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No. 3

Deep Diving Behavior of the Loggerhead Turtle near the Frontal Zone*1

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Loggerhead turtles can maintain a body temperature several degrees warmer than their environment. Stomach temperature data were compiled in order to see how the female loggerhead turtle adapted her body temperature to the different water temperatures near the frontal zone. She passed from the warm water into the cooler water and out again. In the cooler water, the stomach temperature gradually went down. Although this was largely due to thermodynamic transfer of heat from the skin, it was also found that the female loggerhead turtle drinks cold water during a deep dive, thereby cooling body temperature from the inside. Coming out of the cooler water again, she would make continuous and repeated dives in the shallower layer and raise her body temperature once again through kinetic energy consumption.

Previous papers dealt with the migration of the female loggerhead turtle, *Caretta caretta*, during inter-nesting periods; her estimated route, circadian rhythm and fluctuation due to oceanic environmental conditions.[1,2] Several remarkable dives were found on the Time Depth Recorder (TDR). These occurred when passing through the frontal zone or during typhoons. However, the diving behavior near the frontal zone was different from that when avoiding typhoons both in terms of underwater duration and maximum depth. This was perhaps a result of thermal adaptation to different water temperatures.

A maximum diving depth of 233 m was recorded on June 16 1988 when the turtle encountered the frontal zone. The horizontal temperature gradient rose 4°C from 25°C to 21°C between the warmer water side and cooler water side. The turtle was passing from the warmer to cooler water and began deep dives the moment she encountered the cooler water. A similar deep dive of 211 m was recorded on the TDR on June 21 when the turtle passed out of the cooler water.

If the turtle had to drop her body temperature when encountering the frontal zone in order to adapt to the surrounding cooler water, the deep dives would be effective because the deeper water has a lower temperature. However, a dive of 211 m, as recorded on June 21, seems unnecessary if the turtle wanted to raise body temperature when coming out of the cooler water. In this paper, we tried to find the reason for such deep dives, by correlating stomach temperature with surrounding water temperature.

Method

The time series of water temperatures was compared with the stomach temperatures throughout the first inter-nesting migration period. Then the diving patterns near the frontal zone were compared with the vertical temperature gradient. The stomach temperature did not change as quickly as the water temperature. This was for two different reasons: one was the so-called thermal inertia, in other words the thermal time lag between the turtle's body and its environment;[3-6] the other was the difference in rotation speed of the micro motor which drives the pressure sensitive paper in the Time Temperature Recorder (TTR). The latter mechanical difference could easily be rectified so as to correlate with each time mark.

Any rise or fall in stomach temperature always lagged behind the fluctuation in water temperature.

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However the time constant seemed to be influenced more or less by the difference in the environmental thermal gradient. The highest or lowest values and the other remarkable fluctuation on both temperature records were checked every 6 hours. Thereafter the stomach temperatures were overlaid on the water temperature records. Although it is impossible to estimate thermal inertia through such data processing, some idea may be gained of the correlation between the two temperature fluctuations.

As the deeper layer water was lower in temperature, the temperature fluctuations on the TTRs depended upon the frequency and depth of the dive. The time difference of several minutes between diving depth and water temperature was also indicated on the time series data. This was due to the different mechanical gear ratio of the TTR and the TDR. We overlaid the portion of the deepest layer onto the lowest temperature in the time series each hour with reference to the time mark. After overlaying the depth and water temperature data, isotherms were drawn. A standardized time axis used, based on the water temperature series the same as that used in the first report on the migration process.[1]

The diving depth was plotted every minute over a period of 8 hours, before and after entering the cooler water, from 14:00 to 22:00 on June 16. It was also plotted for a period of 8 hours as the turtle passed out of the cooler water mass, from 18:00 to 02:00, June 20 and 21.

