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Source: Chelonian Conservation and Biology, 19(1) : 101-110

Published By: Chelonian Research Foundation and Turtle Conservancy

URL: https://doi.org/10.2744/CCB-1428.1

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Quarter-Century (1993–2018) Nesting Trends in the Peripheral Populations of Three Sea Turtle Species at Ishigakijima Island, Japan

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Abstract. – Three sea turtle species (loggerhead [*Caretta caretta*], green [*Chelonia mydas*], and hawksbill [*Eretmochelys imbricata*] turtles) have nesting sites at Ishigakijima Island, which is located in the southwestern part of Japan. This island is known as the geographic southern (low-latitude) limit of north Pacific loggerhead turtles' nesting sites and close to the northern (high-latitude) limit of northwest Pacific green and hawksbill turtles' nesting sites. Our 26-yr nesting survey (1993–2018) revealed that the number of nesting events of loggerhead turtles decreased (with a temporal increment between 2006 and 2008), while the other study reported that the entire Japanese loggerhead nesting population continued to increase substantially from 2006 to, at least, 2012. In contrast, the green turtle population increased gradually, with fluctuations. Hawksbill turtles had several nests annually. The sea surface temperature during the nesting season was significantly related to the annual number of nesting events in loggerhead turtles but not in green and hawksbill turtles. Thus, warming temperature may have caused a reduction in the nesting population of loggerhead turtles at Ishigakijima Island, which is the southern limit of their nesting distribution.

Key Words – *Caretta caretta*; *Chelonia mydas*; citizen science; climate change; distribution shift; *Eretmochelys imbricata*; phenology

要旨. – 日本の南西諸島に位置する石垣島は、アカウミガメ、アオウミガメ、タイマイの三種のウミガメが産卵することで知られる。石垣島はアカウミガメの北太平洋における産卵域の南限（低緯度）に位置し、一方アオウミガメとタイマイは、北西太平洋における産卵域の北限（高緯度）に近いことで知られる。**1993**年から**2018**年までの**26**年間におよぶ産卵調査の結果、石垣島におけるアカウミガメの産卵数は**2006**年から**2008**年に一時的に増加したものの、年々減少していることがわかった。これは、**2000**年代初頭から**2012**年までにおいて日本全体で見られた増加傾向と一致しない。一方、アオウミガメの産卵数は増減を繰り返しながらも増加傾向にあった。タイマイは毎年数回の産卵がみられた。産卵期間中の石垣島周辺の海面水温は、アカウミガメの毎年の産卵数と有意な相関がみられたが、アオウミガメとタイマイではみられなかった。このため、産卵域の南限である石垣島におけるアカウミガメの産卵数の減少は温暖化と関係があるかもしれない。

Sea turtles are ectotherms; thus, their physiology, behavior, and ecological traits are heavily affected by ambient temperature (Spotila et al. 1997). More specifically, research has shown that the sex of sea turtles is determined by the clutch temperature during the middle third of incubation (Mrosovsky 1994). Therefore, climate change may, potentially, have a significant impact on the reproductive output of turtles at breeding sites as well as on the efficiency of energy acquisition at foraging sites (Hawkes et al. 2009). In fact, the potential impact of climate change on sea turtles has been observed in the sex ratio of foraging populations (Jensen et al. 2018), hatchling mortality (Laloë et al. 2017), nesting season (Weishampel et al. 2004; Hawkes et al. 2007), and remigration intervals in nesting turtles (Solow et al. 2002). The accumulation of such effects may result in changes in the distribution and reduce the survival rate of sea turtles. However, to our knowledge, the effect of climate change on the distribution of sea turtles' nesting places has rarely been investigated (but see Maffucci et al. 2016). Although sea turtles are known for their nest site fidelity (Lohmann et al. 1997), they may find other nesting sites if the current ones become unsuitable (Hawkes et al. 2009). Previously unsuitable habitats (e.g., beaches at higher latitudes than current nesting areas) may become suitable for successful egg incubation after an increase in air, beach, and sand temperatures. This apparently occurred in the past, when warmer temperatures during interglacial periods facilitated the expansion of loggerhead sea turtles into higher latitudes (Bowen et al. 1994). In contrast, there is also the possibility that a site on a lower-latitude beach that currently has suitable nesting conditions will become unsuitable as an optimal breeding site because of excessively elevated temperatures; this is particularly true for temperate species.

