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## Seasonal fluctuations in sand temperature: effects on the incubation period and mortality of loggerhead sea turtle (*Caretta caretta*) pre-emergent hatchlings in Minabe, Japan

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**Abstract** Incubation period, hatching success, and emergence percentage in loggerhead (*Caretta caretta*) nests were quantified during the 1993 and 1995 nesting seasons and following incubation seasons in Minabe, Wakayama, Japan. Sand and nest temperatures were also monitored. Over the seasons, daily mean sand temperature at nest depth fluctuated between 18.0°C and 33.3°C, with a steep increase in the second week of July and a peak in late August. Temperatures inside the nest chambers were a few degrees above those of the surrounding sand at the end of incubation. The incubation period ranged from 46 to 82 days. A significant negative correlation was found between mean sand temperature and incubation period. The relationship conformed to the day-degree concept. There was no significant seasonal trend in hatching success, but many pre-emergent hatchlings were found dead in most of the clutches during the warmest part of the season. Emergence percent-

age was correlated with mean sand temperature calculated for 4 days before emergence, suggesting that mortality may be due to heat. This heat-related mortality is considered to be a common phenomenon at our study site, because the peak in emergences coincides with the peak in high temperatures. These temperature effects on hatchling mortality must be taken into account in estimates of hatchling sex ratios. Because sand temperatures already exceed the optimal thermal range for incubation, this population is vulnerable to even small temperature increases resulting from global warming.

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### Introduction

Although sea turtles spend most of their lives in the sea, embryonic development and hatchling emergence from the eggs occur in nests excavated in sandy beaches. It is essential that environmental conditions surrounding the egg clutch remain within the range that will allow embryonic development.

Among other physical factors, temperature has important effects on sea turtle eggs, as in other reptiles (Packard and Packard 1988). Laboratory experiments have shown that sea turtle eggs seldom hatch if incubated at constant temperatures <24°C or >33°C for some extended period of time (Bustard and Greenham 1968; McGehee 1979; Yntema and Mrosovsky 1980; Miller 1982). Incubation period decreases with increasing temperature (Bustard and Greenham 1968; McGehee 1979; Miller 1982; Limpus et al. 1983), and sex determination is also influenced by temperature during the middle third of incubation (Yntema and Mrosovsky 1982).

In natural conditions, the thermal environment in sea turtle nests is not as stable as in incubators, although the diurnal fluctuation in sand temperature at nest depth is less than that to which fresh water turtle species are exposed in their shallower nests (Packard and Packard 1988). A sea turtle clutch generally consists of about 100 or more large eggs (Hirth 1980). Such a large mass of

embryos in late incubation generates more heat than is transported away from the cavity, and consequently temperature inside the chamber increases by a few degrees above that of the adjacent sand (Kraemer 1979; McGehee 1979; Maxwell et al. 1988; Maloney et al. 1990; Godfrey et al. 1997). Moreover, the sand temperature itself can exhibit a considerable seasonal change. Seasonal variation is especially likely to occur at loggerhead sea turtle (*Caretta caretta*) rookeries that are generally distributed at a higher latitudinal range than other sea turtle species (Dodd 1988). For example, sand temperature at nest depth varied from 25°C to 32°C for most of the nesting season at the loggerhead nesting beach in Mon Repos, Australia (Limpus et al. 1983).

Seasonal changes in sand temperature that result in temperatures outside of the viable range can induce seasonal changes in mortality. Hatching success may decrease for nests in which sand temperature exceeds 33°C during the incubation for an extended period of time. Even if the ambient sand temperature remains below the lethal limit, increasing metabolic heat in later developmental stages may raise the nest temperatures above the viable limit and kill the embryos or pre-emergent hatchlings. Therefore, the timing of hatching is crucial for embryonic survival. In this sense, the relationship between temperature and incubation period is significant. However, few field studies have addressed these aspects. Most studies dealing with sand or nest temperatures have focused on hatchling sex ratios.

In the present study we examine seasonal changes in sand temperature, incubation period, hatching success, and emergence percentage in loggerhead nests on one of their major nesting grounds in Japan. We then evaluate the inter-relationships of these parameters in the field.

