

Nest Site Sand Temperatures from 1897 to 2023 for Three Sea Turtle Species at Kuroshima Island, Ryukyu Archipelago, Japan

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ABSTRACT. – To monitor the impact of climate change on sea turtle nesting beaches, we measured the sand temperature at 3 specific nesting locations for loggerhead turtles (*Caretta caretta*), green turtles (*Chelonia mydas*), and hawksbill turtles (*Eretmochelys imbricata*) at Nishinohama Beach on Kuroshima Island, Ryukyu Archipelago, Japan. During the major incubation periods (peak of nesting season) from 2009 to 2023, sand temperature surrounding nests ranged from 28.72°C to 30.45°C for loggerheads, 28.46°C to 30.04°C for green turtles, and 28.60°C to 29.36°C for hawksbills. Estimated historical (since 1897) sand temperatures based on recorded climatology data indicate that sand temperatures at nesting microsite locations increased by 1.29°C, 1.12°C, and 1.18°C per 100 yrs for loggerheads, green turtles, and hawksbills, respectively.

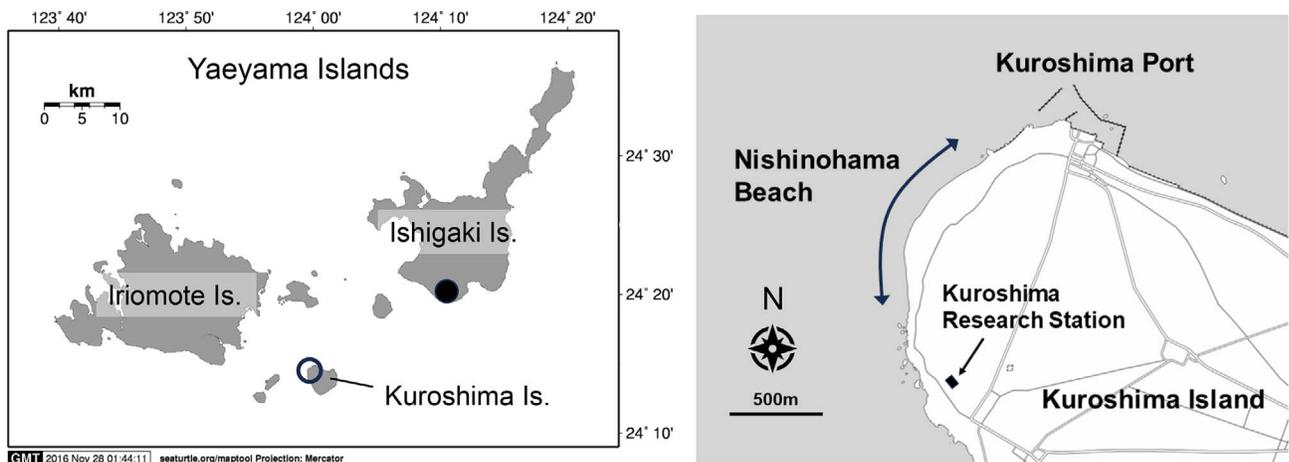
KEY WORDS. – loggerhead turtle; green turtle; hawksbill turtle; global warming; sand temperature

Many sea turtle populations are classified as vulnerable, endangered, or critically endangered by the International Union for the Conservation of Nature (IUCN 2023). For species conservation, preserving nesting and breeding areas is of utmost importance. In sea turtle species, embryonic development is influenced by incubation temperature. In particular, sea turtle embryos develop at a range of temperatures 24°–35°C (Ackerman 1997), and hatchlings' morphology and locomotor performance can be influenced by incubation temperature (Booth 2017). In addition, sea turtles exhibit temperature-dependent sex determination, with high incubation temperatures producing more females (Morreale et al. 1982). As a result, global warming is expected to affect the incubation success, survival rates, and sex ratios of sea turtle hatchlings (Hamann et al. 2007; Hawkes et al. 2009; Booth 2017). Related to this, there have been increasing examples of strong female biases (i.e., feminization) in sea turtle populations around the world (e.g., Jensen et al. 2018; Tanabe et al. 2020).