It is assumed that the effects of climate change on species (e.g., a shift in their geographic range) would be clearly recognized at the range margins of their geographical distribution (Hampe and Petit 2005). Therefore, the continuous monitoring of the status of populations at the range margin of their distribution is an adequate approach to assess the potential effect of climate change on species. Ishigakijima Island, which is located in the southwestern part of Japan (lat 24.4°N, long 124.2°E; Fig. 1), provides nesting places for 3 sea turtle species: loggerhead (*Caretta caretta*), green (*Chelonia mydas*), and hawksbill (*Eretmochelys imbricata*) turtles (Uchida and Nishiwaki 1982; Kamezaki 1991). It is known as the geographic southern (low-latitude) limit of north Pacific loggerhead turtles' nesting sites, alongside adjacent islands Kuroshima and Iriomotejima (Kamezaki et al. 2003; Kameda et al. 2007) (Fig. 1A–B). Meanwhile, the island is close to the northern (high-latitude) limit of northwest Pacific green and hawksbill turtles' nesting sites (Kamezaki 1991) (Fig. 1A). Therefore, Ishigakijima Island incorporates range margins of nesting populations from 3 sea turtle species; this may make it a suitable place to examine the effect of climate change on the distribution of sea turtles' nesting sites through the long-term monitoring of their nesting trends. Here, we reported the quarter-century trends of nesting populations of 3 sea turtle species on Ishigakijima