Results

Correlation of Water Temperature and Stomach Temperature

We can show the correlation of water temperature and stomach temperature in Fig. 1. The loggerhead turtle maintains a stomach temperature several degrees warmer than the water temperature.[1-3] As shown in Fig. 1, stomach temperatures range from 20.7°C to 28.2°C whereas water temperatures range form 12.0°C to 25.5°C. The stomach warming process is partially indicated on the right edge of Fig. 1. We found that temperatures rise up to 28.2°C in proportion to the surrounding water temperature. There tends to be a wide range in the highest stomach temperature and the fluctuation in water temperature, because the change in stomach temperature lags more than one hour behind the change in water temperature

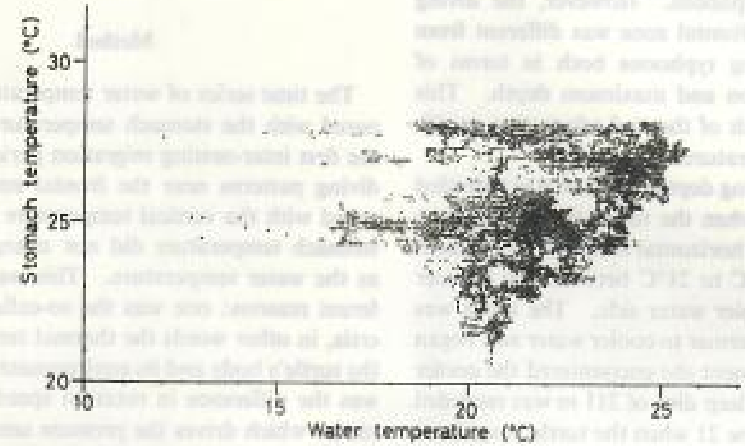

Fig. 1. Correlation of stomach temperature and water temperature throughout the whole internesting periods.

Table 1. Physical parameters of deep dives near the frontal zone

	Cooling			Warming			
	No. 1	No. 2	No. 3	No. 1	No. 2	No. 3	No. 4
Depth (m)	94	170	233	139	211	118	104
Diving speed (m/min)	13.4	42.5	58.3	23.2	35.2	16.9	13.0
Underwater duration (min)	14	8	8	12	12	14	16
Mean temp. gradient (°C/m)	0.06	0.05	0.04	0.05	0.04	0.05	0.05

Table 2. Hourly mean water temperature on the TTR with relation to experiential mean temperature (T_E), and sea surface temperature estimated by the TDR and the TTR (T_S) when swimming from the warmer water to the cooler (A), and the cooler water to the warmer (B)

A. (16:00–22:00, June 16)				B. (18:00–22:00, June 20)			
Time	T_S	T_E	T_E/T_S	Time	T_S	T_E	T_E/T_S
16:00	24.0	—	—				
17:00	23.0	22.6	0.98				
18:00	22.5	21.7	0.96	18:00	21.3	—	—
19:00	21.5	21.7	1.01	19:00	22.0	20.7	0.94
20:00	21.5	20.8	0.97	20:00	22.0	20.3	0.92
21:00	21.0	21.7	1.03	21:00	21.5	20.9	0.97
22:00	21.0	20.8	0.99	22:00	22·00	20.7	0.94
			mean 0.99				mean 0.94

which varied frequently according to oceanic environment and the turtle's swimming behavior.

The cooling process versus water temperature is clustered on the left hand side. This shows a varying correlation with the surrounding water temperature, especially in the range between 25°C and 27°C, when stomach temperatures fluctuate considerably with the many different water temperatures. As the warming and cooling trends are shown by a hysteresis, the correlation pattern has several blank spots near the central part of Fig. 1.

The Deep Dives Near the Frontal Zone

The thermal adaptation of the loggerhead turtle in the open sea seemed to be different from warming and cooling to the surrounding water temperature. The difference should be reflected more or less in terms of diving behavior near the frontal zone since the turtle had to adapt her body temperature as soon as she encountered a different water mass. The physical parameters of the deep dives are summarized in Table 1. The value of diving depths gradually increased during cooling and the vertical swimming speed, ascending and descending speed, became faster in proportion to the diving depth.

The hourly surface water temperature, T_S was compared with the mean hourly temperature of the turtle while swimming, T_E, as recorded on the TTR. This is shown in Table 2. If there was no horizontal thermal gradient such as the frontal zone, the turtle would spend most of the day time at the surface layer. A close correlation was made between the deep dives and the horizontal thermal gradient. As the turtle swam near the front there were discontinuous changes in the temperature registering stress on the thermal gradient. The ratio of T_E/T_S is that between the change in surface water temperature from one hour to the next and the change in hourly mean temperature from one hour to the next. During the cooling process, they are nearly equal to 1.00, but during the warming process, no remarkable correlation is to be found.