## Materials and methods

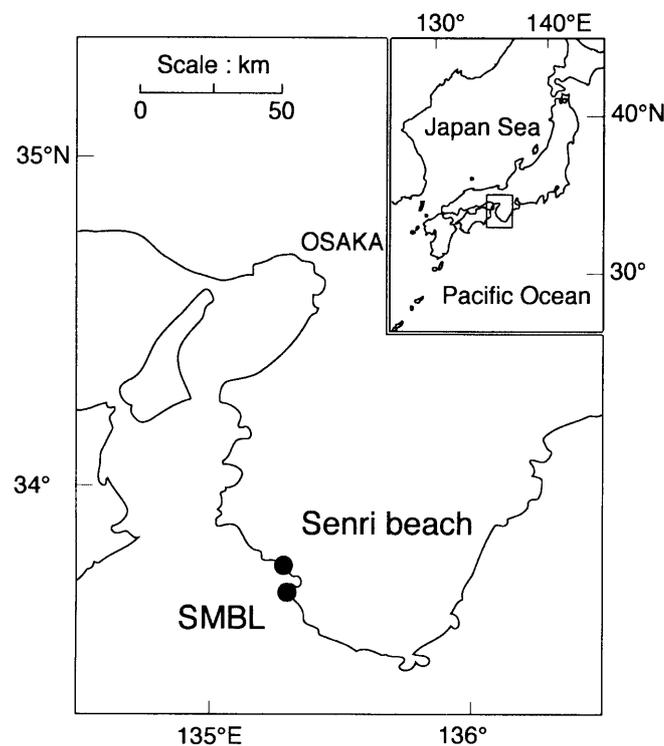
Observations and measurements were made on Senri Beach (33°46'N; 135°15'E), Minabe, Wakayama, Japan (Fig. 1). The beach is 1360 m long and has a maximum width of 50 m. This is one of the important nesting grounds for loggerhead turtles (*Caretta caretta*) in Japan (Sato et al. 1997).

From May to October in 1993 and 1995, sand temperature was measured in the hatchery (a fenced in area of sand) on an area of high beach where egg deposition has been known to occur naturally. We used time-temperature recorders (MDS-T II: Alec Electronics, Kobe, Japan) that were 165 mm long and 26 mm in diameter. The accuracy was  $\pm 0.15^\circ\text{C}$ ; the response time of the thermistor was 2 s. Details about this recorder have been reported by Sakamoto and Yuzuriha (1993). Calibration of the data loggers was conducted in controllable, custom-made water baths with a quartz thermometer (model 2804A: Hewlett-Packard) which was calibrated using a water triple point cell (model A13: Jarret Instruments). The recorders were placed at a depth of 50 cm, and measured sand temperature every hour. This depth corresponds to that of the natural egg chamber; the depths at the top and bottom of 82 loggerhead clutches averaged 31.6 and 54.4 cm, respectively, on this beach (Matsuzawa et al. 1995). Hourly rainfall was recorded automatically to 0.5 mm at Seto Marine Biological Laboratory of Kyoto University, Shirahama, about 8 km south of the research area.

To control for spatial variation in sand temperature that may occur along the nesting beach and to focus only on the temporal variation, 19 loggerhead nests were collected from the beach

immediately after deposition, and relocated to the hatchery. Ten nests were collected in 1993, and nine, in 1995. One or two clutches were collected at intervals of about 10 days throughout the nesting season (Table 1). To maintain uniform dimensions and depth of the artificial egg chambers, a plastic pipe (diameter = 20 cm, length = 100 cm) was first buried. The number of eggs in each artificial chamber was consistent. After 100 eggs of the clutch were placed in the pipe, maintaining the top and bottom of the egg chamber at the depths of 40 and 60 cm, respectively, the pipe was pulled out and the eggs left in the sand. Sand was placed above the reburied nest and compacted by hand; the surface was smoothed. To avoid movement-induced mortality of the eggs (Limpus et al. 1979), each relocation was completed within 3 h of oviposition. The time-temperature recorder was placed 1 m away from the nearest chamber (i.e. outside). Clutches were also separated by 1 m. To examine thermal differences between the inside and outside of egg chambers, time-temperature recorders were placed in the center of nest cavities laid on 20 June 1993 (no. 9304) and on 10 July 1995 (no. 9506).

