Thermoconservation mechanisms inferred from peritoneal cavity temperature in free-swimming Pacific bluefin tuna *Thunnus thynnus orientalis*

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ABSTRACT: Immature Pacific bluefin tuna *Thunnus thynnus orientalis*, marked with archival tags, were released near Tsushima Island in the eastern East China Sea (58 fish on 7–14 Dec 1995; 47 fish on 29 Nov 1996), to investigate thermoconservation mechanisms of immature bluefin under low ambient temperature. A total of 15 fish were recovered and time-series data for ambient water and peritoneal cavity temperatures, recorded every 128 s, were analyzed. In winter, the difference between ambient and peritoneal cavity temperatures increased only slightly as ambient temperature decreased. In summer the difference became appreciably large, as ambient temperature decreased due to repeated dives to depths below the thermocline for short periods (~640 s), perhaps for feeding. This suggests that peritoneal cavity temperature is maintained during dives. A heat budget model revealed that thermal inertia, or internal heat production in the daytime, was important for thermoconservation during dives. As bluefin could only maintain body temperature for a short period, they had to avoid rapid temperature change at the thermocline through behavioral thermoregulation. This is quite different from the situation for bigeye tuna, as reported elsewhere. The mean temperature difference for a half-day period was larger in summer than in winter and in addition, the difference increased with body size. These results imply that the ability to maintain peritoneal cavity temperature develops with growth from winter to summer. The heat budget model further suggests that an ability to maintain peritoneal cavity temperature could result from decreasing both the whole-body heat-transfer coefficient (k) and internal heat production ($\dot{T}_m$), and that the significant increase in temperature difference from winter to summer could be attributed to a lower decreasing rate of $\dot{T}_m$ compared with that of k during this period. The significantly larger temperature difference in the daytime, compared to that in the nighttime, suggested higher internal heat production resulting from higher internal activity in the daytime. However, it was also revealed that vertical diving activity could be related to physical conditions such as light intensity. The bluefin made few dives on days when solar radiation was comparatively low, implying that low visibility may prevent dives to depths below the thermocline.

KEY WORDS: Pacific bluefin tuna · Archival tag · Thermoconservation · Peritoneal cavity temperature · Heat budget model · Behavioral thermoregulation · Internal heat production · *Thunnus thynnus orientalis*

INTRODUCTION

Pacific bluefin tuna *Thunnus thynnus orientalis* are one of the most important fishery resources in the neritic region of Japan. Basic scientific knowledge on their distribution and movement is therefore required for proper stock management. The relationship between abundance of bluefin and various oceanic conditions has been reported (Uda 1957, 1973, Sund et al. 1981, Yamanaka 1981, Koido & Mizuno 1989, Matsumura 1989, Ogawa & Ishida 1989a,b, Bayliff 1994).

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This includes the effect of water temperature on bluefin distribution and movement. However, most of this information is still very fragmented.

With regard to factors affecting stock abundance, it has been suggested that periodic changes in the bluefin population off Japan could be attributed to oceanographic events such as the abnormal southern intrusion of the cold Oyashio Current (Uda 1957, 1973, Ogawa & Ishida 1989a,b). Immature bluefin migrate northward from spring to summer along both the east and west coasts of Japan, and southward from fall to winter near the boundary with cooler coastal water. They are often located near the boundaries of cold water masses, or offshore eddies caused by localized upwelling (Uda 1973). The dependence of bluefin distribution and movement on temperature was also reported in the eastern Pacific (Sund et al. 1981). However, the temperature effects did not always prove to be causal (Brill 1994a), and they could be seriously biased by biological factors such as the physiological abilities of bluefin. In this regard *Thunnus* is well known as a fish genus with an elevated body temperature (Kishinoue 1923, Barrett & Hester 1964, Carey et al. 1971, Carey 1973, Stevens et al. 1974, 2000). Therefore it is of great importance to clarify the mechanisms that regulate body temperature under ambient water temperatures that can change greatly as bluefin move horizontally or vertically.

Carey & Lawson (1973) observed thermoregulation in 250 kg bluefin. However, thermoregulation could not be unequivocally separated from the effect of simple thermal inertia in such a large fish (Neill & Stevens 1974). Neill et al. (1976) postulated that skipjack tuna *Katsuwonus pelamis* could face an overheating problem and that its activity could be limited in warm waters. Other laboratory studies were also undertaken to detect the physiological thermoregulatory abilities of skipjack and yellowfin *Thunnus albacares* (Brill et al. 1978, Dizon et at. 1978, Dizon & Brill 1979, Dewar et al. 1994). In the 1990s, using ultrasonic transmitters attached to free ranging bigeye tuna *T. obesus*, Holland et al. (1990, 1992) and Holland & Sibert (1994) measured swimming depth and muscle temperature simultaneously. They found that the fish spent most daylight hours well below the thermocline (in 15°C water) but made regular, brief, upward excursions into the mixed layer. Holland et al. (1992) and Holland & Sibert (1994) further discuss the thermoregulation mechanism of the bigeye and report that they reduce the efficacy of their vascular counter current heat exchangers while gaining heat from the environment, then increase it again when they return to depths below the thermocline.

The thermoregulatory mechanisms of tunas other than bigeye or yellowfin have not yet been reported.

Owing to a serious lack of detailed information about the mechanisms maintaining the body temperature of free-swimming tunas, most of the effects of seasonal and spatial changes in oceanic conditions on body temperature are not yet fully understood. Some hypotheses have been proposed on the ecological or physiological importance of the maintenance of body temperature above ambient water temperature (Carey & Teal 1966, Neill & Stevens 1974, Graham 1975, Carey et al. 1984, Block et al. 1993, Brill 1994a, 1996, Stevens et al. 2000). Although the ability to maintain temperature may enable rapid digestion, rapid growth, and rapid recovery from exhaustive exercise (Brill 1996), all these hypotheses need to be verified using field data. To obtain such long-term behavioral and physiological data in the field, it is necessary to develop data logging techniques.