The diving behavior and isotherms are shown in Fig. 2 when the turtle encountered the cooler water from the warmer water. She swam until 16:30 on the 16th in a surface layer which was 24°C in temperature. Between 17:00 and 20:00, the water temperature gradually cooled from 24°C to 21°C and the turtle progressed to the front. Three deep dives were recorded between 17:00 and 21:00 as she approached the frontal zone. Diving depths gradually increased, first 74 m, then 170 m and finally a maximum depth of 233 m. The deepest dive took a total of 8 minutes. After these deep dives she continued to swim in the surface layer. The average temperature between 17:00 to 21:00 was 21.1°C, which was lower than that of the surface layer of the boundary and was a result of the frequent dives. In fact, it was almost the same as the surface layer water temperature in the cooler water mass, which was 21.0°C.

On the 20th, there were similar continuous and repeated deep dives as the turtle passed through the cooler water mass. These are shown in Fig. 3. She first descended to a depth of 133 m, and then, 50 minutes later, made a 10 minute dive to a depth of 211 m. These typical deep dives were repeated four times, of which the latter gradually becomes shallower. Thereafter, she made repeated continuous dives, different both in term of underwater duration and diving depth. Their mean underwater duration was 17 minutes and mean diving depth 54 m, 1.5 times longer and 0.4 times shallower than the previous four deep dives.

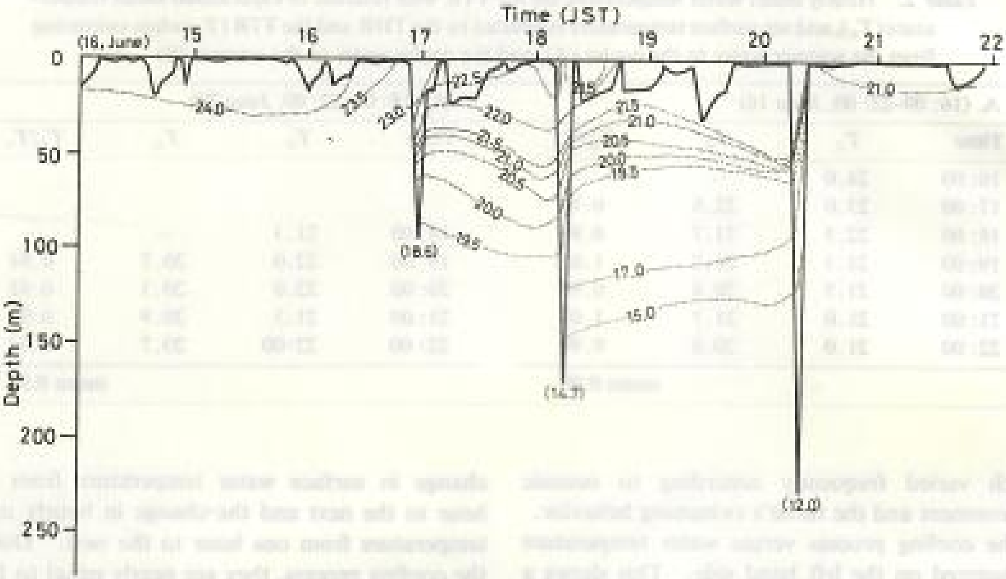

Fig. 2. Diving behavior of the loggerhead turtle when swimming from warmer water to cooler water boundaries (solid line) and isotherms (thin dotted line).