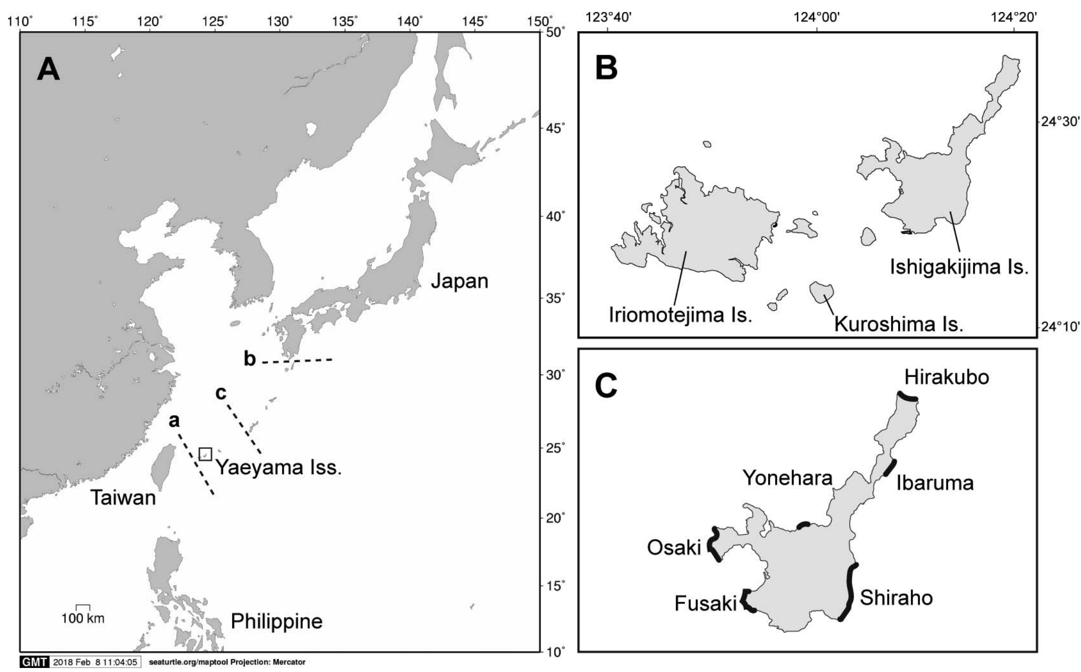

Figure 1. (A) Map showing the location of the Yaeyama Islands and the geographical limits of the nesting distribution of sea turtles in the northwest Pacific (a represents the southern limit of loggerhead nesting sites, while b and c represent the northern limits of green and hawksbill turtles) (Biodiversity Center of Japan 2016). (B) Map showing Ishigakijima, Kuroshima, and Iriomotejima islands, which make up the Yaeyama Islands. (C) Map showing 6 major nesting beaches on Ishigakijima Island. Bold black lines represent the beach lines of each nesting site. The map on the left side was drawn by using the Maptool program (http://www.seaturtle.org).

Island during the 1993–2018 period and investigated the potential effect of climate change on these trends.

METHODS

Nesting Survey. — In 1993, we started collecting nesting data along 3.0 km of the Ibaruma beach on Ishigakijima Island, where sea turtle nests have been observed to be most abundant (Abe et al. 2004) (Fig. 1C). The nesting survey area gradually expanded to almost all beaches by 2002. Thus, nesting data collected from major beaches other than Ibaruma (Osaki [3.4 km], Hirakubo [1.3 km], Fusaki [2.1 km], Shiraho [7.0 km], and Yonehara [1.1 km] beaches) (Fig. 1C) were used for the analysis of the nesting trends on the entire Ishigakijima Island since 2002.

Nesting surveys were conducted during the day or night throughout the nesting season (that generally lasted from April to September) from 1993 to 2018. The surveys were conducted intermittently with various interval ranges that lasted anywhere between 1 d and about 1 mo. In this study, a nesting event was defined as the behavior that a female completed nesting activities (e.g., digging an egg chamber, laying eggs, and camouflaging the site), while a landing event included the behavior that a female came ashore but returned to the sea without any nesting success in addition to a nesting event. In the surveys, the numbers of landing and nesting events were counted; the date when those events occurred was estimated based on the conditions of crawl tracks. The nesting success was judged by whether a crawl track was accompanied by digging a body pit/egg chamber, abandoned nesting attempts, and emergence of hatchlings from the nests. The species of the turtles engaging in nesting activities was identified by the morphology of the nesting females, hatchlings, or adequately developed embryos in dead eggs and by the characteristics of the crawl tracks. Several typhoons passed by Ishigakijima Island every year. Thus, high tide caused by the typhoons washed out the traces of nesting sites and crawls. Therefore, in this study, we included the minimum count of sea turtle nesting or landing events.

If turtles were encountered during night patrols, the straight carapace length (SCL) of nesting individuals was measured. Then they were tagged internally using passive integrated transponder tags and externally using metal (inconel) and plastic tags on both hind flippers. These procedures took place after the turtles completed their nests or before they returned to sea after they had abandoned the nests. Moreover, a green turtle (SCL, 927 mm) nesting at Ibaruma beach was deployed with a Fastloc GPS-Argos tag (Mk10-AF, Wildlife Computers, Redmond, WA) in July 2014 and was tracked to examine the potential foraging habitat of green turtles nesting on Ishigakijima Island. The nest locations were often lost because high tide caused by typhoons washed out the nesting traces. The ratio of emergence success was investigated only for the nests the locations of which were still identified after hatchlings emerged.