Several days before expected emergence, cylindrical wire cages (diameter = 1.0 m, height = 0.6 m, mesh size < 8 mm) were placed over the nest, and checked each morning. All hatchlings found in the trap were counted as those that had emerged during the previous night and were released from the hatchery. We defined incubation period as the number of days between the date of laying and the date of first emergence from the nest. In loggerheads, emergence has been observed to occur over a maximum of 11 nights (Hays et al. 1992). Therefore, nests were excavated after 11 days of first emergence. Dead hatchlings free of the egg shell were counted as hatched, whereas dead hatchlings that had pipped but not emerged from the egg shell were not counted as hatched. Hatching success was defined as the ratio of number of hatched eggs to number of reburied eggs (100). Live hatchlings found in the nest after 11 days were not considered emerging hatchlings, because it was unlikely that they would emerge to the surface. Emergence percentage in this paper is the ratio of hatchlings that



**Fig. 1** *Caretta caretta*. Senri Beach in Minabe town and Seto Marine Biological Laboratory (SMBL) in Shirahama town where precipitation was monitored

**Table 1** *Caretta caretta*. Experimental data on 19 clutches reburied in experimental hatchery

Year, clutch no.	Nesting date	Emergence date	Incubation period (days)	Hatching success (%)	Emergence percentage (%)
1993					
9301	23 May	12 Aug	81	71	100
9302	31 May	14 Aug	75	83	96.4
9303	10 Jun	21 Aug	72	71	100
9304	20 Jun	25 Aug	66	63	92.1
9305	30 Jun	27 Aug	58	83	94.0
9306	30 Jun	29 Aug	60	91	80.2
9307	10 Jul	4 Sep	56	71	85.9
9308	20 Jul	14 Sep	56	87	92.0
9309	30 Jul	22 Sep	54	92	91.3
9310	11 Aug	—	—	0	—
1995					
9501	20 May	5 Aug	77	74	17.6
9502	30 May	6 Aug	68	79	29.1
9503	10 Jun	12 Aug	63	63	31.7
9504	20 Jun	15 Aug	56	91	28.6
9505	1 Jul	18 Aug	48	61	8.2
9506	10 Jul	25 Aug	46	40	10.0
9507	20 Jul	4 Sep	46	46	37.0
9508	31 Jul	15 Sep	46	86	89.5
9509	9 Aug	25 Sep	47	98	93.8

emerged from the sand to hatched eggs. For convenience of data analyses, we assumed that all oviposition and emergence events occurred at midnight.

Although effects of temperature on incubation period have been quantified and regression equations have been generated in some earlier laboratory studies, these studies have not explored the basis of the relationship (but see Ackerman 1994). We quantified the effect on the basis of the day-degree concept, described in the following equation:

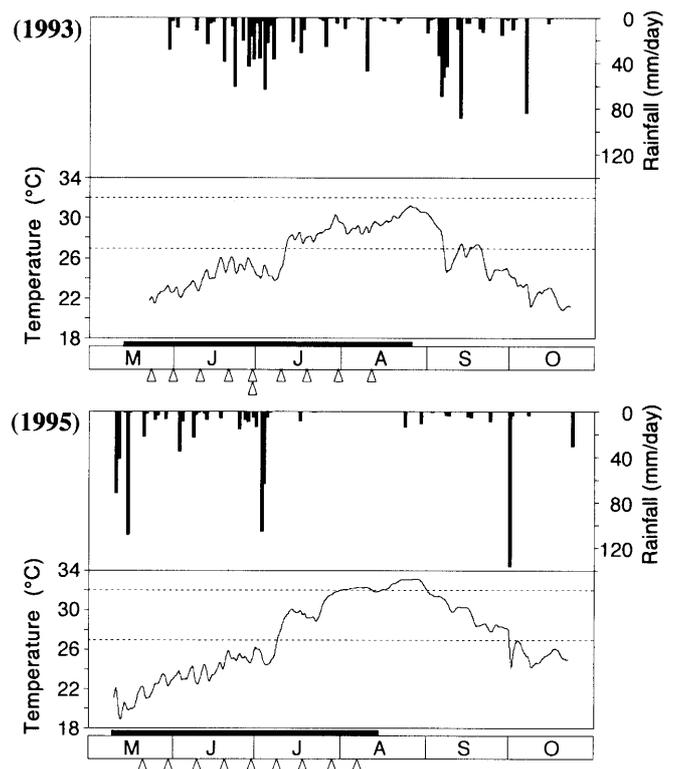
$$D = K(T - T_0)^{-1} \quad (1)$$

where  $D$  is the incubation period (days) at a given mean sand temperature  $T$  ( $^{\circ}\text{C}$ ),  $T_0$  ( $^{\circ}\text{C}$ ) is a constant that represents developmental zero temperature below which it is assumed that development ceases,  $K$  (day-degrees) is a constant that represents the day-degrees required to complete development. This equation states that the first emergence event for each egg chamber will occur when the value of the integral of the sand temperature above  $T_0$  ( $^{\circ}\text{C}$ ) reaches  $K$  (day-degrees). To transform the equation into a simple linear regression equation, the incubation period (days) for each clutch was transformed into the reciprocal. The simple linear regression equation was calculated using the method of least squares; then the constants  $T_0$  and  $K$  were calculated. This model is often used to describe the relationship between incubation period and temperature for ectotherms like insects (Begon et al. 1990) and fish (Itazawa 1991) even in variable and unstable thermal environments. KaleidaGraph and StatView were used for data analysis.