In recent years, micro dataloggers, or 'archival tags', have been developed and applied to a few free-ranging fishes (Boehlert 1997, Metcalfe & Arnold 1997, Ogura 1997, Block et al. 1998a,b, Tanaka et al. 1998, 2000, Gunn et al. 1999, Lutcavage et al. 1999, Kitagawa et al. 2000, Naito et al. 2000). The behavior of tunas has also been observed using such tags (Block et al. 1998a,b, Lutcavage et al. 1999, Kitagawa et al. 2000), and behavior, physiology, and ecology are being gradually clarified. Kitagawa et al. (2000) largely discussed the vertical distribution and movement of bluefin in relation to ambient water temperature, and suggested that bluefin used behavioral thermoregulation to avoid a rapid temperature drop at the thermocline, and that they used repeated, short period dives for feeding. The main objective of this study is to investigate in detail the thermoconservation mechanism of free-swimming, immature bluefin under low ambient temperatures, by analyzing ambient water and peritoneal cavity temperature records obtained from archival tags. We focus on the influence of temporal and spatial changes in ambient water temperature on the peritoneal cavity temperature. Effect of body size on the regulation of peritoneal cavity temperature is also examined. Finally, we discuss the reason why immature bluefin adopt behavioral thermoregulation (Kitagawa et al. 2000) by comparison with the characteristics of thermoregulation exhibited in bigeye (Holland et al. 1992).

MATERIALS AND METHODS

The archival tag used for the present study (Northwest Marine Technology Inc., WA) measures and records external and internal temperatures, swimming depth, and ambient light levels every 128 s (675 data

d⁻¹) for a maximum of 80 d. In addition, fish location is roughly estimated every day at sunrise and sunset, as detected by the light sensor. Detailed specification of the archival tag has been described elsewhere (Anonymous 1994, Block et al. 1998a).

Pacific bluefin tunas were captured by trolling near Tsushima Island (Fig. 1). Of these, 105 immature tunas with fork lengths of 45 to 78 cm, ≤1 yr old (Yukinawa & Yabuta 1967) were selected for tagging. The tunas marked with the archival tags to the peritoneal cavity were released near the Tsushima Island on 2 different occasions: 58 fish on 7–14 Dec 1995 and 47 fish on 29 Nov 1996. Of the 105 individuals released, 15 (5 in 1995 and 10 in 1996) were recovered by fisheries in the

Fig. 1. (■) Release site for Pacific bluefin tuna marked with archival tags; (□) Izuhara Meteorological Observatory

East China Sea, where they migrate in winter. Of the 15 individuals, 9 were recovered within 2 mo, while the other 6 were recovered within 4 to 7 mo after release. Details of these data are described in our previous paper (Kitagawa et al. 2000).

The heat balance in the peritoneal cavity is described using the equation proposed by Schmidt-Nielsen (1990):

Storage of heat = Heat production
+ Conductive heat exchange

This equation indicates that heat production and conductive heat exchange could play important roles in temperature fluctuation of the peritoneal cavity of bluefin. Thus, the more that heat is stored, the greater the temperature difference between the peritoneal cavity and the ambient water. To clarify how high bluefin maintain body temperature, we processed the temperature differences from the tag data, and discuss the relationship between temperature difference and ambient temperature. Thermoregulatory characteristics of the bluefin, suggested by Kitagawa et al. (2000), are compared with those of bigeye using the following heat budget model.

Heat budget model. To examine the variable relationship between ambient water and peritoneal cavity temperatures, a heat budget model is developed. Heat loss or gain (i.e. storage of heat) is proportional to the difference between body temperature and ambient water temperature (Holland et al. 1992, Brill 1994b) as demonstrated in Eq. (1):

$$\frac{\mathrm{d}T_b}{\mathrm{d}t} = k(T_a - T_b) + \dot{T}_m \tag{1}$$

where k is the whole-body heat-transfer coefficient (°C s⁻¹°C⁻¹), $\dot{T}_m$ is the rate of temperature change due to internal heat production (°C s⁻¹), T_a is the ambient water temperature (°C) and T_b is body (peritoneal cavity) temperature (°C). The first term on the right-hand side corresponds to 'conductive heat exchange'. In order to derive an equation that allows the calculation of the values of k and $\dot{T}_m$ by data fitting, Eq. (1) is integrated with respect to time t and expressed as follows:

$$T_b(t) = (T_b(0) - T_e)e^{-k(t-L)} + T_e \tag{2}$$

$$T_e = T_a + \dot{T}_m/k \tag{3}$$

where T_e is the body temperature at steady state and L is the time-lag from the change in T_a to the change in T_b. Eq. (2) indicates that for $t > L$, body temperature changes exponentially when T_a, $\dot{T}_m$ and k are constant.