One approach to gauge the impact of climate warming on sea turtle primary sex ratios is the measurement of beach sand temperatures, as beach warming can lead to feminization. The sand temperatures of sea turtle rookeries have been measured worldwide to assess the effects of global warming on sea turtle hatchlings in particular (reviewed by Patrício et al. 2021). Previous studies have used the correlation between sand temperature and air temperature, and efforts have been made to predict past and future sand temperatures via ex situ approaches

(Hays et al. 2003; Fuentes et al. 2009; Laloë et al. 2016). However, sand temperatures on nesting beaches are affected by additional factors, such as sand color, shading, and nest depth (Godfrey and Mrosovsky 1999; Hays et al. 2001; Wood et al. 2014), and, therefore, measuring sand temperature at the nesting site level is important.

The Yaeyama Islands are located at the southern end of the Ryukyu Archipelago, Japan. This region includes nesting beaches for loggerhead turtles (*Caretta caretta*), green turtles (*Chelonia mydas*), and hawksbill turtles (*Eretmochelys imbricata*). Moreover, the Yaeyama Islands are considered the southern limit of the North Pacific loggerhead turtle nesting area (Kamezaki et al. 2003) and close to the northern limit for nesting by Northwest Pacific green turtles and hawksbill turtles (Kamezaki 1991). Our research group monitored the sand temperatures of a major nesting beach (Nishinohama Beach) on Kuroshima Island of the Yaeyama Islands from 2009 to 2023. We measured sand temperatures at 3 locations on the beach, corresponding to nest locations for each of the 3 sea turtle species. Using sand temperature measurements and estimating sand temperatures during the last century, we assessed the long-term effects of changing beach sand temperatures on each species. First, we summarized the monthly nesting activity of each sea turtle species for the known major nesting and incubation periods from 2009 to 2023. We then estimated the trend of historical sand temperature from 1897 to 2008 by combining the air and sand temperature relationships to match the incubation season of each species. In doing so,



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Figure 1. Location of Kuroshima Island, Yaeyama Islands, Ryukyu Archipelago, and photograph of Nishinohama Beach in Kuroshima Island. ●: Point for measurement of air temperature (Ishigaki Meteorological Office); ○: Point for measurement of sand temperature. Photo by Kazunari Kameda

we generated a 126-yr time series (1897–2023) of sand temperatures that can be used to look at potential impacts of changing mean temperatures to primary sex ratios of hatchlings emerging from Nishinohama Beach.

METHODS

Study Area

The Yaeyama Islands are located at the southern end of the Ryukyu Archipelago in the Northwest Pacific (lat 24°00'N–24°40'N, long 122°45'E–124°30'E; Fig. 1). This region is classified as a subtropical area and is one of the largest coral reefs in Japan. Many beaches of the Yaeyama Islands serve as sea turtle nesting sites (Kamezaki 1991).

Sea turtles were monitored, and sand temperatures were measured at Nishinohama Beach on Kuroshima Island. This beach is approximately 1 km long and 20 m wide, mainly composed of corals, shells, and foraminifera. Nishinohama Beach is dominated by vegetation, including tall trees and shrubs, and the sand-grain diameter is 0.5–1.0 mm at the vegetation line (Kameda and Wakatsuki 2017). Kuroshima Island is designated as part of Iriomote Ishigaki National Park by the Japanese Ministry of the Environment. Since 1978, sea turtle nests have been monitored on this beach, with loggerhead nesting showing a declining trend, green turtle nesting showing an increasing trend, and hawksbill nesting remaining stable (Kameda and Wakatsuki 2017).

