = k_{\rm w-rm}(T_{\rm a} - T_{\rm rm}) + \dot{T}_{\rm p}$$
, (1)

$$dT_s / dt = k_{rm-s}(T_{rm}-T_s)$$
. (2)

Here k_{w-rm} is the rate constant for heat transfer between the ambient water and the red muscle, k_{rm-s} is the rate constant for heat transfer between the red muscle and the temperature sensor on the archival tag, T_p is the potential rate of temperature increase due to metabolic heat production; and T_a , T_{rm} and T_s are ambient water, red muscle and sensor (i.e. visceral cavity) temperatures, respectively. (A derivation of the equations and a more detailed account of the meaning of the different terms are given in the Appendix.) In order to allow for active thermoregulation in the model, the value of k_{w-rm} was made variable according to:

$$k_{\rm w-rm} = k_{\rm low} \{ 1 + n[1 + \text{Sign}(T_{\rm a} - T_{\rm rm})] \} , \qquad (3)$$

where *n* is any positive number. The Sign(x) function attained a value of 1 when x>0, -1 when x<0 and 0 when x=0. Thus k_{w-rm} attained a low value (k_{low}) whenever $T_a < T_{rm}$, and increased to a high value (k_{high}) that was (2*n*+1) times k_{low} when $T_a > T_{rm}$.

It is generally only possible to find analytical solutions to the above system of equations in cases where k_{w-rm} , k_{rm-s} , \dot{T}_p and T_a are either constant or vary in time according to some simple analytical function (e.g. a Sine function). The system of equations was therefore solved numerically using commercial software (Mathematica, Wolfram Research, Champaign, IL, USA). If the model is adequate, taking the measured T_a as input and supplying reasonable values for k_{w-rm} , k_{rm-s} and \dot{T}_p should result in predicted values for T_s that closely follow the recorded values. The values of k_{low} and n that gave the smallest discrepancy between the measured T_s and the modeled T_s were found for each daytime period for individual fish as follows.

(1) As is evident from the equations, $\dot{T}_{p}=k_{w-rm}(T_{rm}-T_{a})$ whenever the fish is in thermal steady state $(dT_{rm}/dt=dT_{s}/dt=0)$. The value of $(T_{rm}-T_{a})=\Delta T_{ss}$ (i.e. steady-state red muscle temperature excess) was calculated for each period lasting more than 120 min during the whole night-time period and averaged. The potential rate of temperature increase due to metabolic heat production was then calculated as $\dot{T}_{p}=k_{w-rm}\Delta T_{ss}$. An actual \dot{T}_{p} , which took into account the red muscle temperature and the swimming speed, was calculated assuming exponential relationships between metabolic heat production and temperature as well as between metabolic heat production and swimming speed according to Eqn 4:

$$\dot{T}_{\rm p} = k_{\rm w-rm} \Delta T_{\rm ss} Q_{10}^{(T_{\rm rm} - T_{\rm ref})/10} 10^{\rm mV}$$
 (4)

Here $T_{\rm ref}$ is the average water temperature during the steady state periods (i.e. when $T_{\rm rm}$ is not changing) and V is the vertical swimming speed calculated from the changes in depth recorded by the archival tag. The values for Q₁₀ (i.e. effect of temperature on metabolic rate) and 'm' (the exponent in the equation describing the increase in metabolic rate with swimming speed) for an equally sized yellowfin tuna (*Thunnus albacares*) were taken from the literature (Dewar and Graham, 1994). $T_{\rm rm}$ was calculated from the sensor temperature according to:

$$T_{\rm rm} = T_{\rm s} + (1/k_{\rm rm-s}) ({\rm d}T_{\rm s}/{\rm d}t) .$$
(5)

The above equation follows directly from Eqn 2.



Fig. 1. 3-day depth record for Fish 241, illustrating the typical pattern observed in bigeye tuna not associated with floating objects or seamounts (from Musyl et al., 2003). The black horizontal bars indicate the night time.

(2) The value of $k_{\rm rm-s}$ takes into account the time constant for the temperature sensor built into the archival tag. This was largely determined by the size and construction of the tag and the tag's location within the visceral cavity. We assumed the value for $k_{\rm rm-s}$ to be constant for any fish and to vary only little among the different fish. A value was guessed which was finetuned after the best values of $k_{\rm low}$ and *n* (as defined in Eqn 3) had been fitted (see below). This was done once for each fish and this value of $k_{\rm rm-s}$ was used when fitting $k_{\rm low}$ and *n* for all the daytime periods.

(3) The best value of k_{low} and *n* for each daytime period were found by a least-squares method, the minimized entity being:

SS =
$$\sum_{i} [f_{\rm ns}(i) - T_{\rm s}(i)]^2$$
, (6)

where $T_s(i)$ is the measured visceral cavity temperature at time *i* and $f_{ns}(i)$ is the function value (i.e. the value given by the numerical solution at that time).