By assuming a steady state (dT_b/dt = 0) in the same manner as above, $\dot{T}_m$ should be equal to the 'conductive heat exchange' as follows:
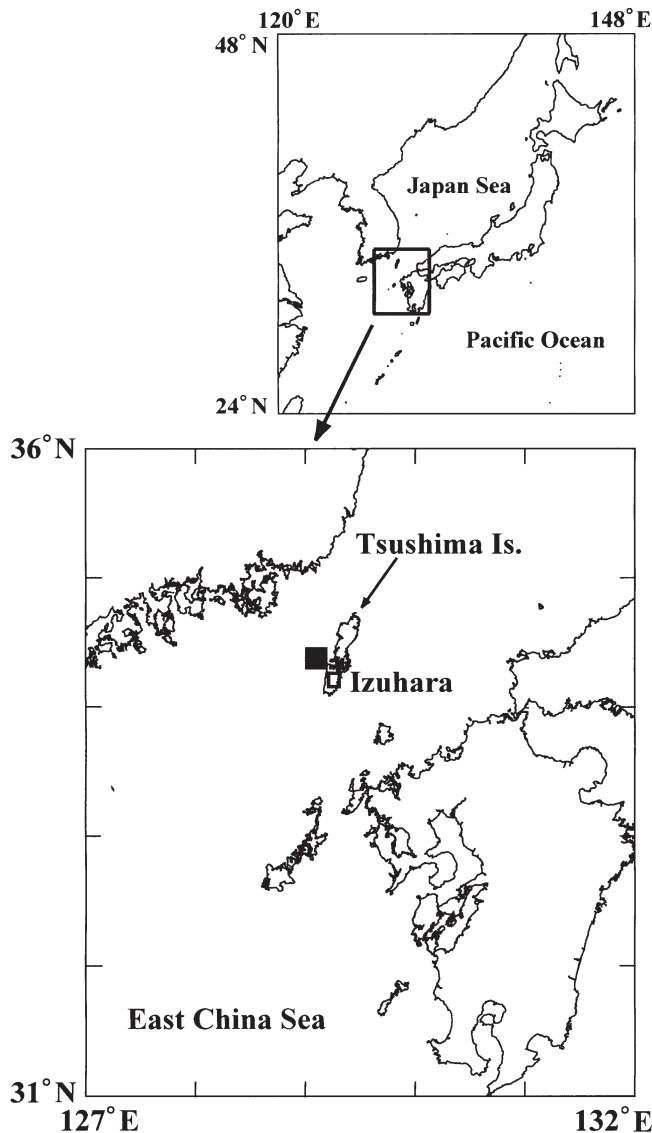
$$\dot{T}_m \ = \ k(T_e - T_a) \tag{4}$$

Eq. (4) suggests that in steady state, heat production is estimated by the heat-transfer coefficient and the temperature difference. Using the above equations to represent the heat budget, we quantified the characteristics of body temperature maintenance in bluefin and tried to simulate the change of peritoneal cavity temperature in relation to ambient water temperature using values of k and $\dot{T}_m$ estimated from time-series data.

RESULTS

Relationship between ambient water and peritoneal cavity temperatures

Bluefin spent most of their time at the surface, responding to the development of the thermocline in summer (March to June), and avoiding the effect of cool water below the thermocline (Kitagawa et al. 2000). However, during the daytime, they made repeated dives to a cool water depth in order to feed. Mean dive duration for all individuals in June, from departure at the surface (0–9 m) to the return, ranged from 335 s to 670 s. Based on this time range, we first looked at the relationship between the 5 (640 s) mean values of ambient water and peritoneal cavity temperature.

The relationship between ambient water temperature and the difference between ambient water and peritoneal cavity temperatures, for the individual Bluefin 177, during the daytime in December and June is shown in Fig. 2. Similar patterns to that shown in Fig. 2 were also obtained from the other individuals. In December, the range in ambient water temperature was comparatively narrow because of vertical mixing, and the differences between ambient water and peritoneal cavity temperatures only slightly increased as ambient water temperature decreased. In June, on the other hand, the range in ambient water temperature was wider, because of repeated dives through the thermocline in the daytime. The temperature differences were much larger than those in December, and the differences increased as ambient water temperatures decreased. The results of Spearman rank correlation analysis for the relationship between ambient water temperature and temperature difference in December and June are summarized for all individuals in Table 1. In December, the relationship was ambiguous because of the small range in ambient water temperature and temperature difference, although it was significant for most individuals. On the other hand, in June, significant negative correlations were found for all individuals. This indicates that peritoneal cavity temperature is maintained on a short time scale (640 s) when the bluefin makes repeated dives through the thermocline into depths with lower ambient temperature.

Mean values for ambient water and peritoneal cavity temperatures in the daytime or nighttime were calculated. The relationship between ambient water and
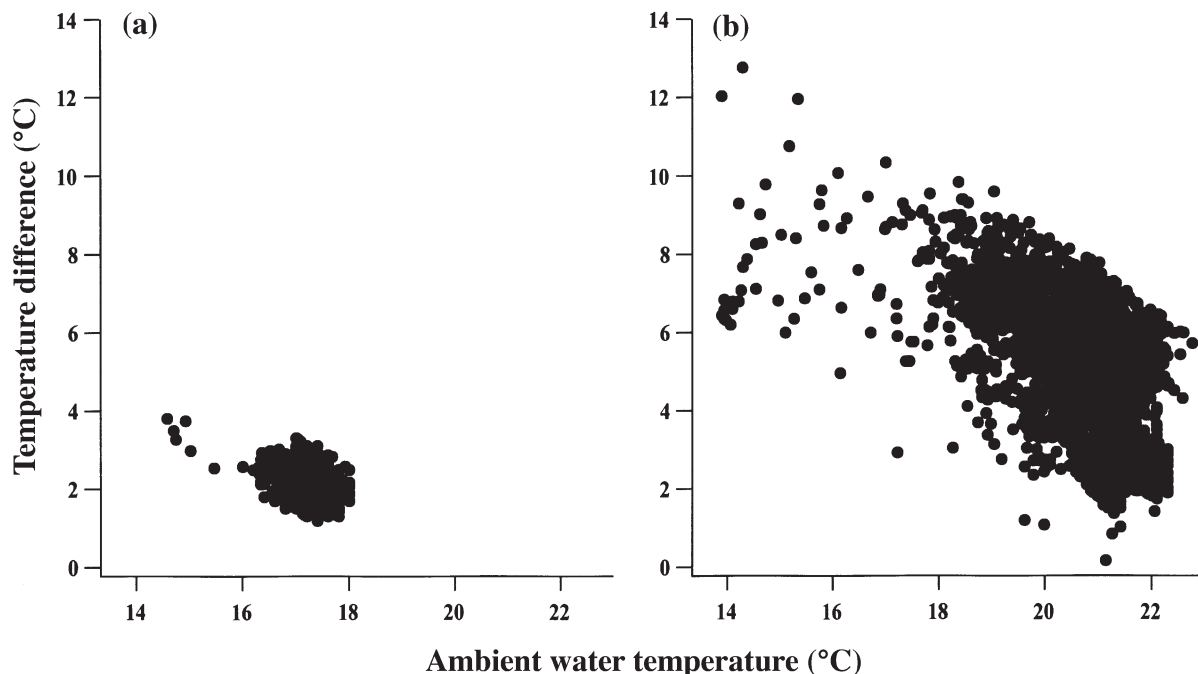