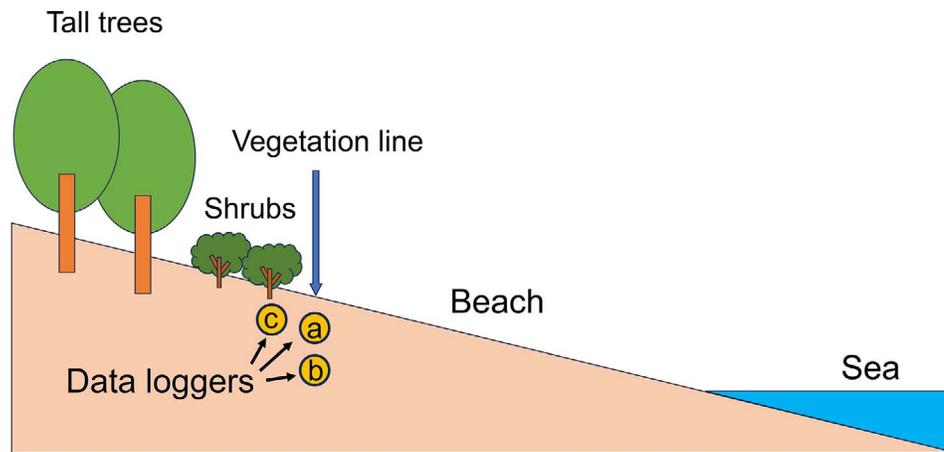


Figure 2. Setting data loggers for each species. (a) Loggerhead turtle nesting location, at vegetation line and 40 cm depth; (b) green turtle nesting location, at vegetation line and 60 cm depth; (c) hawksbill turtle nesting location, in vegetation area and 40 cm depth.

Monitoring of Sea Turtle Nests and Sand Temperature

Nesting surveys on Nishinohama Beach (i.e., patrolling for sea turtle nests) were conducted from March to October at intervals of 1–3 days from 2009 to 2023. Sea turtle species were determined by identifying the turtle track on the beach and measuring egg diameters (Kamezaki et al. 1994). When the species could not be identified from the tracks and egg diameters, we sampled 5 eggs per nest and moved them to an incubator for species identification upon hatching, based on the hatchlings' external morphology (Kamezaki et al. 1994).

The sand temperatures were measured from June to October in 2009, 2010, 2014, 2016, and 2020, and from May to October in 2011–2013 and 2018–2023. Surveys were not conducted in 2015 and 2017. Because Nishinohama Beach has uniform elevation from the high tide line to the vegetation line (where shrubs and tall trees are found), temperature data loggers were deployed at the central location on the beach (lat 24°14'58.0"N, long 123°59'32.8"E). Each sea turtle species lays eggs at different locations and depths, and temperature logger placement corresponded with the typical location on the beach and nest depth of each species (Fig. 2; Godfrey and Mrosovsky 1999; Laloë et al. 2016). In this region, loggerhead and green turtles mainly nest near the vegetation line, at the border between shrubland and beach sand (Kamezaki et al. 1994); this location is shaded by shrubs and tall trees for 2–3 hrs around dawn. Hawksbill turtle nests have been reported further into the vegetation (Kameda and Wakatsuki 2011), approximately 2–3 m inland from the vegetation line; this location is shaded by shrubs all day. In this region, loggerhead and hawksbill turtle nests were observed at an average depth of 40 cm, whereas green turtle nests occurred at an average depth of 60 cm (Matsuzawa et al. 1995; STAJ unpublished). Therefore, temperature data loggers (HOBO TidbiT v2, Onset Computer Corporation) were placed at these depths (40 cm for loggerheads and hawksbills; 60 cm for green turtles) to measure sand temperatures as close as possible to where a

typical nest would be deposited for each species; temperature data were recorded hourly from 2009 to 2023.

Data Analysis

Ten loggerhead, 125 green, and 49 hawksbill turtle nests were confirmed from 2009 to 2023. We pooled the sea turtle nesting dates by month to determine the major nesting months for each species. Sea turtle eggs generally hatch after approximately 50–80 days of incubation (Ackerman 1997). Therefore, the peak in the number of nests on the beach occurred later than the nesting peaks. In this study, we defined the major incubation period as a month post-nesting and estimated the incubation temperature for each species by calculating the average monthly sand temperatures from 2009 to 2023 during major incubation periods.