Environmental Data. — The mean sea surface temperature (SST) values during the annual nesting season for each turtle species (loggerhead: April–July; green and hawksbill: May–September) at the waters around Ishigakijima Island between 1982 and 2018 were obtained from the Japan Meteorological Agency database. Moreover, the mean air temperature was used to estimate the sand temperature in the clutch during the annual incubation period (loggerhead: April–August; green and hawksbill: May–October). The following conversion equation for beaches with light sand by Laloë et al. (2014) was used to estimate sand temperature from air temperature:

$$T_{\mathrm{sand}} = 1.15 \times T_{\mathrm{air}} - 1.70$$

where T_{sand} represents the estimated sand temperature in the clutch incorporating metabolic heating (0.5°C, Laloë et al. 2014) and T_{air} represented the air temperature.

The annual data of Earth's magnetic field between 1980 and 2015 were used to compare the secular change in magnetic inclination at Ishigakijima Island and the nesting trend; these data were obtained by the Geospatial Information Authority of Japan.

Statistical Analysis. — A generalized linear model (GLM) with a Poisson distribution and a log link function was used to determine the relationship between the number of nesting events in each species and SST. SST was treated as an explanatory variable (fixed effect). Moreover, GLMs with Gaussian and binomial distributions were used to examine the trends of the number of eggs in a single clutch and the emergence ratio of hatchlings over the research period, respectively. In this analysis, year was treated as an explanatory variable. Considering that data on nesting dates between 1993 and 2001 were available only for Ibaruma beach, the number of data was different between 1993–2001 and 2002–2018. Thus, the median date of all nesting events in the annual nesting season of each species was calculated to determine the long-term change of nesting dates on Ishigakijima Island. In this assessment, a GLM with Gaussian distribution was also used, and year was treated as an explanatory variable. We used the "lme4" package in the software R version 3.52 (R Development Core Team 2018) to run the GLM analyses. All data are reported as average ± standard deviation.

RESULTS

Nesting Trends. — At Ibaruma beach, 1.8 ± 2.5 loggerhead (range, 0–9), 38.7 ± 22.1 green (range, 12–110), and 0.3 ± 0.6 hawksbill (range, 0–2) nests were laid annually from 1993 to 2018 (Fig. 2A, C, E). Meanwhile, the annual number of landing events for loggerhead, green, and hawksbill turtles was 3.4 ± 5.0 (range, 0–18), 94.5 ± 54.5 (range, 33–235), and 0.4 ± 0.6 (range, 0–2), respectively (Fig. 2A, C, E). The nesting trends showed