## Results

Temperatures were exceptionally cool in 1993, whereas 1995 had normal temperatures. The nesting seasons for *Caretta caretta* in 1993 and 1995 were from 13 May to 26 August and from 11 May to 14 August, respectively (see also Sato et al. 1997). Most of the nests in each season (93.2% in 1993; 97.7% in 1995) were laid during our reburial experimental period.

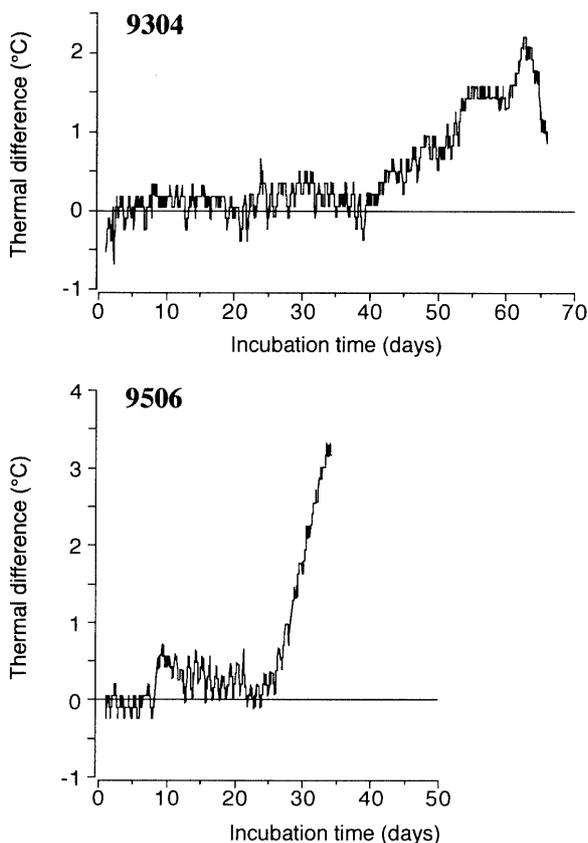
A typical pattern of seasonal thermal change was observed in both years (Fig. 2). The minimum temperature of  $18.0^{\circ}\text{C}$  was recorded in May 1995. The sand



**Fig. 2** *Caretta caretta*. Sand temperature at a depth of 50 cm in Senri Beach, Wakayama, Japan and daily rainfall measured 8 km south of the beach in 1993 and in 1995. Sand temperature data have been smoothed with a 24 h running mean to exclude diurnal fluctuation. Dashed lines indicate the optimal thermal range ( $27\text{--}32^{\circ}\text{C}$ ) for incubation. Solid bar shows the range of the nesting season. Arrowheads indicate the dates on which the clutches of eggs were laid and reburied

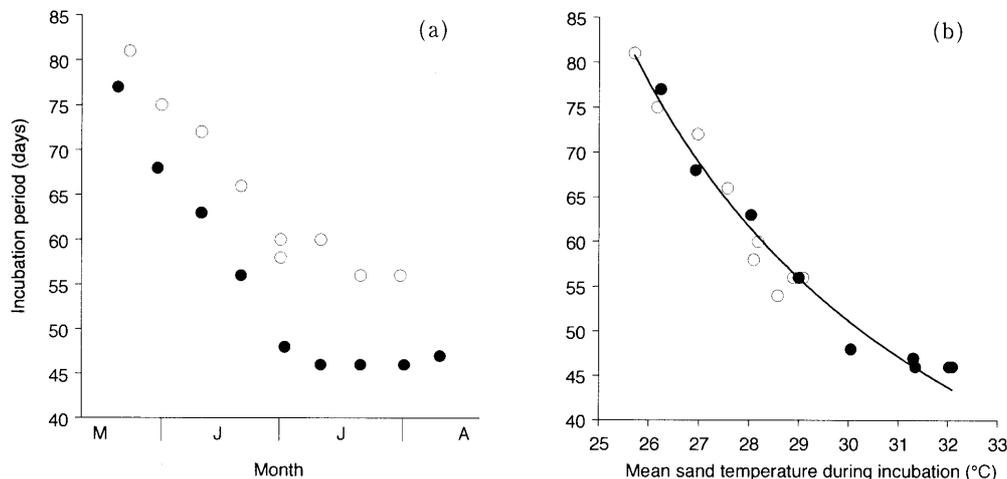
temperatures increased rapidly after the rainy season (June and the first third of July), and at the end of