Fig. 2. Relationship between temperature difference (peritoneal cavity temperature minus ambient water temperature) and ambient water temperature for daytime data in (a) December, and (b) June, for Bluefin 177

Table 1. Results of Spearman rank correlation analysis for relationship between ambient water temperature and the difference between peritoneal cavity and ambient water temperatures, p < 0.0001 unless otherwise stated. Data for December and June (May for Bluefin 282). Duration of data record for each individual also shown

Bluefin no.	Daytime in December Spearman rank correlation coefficient	Duration of data recorded	Daytime in June or May Spearman rank correlation coefficient	Duration of data recorded
177	−0.428	15 Dec 1995–21 Jan 1996	−0.499	24 May 1996–30 Jun 1996
232	−0.313	30 Nov 1996–18 Dec 1996	−0.294	24 May 1997–26 Jun 1997
256	0.041 (p = 0.1614)	30 Nov 1996–18 Dec 1996	−0.089	2 May 1997–24 Jun 1997
282	−0.247	30 Nov 1996–18 Dec 1996	−0.605	21 Mar 1997–15 May 1997
321	−0.022 (p = 0.4521)	30 Nov 1996–18 Dec 1996	−0.422	2 May 1997–24 Jun 1997
328	−0.125	30 Nov 1996–18 Dec 1996	−0.336	1 May 1997–24 Jun 1997
131	0.363	11 Dec 1995–21 Dec 1995		
138	−0.357	11 Dec 1995–27 Dec 1995		
170	−0.346	10 Dec 1995–10 Jan 1996		
174	0.001 (p = 0.991)	12 Dec 1995–20 Dec 1995		
272	0.666	30 Nov 1996–10 Jan 1997		
289	−0.294	30 Nov 1996–22 Dec 1996		
293	−0.242	30 Nov 1996–23 Dec 1996		
301	0.159	30 Nov 1996–18 Dec 1996		
303	−0.139	30 Nov 1996–15 Dec 1996		

peritoneal cavity temperatures on this time scale for Bluefin 177 is shown in Fig. 3. In both winter (November to January) and summer, positive correlations (although low coefficients) were found between these two, suggesting that ambient water temperature in the surface mixed layer affected peritoneal cavity temperature on such a time scale, since the bluefin stayed for an appreciably long time in the mixed layer (Kitagawa et al. 2000). Table 2 further shows the result of Pearson's correlation analysis for all individuals. Higher positive correlations were found for most cases, especially in summer.

The differences between peritoneal cavity and ambient water temperatures were largest during the summer daytime and smallest during the winter nighttime, as seen in Fig. 3. The statistical analysis of these differences is summarized in Table 3. The temperature differences in summer were significantly larger than those in winter (2 sample *t*-test with Welch's correction, p < 0.0001) during both daytime and nighttime. In addition, in summer the differences in the daytime were significantly higher than those in the nighttime. On the other hand, in winter, the temperature differences during daytime were not significantly different from those during nighttime in most cases. These results imply that the rate of internal heat production, or the ability to conserve peritoneal cavity temperature especially during daytime, increases from winter to summer.

In Fig. 4 the mean difference between peritoneal cavity and ambient water temperatures during daytime in winter is related to the fork lengths of the fish, which were measured when they were released (fork length data not obtained in summer). A positive correlation was found (correlation coefficient 0.74, n = 14, p < 0.05), which was also significant for nighttime data (correlation coefficient 0.82, n = 14, p < 0.05).

Estimation from a heat budget model

To look at the mechanism of thermoconservation in bluefin, we examined the heat balance relating to the
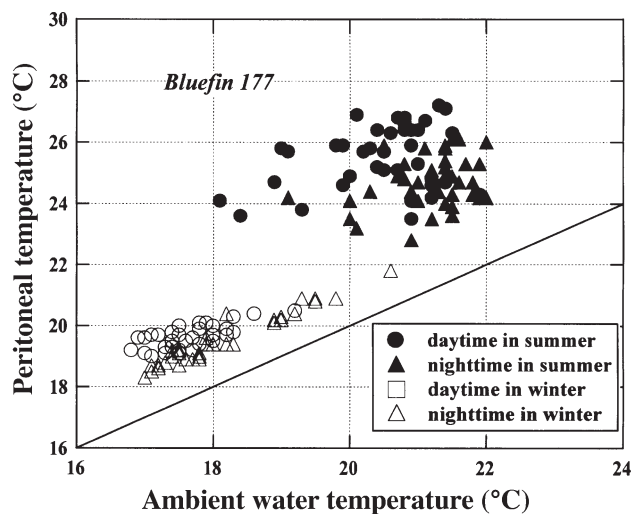

Fig. 3. Relationship between ambient water temperature and peritoneal cavity temperature. Mean values for daytime and nighttime in winter and summer from Bluefin 177. Solid line where peritoneal cavity temperature equals ambient water temperature

Table 2. Results of Pearson correlation analysis for relationship between ambient water temperature and peritoneal cavity temperature; p < 0.0001 unless otherwise stated. Analysis conducted on each data set for winter nighttime, winter daytime, summer nighttime and summer daytime