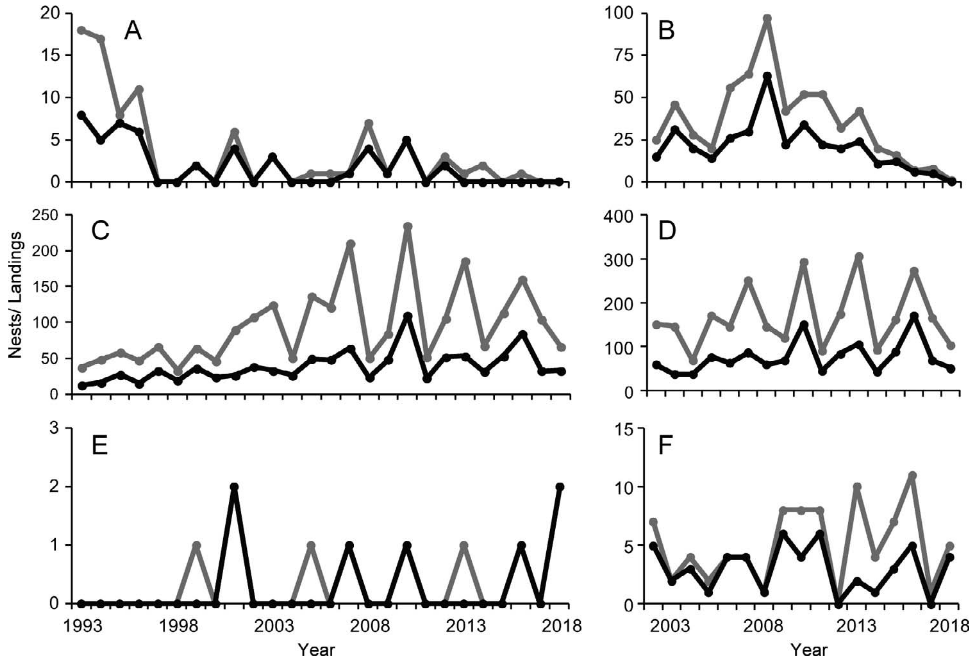

Figure 2. The nesting (black) and landing (gray) trends of (A, B) loggerhead, (C, D) green, and (E, F) hawksbill turtles. Data were calculated for (A, C, E) Ibaruma beach and (B, D, F) 6 major nesting beaches.

that the number of loggerhead nests decreased drastically from 1993 to 1997. No loggerhead nest has been recorded at Ibraruma beach since 2013. Green turtle nests, on the other hand, increased gradually every year (Fig. 2A, C). Hawksbill turtles laid only a few nests every year (Fig. 2D).

At the 6 major nesting beaches of Ishigakijima Island, 19.9 ± 14.3 loggerhead (range, 0–63), 76.1 ± 37.3 green (range, 37–170), and 3.0 ± 2.0 hawksbill (range, 0–6) nests were laid annually from 2002 to 2018 (Fig. 2B, D, F). Meanwhile, the number of landing events for loggerhead, green, and hawksbill turtles was 34.9 ± 23.7 (range, 1–97), 168.0 ± 71.8 (range, 68–306), and 5.1 ± 3.3 (range, 0–11), respectively (Fig. 2B, D, F). The nesting trends showed that the number of nesting loggerheads decreased after peaking at 2008 and then no nest was recorded at any of the major nesting beaches in 2018 (Fig. 2B); however, we counted 1 nest in a minor beach. The green turtles showed a similar nesting trend at Ibaruma beach, which gradually increased annually with considerable fluctuation (Fig. 2D); there was not a significant nesting trend for hawksbill turtles during the survey period (Fig. 2E).

The mean SSTs around the waters of Ishigakijima Island during the nesting seasons for loggerheads (April–July) and green and hawksbill turtles (May–September) between 1982 and 2018 were 26.9°C ± 0.3°C and 28.3°C ± 0.4°C, respectively. These temperatures gradually increased since 1982 (Fig. 3A). GLM analysis showed that the annual number of loggerhead nests decreased significantly between 2002 and 2018 with higher water temperatures (Wald test, $n = 17$, $z = -2.56$, $p < 0.001$; Fig. 3B); meanwhile, no temperature effect was observed for green ($n = 17$, $z = 0.91$, $p = 0.36$; Fig. 3C) and hawksbill ($n = 17$, $z = -0.60$, $p = 0.55$; Fig. 3D) turtles.

Nesting Turtles. — The mean SCLs were 872 ± 60 mm ($n = 19$), 979 ± 46 mm ($n = 110$), and 816 ± 29 mm ($n = 11$) for the loggerhead, green, and hawksbill turtles that we encountered during the surveys, respectively (Table 1). The tag identification of individuals revealed that green turtles nested 3.6 ± 1.1 times during a nesting season (Table 1). The mean remigration interval was 3.9 ± 1.2 yrs (Table 1). The turtle that we preliminary tagged in 1992 was encountered 7 times over 22 yrs (1992–2013). The remigration interval of this turtle was 3.5 ± 0.5 yrs. Meanwhile, the tagged loggerhead turtle was encountered only once at the next nesting event within a season. Furthermore, hawksbill turtles were not encountered again over the 26-yr research period (Table 1).

GPS-Argos tracking revealed that a nesting green turtle migrated to Iejima Island after her nesting season and stayed around there for 2 mo until the battery expired (Fig. 4). Two tagged nesting green turtles were found at the coastal area of Okinawajima Island (Fig. 4).