Results

Red muscle temperature regulation

Fig. 1 shows the time-depth data for Fish 241 recorded during a typical 3-day period [fish identification numbers match those given in Musyl et al. (Musyl et al., 2003)]. At night the fish stayed in the upper \approx 50–100 m of the water column (the uniform-temperature surface layer), whereas in the daytime it descended to approximately 350 m. It subsequently made regular excursions to the uniform-temperature surface layer. This pattern of night- and daytime activity continued for extended periods (Musyl et al., 2003). A typical example of water temperature, sensor temperature, as well as the modeled sensor temperature during daytime for Fish 241, is shown in Fig. 2A. As the fish descended, the T_a decreased rapidly, whereas T_s decreased much more slowly. For every excursion to the uniform-temperature surface layer, there was a rapid increase in T_s , followed by a slow decrease after return to depth. This resulted in a substantial magnification of the difference between T_s and T_a . The modeled T_s follow the recorded T_s remarkably well, and only during the last three surface excursions was a small discrepancy observed. The close fit can better be appreciated in Fig. 2B, which shows an expanded section of Fig. 2A. For this particular period, the fitted values for k_{low} and k_{high} were 0.030 min⁻¹ and 0.45 min⁻¹, respectively. When, in the model, physiological thermoregulation was prevented by keeping k_{w-rm} constant at either the low or the high value, the modeled T_s did not in any way resemble the measured values (data not shown).

In Fig. 3 we have plotted the fitted k_{low} and k_{high} values of each fish during the whole sampling period. It was only possible to calculate k_{low} and k_{high} values on days when fish made regular vertical excursions and the lack of any such account for the missing values. These difficulties were primarily found in the individuals associated with Buoy 3 (Fish 301, Fish 390, Fish 392), due to their irregular swimming patterns. However, Fish 241 also showed association with a floating object for a number of days as described previously (Musyl et al., 2003). This made some days unsuited for modeling. In all of the fish, both k_{low}



Fig. 2. Ambient (T_a) and sensor (T_s) temperature records (the latter located within the body of an archival tag placed in the visceral cavity) during a typical daytime period for Fish 241, along with the fitted T_s data. (A) An entire daytime period; (B) the 300–400 min portion in A expanded.



Fig. 3. The fitted values of k_{high} and k_{low} for each daytime period of each fish from the entire data records. Missing values typically resulted from the fish being associated with a Buoy 3 (Fish 301, Fish 390, Fish 392) or Cross Seamount (Fish 224), making fitting impossible. Fish 224 had an apparent constant displacement of the recorded ambient temperature. When this was adjusted by a constant value, such that the nighttime sensor temperature excess was similar to that of the other fish, it gave similar fitted values for k_{low} and k_{high} and therefore the results were included in the figure.

and k_{high} remained fairly constant throughout the sampling period, with k_{low} being less variable. There was, however, clearly less constancy in the values obtained from the fish



Fig. 4. The fitted k_{low} values from all fish plotted as a function of k_{high} .

k_{high} (min⁻¹)

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associated with Buoy 3 than from those not associated with the floating objects. In Fig. 4 we have plotted k_{low} as a function of k_{high}. There was no clear correlation between the two rate constants; k_{low} was generally 0.02–0.04 min⁻¹ and k_{high} between 0.2 and 0.6 min⁻¹. The k_{high} -values were not correlated with fish body mass, although there was a small but statistically significant decrease in k_{low} with size. The weighted linear leastsquare regression (fitted using the reciprocals of the s.e.m. as weight) was $k_{low}=0.0536-0.000316 FL$ (in cm) ($r^2=0.75$, P=0.042). When fitting k-values, T_p was allowed to vary with swimming speed and red muscle temperature according to Eqn 4. Keeping \dot{T}_{p} constant, and at a value corresponding to the standard metabolic rate at one particular temperature, only marginally affected the fitted k-values however. The average deviations between k-values found with varying or constant \dot{T}_{p} on a sub-sample of eight randomly chosen days from Fish 241 was 4.85% (range: 1.18–7.33%) for k_{low} , and 3.68% (range: 0.587-5.66%) for k_{high} .

The ability of bigeve tuna to rapidly modify the efficiency of



Fig. 5. (A) Red muscle temperature ($T_{\rm rm}$) of Fish 241 (calculated from the measured sensor temperature) as a function of ambient temperature ($T_{\rm a}$) during one day. The data points are joined to illustrate the behavior of the fish and how this affects its $T_{\rm rm}$. (B) The distribution of calculated $T_{\rm rm}$ for an ambient temperature interval of 10.0–25.5°C. (C) Density plot of the number of observations (i.e. the number of observations per °C²) of a given combination of ambient and calculated red muscle temperature. This plot is based on the combined set of observations (all days and nights for the entire time of deployment) for Fish 241, Fish 290, Fish 292, Fish 301 and Fish 625, for a total of 921,592 observations. The dotted straight lines in A and C show $T_{\rm a}=T_{\rm rm}$.

their vascular counter current heat exchangers (i.e. physiologically thermoregulate) and thus exert some control over $T_{\rm rm}$ may be best appreciated from Fig. 5. Fig. 5A is a plot of $T_{\rm rm}$ versus $T_{\rm a}$ for Fish 241 during one day. As the fish ascended and descended, $T_{\rm a}$ cycled between 10 and 25°C, whereas $T_{\rm rm}$ changed by only 5°C with a mean of about 19°C. In Fig. 5B, the frequency distribution of red muscle temperatures at an ambient temperature of 10.0–10.5°C (as calculated from the sensor temperature by Eqn 5) is shown for five fish (Fish 241, Fish 301, Fish 390, Fish 392 and Fish 625) for the entire time that data



Fig. 6. Vertical swimming speed as a function of depth during one day for Fish 241. As indicated by the arrows, the left side of the figure shows descents and right side ascents.

were collected. This panel clearly shows the substantial elevation of red muscle temperature above the ambient temperature. The distribution is obviously skewed, with relatively few recordings below the modal value and many above. Fig. 5C is a density plot of the total number of matched ambient temperatures and calculated red muscle temperatures for the five fish for the entire time that data were collected. The figure very clearly shows thermoregulating animals, but it also re-emphasizes the importance of monitoring internal temperatures in swimming fish first noted by Dizon and Brill (Dizon and Brill, 1979a; Dizon and Brill, 1979b); and that a random point measurement of temperature of a fish hauled on deck and compared to surface water temperature may not reflect the average red muscle temperature elevation or thermoregulatory ability.