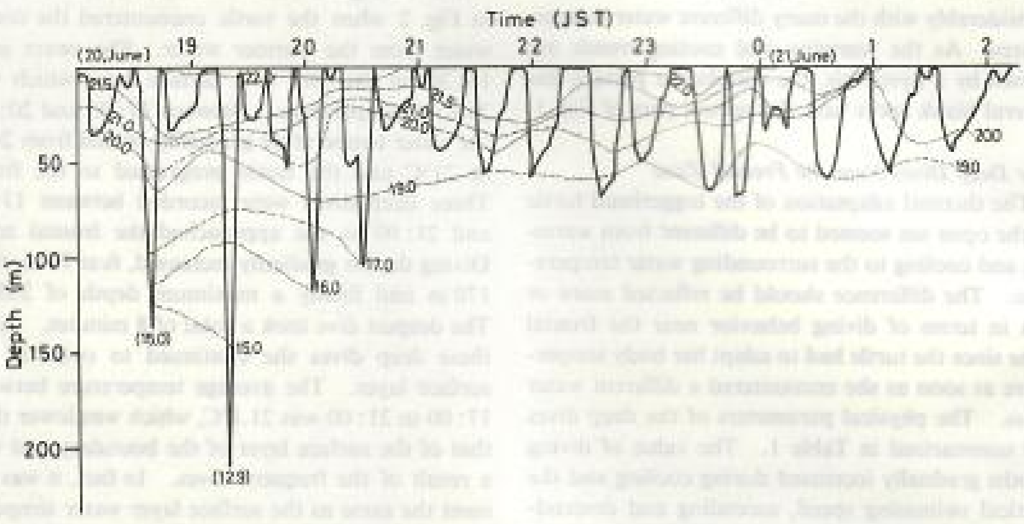

Fig. 3. Diving behavior of the loggerhead turtle when passing from cooler water to warmer water (solid line) and isotherms (thin dotted line).

The stomach temperature drop process is shown in Fig. 4, together with time series of the water temperature fluctuation. However, as mentioned in the data processing, the time difference cannot be described. The step-like drop in stomach temperature is shown with the rapid drop in water temperature. The cooling process therefore does not follow the exponential curve suggested by Neill and Stevens.[3]

Remarkable Difference in Diving Behavior between that Caused by Thermal Adaptation near the Frontal Zone and that Caused by Avoidance of Rough Sea Surface Conditions

The diving patterns near the frontal zone are different from those shown when the turtle is avoiding typhoons as shown in Fig. 5. The turtle appeared to encounter a turbulent surface at 05:00 on the 24th. She made repeated and frequent dives to the 60 m layer after 05:00, and isotherms could be drawn in Fig. 5 referring to

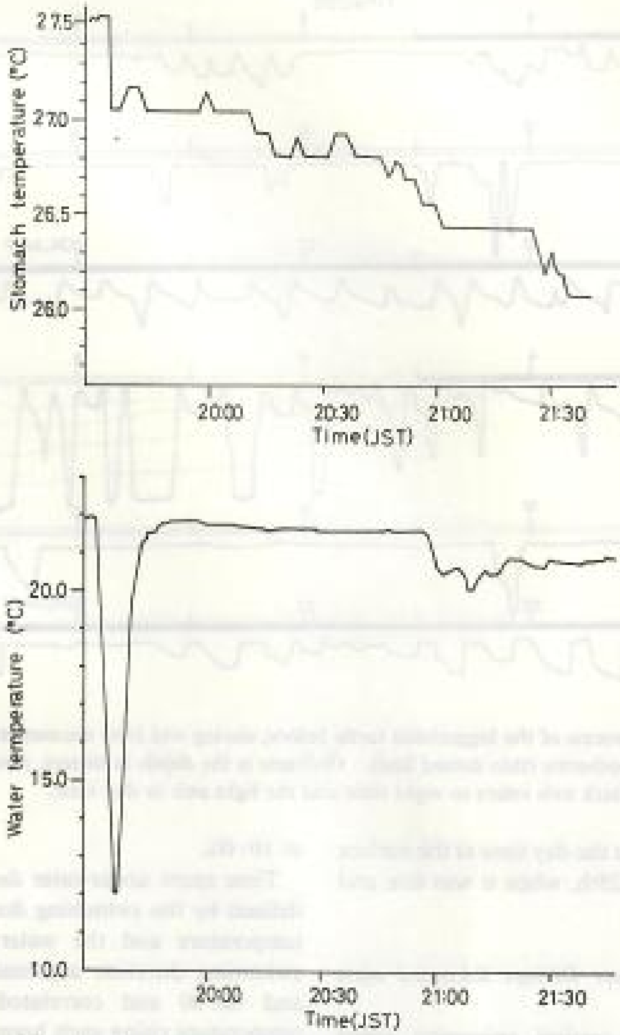

Fig. 4. Process of the drop in stomach temperature (upper panel) and water temperature (lower) after the deepest dives. Abscissa is the time on June 16 (JST).

water temperatures. The thermal distribution is quite different from the former two types near the frontal zone (Figs. 2 and 3). As shown in Fig. 5, between 05:00 and 07:00 on the 24th, no vertical thermal gradient could be found above the 10 m layer, and below the 10 m it was very small.