Nesting Season. — The nesting season of loggerhead turtles ranged from 31 March to 20 July, and the median was 23 May (Table 1; Fig. 5). In green turtles, the nesting season peak was about 1 mo after that of loggerheads (Fig. 5). Green turtle nests were observed mainly during the summer (May–September), while there were a few nests during the winter (November–January) (Table 1; Fig. 5). Hawksbills' peak nesting season was similar to that of green turtles as it ranged approximately from May to September (Table 1; Fig. 5).

The median nesting date of loggerheads (Wald test, $n = 25$, $t = 2.24$, $p < 0.05$; Fig. 6A) and hawksbills

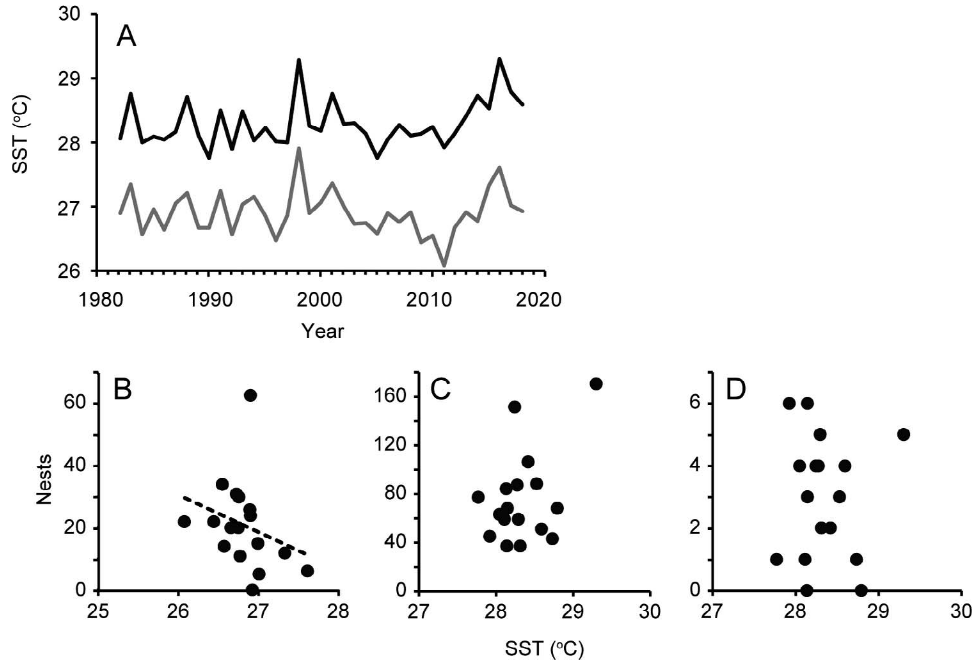

Figure 3. (A) Mean annual sea surface temperature (SST) during the nesting season of loggerhead (April–July, gray) and green and hawksbill (May–September, black) turtles at the waters around Ishigakijima Island. The relationships between the nest numbers at major nesting sites on Ishigakijima Island from 2002 to 2018 and SST during each nesting season for (B) loggerhead, (C) green, and (D) hawksbill turtles are depicted.

(n = 19, t = 2.89, $p < 0.05$; Fig. 6C) was significantly delayed each year during the survey period (1993–2018); the nesting date of green turtles, on the other hand, did not shift significantly over the course of the research period (n = 26, t = –0.32, p = 0.76; Fig. 6B).

Clutch Size, Emergence of Hatchlings, and Estimated Incubation Temperature. — The number of eggs in a single clutch was similar between loggerhead (103.4 ± 23.3) and green (104.1 ± 22.2) turtles, while hawksbills laid more eggs (137.9 ± 26.3; Table 1). No significant trends were observed in the clutch sizes of loggerhead (Wald test, n = 261, t = –0.5, p = 0.61) and green (n = 844, t = –1.69, p = 0.09) turtles over the research period, but a significantly decreasing trend was observed in hawksbill turtles (n = 55, t = –2.6, $p < 0.05$).