August reached a peak of 31.4°C in 1993 and 33.3°C in 1995. Even the daily minimum temperature rarely fell below 32°C in August 1995. In September, sand temperatures decreased, and sporadic heavy rain accompanied by typhoons accelerated the decline. The diurnal fluctuation in sand temperatures at a depth of 50 cm averaged 0.69°C (SD = 0.48,  $n = 320$  days from 1993 and 1995 combined).



**Fig. 3** *Caretta caretta*. Thermal differences between chamber and ambient sand for nest no. 9304 and nest no. 9506. The temperature inside the chamber of no. 9506 exceeded the measurable range of the time-temperature recorder on the 34th day of incubation and stayed above the range for the rest of the incubation period

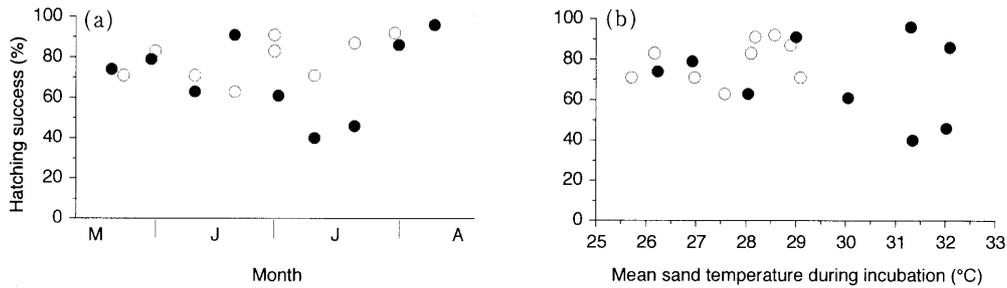
**Fig. 4a, b** *Caretta caretta*. Incubation period for each clutch deposited at different times of the nesting season (a) and relationship between mean sand temperature at 50 cm during incubation ( $T$ ) and incubation period ( $D$ ) for 18 clutches (b). Incubation period is the number of days from oviposition to first emergence, including the period from hatching to emergence. Open circles and solid circles indicate clutches in 1993 and 1995, respectively. The curve was fitted by the least-squares regression:  $D = 639.8(T - 17.6)^{-1}$  ( $r^2 = 0.957$ ,  $F = 360.143$ ,  $n = 18$ ,  $P < 0.0001$ )



Temperatures measured within clutches were different from those outside clutches. For clutch no. 9304, the maximum thermal difference of 2.2°C (nest: 32.1°C; sand: 29.9°C) was recorded on the 63rd day of incubation, which was about 3.5 days prior to first emergence (Fig. 3). The center of the nest was warmer (on average 1.7°C) than the outer sand at the same depth for the last 4 days before first emergence. For the other clutch (no. 9506), nest temperature started to increase more rapidly, and it reached the upper limit of the measurable range of the recorder (35.4°C) on the 34th day of incubation. The nest temperature never decreased below 35.4°C for the remainder of the incubation period.

Incubation periods ranged from 46 to 81 days and varied with time of season when the eggs were deposited (Fig. 4a). The later the clutches were deposited, the shorter the incubation period was in both years (in 1993: Spearman rank correlation coefficient = -0.958,  $n = 9$ ,  $P < 0.01$ ; in 1995: Spearman rank correlation coefficient = -0.881,  $n = 9$ ,  $P < 0.05$ ). There was a significant negative correlation between incubation period (days) and mean ambient sand temperature during incubation (Spearman rank correlation coefficient = -0.977,  $n = 18$ ,  $P < 0.0001$ ; Fig. 4b). The simple linear regression equation was calculated using the method of least squares ( $r^2 = 0.957$ ,  $F = 360.143$ ,  $n = 18$ ,  $P < 0.0001$ ), and the constants  $T_0$  and  $K$  in Eq. 1 were calculated as 17.6 (°C) and 639.8 (day-degrees), respectively.