Isotherms are drawn parallel to the horizontal component. These isothermal patterns suggest that there was vertical water mixing due to the turbulence caused by the wind or the other physical factors. The loggerhead turtle would have to dive to a deeper layer quickly after drawing breath on the rough sea surface in order to save kinetic energy. This is because turbulent hydrolic energy decreases exponentially for the deeper the layer. Table 3 shows a comparison between vertical swimming speed in rough sea conditions and the frequent dives near the frontal zone as she passed from the cooler to the warmer water. Mean descent and ascent speeds near the frontal zone were 12.7 m/min and 5.0 m/min respectively compared with 13.8 m/min and 21.7 m/min in rough sea conditions.

The mean "duration at the bottom layer (DBL)" in the frontal zone was 1.4 min/dive, but in rough sea it was 5.8 min/dive. In the latter case, the longest duration was 21 minutes, which means that descending and ascending speeds were faster than at the frontal zone. This was probably in order to get to a deeper calm level as quickly as possible, where she could spend a longer period of time. On the other hand, as the diving patterns

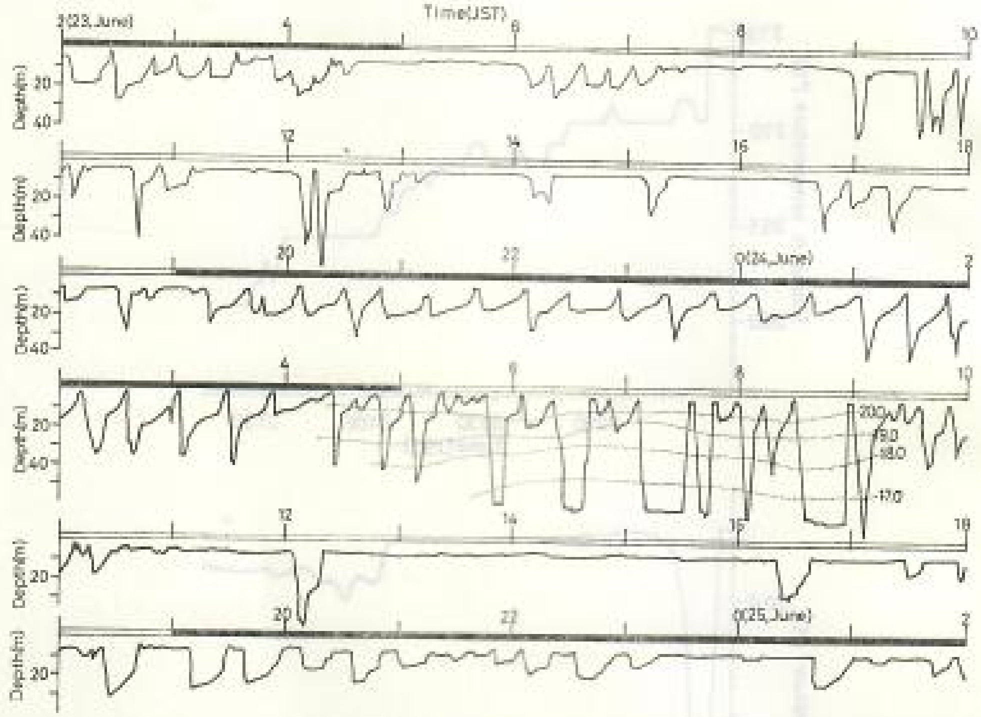

Fig. 5. Diving process of the loggerhead turtle before, during and after encountering the typhoon (solid line), isotherms (thin dotted line). Ordinate is the depth in meters, abscissa is the time (JST). The dark axis refers to night time and the light axis to day time.

in Fig. 5 show, she spent the day time at the surface layer on the 23rd and 25th, when it was fine and sea was calm.