Vertical swimming speed

The vertical swimming speed for Fish 241 as a function of depth is shown in Fig. 6. There was a gradual increase in swimming speed (reaching a maximum of approximately 2 m s⁻¹) close to the mid-point depth during vertical movements and then a gradual decrease. The velocity-distance curves for ascents and descents of Fish 241 were clearly similar. Fig. 7 shows average maximum velocities of all ascents and descents during the entire sampling period as a function of size. Maximum vertical swimming speeds during the two periods were not statistically different. There was, however, a weak negative correlation between maximum swimming speed (in FL s⁻¹) and fork length (FL; cm). Along with the averages of all the maximal vertical swimming speeds, we have plotted the maximal value of vertical swimming speed observed during the entire sampling period of each fish (filled triangles). These values ranged from ≈ 4 to 7 FL s⁻¹ with no apparent sizedependency.



Fig. 7. Mean of all the observed maximal ascent and descent speeds (\pm s.e.m) during vertical excursions for (from left to right) Fish 390, Fish 392, Fish 301, Fish 298, Fish 625, Fish 241 and Fish 224, plotted as a function of size (fork length, *FL*). The regression lines were fitted with a weighted linear least-square procedure using the reciprocals of the s.e.m. as weight and are: y=3.627-0.0192x (for descents, $r^2=0.985$, P=0.00015) and y=3.439-0.0195x (for ascents, $r^2=0.945$, P=0.001). Note that the s.e.m. for each point is so small that it is not distinguishable from the symbol. Also the maximal vertical speeds observed for each fish during their entire tag deployment period are shown (filled triangles).

The average maximal swimming speeds calculated from the depth measurements represent the minimum estimates of the true swimming speeds, as only the vertical component was known (Fig. 6). Nevertheless, the recorded vertical swimming speeds were surprisingly high (Fig. 7). Thus the two largest specimens (*FL*=79 and 86 cm) on every excursion reached Reynolds numbers in excess of 1.2×10^6 and 1.4×10^6 , respectively, which is above the range where the boundary layer would be expected to shift from laminar to turbulent (Webb, 1975).

Discussion

The routine metabolic rates of southern bluefin tuna have been shown to increase by 2.8 times following food ingestion, due to increased swimming speed and specific dynamic action (SDA) (Fitzgibbon et al., 2007). We have, however, specifically excluded the effect of feeding on metabolic heat production and any influence of visceral warming following food intake from our modeling efforts for three reasons. First, neither Musyl et al. (Musyl et al., 2003) nor Schaefer and Fuller (Schaefer and Fuller, 2002) reported any obvious increases in visceral temperatures in bigeye tuna in their extensive data sets that were equivalent in magnitude and duration (20-40 h) to those reported by Gunn et al. (Gunn et al., 2001) occurring in southern bluefin tuna (Thunnus maycoyii) following feeding. We admit that this was surprising given that bigeye tuna do have vascular counter-current heat exchangers associated with the liver (as do both southern and Atlantic bluefin tunas) (Graham and Dickson, 2001). Bigeye tuna should, therefore, also be expected to warm their viscera following feeding (Stevens and McLeese, 1984; Gunn et al., 2001). We have no explanation why they did not. Second, we have no data on the feeding frequency of bigeye tuna. As such, including this 'SDA-effect' would have been pure speculation. Third, and most importantly, even though we included increases in metabolic rate and red muscle temperature due to increases in swimming speed in our calculations, this actually had little or no effect on the modeled values for the rate constants of heat transfer (k_{low} and k_{high}) accompanying the vertical movements of bigeye tuna. We suspect that any increases in metabolic rate following feeding would likewise not effect our conclusions.

Modulation of heat transfer: thermoregulation

Our results do show that differential heating and cooling rates were a necessary assumption to predict successfully the temperatures recorded by archival tags placed in the visceral cavity of bigeye tuna. Although we made direct efforts to correct for the fact that the temperature data were recorded by a sensor that was part of an archival tag, rather than a small separate temperature sensor placed in the red muscle, the average ratio between heating and cooling rates that we calculated may still have underestimated the true value. Indeed, Holland et al. (Holland et al., 1992) and Holland and Sibert (Holland and Sibert, 1994), using data from acoustic tags with a thermistor placed directly into the red muscle of bigeye tuna, found higher ratios (100–1000).