We calculated the monthly sand temperature for each year by calculating the average hourly sand temperature of the nesting zones of each sea turtle species. We compared sand temperature with air temperature from 2009 to 2023, and used this relationship to backcast annual mean sand temperatures to 1897. Briefly, we searched the Japan Meteorological Agency Website (<https://www.jma.go.jp/jma/index.html>) to obtain the monthly air temperatures on Ishigaki Island, 20 km from Kuroshima Island, from 1897 to 2023. Second, we constructed linear regression models of the relationship between each species' nest locations' monthly sand and air temperatures during the major incubation periods from 2009 to 2023. Then, using these regression models with historical air temperatures, we estimated sand temperatures from 1897 to 2023. All the statistical analyses were performed using Microsoft Excel.

RESULTS

Nesting Seasons for the 3 Sea Turtle Species

From 2009 to 2023, loggerhead turtle nesting was confirmed from April to June (Fig. 3), and the major nesting periods were May and June (90% of total nests).

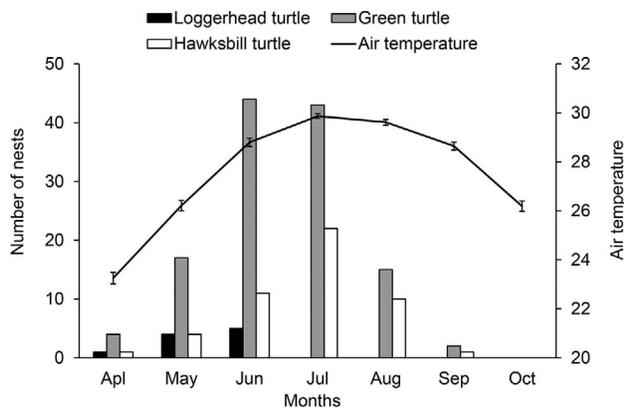


Figure 3. Seasonal distribution of nest numbers in loggerhead ($n = 10$), green ($n = 125$), and hawksbill turtles ($n = 49$) from 2009 to 2023 on Kuroshima Island; Air temperature was measured on Ishigaki Meteorological Office. Bar: Standard error.

Green turtle nesting was confirmed from April to September, and the major nesting period was from May to August (95% of total nests). Hawksbill turtle nesting was confirmed from April to September, and the major nesting period was from June to August (88% of the total nests). Accordingly, the major incubation periods for loggerheads, green turtle, and hawksbills were June to July, June to September, and July to September, respectively. Monthly air temperatures during the major incubation periods were $28.80^{\circ}\text{C} \pm 0.67^{\circ}\text{C}$ (mean \pm SE) in June, $29.87^{\circ}\text{C} \pm 0.36^{\circ}\text{C}$ (mean \pm SE) in July, $29.62^{\circ}\text{C} \pm 0.45^{\circ}\text{C}$ (mean \pm SE) in August, and $28.65^{\circ}\text{C} \pm 0.63^{\circ}\text{C}$ (mean \pm SE) in September.

Seasonal Sand Temperatures from 2009 to 2023

At each sea turtle nesting location, the mean monthly sand temperatures from 2009 to 2023 showed similar seasonal changes, with peak temperatures in July (Fig. 4). The range of sand temperatures during the major incubation period for loggerhead turtle nesting locations was from $28.72^{\circ}\text{C} \pm 0.14^{\circ}\text{C}$ (mean \pm SE, June) to $30.45^{\circ}\text{C} \pm 0.14^{\circ}\text{C}$ (July), the range for green turtles was from $28.46^{\circ}\text{C} \pm 0.21^{\circ}\text{C}$ (June) to $30.04^{\circ}\text{C} \pm 0.20^{\circ}\text{C}$ (July), and that for hawksbill turtles was from $28.60^{\circ}\text{C} \pm 0.22^{\circ}\text{C}$ (September) to $29.36^{\circ}\text{C} \pm 0.15^{\circ}\text{C}$ (July).