Bluefin no.	Winter nighttime Pearson correlation coefficient	Sample size	Daytime Pearson correlation coefficient	Sample size	Summer nighttime Pearson correlation coefficient	Sample size	Daytime Pearson correlation coefficient	Sample size
177	0.969	37	0.688	38	0.318 (p = 0.0546)	37	0.299 (p = 0.0677)	38
232	0.893	18	0.826	19	0.96	33	0.816	34
256	0.864	18	0.908	19	0.927	53	0.885	54
282	0.877	18	0.798	19	0.938	55	0.898	56
321	0.969	18	0.967	19	0.722	53	0.531	54
328	0.981	18	0.98	19	0.866	54	0.905	55
131	0.798 (p = 0.0038)	10	0.507 (p = 0.1138)	11				
138	0.782 (p = 0.0002)	16	0.552 (p = 0.02)	17				
170	0.472 (p = 0.0067)	31	0.307 (p = 0.0872)	32				
272	0.824	41	0.711	42				
289	0.957	22	0.886	23				
293	0.87	23	0.894	24				
301	0.914	18	0.959	19				
303	0.961	15	0.944	16				

time series of peritoneal cavity temperature using the heat budget model described in the 'Materials and methods'. We first focused on Bluefin 177 for 1 June 1996, when the tuna swam below the thermocline for a relatively long time. Values of k for bigeye, measured during upward excursions into surface water, exceed values when swimming in cold water below the thermocline by 2 orders of magnitude (Holland et al. 1992). Therefore, we examined the difference in the value of k of bluefin using Eq. (2). The time-series data of ambient water and peritoneal cavity temperatures used for

the analysis are shown in Fig. 5. Regression curves based on a calculation using Eq. (2) for the time changes in peritoneal cavity temperature are shown in Fig. 5a,b. The duration of Fig. 5a is from 10:59:28 to 13:41:36, when the bluefin was swimming below the thermocline (i.e. cooling). Assuming a mean value for T_a of 14.2°C and $T_b(0)$ of 23.8°C, values of 3.70×10^{-4} for k and 2.20×10^{-3} for $\dot{T}_m$ were required for the best regression, with a time-lag (L) of 4 data (512 s). It is difficult to determine the values of k for other individuals in the same manner because they swam below the

Table 3. Statistical significance for temperature differences between winter and summer, and between day and night; p < 0.0001 unless otherwise stated. D, daytime; N, nighttime; S, summer; W, winter

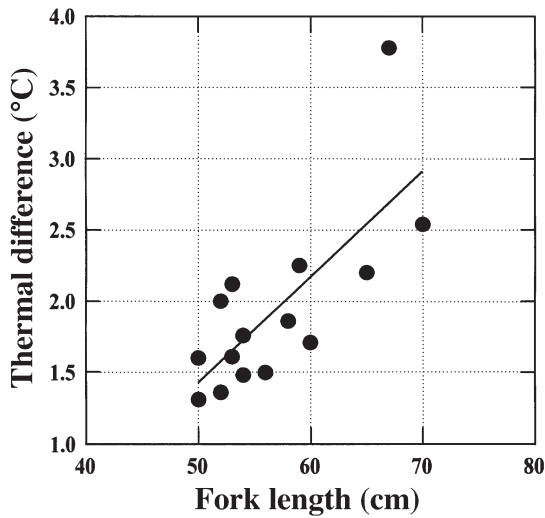| Bluefin no.	Temperature difference between N and D in winter paired t-test mean difference (°C)	Temperature difference between N and D in summer paired t-test mean difference (°C)	Temperature difference between W and S in nighttime 2 sample t-test with Welch's correction mean difference (°C)	Temperature difference between W and S in daytime 2 sample t-test with Welch's correction mean difference (°C)
177	0.582	1.519	2.13	3.05
232	0.068 (p = 0.1695)	1.487	1.17	2.62
256	0.069 (p = 0.3344)	1.489	0.93	2.38
282	0.246 (p = 0.003)	1.188	1.62	2.55
321	0.085 (p = 0.035)	2.038	2.26	4.23
328	0.001 (p = 0.9684)	1.895	3.92	3.91
131	0.373 (p = 0.0398)			
138	0.621			
170	0.572 (p = 0.0051)			
272	0.233 (p = 0.0002)			
289	0.172 (p = 0.0004)			
293	0.237 (p = 0.002)			
301	0.1 (p = 0.0862)			
303	0.137 (p = 0.0038)			

Fig. 4. Relationship between fork length of individuals at time of release and mean difference between peritoneal cavity and ambient water temperatures recorded in winter, shortly after release. Only daytime data plotted. Solid line is linear regression

thermocline for only a short period. The duration of Fig. 5b is from 13:48:00 to 15:21:52, when the bluefin returned to the surface from the cold water (i.e. warming). Assuming a mean value for T_a of 20.1°C and $T_b(0)$ of 20.3°C, estimated values for k and $\dot{T}_m$ for the best regression are 3.6×10^{-4} and 2.8×10^{-3} respectively, with a time-lag (L) of 1 data (128 s). It should be noted that there is little difference in values of k between these 2 estimates, whereas there is a significant difference in the values of $\dot{T}_m$, suggesting that the internal heat production ($\dot{T}_m$) contributes more than the heat transfer (k) to the temperature change in the peritoneal cavity. The values of k (2.16×10^{-4} to 6.01×10^{-4}°C s^{-1}°C^{-1}) and $\dot{T}_m$ (1.09×10^{-3} to 3.12×10^{-3} °C s^{-1}) for 5 other individuals were also of the same magnitude, and all values of $\dot{T}_m$ were higher than those of bigeye described by Holland et al. (1992). It is difficult to estimate k from the data in winter because the changes in ambient water and peritoneal cavity temperature differences are quite small.

To verify the estimated values of k and $\dot{T}_m$, the time series for peritoneal cavity temperature from 24 May to 30 June was simulated for Bluefin 177. Here, the differential term on the left side of Eq. (1) was replaced by $\Delta T_b/\Delta t$ as follows:

$$\frac{\Delta T_b}{\Delta t} \;=\; k(T_a - T_b) + \dot{T}_m \tag{5}$$

where Δt is 128 s and k is assumed to be constant (3.65×10^{-4}°C s^{-1}°C^{-1}, mean value) following the previous estimates. The rate of internal heat production $\dot{T}_m$ was fixed at 2.5×10^{-3} °C s^{-1} (mean value) during the daytime, when the fish made repeated dives. Since