Nonetheless, bigeve tuna clearly have extensive thermoregulatory abilities that appear to exceed those of yellowfin tuna. The ratios of k_{low} to k_{high} that we calculated when bigeye tuna were warming and cooling were much higher than those found for swimming yellowfin tuna during laboratory studies (Dewar et al., 1994). We cannot state with certainty to what degree the difference in the ratios of heating and cooling rates for bigeye and yellowfin tunas reflect true physiological and anatomical differences (Dickson and Graham, 2004; Graham and Dickson, 2004), or a difference between unrestrained fish performing natural behavior and specimens in a laboratory swimming tunnel. Yellowfin tuna are, however, generally thought to have a lesser ability to physiologically thermoregulate (Dizon and Brill, 1979a; Dewar et al., 1994).

Yellowfin tuna have a central heat exchanger and relatively small lateral heat exchangers and it has been suggested that this limits their ability to make large, abrupt changes in heat transfer rates (Graham, 1975; Dewar et al., 1994). Atlantic bluefin tuna (Thunnus thynnus), in contrast, have large lateral heat exchangers but a much reduced dorsal aorta and an incomplete post-cardinal vein. Without a large dorsal aorta and a complete post-cardinal vein, Atlantic bluefin may likewise be limited in their thermoregulatory abilities as they may not be able to alter blood flow to the red muscle to pathways that do not pass through the lateral vascular counter current heat exchangers. The large size of adult Atlantic bluefin tuna, and their apparently efficient heat exchangers, do allow this species to maintain a larger difference between red muscle and water temperatures when in cold water than is seen in other endothermic fishes (Carey and Teal, 1969; Carey and Lawson, 1973; Neill and Stevens, 1974; Stevens et al., 2000; Block et al., 2001), including the Pacific bluefin tuna (Gunn and Block, 2001; Marcinek et al., 2001). It is plausible, therefore, that Atlantic bluefin tuna would not benefit further from having a large ability to modulate heat transfer rates, unless it would be to avoid overheating during spawning periods in the warm surface waters of the Gulf of Mexico (Block et al., 2001).

Bigeye tuna are anatomically intermediate between yellowfin tuna and Atlantic bluefin tuna. Bigeye tuna have a more developed dorsal aorta than Atlantic bluefin tuna, and a complete post cardinal vein (Kishinouye, 1923; Gibbs and Collette, 1967; Collette et al., 2001). In bigeye tuna, however, the dorsal aorta and post cardinal vein lack the well developed counter current heat exchangers (arterioles and venules) arising from them that are present in yellowfin tuna (Graham and Dickson, 2001). We suggest that the lack of a central vascular counter current heat exchanger may actually allow changes in relative blood flow between the central and lateral circulations (the latter supplying the lateral vascular counter current heat exchangers) to regulate heat transfer to and from the water *via* the circulatory system and gills.

The physiological adjustments needed to obtain heating rates more than an order of magnitude greater than the cooling rates are substantial. A simple passive mechanism that would decrease heat exchanger efficiency and increase heating rate during warming (such as an increased blood supply to the muscle via the lateral the heat exchanger) seems unlikely. As described above, it is more probable that blood supply to the red muscle is shunted from the lateral blood vessels to the dorsal aorta and post cardinal vein. This hypothesis is supported by the fact that the vertical swimming speed was invariably maximal approximately midway on the vertical excursions (Figs 6 and 7). This was at ambient temperatures that were lower than red muscle temperature and where the fish was in a thermoconserving mode (Fig. 2). The increase in blood flow accompanying an increased swimming speed would, therefore, not necessarily be reflected in a change in the rate constant for heat transfer. Furthermore, attempts to model the internal temperature by letting the k-value become directly proportional to swimming speed proved unsuccessful. It appears, therefore, that bigeye tuna utilize a combination of physiological and behavioral thermoregulation in order to maintain red muscle temperatures well above the water temperature. As described by Lowe et al. (Lowe et al., 2000), sustained elevated muscle temperatures appear critical to the ability of bigeye tuna to withstand low ambient oxygen levels (approaching $1-2 \text{ mg } l^{-1}$) occurring at depth (Hanmoto, 1987), by allowing their blood to have a high oxygen affinity as it passes through the gills (typical of sluggish hypoxia tolerant fish species) and a lower oxygen affinity blood typical of other (less hypoxia tolerant, but likewise high energy demand) tuna species after it is warmed in the vascular counter current heat exchangers.

All these adaptations appear to give bigeye tuna the ability to have extensive vertical movement patterns suggestive of a strong association with the movements of the SSL, both during the daytime and the night time (Fig. 1). This association is stronger than in other tuna species that are less able to follow the SSL during the daytime when it descends to depths >350–400 m and water temperatures below well below 10°C (Marchal et al., 1993). For example, in contrast to the vertical movement pattern of bigeye tuna, yellowfin tuna generally remain in the uniformtemperature surface layer, generally just entering the thermocline (Holland et al., 1990; Block et al., 1997; Brill et al., 1999) and only very occasionally descending to depths with water temperatures below 10°C (Dagorn et al., 2006). Although these differences in the vertical movements have been hypothesized to be due to effects of acute reductions in ambient temperature on cardiac function (Brill and Bushnell, 2001; Blank et al., 2004; Landeira-Fernandez et al., 2004; Shiels et al., 2004), such species-specific differences in behavior could also be a result of differences in physiological thermoregulatory abilities. Yellowfin tuna do show different heating and cooling rates in visceral temperature during these extensive (albeit very occasional) vertical movements (Dagorn et al., 2006), but these data have not yet been analyzed in a way equivalent to that presented here.