The percentages of emergence success of hatchlings from the nest were 75.4% ± 23.5%, 80.0% ± 23.4%, and 84.2% ± 17.4% for loggerhead, green, and hawksbill turtles, respectively (Table 1). The presumed causes of emergence failure were the submergence of nests due to typhoons and the predation by ghost crabs (*Ocypode* spp.). No significant trends in emergence success were observed over the research period for all 3 species (loggerheads: Wald test, n = 251, z = –0.68, p = 0.50; greens: n = 804, z = 1.47, p = 0.14; hawksbills: n = 52, z = –0.40, p = 0.69).

The annual mean estimated sand temperatures in the clutch during the incubation period of loggerhead (April–August) and green and hawksbill (May–October) turtles were 30.1°C ± 0.5°C and 30.8°C ± 0.5°C between 1980 and 2018, respectively. These temperatures increased annually in a gradual manner, as was the case with SST (Fig. 7).

Earth's Magnetic Field. — The components of earth's magnetic field at Ishigakijima Island showed subtle annual changes between 1980 and 2015. The inclination

Table 1. Characteristics of 3 species of nesting sea turtles and their reproductive performance at Ishigakijima Island.[a]

	Loggerhead			Green			Hawksbill		
	Mean ± SD	Range	n	Mean ± SD	Range	n	Mean ± SD	Range	n
SCL (mm)	872 ± 60	768–969	19	979 ± 46	873–1067	110	820 ± 53	690–870	12
Clutch size (no. of eggs)	103.4 ± 23.3	5–161	263	104.1 ± 22.2	22–181	844	137.9 ± 26.3	68–191	55
Emergence success (%)	75.4 ± 23.5	0–100	255	80.0 ± 23.4	0–100	798	84.2 ± 17.4	21.7–99.2	52
Date of nesting (Julian day)	144 ± 21.8	89–202	346	190 ± 36.5	18–362	1163	181 ± 32.1	120–251	50
Clutch frequency (no. of clutches)	2	2	1	3.6 ± 1.1	1–6	60	—	—	0
Remigration interval within an individual (yrs)	—	—	0	3.9 ± 1.2	2–8	74	—	—	0

[a] n = number of data; SCL = straight carapace length.

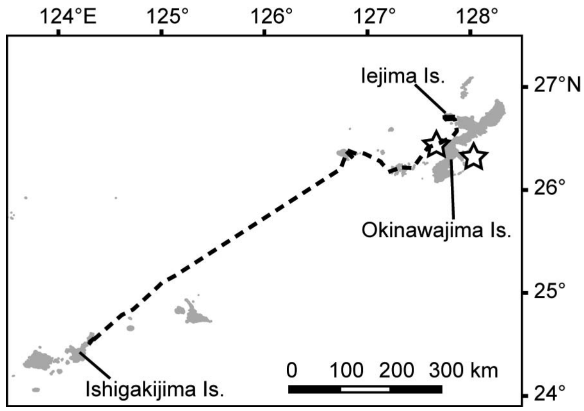

Figure 4. A map showing the postnesting migration of a green turtle nesting at Ibaruma beach and the tag-recapture sites of 2 other individuals. A dashed line and white stars represent the migration route determined by GPS-Argos tracking and tag–recapture sites, respectively.

angle increased gradually from 33.8° in 1980 to 35.5° in 2015. The total and vertical intensities of the magnetic field also increased from 43,889 and 24,396 nT in 1980 to 44,471 and 25,848 nT in 2015, respectively. Meanwhile, the horizontal intensity decreased gradually from 36,484 nT in 1980 to 36,184 nT in 2015.