nighttime is regarded as an inactive period, during which peritoneal cavity temperature is constant, the rate of internal heat production was estimated to be 8.40×10^{-4}°C s^{-1}, assuming the temperature difference, $T_e - T_a$ in Eq. (4) to be 2.30°C, which is the modal value for the nighttime data. The time-lag (L) is estimated to be 3 data (384 s, mean value). An initial peritoneal cavity temperature $T_b(0)$ of 23.4°C was selected for 0:00:16 on 24 May. The result of the calculation together with the time-series data is shown in Fig. 6. The coefficient of determination for Bluefin 177 is 0.220, while the coefficients for the other individuals are relatively high (Table 4). For Bluefin 177, the estimated peritoneal cavity temperature (green) corresponds well with the actual temperature (red) during the period from 24 May to 7 June. However, mean residuals from the actual temperature significantly increased in the following days (Student's *t*-test, p < 0.05) and frequency of vertical migration often decreased during this period.
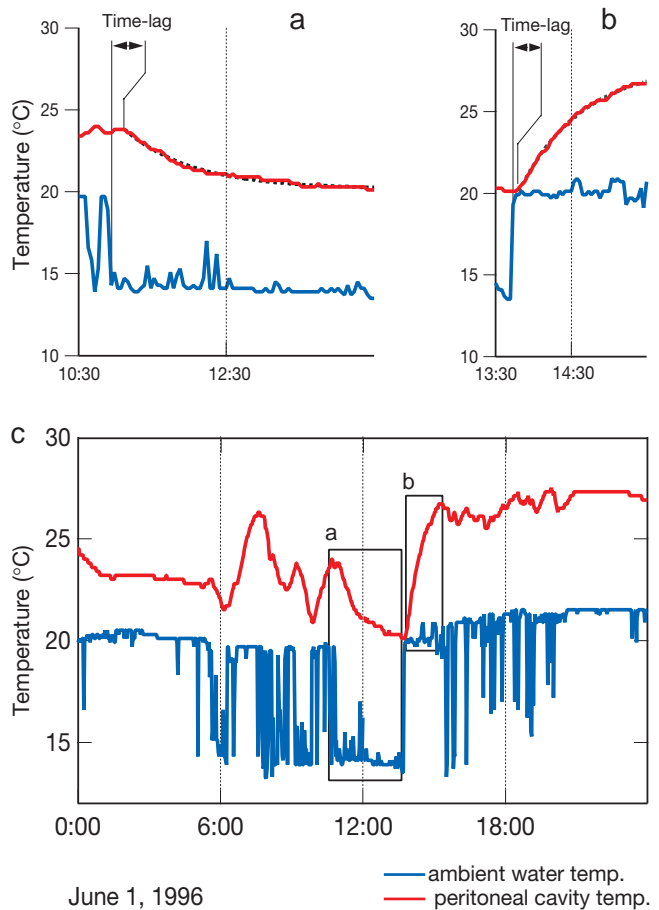

Fig. 5. Time-series data recorded for Bluefin 177 on June 1, 1996. Enlarged times-series data for: (a) 10:59:28 to 13:41:36, and (b) 13:48:00 to 15:21:52. Dotted lines in a,b represent regression curves: (a) $T_b(t) = 20.17 + 3.65 \exp(-3.70 \times 10^{-4})$, (b) $T_b(t) = 27.87 + 7.76 \exp(-3.60 \times 10^{-4})$
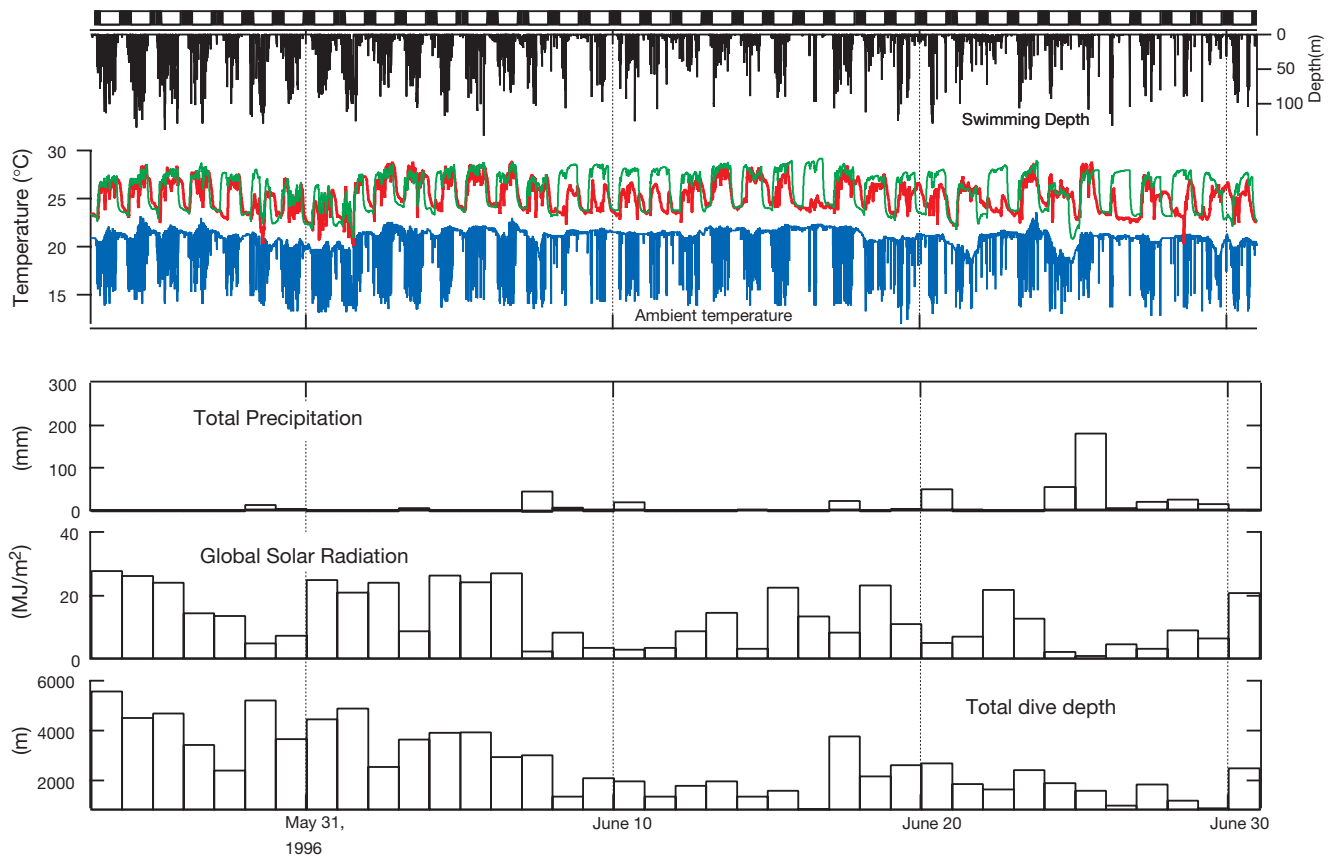
Fig. 6. Comparison between actual (red) and calculated (green) peritoneal cavity temperature based on observed ambient water temperature and assumed heat production for Bluefin 177 from 24 May to 30 June 1996. Peritoneal cavity temperature calculated from internal heat production, $2.5 \times 10^{-3}\,°C\,s^{-1}$ during daytime (active diving) and $8.40 \times 10^{-4}\,°C\,s^{-1}$ during nighttime (inactive period). Blue and black lines indicate changes in ambient water temperature and swimming depth during same period. Shaded time zones at top of figure denote day/night. Time series of global solar radiation and precipitation at Izuhara Meteorological Observatory (see Fig. 1) also shown, together with total dive depth recorded per day