No hatchlings were obtained from the clutch laid on 11 August 1993. We examined the unhatched eggs from the clutch and found no evidence of development. Hatching success of other clutches varied from 40% to 96% (mean = 74.9%, SD = 15.8,  $n = 18$ ). There was no seasonal trend in hatching success except for low values for two clutches laid in mid-July 1995 (Fig. 5a). No significant correlation was found between hatching success and mean sand temperature (Spearman rank correlation coefficient = -0.011,  $n = 18$ ,  $P = 0.9625$ ; Fig. 5b), although there was greater variation at higher temperatures. All dead embryos from no. 9506 were classified using Miller's developmental stage of 29 or 30. Although we did not examine



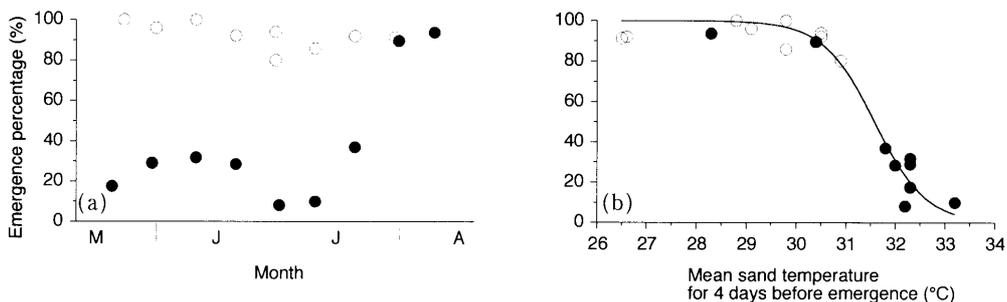
**Fig. 5a, b** *Caretta caretta*. Hatching success for each clutch laid at different times of the nesting season (a) and relationship between mean sand temperature during incubation and hatching success (b). Open circles and solid circles indicate clutches in 1993 and 1995, respectively. There is no significant correlation between hatching success and temperature (Spearman rank correlation coefficient =  $-0.011$ ,  $P=0.9625$ )

developmental stages of all unhatched eggs for other clutches, most of them in 1995 had developed nearly completely or had pipped but died without emerging from the egg shell.

Emergence percentage for each clutch is plotted against the date of oviposition in Fig. 6a. In 1993, most of the hatchlings emerged from the nests, and there was no seasonal trend in the emergence percentage (range = 80.2% to 100%, mean = 92.4%, SD = 6.4,  $n=9$ ). However, there was a wide fluctuation in emergence percentage in 1995. For the first seven clutches that emerged in August, emergence percentage was remarkably low (8.2–37.0%). Emergence percentage improved for the last two clutches emerging in September (89.5% and 93.8%).

Emergence percentage did not correlate with mean sand temperature during incubation duration (Spearman rank correlation coefficient =  $-0.381$ ,  $n=18$ ,  $P=0.1162$ ). However, there was a significant negative correlation between emergence percentage and mean sand temperature for 4 days before first emergence (Spearman rank correlation coefficient =  $-0.762$ ,  $n=18$ ,  $P=0.0017$ ; Fig. 6b). The 4 day duration is based on

**Fig. 6a, b** *Caretta caretta*. Emergence percentage for each clutch laid at different times of the nesting season (a) and relationship between mean sand temperature for 4 days before first emergence ( $T_1$ ) and emergence percentage ( $E$ ) for 18 clutches (b). Emergence percentage is the ratio of emerging hatchlings to hatching eggs. Open circles and solid circles indicate clutches in 1993 and 1995, respectively. The curve was fitted by least-squares regression:  $E = 100\{1 + \exp[1.9(T_1 - 31.6)]\}^{-1}$  ( $r^2 = 0.960$ ,  $n = 18$ )



4.1 days of mean estimated time between hatching and emergence for loggerheads (Godfrey and Mrosovsky 1997) and 3.5 days between maximum peak of nest heat and emergence (Fig. 3). The mean emergence percentage for the seven nests at temperatures  $<30^\circ\text{C}$  is 94.2%. There is a steep drop between  $31^\circ\text{C}$  and  $32^\circ\text{C}$  (Fig. 6b).