Frequent Shallower Layer Divings Recorded when Leaving Cooler Water

Factors controlling vertical swimming speed when leaving the cooler water mass correlate with kinetic energy consumption. The fact that DBL was less between 21:00 and 02:00 suggests that the turtle did not rest at either the deeper layer or the surface layer, but ascended and descended continuously. A lower ascending speed might have been necessary to ensure that the rise in stomach temperature was gradual. One of the reason was thought that the turtle was swimming against gravity and therefore needed much more kinetic energy than when descending. Such energy was used to raise the stomach temperature rather than to travel a longer distance. This tendency in the ascending motion is illustrated in Table 3, where the mean descending speed was 18.2 m/min and the ascending speed was 7.4 m/min. Stomach temperature increased from 24.5°C to 25.0°C between 21:00 and 00:00, and then fluctuated about 25.0°C going up again to 26.0°C at 10:00.

Time spent underwater during those periods is defined by the swimming duration to adapt body temperature and the water temperature. Each swimming duration accumulated between 21:00 and 00:00 and correlated with the stomach temperature rising each hour. That is, the swimming duration accounted for 40 minutes out of one hour between 21:00 to 22:00. At this time the stomach temperature changed from 24.5°C to 24.6°C. In the period from 22:00 to 23:00, the

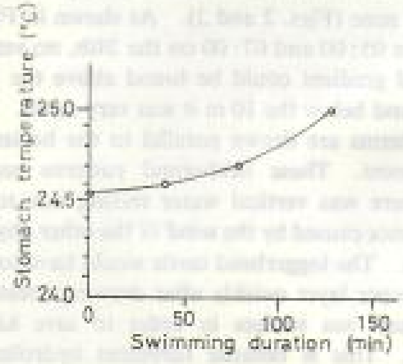

Fig. 6. Correlation between stomach temperature rise and swimming duration.

Table 3. Remarks on continuous diving motion at the frontal zone and in the rough sea surface: descending duration (DD); descending speed (DS); depth (Dep), duration at the bottom layer (DBL); ascending duration (AD) and ascending speed (AS)

A. Frontal zone

Time	DD (min)	DS (m/min)	Dep (m)	DBL (min)	AD (min)	AS (m/min)
20:00–21:00	3	12.7	38	1	14	2.7
21:00–22:00	3	16.0	48	1	12	4.0
	5	12.0	60	1	13	4.6
	(shallow layer diving 5 min)				—	—
22:00–23:00	2	31.0	62	1	16	3.9
	6	12.2	73	0	14	5.2
23:00–00:00	5	10.8	54	3	12	4.5
	8	8.8	70	2	7	10.0
	5	14.6	73	3	8	9.1
00:00–01:00	5	8.0	40	0	14	2.9
	4	16.0	64	3	9	7.1
	(shallow layer diving 5 min)				—	—
01:00–02:00	11	5.6	62	0	16	3.9
	7	7.1	50	2	21	2.4
	(shallow layer diving 4 min)				—	—
Total	64	—	694	17	156	—
Mean	5.3	12.9	57.8	1.4	13.0	5.0

B. Rough sea surface condition

Time	DD (min)	DS (m/min)	Dep (m)	DBL (min)	AD (min)	AS (m/min)
05:00–06:00	4	13.0	52	2	8	6.5
	4	15.0	60	4	2	30.0
06:00–07:00	6	10.3	62	8	3	20.7
07:00–08:00	5	12.4	62	10	2	31.0
	5	13.0	65	4	2	32.5
08:00–09:00	3	22.0	66	2	6	11.0
	4	10.5	42	0	8	5.3
	5	13.6	68	21	2	34.0
09:00–10:00	5	14.4	72	1	3	24.0
Total	41	—	549	52	36	—
Mean	4.6	13.8	61.0	5.8	4.0	21.7

swimming duration was 37 minutes and temperature was raised from 24.6°C to 24.7°C. The second duration was added to the first (40+37). The total swimming duration was 127 minutes (40+37+48) whereas stomach temperature increased to 25.0°C. The correlation between stomach temperature and swimming duration is shown in Fig. 6.