Our data also show a significant negative relationship between k_{low} and size was based on few individuals and limited size range. This relationship would be expected due to a relative decrease in heat loss to the water *via* the body surface, which could be, in turn, due to a simple decrease of the surface-tovolume ratio in larger individuals. In skipjack tuna (*Katsuwonus pelamis*), measured surface heat loss has been found to be over 50% of calculated metabolic heat production (Brill et al., 1978). The decrease in k_{low} with size is likewise consistent with the observation that thermal inertia increases with body size in tunas (Neill et al., 1976).

Vertical swimming speed

The maximal observed vertical swimming speeds of bigeye tuna (Fig. 7) were higher than those measured in Pacific bluefin tuna $(2.58-3.99 \text{ body length s}^{-1})$ (Marcinek et al., 2001) and to be above predicted maximum sustained swimming speeds of vellowfin tuna (Bushnell and Brill, 1991; Korsmeyer et al., 1996). Also, the speeds seen during vertical movements were greater than the horizontal speed measured for large bigeye tuna around the Hawaiian Islands, further validating the use of vertical speeds to estimate maximum swimming speeds (Dagorn et al., 2000). Vertical swimming speeds based on rates of ascent do not, however, take into account any horizontal component and it was unlikely that the fish was swimming straight up. In order to measure accurate swimming speeds, a speed telemetry device would be necessary as employed by Block et al. (Block et al., 1992). Such detailed measurement would better elucidate whether swimming speeds are the same at different depths and during descent and ascent. Pacific bluefin tuna, blue marlin (Makaira nigricans), and yellowfin tuna all appear to increase swimming speeds during descents into cool water (Marcinek et al., 2001; Block et al., 1992; Dagorn et al., 2006) which may represent part of an energy saving 'swim-glide' behavior (Weihs, 1973).

Merits and limitations of the model

Our model is the most parsimonious one that can analyze simultaneously recorded ambient and internal temperatures and estimate cooling and heating rates. The model provided close fits between the observed and the modeled T_s on specimens of bigeye tuna that swum up and down in the water column during daytime. The key feature of the model was the way thermoregulation was implemented. This was done with a very simple switch: whenever T_a was above T_{rm} the rate constant for temperature change attained a high value; and whenever T_a was below T_{rm} it attained a low value. This bistate switching was sufficient to account for the recorded temperatures. The simplicity of the model makes it suitable for analysis of recorded temperature (simultaneous

internal and external) data of many species. The time resolution of the data is crucial, however. In our analyses, the data we had available were recorded with a time resolution of 1 min. Nevertheless, using data with higher time resolution together with faster responding tags might have yielded higher separation between the estimated rates for cooling and heating, closer to those reported by Holland et al. (Holland et al., 1992) and Holland and Sibert (Holland and Sibert, 1994). Moreover, when we tried to analyze data recorded with a time resolution of 5 min, we were unsuccessful. While our model is attractive for its simplicity, it can only yield rate constants for cooling and heating and this in itself provides little information on the mechanism of thermoregulation. To extract more precise information on the mechanisms, the data would have to be analyzed in terms of a two- (or three-)dimensional model that could take into account differential heat production in different types of muscle, heat exchanger efficiency, routes of heat loss to the water, etc.

Conclusions

Bigeye tuna use both behavioral and physiological thermoregulation to help maintain elevated red muscle temperature. Their ability to modulate heat transfer rates is independent of swimming speed and ambient temperature. During the regular vertical sojourns, bigeye tuna can modulate heat transfer rates on average by a factor 12. There appears to be a tendency for the ability of the bigeye tuna to sustain elevated red muscle temperatures to increase with size, primarily by a significant decrease in k_{low} and perhaps increases in thermal inertia (Neill et al., 1976).

Appendix

Model development

In developing our mathematical model, we made the following assumptions:

(1) The red muscle temperature distribution and heat production were uniform.

(2) Blood returning from the gills was at ambient temperature and reached the red muscle through vascular counter current heat exchangers, as well as directly.

(3) In addition to the convective cooling by the blood, there was conductive heat loss to the water through the body surface (Brill et al., 1978).

(4) The temperature sensor was insulated to some degree and thus the recorded temperature lagged behind the changes in muscle temperature.

With these assumptions, the heat balance model requires two coupled, first-order ordinary differential equations:

$$\frac{dH_{\rm rm}}{dt} = G_{\rm c}[1 - \epsilon(1 - f)](T_{\rm a} - T_{\rm rm}) + G_{\rm d}(T_{\rm a} - T_{\rm rm}) + \dot{H}_{\rm p} - G_{\rm rm-s}(T_{\rm rm} - T_{\rm s}), \quad (A1)$$

$$\frac{\mathrm{d}H_{\mathrm{s}}}{\mathrm{d}t} = G_{\mathrm{rm-s}}(T_{\mathrm{rm}} - T_{\mathrm{s}}) \ . \tag{A2}$$

 $H_{\rm rm}$ and $H_{\rm s}$ are the heat contents of the red muscle and the sensor; $G_{\rm c}$ and $G_{\rm d}$ are the convective (by blood) and the conductive heat transfer coefficients (respectively) from the fish to the water. $G_{\rm rm-s}$ is the conductive heat transfer coefficient for heat movement between the red muscle and the temperature sensor of the archival tag in the visceral cavity. T_a , T_{rm} and T_s are the ambient, red muscle and visceral cavity temperatures, respectively. \dot{H}_p is red muscle heat production, ϵ is the heat exchanger efficiency (i.e. the fraction of heat carried into the heat exchanger by the venous blood that is transferred to the arterial blood), *f* the fraction of the blood flow supplying the red muscle directly, and (1–*f*) the fraction of the blood flow supplying the red muscle through the vascular counter-current heat exchangers. Note that if ϵ =1 and *f*=0, convective heat transfer would be reduced to zero (the first term in Eqn A1 vanishes). If, on the other hand, ϵ =0 or *f*=1, the effect of the heat exchanger would be eliminated (the terms in the square bracket=1).