## Discussion

### Sand and nest temperatures

Our data demonstrate that sand temperatures at Senri Beach exhibit two distinctive features. First, the sand temperature fluctuations were greater than those reported from any other loggerhead rookery. Both the minimum of  $18^\circ\text{C}$  and the maximum of  $33.3^\circ\text{C}$  are remarkable compared to those of other rookeries: e.g.  $24.7^\circ\text{C}$  and  $30.3^\circ\text{C}$  at Merritt Island, Florida (McGehee 1979) and  $25^\circ\text{C}$  and  $32^\circ\text{C}$  at Mon Repos in Australia (Limpus et al. 1983). Secondly, sand temperature increased steeply as the rainy season ended. Consequently, for more than half of the nesting season and following incubation season, the sand temperatures were out of the optimal range ( $27\text{--}32^\circ\text{C}$ ) for sea turtle incubation (Bustard 1972). These features ensure that sand temperatures fluctuate during incubation and that eggs are exposed to quite different temperature regimes based on the time of season when they are deposited.

The thermal difference between the center of an egg chamber and the adjacent sand occurs due to a thermo-diffusion process of metabolic heat into ambient sand (Ackerman et al. 1985). The pattern of oxygen uptake with time, which corresponds to the pattern of metabolic heat production, is sigmoidal, peaking at about the time that hatching occurs (Ackerman 1980). Correspondingly,

actual measurements showed that thermal differences in a *Caretta caretta* egg chamber were negligible earlier in incubation, but increased gradually as development proceeded and peaked about the time of hatching (Kramer 1979; McGehee 1979). Our nest no. 9304 also exhibited a similar pattern. The period from the peak temperature to the first emergence for this clutch (3.5 days) is similar to the estimated time from hatching to emergence of 4.1 days (Godfrey and Mrosovsky 1997).

#### Incubation period

In our study, a greater seasonal variation in incubation period was found than recorded for any other loggerhead rookery (Dodd 1988; Mrosovsky 1988; Kaska et al. 1998), reflecting greater seasonal variation in sand temperature. Although few studies have attempted to apply the day-degree concept to reptiles, our results support the validity of applying this concept to loggerhead eggs. The high value of the coefficient of determination indicates that incubation period can be predicted from sand temperatures at similar depths.

The regression equation based on the day-degree concept has several advantages. For example, it helps standardize chronology of embryonic development. This is necessary for estimation of hatchling sex ratios on beaches with widely fluctuating sand temperatures like those at our study site. It has been assumed that the thermosensitive period for sex determination corresponds to the middle third of the incubation period (e.g. Hanson et al. 1998). However, the developmental stages of eggs incubated under increasing or decreasing temperatures cannot correspond to the stages of eggs incubated under constant temperature for the same percentage of the incubation period, because development rates vary with temperature (Matsuzawa et al., unpublished data). Standardization of embryonic development makes it possible also to estimate the approximate time of death for unhatched eggs and to detect responsible factors (Matsuzawa et al., unpublished data).

It should be noted that we did not determine that all development processes ceased at 17.6°C. The linearity between temperature and development rate is generally maintained only within the viable range, and developmental zero is merely the intercept. No visible signs of embryonic development were found for loggerhead eggs incubated at 20°C (McGehee 1979). It should also be noted that our regression does not represent the relationship as precisely as regressions from laboratory experiments. In our equation, incubation period includes the period from hatching to emergence, and mean sand temperature is cooler than mean temperatures to which eggs are actually exposed. Nevertheless, the equation we generated represents the physiological relationship. In addition, our equation has practical applications for field studies.

#### Hatching success

No seasonal trend in hatching success was found in this study. A mean hatching success of 75% is similar to values in previous reports from loggerhead rookeries (Wyneken et al. 1988; Christens 1990; Peters et al. 1994; Kaska et al. 1998). However, it appears that thermal deviation from the viable range for development caused mortality to some extent in some clutches. The hatching success of two clutches (nos. 9506 and 9507) laid in the middle of July 1995 was < 50%. Most of the unhatched embryos had almost completed development. The first emergence from these nests occurred on 25 August and 4 September, indicating that the embryos died in the last third of August when sand temperatures peaked at about 33°C (Fig. 2). Sea turtle eggs seldom hatch when incubated at constant temperatures > 33°C for some extended period (Bustard and Greenham 1968; McGehee 1979; Yntema and Mrosovsky 1980; Miller 1982). Due to the rapid increase in metabolic heat, the center of egg chamber no. 9506 rose to at least 35.4°C, and a similar increase must have occurred in no. 9507. The eggs were exposed to lethal temperature levels and presumably died of excess heating.