Historical Sand Temperature and Nest Temperature from 1897 to 2008

Regression models of the relationship between sand temperature and air temperature during major incubation periods were calculated for the 3 sea turtle species (Fig. 5). Sand and air temperatures showed statistically significant correlations at all depths: loggerhead turtles, sand temperature = $0.962 \times$ air temperature + 1.449 ($r = 0.95$, $n = 73$, $p < 0.01$); green turtles, sand temperature = $0.808 \times$ air temperature + 5.703 ($r = 0.92$, $n = 23$, $p < 0.01$); and hawksbill turtles, sand temperature = $0.779 \times$ air temperature + 6.036 ($r = 0.88$, $n = 73$, $p < 0.01$). Regression

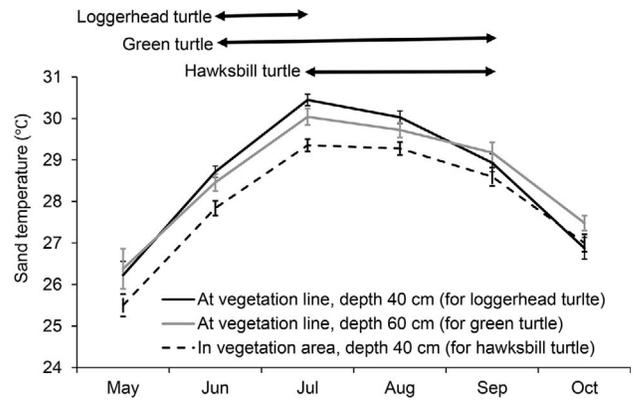


Figure 4. Seasonal changes in sand temperatures for each sea turtle species nesting location. Measurement periods for loggerhead turtle and hawksbill turtle locations are from 2009 to 2023, and for green turtle locations from 2019 to 2023. Bar: Standard error. Arrow: major incubation period in this study.

models were then used to predict the historical sand temperatures from 1897 to 2008 (Fig. 6). The slope of the linear regression model in historical sand temperatures increased 1.29°C , 1.12°C , and 1.18°C per 100 yrs for loggerhead, green, and hawksbill turtles, respectively.

DISCUSSION

In the Yaeyama Islands, the ranges of sand temperature during the major incubation periods were $28.72^{\circ}\text{--}30.45^{\circ}\text{C}$, $28.46^{\circ}\text{--}30.04^{\circ}\text{C}$ and $28.60^{\circ}\text{--}29.36^{\circ}\text{C}$ for loggerhead, green turtle, and hawksbill nesting locations, respectively. Previous studies reported that the sand temperatures of loggerhead turtle nesting beaches were $29.5^{\circ}\text{--}33.2^{\circ}\text{C}$ in Greece, Mediterranean (Godley et al. 2001), and 29.4°C (mean) in Queensland, Australia (Wood et al. 2014). Those of green turtle nesting beaches were $28.7^{\circ}\text{--}31.3^{\circ}\text{C}$ for a light-colored beach in Ascension Island, central Atlantic (Godley et al. 2002), $30.4^{\circ}\text{--}32.3^{\circ}\text{C}$ in Taiwan, Northwest Pacific (King et al. 2013), 29.0°C (mean) in Raine Island, Australia (Fuentes et al. 2009), and $<28.5^{\circ}\text{C}$ at a remote South Pacific location (Laloë et al. 2020). Those of hawksbill turtle nesting beaches were $30.3^{\circ}\text{--}32.4^{\circ}\text{C}$ in Barbados, Caribbean (Horrocks and Scott 1991), and $29.8^{\circ}\text{--}31.0^{\circ}\text{C}$ in the western Yucatán Peninsula, Mexico (Flores-Aguirre et al. 2020). The temperatures of green and hawksbill turtles nesting beaches were $29.1^{\circ}\text{--}33.3^{\circ}\text{C}$ on the island of St. Eustatius in the northeastern Caribbean (Laloë et al. 2016). The sand temperature at Nishinohama Beach's nesting season was lower than at any other, likely because of the white sand color and shading of vegetation on this beach, as researchers have linked shading and white sand color to lower sand temperatures (Hays et al. 2001; Wood et al. 2014).