The relation between heat and temperature is given by $dH=V_mc_p\rho dT$, where V_m is the volume, c_p the average heat capacity, and ρ the average density of the fish. Substituting this identity into Eqn A1 and Eqn A2 gives:

$$\frac{dT_{\rm rm}}{dt} = \frac{G_{\rm c}}{V_{\rm m}c_{\rm p}\rho} \left[1 - \epsilon (1 - f)\right](T_{\rm a} - T_{\rm rm}) + \frac{\dot{H}_{\rm p}}{V_{\rm m}c_{\rm p}\rho} - \frac{G_{\rm rm-s}}{V_{\rm m}c_{\rm p}\rho} (T_{\rm rm} - T_{\rm s}), \quad (A3)$$

$$\frac{\mathrm{d}T_{\mathrm{s}}}{\mathrm{d}t} = \frac{G_{\mathrm{rm-s}}}{V_{\mathrm{m}}c_{\mathrm{p}}\rho} \left(T_{\mathrm{rm}} - T_{\mathrm{s}}\right) \,. \tag{A4}$$

The last term in Eqn A3 is small compared to the others and may be neglected.

Introducing the rate constants $k_c=G_c/(V_mc_p\rho)$, $k_d=G_d/(V_mc_p\rho)$, $k_{rm-s}=G_{rm-s}/(V_mc_p\rho)$, and the potential rate of temperature increase due to metabolic heat production $[\dot{T}_p=\dot{H}_p(V_mc_p\rho)]$, then rearranging leads to:

$$\frac{dT_{\rm rm}}{dt} = \{k_{\rm c}[1 - \epsilon(1 - f)] + k_{\rm d}\}(T_{\rm a} - T_{\rm rm}) + \dot{T}_{\rm p}, \qquad (A5)$$

$$\frac{\mathrm{d}T_{\mathrm{s}}}{\mathrm{d}t} = k_{\mathrm{rm-s}}(T_{\mathrm{rm}} - T_{\mathrm{s}}) \;. \tag{A6}$$

This can be further simplified to:

$$\frac{\mathrm{d}T_{\mathrm{rm}}}{\mathrm{d}t} = k_{\mathrm{w-rm}}(T_{\mathrm{a}} - T_{\mathrm{rm}}) + \dot{T}_{\mathrm{p}} , \qquad (A7)$$

$$\frac{\mathrm{d}T_{\mathrm{s}}}{\mathrm{d}t} = k_{\mathrm{rm-s}}(T_{\mathrm{rm}} - T_{\mathrm{s}}) , \qquad (A8)$$

where we have introduced a new rate constant, k_{w-rm} , given by:

$$k_{\text{w-rm}} = k_{\text{c}}[1 - \epsilon(1 - f)] + k_{\text{d}}.$$
(A9)