#### Emergence percentage

In 1995, pre-emergent hatchlings suffered high mortality in the nest chamber. There have been several reports of mortality of pre-emergent hatchlings. Mortimer (1990) suggested desiccation and cave-ins can depress success of pre-emergent green turtles at Ascension Island. Peters et al. (1994) indicated that compactness of beach sand can obstruct emergence of loggerheads in Turkey. Both studies reported differences in mortality among beaches with different types of sand, whereas we found differences within the same sand type. Although we did not measure water potential, the sand was sufficiently wet not to collapse when the chambers were excavated. Additionally, unhatched eggs remained turgid at excavation. These observations indicate that desiccation and cave-ins were not the cause of mortality in our study.

Our results demonstrated that mortality was significantly related to high temperatures during pipping and emergence (Fig. 6b). Similar high mortality of pre-emergent hatchlings is often found during the hot season in in situ nests on the same beach (Matsuzawa, personal observation) and occasionally at other nesting sites in Japan (Yamashita 1995), supporting this correlation. Mortality may result from the following processes. First, heat can directly cause death. Emergence percentage fell steeply between 31°C and 32°C. In view of the thermal difference between the inner and outer egg chamber (Fig. 3), nest temperatures of clutches suffering considerable mortality must be higher than the lethal level, as discussed above. Secondly, the hatchlings can be trapped in their chambers due to heat. Activity of sea turtle hatchlings decreases at high temperatures, probably

because of thermal inhibition of coordinated muscle movement (Mrosovsky 1968; O'Hara 1980; Moran et al. 1999). The critical threshold temperature above which hatchlings do not emerge is 32.4°C for loggerheads (Moran et al. 1999). This physiological mechanism probably applies from the time of pipping. Preliminary observations with a stethoscope indicate that pre-emergent hatchlings often make their way to the subsurface during the daytime when temperatures in the nests are low (Matsuzawa, personal observation). Hatchlings pipping out in August 1995, when even the minimum sand temperature at the nest depth rarely fell below 32°C, might have been unable to leave the nest chambers. Finally, poor gas exchange may influence mortality (Ackerman 1980). Gas diffusion in the sand is restricted, and oxygen consumption in a nest increases as metabolism increases with embryonic development (Ackerman 1980). Consequently, the partial pressures of oxygen in nests drop to roughly 12–14 kPa at time of hatching (Ackerman 1977). Therefore, when high temperatures accelerate the metabolic rate, suffocation may follow.

The peak of the nesting season in this rookery spans from the end of June to the beginning of July (Sato et al. 1997). Hatchlings from nests laid during this period emerge during the second half of August (Table 1). This approximately corresponds to the peak of high temperatures (Fig. 2). Moreover, emergence dates for earlier clutches are also during this period, because earlier clutches have longer incubation periods due to cool initial temperatures (Fig. 4a). Therefore, many nests in this rookery are subjected to the mortality risk from high temperatures. Except for those years with unusually low temperatures, such as 1993, high mortality in the egg chambers in this rookery seems to be a common phenomenon.

#### Implications for conservation and further studies

The results of the present study provide important information for management and conservation of sea turtles. Embryos and pre-emergent hatchlings may die as a result of high nest temperatures in rookeries where sand temperatures are as high as at our study site. If high mortality occurs as a result of high sand temperatures, especially in rookeries where the number of nesting females has decreased rapidly like at loggerhead rookeries in Japan (Sato et al. 1997), protective measures may be needed. By monitoring sand temperature and calculating the day-degree, dates of hatching and emergence can be predicted. When sand temperature at nest depth exceeds the threshold, cooling of the nests that are about to hatch, for example by partial shading or sprinkling with water, could protect pre-emergent hatchlings from the heat.

Discussion of the effects of global warming on sea turtle populations have focused on loss of nesting beach habitat as a result of sea level rise and on skewed sex ratios as a result of temperature increases on tempera-

ture-dependent sex determination (Davenport 1997). The loggerhead population at Senri Beach is nesting in a habitat near the extreme of its range of thermal tolerance. This population and others in similar thermal regimes are vulnerable to even slight increases in temperature as a result of global warming. These populations could experience excessive nest failure as a result of global warming before they are threatened by sea level rise or skewed sex ratios.

Our findings also have implications for studies of sea turtle demography. Hatchling sex ratios are usually estimated by combining nesting frequency at different times of the season with the sex ratios of hatchlings sampled at those times (reviewed by Mrosovsky 1994). Many of these studies are based on the implicit assumption of uniform mortality. However, as Godfrey and Mrosovsky (1999) pointed out, significant seasonal or spatial differences in mortality or clutch size must be taken into account in sex ratio estimates to avoid substantial errors. Heat-related mortality may be one such factor.

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