Discussion

Stomach Temperature Cooling Process

The Kuroshio often has the formation of eddies on either side.[7,8] Cold eddies off the Kii-peninsula have received attention because of their role in the transportation of pelagic fish larvae.[8] The cold water is separated by the sharp horizontal thermal gradient over a short distance, as shown in Fig. 2. The deep dives are thought to correlate with the sharp horizontal thermal gradient. The thermal time constant is estimated at 3 to 4 hours although turtles are able to alter their heat exchange rates.[10]

Live sea turtles usually heat faster than they cool.[10] It has been suggested that the process is a result of a hysteresis in warming and cooling, as shown in Fig. 1. Smith *et al.*[11], in their experiments with green turtles in styroform boxes, reported differences in water temperature compensation between warming and cooling. They also reported that the turtles usually remained relatively still when warming. However, when entering cool water, all the turtles swam vigorously and tried to escape. They measured the thermal time constant over a large temperature range of 15°C to 35°C. The gradient seemed too steep bearing in mind the physiological thermal stimulus, thus forcing them try to escape.

Under natural oceanic conditions, the turtle would pass through directly without any vertical deep dives if the horizontal thermal gradient is lower to compare with the horizontal swimming speed, since thermal stimulus during swimming is controllable. If the horizontal thermal gradient is high, she would have to cool her body to adapt the surrounding water temperature. However, she could not stay in the lower temperature zone for longer periods as shown in Table 1. Deep dives were repeated 3 times with an underwater duration of 8 to 14 minutes. The diving depth and duration may be correlated with the thermal stimulus.

Kuroki[13] reported that in general, the thermal stimulus of fish has two physical parameters, *i.e.* temperature gradient and thermal time constant. When considering the swimming behavior of sea turtles, thermal stimulus should be discussed in terms of the quantitative value of the stimulus (ΔQ).[13] In vertical swimming motion near the frontal zone, four additional factors are necessary: vertical temperature gradient ($\Delta T_z/\Delta Z$); individual vertical swimming speed ($\Delta Z/\Delta t$); time spent underwater (Δt); number of dives (N). Although the correlation between numerical thermal difference (ΔT_0) and the quantitative value of stimulus (ΔQ) is not yet clear, ΔQ may be a function of ΔT_0, and is given as:

$$\Delta T_0 \propto (\Delta T_z/\Delta Z)(\Delta Z/\Delta t)\Delta t N$$

If the loggerhead turtles want to decrease thermal stimulus in a high horizontal temperature gradient, frequent dives must be repeated with a slow vertical swimming speed. However, their speed cannot be too slow since underwater duration is limited by their need for breath at the surface.

The correlation is not easily determinable. To compare behavior on the frontal zone and the horizontal thermal gradient, we require many cases. The ratio, T_E/T_S in Table 2 gives some idea of the results of the turtle's thermal control at the boundaries between the warmer and the cooler water because the ratio when entering the front is the constant. That is to say, the mean experiential temperature is equal to the surface water temperature of the cooler water and the turtle swam continuously in the surface layer after passing through the boundaries.

It is impossible to fit the cooling process into an exponential curve since several step-like shapes are shown (Fig. 5). These should be some correlation between drinking cool water or eating food, which has the effect of dropping body temperature from the inside. An absence of an exponential in the cooling process was also reported with the red muscle of a skipjack tuna.[4] It is important to estimate the time constant of stomach temperature as she adjusts herself down to that of the surrounding water temperature in oceanic conditions.

Stomach Temperature Warming Process

The warming process is different from the thermodynamical cooling process because we cannot find any higher temperature zone in which to raise stomach temperature. The loggerhead turtle has to generate energy to raise her own stomach temperature when approaching the warmer water mass. Diving depths shown in Table 1 suggest that the turtle detected the thermal gradient near the frontal zone. Those deep dives were not so effective in raising stomach temperature, therefore a constant value was maintained during repeated deep divings, and was raised two hours after those dives.