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References

- Blank, J. M., Morrissette, J. M., Landeira-Fernandez, A. M., Blackwell, S. B., Williams, T. D. and Block, B. A. (2004). *In situ* cardiac performance of Pacific bluefin tuna hearts in response to acute temperature change. *J. Exp. Biol.* 207, 881-890.
- Block, B. A., Booth, D. T. and Carey, F. G. (1992). Direct measurement of swimming speeds and depth of blue marlin. J. Exp. Biol. 166, 267-284.
- Block, B., Finnerty, J. R., Stewart, A. F. R. and Kidd, J. (1993). Evolution of endothermy in fish: mapping physiological traits on a molecular phylogeny. *Science* 260, 210-214.
- Block, B. A., Keen, J. E., Castillo, B., Dewar, H., Freund, E. V., Marcinek, D. J., Brill, R. W. and Farwell, C. (1997). Environmental preferences of yellowfin tuna (*Thunnus albacares*) at the northern extent of its range. *Mar. Biol.* 130, 119-132.
- Block, B. A., Dewar, H., Blackwell, S. B., Williams, T. D., Prince, E. D., Farwell, C. J., Boustany, A., Teo, S. L. H., Seitz, A., Walli, A. et al. (2001). Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science* 293, 1310-1314.
- Brill, R. W. and Bushnell, P. G. (2001). The cardiovascular system of tunas. In *Tuna. Physiology, Ecology and Evolution (Fish Physiology, Vol. 19)* (ed. B. A. Block and E. D. Stevens), pp. 79-120. San Diego: Academic Press.
- Brill, R. W., Guernsey, D. L. and Stevens, E. D. (1978). Body surface and gill heat loss in restrained skipjack tuna. In *The Physiological Ecology of Tunas* (ed. G. D. Sharp and A. E. Dizon), pp. 261-276. San Diego: Academic Press.
- Brill, R. W., Dewar, H. and Graham, J. B. (1994). Basic concepts in steady state and non-steady state heat transfer in fishes, and their use in determining thermoregulatory abilities in tunas. *Environ. Biol. Fishes* 40, 109-124.
- Brill, R. W., Block, B. A., Boggs, C. H., Bigelow, K. A., Freund, E. V. and Marcinek, D. J. (1999). Horizontal movements and depth distribution of large adult yellowfin tuna (*Thunnus albacares*) near the Hawaiian Islands, recorded using ultrasonic telemetry: implications for the physiological ecology of pelagic fishes. *Mar. Biol.* 133, 395-408.
- Bushnell, P. G. and Brill, R. W. (1991). Responses of swimming skipjack (*Katsuwonus pelamis*) and yellowfin (*Thunnus albacares*) tunas exposed to acute hypoxia, and a model of their cardio-respiratory function. *Physiol. Zool.* 64, 787-811.
- Carey, F. G. and Lawson, K. D. (1973). Temperature regulation in a freeswimming bluefin tuna. *Comp. Biochem. Physiol.* 44A, 375-392.
- Carey, F. G. and Teal, J. M. (1969). Regulation of body temperature by the bluefin tuna. Comp. Biochem. Physiol. 28, 205-213.
- Collette, B. B., Reeb, C. and Block, B. A. (2001). Systematics of the tunas and mackerels (Scombridae). In *Tuna. Physiology, Ecology and Evolution (Fish Physiology, Vol. 19)* (ed. B. A. Block and E. D. Stevens), pp. 1-33. San Diego: Academic Press.
- Dagorn, L., Bach, P. and Josse, E. (2000). Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean, determined using ultrasonic telemetry. *Mar. Biol.* 136, 361-371.
- Dagorn, L., Holland, K. N., Hallier, J.-P., Taquet, M., Moreno, G., Sancho, G., Itano, D. G., Aumeeruddy, R., Girard, C., Million, J. et al. (2006). Deep diving behavior observed in yellowfin tuna (*Thunnus albacares*). Aquat. Living Resour. 19, 85-88.
- Dewar, H. and Graham, J. (1994). Studies of tropical tuna swimming performance in a large water tunnel energetics. J. Exp. Biol. 192, 13-31.
- Dewar, H., Graham, J. B. and Brill, R. W. (1994). Studies of tropical tuna swimming performance in a large water tunnel – thermoregulation. J. Exp. Biol. 192, 33-44.
- Dickson, K. A. and Graham, J. B. (2004). Evolution and consequences of endothermy in fishes. *Physiol. Biochem. Zool.* 77, 998-1018.
- Dizon, A. E. and Brill, R. W. (1979a). Thermoregulation in yellowfin tuna, *Thunnus albacares. Physiol. Zool.* 52, 581-593.
- Dizon, A. E. and Brill, R. W. (1979b). Thermoregulation in tuna. Am. Zool. 19, 249-265.
- Fitzgibbon, Q. P., Seymour, R. S., Ellis, D. and Buchanan, J. (2007). The energetic consequence of specific dynamic action in southern bluefin tuna *Thunnus maccoyi. J. Exp. Biol.* 210, 290-298.
- Gibbs, R. and Collette, B. B. (1967). Comparative anatomy of the tunas, genus *Thunnus. Fish. Bull. U. S.* 66, 65-130.
- Graham, J. B. (1975). Heat exchange in the yellowfin tuna, *Thunnus albacares*, and skipjack tuna, *Katsuwonus pelamis*, and the adaptive significance of elevated body temperature in scombrid fishes. *Fish. Bull. U. S.* **73**, 219-229.
- Graham, J. B. and Dickson, K. A. (1981). Physiological thermoregulation in the albacore *Thunnus alalunga*. Physiol. Zool. 54, 470-486.
- Graham, J. B. and Dickson, K. A. (2001). Anatomical and physiological specializations for endothermy. In *Tuna. Physiology, Ecology and Evolution* (*Fish Physiology, Vol. 19*) (ed. B. A. Block and E. D. Stevens), pp. 121-166. San Diego: Academic Press.
- Graham, J. B. and Dickson, K. A. (2004). Tuna comparative physiology. J. Exp Biol. 207, 4015-4024.
- Gunn, J. and Block, B. (2001). Advances in acoustic, archival, and satellite tagging

of tunas. In *Tuna. Physiology, Ecology and Evolution (Fish Physiology, Vol. 19)* (ed. B. A. Block and E. D. Stevens), pp. 167-224. San Diego: Academic Press.