The sand temperature is affected by seasonal air temperature, sand depth, and sun exposure (Matsuzawa et al. 1995, 2002; Wood et al. 2014). The sand temperature at shallower depths is generally higher than at deeper depths (Laloë et al. 2016). Our results showed that, from June to

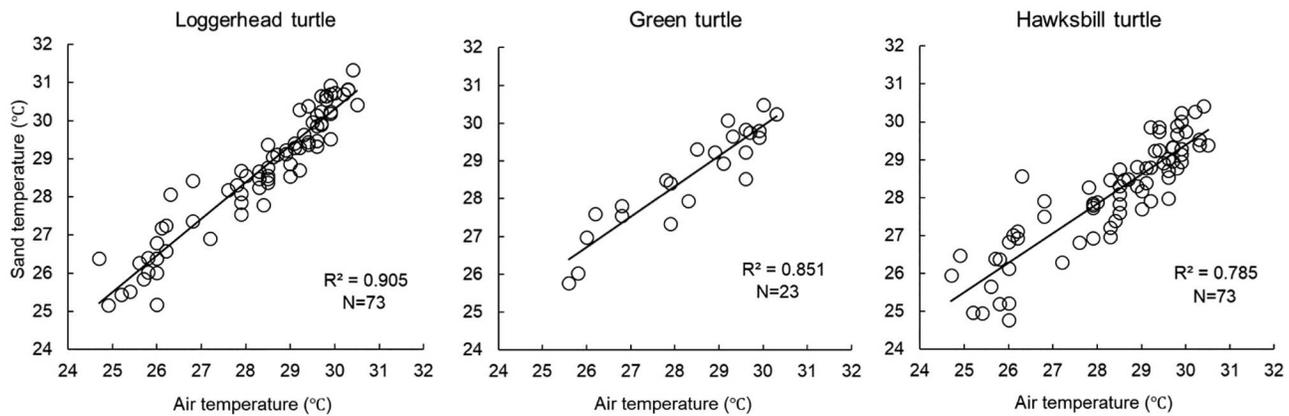


Figure 5. Regression analysis of mean monthly air temperature and mean monthly sand temperature for each nesting location from 2009 to 2023. In all cases, $p < 0.01$.

August, the sand temperature at the vegetation line at 40 cm depth was higher than at the vegetation line at 60 cm depth. However, the sand temperature at the vegetation line at the depth of 40 cm was cooler than those at