What then, is the reason why bluefin often became inactive during the daytime? Light conditions in the subsurface water are a possible factor affecting the vertical movements of bluefin, as they are a visual predator and are perhaps diving for food. We therefore looked at the time series of global solar radiation in relation to

changes in behavioral patterns of the bluefin. The lower series in Fig. 6 show the total dive depths per day (an integration of the depth record for 1 d) as an index of activity, in relation to global solar radiation and precipitation. The latter 2 data sets were obtained from Izuhara Meteorological Observatory, Tsushima Island (Fig. 1), near where the bluefin tended to swim over the period 24 May 1996 to 30 June 1996. Bluefin only made a few dives on days when the radiation was low (Pearson's correlation coefficient $R = 0.490$, $p < 0.05$).

Table 4. k and $\dot{T}_m$ input values used in heat budget model to simulate peritoneal cavity temperature of each individual. Coefficient of determination of calculated temperature also shown

Bluefin no.	Heat transfer coefficient $(°C\,s^{-1}\,°C^{-1})$	Heat production in the daytime $(°C\,s^{-1})$	Heat production in the nighttime $(°C\,s^{-1})$	Coefficient of determination
177	3.65×10^{-4}	2.50×10^{-3}	8.40×10^{-4}	0.220
232	3.70×10^{-4}	1.70×10^{-3}	8.80×10^{-4}	0.680
256	2.16×10^{-4}	1.09×10^{-3}	9.20×10^{-4}	0.686
282	2.78×10^{-4}	1.62×10^{-3}	6.90×10^{-4}	0.668
321	2.23×10^{-4}	1.62×10^{-3}	5.80×10^{-4}	0.370
328	6.01×10^{-4}	3.12×10^{-3}	1.50×10^{-4}	0.678

DISCUSSION

According to Holland et al. (1992), bigeye undergo physiological and behavioral thermoregulation by changing the heat-transfer coefficient k by

2 orders of magnitude ($k = 5.22 \times 10^{-4}$ for cooling, 4.01×10^{-2} for warming). Disengaged heat exchangers allow rapid warming as the fish ascends from cold water into warm surface water, and they are reactivated to conserve heat when the fish returns to cold water. However, for bluefin there is almost no difference in values of k ($k = 3.7 \times 10^{-4}$ for cooling, 3.6×10^{-4} for warming), suggesting that the bluefin do not undergo physiological thermoregulation, as do bigeye. In addition, internal heat production ($\dot{T}_m$) contributed much more than heat-transfer to the temperature fluctuation in the peritoneal cavity of bluefin.

We compared the characteristics of the thermoregulation mechanism of bluefin with those of bigeye described in Holland et al. (1992), in terms of time requirements for recovery of body temperature. We assumed initial peritoneal cavity temperatures as 15, 17 and 19°C, and a constant ambient water temperature (21°C). For bluefin, we further specified k as 3.65×10^{-4} and $\dot{T}_m$ as 2.50×10^{-3}, which are the values used in Fig. 6 and referred to by Holland et al. (1992) for bigeye. The time series for peritoneal cavity temperature calculated by using Eq. (2) are shown in Fig. 7. It is noticeable that bigeye are able to raise peritoneal cavity temperature to the level of ambient water temperature within about 120 s, whereas bluefin take at least 600 s to reach the same level. This difference in the recovery process is attributed to the differences in values of k between bigeye and bluefin; the former has a larger value of k by about 2 orders of magnitude, resulting in much less insulation. This enables bigeye to equalize surface water and body temperatures like an ectothermal animal. However, because of their larger insulation, bluefin cannot match the bigeye. Instead, the fraction of their higher internal heat production ($\dot{T}_m$) is retained and used to increase body temperature like endotherms. In other words, bluefin rely more on internal heat production to increase body temperature, whereas bigeye rely more on acquiring heat from the ambient water temperature.

The reason why the peritoneal cavity temperature of bluefin is maintained over short time scales in summer (e.g. 640 s, Fig. 2) could be attributed to thermal inertia, as noted by Neill & Stevens (1974). Higher internal heat production of bluefin (Table 4) in the daytime may be another important mechanism. Since this higher heat production makes the $\mathrm{d}T_b/\mathrm{d}t$ term in Eq. (1) larger when both k and T_a are constant, it could relieve the reduction in the peritoneal cavity temperature due to low ambient water temperature. Both mechanisms are probably responsible for the maintenance of bluefin body temperature while they are diving into depths below the thermocline.