- Gunn, J., Jartog, J. and Rough, K. (2001). The relationship between food intake and visceral warming in southern bluefin tuna (*Thunnus maccoyii*). In *Electronic Tagging and Tracking in Marine Fisheries* (ed. J. R. Sibert and J. L. Nielsen), pp. 109-130. Dordrecht: Kluwer Academic Publishers.
- Hanamoto, E. (1987). Effect of oceanographic environment on bigeye tuna distribution. Bull. Jap. Soc. Fish. Oceanogr. 51, 203-216.
- Holland, K. N. and Sibert, J. R. (1994). Physiological thermoregulation in bigeye tuna, *Thunnus obesus. Environ. Biol. Fishes* 40, 319-327.
- Holland, K. N., Brill, R. W. and Chang, R. K. C. (1990). Horizontal and vertical movements of yellowfin and bigeye tuna associated with fish aggregating devices. *Fish. Bull. U. S.* 88, 493-507.
- Holland, K. N., Brill, R. W., Chang, R. K. C., Sibert, J. R. and Fournier, D. A. (1992). Physiological thermoregulation in bigeye tuna (*Thunnus obesus*). *Nature* 358, 410-412.
- Holland, K. N., Kajiura, S. M. and Itano, D. G. (2001). Tagging techniques can elucidate the biology and exploitation of aggregated pelagic fish species. *Am. Fish. Soc. Symp.* 25, 211-218.
- Josse, E., Bach, P. and Dagorn, L. (1998). Simultaneous observations of tuna movements and their prey by sonic tracking and acoustic surveys. *Hydrobiologia* 371/372, 61-69.
- Katz, S. L. (2002). Design of heterothermic muscle in fish. J. Exp. Biol. 205, 2251-2266.
- Kishinouye, K. (1923). Contributions to the comparative study of the so-called scombroid fishes. J. Coll. Agric. Imperial Uni. Tokyo 8, 365-378.
- Korsmeyer, K. E., Dewar, H., Lai, N. C. and Graham, J. B. (1996). Tuna aerobic swimming performance: physiological and environmental limits based on oxygen supply and demand. *Comp. Biochem. Physiol.* **113B**, 45-56.
- Landeira-Fernandez, A. M., Morrissette, J. M., Blank, J. M. and Block, B. A. (2004). Temperature dependence of the Ca²⁺–ATPase (SERCA2) in the ventricles of tuna and mackerel. Am. J. Physiol. 286, R398-R404.
- Lowe, T., Brill, R. and Cousins, K. (2000). Blood O₂-binding characteristics of bigeye tuna (*Thunnus obesus*), a high-energy-demand teleost that is tolerant of low ambient O₂. *Mar. Biol.* **136**, 1087-1098.
- Marchal, E., Gerlotto, F. and Stequert, B. (1993). On the relationship between scattering layer, thermal structure and tuna abundance in the eastern Atlantic equatorial current system. *Oceanol. Acta* 16, 261-272.
- Marcinek, D. J., Blackwell, S. B., Dewar, H., Freund, E. V., Farwell, C., Dau, D., Seitz, A. C. and Block, B. A. (2001). Depth and muscle temperature of Pacific bluefin tuna examined with acustic and pop-up satellite archival tags. *Mar. Biol.* 138, 869-885.
- Musyl, M. K., Brill, R. W., Curran, D. S., Gunn, J. S., Hartog, J. R., Hill, R. D., Welch, D. W., Eveson, J. P., Boggs, C. H. and Brainard, R. E. (2001). Ability of archival tags to provide estimates of geographical position based on light intensity. In *Electronic Tagging and Tracking in Marine Fisheries* (ed. J. R. Sibert and J. L. Nielsen), pp. 343-367. Dordrecht: Kluwer Academic Publishers.
- Musyl, M. K., Brill, R. W., Boggs, C. H., Curran, D. S., Kazama, K. K. and Seki, M. P. (2003). Vertical movements of bigeye tuna (*Thuanus obesus*) associated with islands, bouys, and seamounts near the main Hawaiian Islands from archival tagging data. *Fish. Oceanogr.* 12, 152-169.
- Neill, W. H. and Stevens, E. D. (1974). Thermal inertia versus themoregulation in 'warm' turtles and tunas. *Science* 184, 1008-1010.
- Neill, W. H., Chang, R. K. C. and Dizon, A. E. (1976). Magnitude and ecological implications of thermal inertia in skipjack tuna, *Katsuwonus pelamis* (Linnaeus). *Environ. Biol. Fishes* 1, 61-80.
- Schaefer, K. M. and Fuller, D. W. (2002). Movements, behavior, and habitat selection of bigeye tuna (*Thunnus obesus*) in the eastern equatorial Pacific, ascertained through archival tags. *Fish. Bull. U. S.* 100, 765-788.
- Schaefer, K. M. and Fuller, D. W. (2005). Behavior of bigeye (*Thunnus obesus*) and skipjack tuna (*Katsuwonus pelamis*) tunas within aggregations associated with floating objects in the equatorial eastern Pacific. *Mar. Biol.* 146, 781-792.
- Shiels, H. A., Blank, J. M., Farrell, A. P. and Block, B. A. (2004). Electrophysiological properties of the L-type Ca²⁺ current in cardiomyocytes from bluefin tuna and Pacific mackerel. *Am. J. Physiol.* 286, R659-R668.
- Sibert, J. R., Musyl, M. K. and Brill, R. W. (2003). Horizontal movements of bigeye tuna (*Thunnus obesus*) near Hawaii determined by Kalman filter analysis of archival tagging data. *Fish. Oceanogr.* 12, 141-151.
- Stevens, E. D. and McLeese, J. M. (1984). Why bluefin tuna have warm tummies: temperature effects on trypsin and chymotrypsin. Am. J. Physiol. 246, R487-R494.
- Stevens, E. D., Kanwisher, J. W. and Carey, F. G. (2000). Muscle temperature in free-swimming giant Atlantic bluefin tuna (*Thunnus thynnus*). J. Thermal Biol. 25, 419-423.
- Webb, P. W. (1975). Hydrodynamics: nonscombroid fish. In Fish Physiology, Vol. VII (ed. W. S. Hoar and D. J. Randall), pp. 189-237. San Diego: Academic Press.
- Weihs, D. (1973). Mechanically efficient swimming technique for fish with negative buoyancy. J. Mar. Res. 31, 194-209.