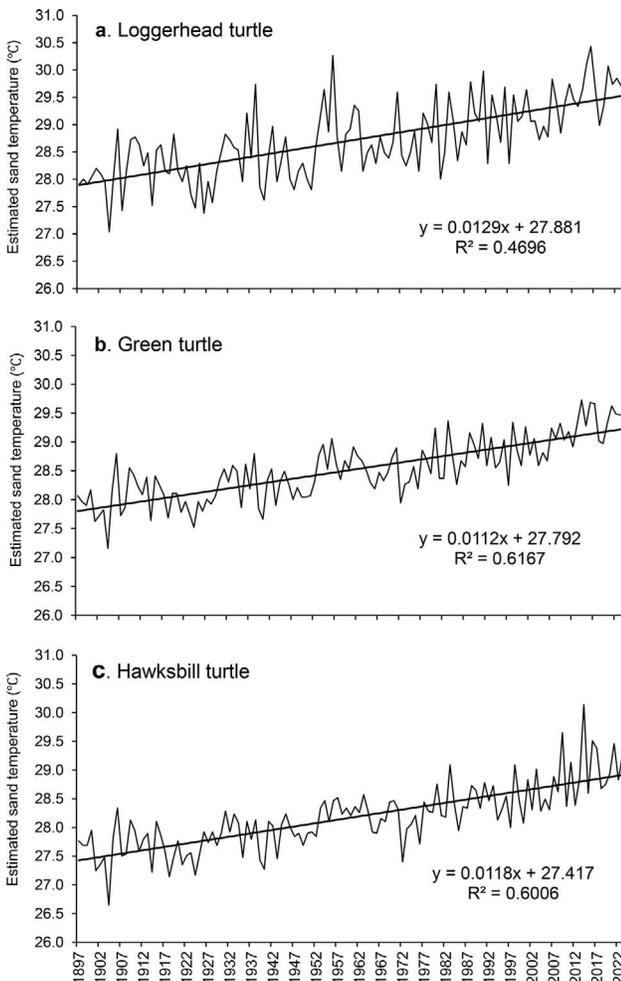


Figure 6. Estimated (1897–2008) and in situ measured (2009–2023) mean sand temperatures during the major incubation period in each sea turtle species nesting on Nishinohama Beach, Kuroshima Island. (a) Loggerhead (June–July), (b) green (June–September), and (c) hawksbill turtles (July–September).

60 cm in May, September, and October (Fig. 4). Seasonal inversion in relative sand temperatures between different depths has also been documented at other sites in Japan and is likely to maintain more stable temperatures at deeper locations because deeper locations have smaller effects of air temperature and sun exposure (Biodiversity Center of Japan 2023). The sand temperature in the vegetation area was cooler than at the vegetation line (Fig. 4). This result shows that vegetation shading is an important factor limiting the increase in sand temperature (Wood et al. 2014; Laloë et al. 2020).

The historical sand temperature for loggerhead turtles was higher than that for green and hawksbill turtles, even though loggerhead turtles had a longer incubation period than the other species (Figs. 4 and 6). These differences may reflect the characteristics of nest location for each sea turtle species; the nesting depth of loggerhead turtles is generally shallower than that of green turtles (Matsuzawa et al. 1995; STAJ unpublished), and they lay eggs in front of vegetation, unlike hawksbill turtles (Kamezaki et al. 1994; Kameda and Wakatsuki 2011). In other words, our results indicate that the embryonic development of loggerhead turtle eggs in this region is likely more strongly affected by global warming than that of green and hawksbill turtles. Our findings suggest that loggerhead turtles in this region may be more prone to feminization in the face of global warming than green and hawksbill turtles.

We found that sand temperatures may have increased by 1.29°C, 1.12°C, and 1.18°C per 100 yrs at the nesting positions for loggerhead, green, and hawksbill turtles on Nishinohama Beach. As Hays et al. (2003) reported, sand temperatures at green turtle nesting locations rose by 0.36–0.49°C every 100 yrs in Ascension Island. Yaeyama Islands are likely to be vulnerable to global warming. Our survey revealed that the nesting seasons of green and hawksbill turtles in this region coincided with the peak air temperature, and that of loggerhead turtles was also close to the peak air temperature for the year (Fig. 2). Sea turtles may adapt to climate change by shifting their nesting seasons and distributions (reviewed by Patrício et al. 2021).

Previous studies have reported that loggerheads are beginning to nest earlier because of climate change (Pike et al. 2006; Hawkes et al. 2007). For example, the nesting season of loggerhead turtles was earlier by 9 Julian days on the Atlantic coast of central Florida from 1983 to 2003 (Pike et al. 2006). However, whether all sea turtle populations can adapt to global warming by nesting earlier is unknown. Okuyama et al. (2020) reported no evidence of an earlier date of the peak of the nesting season for loggerhead, green, and hawksbill turtles on Ishigakijima Island over the past 25 yrs. Accordingly, sea turtles nesting in the Yaeyama Islands probably do not change their nesting season as an adaptation to global warming.

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