On the other hand, high positive correlations were found between the values of peritoneal cavity and
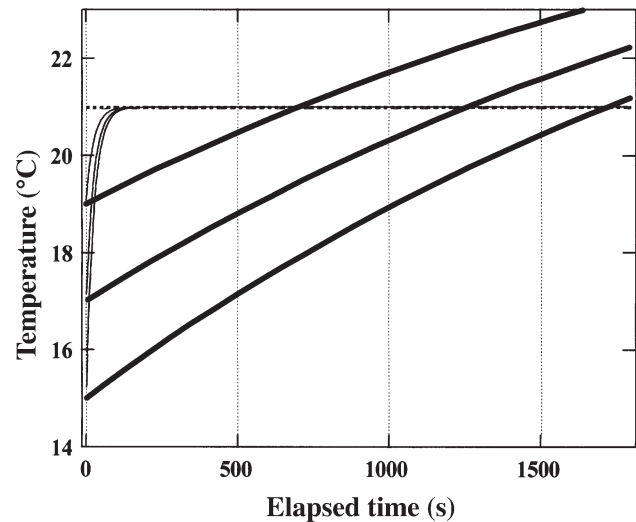

Fig. 7. Comparison of body temperature recovery times for bigeye (thin lines) and bluefin (heavy lines). Body temperature for bigeye calculated using values of $k = 4.01 \times 10^{-2}\,°\mathrm{C\ s^{-1}\,°C^{-1}}$ and $\dot{T}_m = 1.12 \times 10^{-4}\,°\mathrm{C\ s^{-1}}$ (Holland et al. 1992). Body temperature of bluefin calculated using values of $k = 3.65 \times 10^{-4}\,°\mathrm{C\ s^{-1}\,°C^{-1}}$ and $\dot{T}_m = 2.50 \times 10^{-3}\,°\mathrm{C\ s^{-1}}$. Ambient water temperature (21°C), horizontal dotted line

ambient water temperatures averaged over every daytime or nighttime period. This suggests that the peritoneal cavity temperature is greatly influenced by ambient water temperature on this time scale. This could be the reason why bluefin make repeated dives into the cold water below the thermocline and stay there for only a short time. However, Carey & Lawson (1973) report that giant bluefin tuna weighing 250 kg stay for long time periods (~4 h) under the cold temperatures of 5°C. According to Nihira (1996), skipjack tuna over 45 cm in fork length pass through the Kuroshio Front and enter into the cold water of the Kuroshio-Oyashio transition area, but small-sized skipjack do not. In the present study, relatively large-sized immature bluefin (70 cm fork length) maintained appreciably large thermal differences between peritoneal cavity and ambient water temperatures compared with those of smaller-sized bluefin (50 cm fork length) (Fig. 4). This implies that in the immature period the ability to maintain body temperature increases with size, and therefore the effect of low ambient water temperature on behavior may develop with growth. This probably makes it possible for larger bluefin to dive into depths below the thermocline for longer periods.

How then, do bluefin acquire the ability to maintain temperature with growth? Eq. (4) is transformed to:

$$T_e - T_a = \frac{\dot{T}_m}{k} \qquad (6)$$

That is, the temperature difference is equal to the value of heat production divided by the heat-transfer coefficient. The value of k represents insulation ability, and asymptotically decreases to zero with growth because the outer muscle around the peritoneal cavity becomes thicker. In addition, as noted by Neill & Stevens (1974), and Paladino et al. (1992), large-sized animals generally get more physical ability by increasing heat capacity and thermal inertia, resulting in more insulation of their body. Furthermore, the rete system (countercurrent heat exchanger) in the red muscle develops with growth, which may develop the ability to conserve heat (Funakoshi et al. 1985).

It is obvious from Eq. (6) that these physiological developments, in addition to a decrease of the value of k with growth, lead to a continuous increase in the difference between ambient and peritoneal cavity temperatures. If this is true, bluefin may face a severe overheating problem (Neill et al. 1976). However, according to Carey & Teal (1973), or Neill & Stevens (1974), the temperature difference of a penned bluefin (about 220 cm in fork length) was only about 6°C, suggesting that it does not increase indefinitely with growth, probably because the value of $\dot{T}_\mathrm{m}$ decreases as well as the value of k. Using the value of k of this bluefin (2.33×10^{-5} °C s^{-1} °C^{-1}, Neill & Stevens 1974), $\dot{T}_\mathrm{m}$ can be estimated from Eq. (4) as 1.40×10^{-4} °C s^{-1}. This value is, in fact, lower than that of the small-sized individual (8.40×10^{-4} °C s^{-1}), which we estimated from the data during the inactive period (midnight to sunrise) in the present study, assuming that the penned bluefin could be inactive from midnight to sunrise. In conclusion, the development of an ability to maintain body temperature with growth could be derived from decreasing values of both k and $\dot{T}_\mathrm{m}$. It is probable that from winter to summer a slower decrease in the value of $\dot{T}_\mathrm{m}$ compared to that of k could result in a significant increase in temperature difference in summer compared with that in winter (Fig. 3, Table 3).

It was also suggested in the present study that vertical diving activity could be affected by light conditions. Bluefin 177 made few dives during the day, when solar radiation was comparatively low. This may be responsible for the wide variation of peritoneal cavity temperature in Fig. 3, and the weaker correlation of peritoneal cavity temperature with ambient water temperature of Bluefin 177 in summer, compared with that of other individuals (Table 2). According to Kawamura et al. (1981), histological visual acuity of bluefin (min. separable angle, 3.57/3.67 minutes of arc) is low compared with that of other tuna species, such as yellowfin, bigeye, and albacore (2.04–2.52 min). In addition, at lower luminance, skipjack have a lower histological visual acuity (Nakamura 1968). Considering these results, we suggest bluefin would not dive to depths

through the thermocline on such days because light does not penetrate into these depths and they do not have sufficient visibility for feeding. It may also be possible that the counter shading effect of small fishes used as bait requires a certain amount of light.

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