Physically, the energy used to raise stomach temperature had to be generated by the swimming motion which was repeated continuously between 20:00 and 01:00. There is a close correlation between swimming efficiency and the propulsion system. Sea turtles are dorsal ventrally flattened and have large thin flippers for propulsion. The aquatic propulsion system of a rigid body organism such as sea turtles can also be described in terms of drag (D) and propulsive force. Total energy (W) consumed by the loggerhead turtle during the continuous diving is the same as that discussed by Sakamoto *et al.*[14]:

$$\eta W = D(L_V + L_H)$$

where η is overall swimming efficiency, D is drag and L is total swimming distance including both vertical (V) and horizontal (H) components. Drag is the resistance to motion of a body moving in a fluid,

$$D = 1/2 C_d \rho S U^2$$

where U is swimming speed, C_d is drag coefficient, ρ is the density of the surrounding fluid, S is the characteristic area of the turtle. Unfortunately, with the loggerhead turtle, there are no single definitions for S and C_d.

The part of the total power used for overcoming resistance is affected by two efficiency factors: the conversion of chemical energy to mechanical work in the muscles, and the efficiency of converting mechanical work in the swimming muscles to propelling power.[15,16] The remaining part, *i.e.* energy loss in swimmng by using actual propulsion $(1-\eta)$ should be important when considering the energy used in controlling body temperature.

The deep dives contained no horizontal underwater swimming component while the frequent shallow layer divings did. The ratio between time spent at the surface and underwater duration is 38 : 142 in the period from 21 : 00 to 00 : 00. However, the diving pattern is different from avoiding typhoons (see Fig. 5). In the latter, more time spent underwater and the turtle remain at a more constant level than the former. If total energy (W) is available to the loggerhead turtle, a curve of secondary degree as in Fig. 6 is fitted to the body temperature rise and time correlation that is included in U^3.

Swimming behavior near the frontal zone may be an important problem to consider the thermal adaptation of the sea turtles in the course of the long distance navigation.[17-20]

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References

1) Y. Naito, W. Sakamoto, I. Uchida, K. Kureha, and T. Ebisawa: *Nippon Suisan Gakkaishi*, **56**, 255–262 (1990).
2) W. Sakamoto, Y. Naito, I. Uchida, and K. Kureha: *Nippon Suisan Gakkaishi*, **56**, 263–272 (1990).
3) W. H. Neill and E. D. Stevens: *Science*, **184**, 1008–1010 (1974).
4) I. Barrett and F. J. Hester: *Nature*, **203**, 96–97 (1964).
5) E. D. Stevens and F. E. J. Fry: *Comp. Biochem. Physiol.*, **38A**, 203–211 (1971).
6) F. G. Carey and K. D. Lawson: *Comp. Biochem. Physiol.*, **44A**, 375–392 (1973).
7) H. Kawai: in "Kuroshio, physical aspects of the Japan Current, (ed. by H. Stommel and K. Yoshida)," University Washington Press, Seattle, 1972, pp. 371–386.
8) R. E. Cheney: *J. Geoph. Res.*, **82**, 5459–5468 (1977).
9) S. Uehara: *Bull. Tokai. Reg. Fish. Res. Rab.*, **34**, 55–66 (1962).
10) E. A. Standora, J. R. Spotila, and R. E. Foley: *J. Therm. Biol.*, **7**, 159–165 (1982).
11) E. N. Smith, N. C. Long, and J. Wood: *Herpetologica*, **20**, 325–332 (1986).
12) T. Kuroki: *Nippon Suisan Gakkaishi*, **33**, 264–274 (1967).
13) H. Tamiya: *Kagaku*, **19**, 338–349 (1949).
14) W. Sakamoto, Y. Naito, A. C. Huntley, and B. J. Le Boeuf: *Nippon Suisan Gakkaishi*, **55**, 2057–2063 (1989).
15) P. W. Webb: in "Hydrodynamics and energetics of fish propulsion", *Bull. Fish. Res. Board Can.*, **190**, 1975, pp. 1–158.
16) C. E. Brown and B. S. Muir: *J. Fish. Res. Board Can.*, **27**, 1637–1652 (1970).
17) D. Green: *Herpetologica*, **18**, 121–130 (1984).
18) A. Carr: *Sci. Amer.*, **212**, 79–96 (1965).
19) D. L. Stoneburner: *Copeia*, **2**, 400–408 (1982).
20) J. A. Nortimer and K. M. Portier: *Copeia*, **4**, 962–977 (1989).