DISCUSSION

Shift of Dominant Nesting Sea Turtle Species at Ishigakijima Island. — Our nesting survey revealed that 3 sea turtle species showed different nesting trends at Ishigakijima Island over a quarter of a century; the dominant species among the nesting turtles was the green turtle. The dominant species on this island in the 1980s was the loggerhead turtle (Kamezaki 1991); therefore, the dominant species shift occurred from temperate loggerhead to tropical green turtles between the 1980s and 1990s. The same shift was reported at an adjacent island (Kuroshima Island) (Kondo et al. 2000).

Loggerhead Turtles. — The carapace size of nesting loggerhead turtles was larger in the study area than it was in other major nesting beaches in Japan (Minabe and Yakushima Island) (Hatase et al. 2002, 2013). In Japanese nesting populations, larger turtles tend to be neritic foragers migrating to the continental shelf in the East China Sea to feed on benthic prey (Hatase et al. 2002, 2007). Therefore, loggerhead turtles nesting at Ishigakijima Island could have embarked on a foraging migration to the East China Sea after the nesting season.

Our results showed that the nesting population of loggerhead turtles on Ishigakijima Island declined from 1993 to 2005 but temporally increased between 2006 and 2008. This increasing trend corresponded to that of the entire nesting population of loggerheads in Japan (Kamezaki et al. 2003; Biodiversity Center of Japan 2016). However, although the entire Japanese loggerhead population increased substantially and continuously at least until 2012 (Biodiversity Center of Japan 2016), the

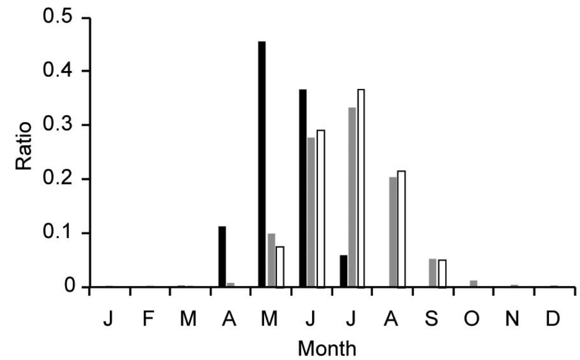

Figure 5. Monthly distribution of loggerhead (black), green (gray), and hawksbill (white) nest ratios from 1993 to 2018 on Ishigakijima Island.

Ishigakijima Island population decreased drastically after 2008 and became almost extinct in 2018. Thus, the decline of the Ishigakijima Island nesting population was, presumably, caused not by common factors affecting the entire Japanese population, such as the environmental condition of foraging grounds (Chaloupka et al. 2008b), but by a specific local factor. However, the recent population reduction (after 2013) could have been partially caused by a common factor because the entire Japanese population also decreased (Biodiversity Center of Japan 2016, 2019).

Ishigakijima Island is the southern (low-latitude) limit of the north Pacific population of loggerhead turtles' nesting distribution. Moreover, the SST around the Ishigakijima Island waters increased over the past decades, and this increment was significantly related to the reduction of nest numbers. Meanwhile, the emergence ratio of loggerhead hatchlings did not change over the research period. These facts may lead to a reliable hypothesis that the loggerheads that used to nest in Ishigakijima Island may not currently be able to access the waters around the island due to high temperatures; consequently, they shifted their nesting sites to regions that are more temperate. This hypothesis is supported by satellite tracking studies reporting that the range of SSTs that these turtles occupy in the central north Pacific is 15°C–25°C (Polovina et al. 2004); moreover, the maximum SST that juvenile and mature loggerhead turtles generally experience in the north Pacific is around 28°C (Kobayashi et al. 2008; Narazaki et al. 2015; J. Okuyama et al., unpubl. data, 2018). The SST during loggerheads' nesting season around Ishigakijima Island has been increasing annually and is currently close to 28°C (Fig. 3). This match between the SST around Ishigakijima Island and the upper SST range that loggerheads normally experience may have prevented them from nesting at Ishigakijima Island. Kondo et al. (2000) also suggested that there is a relationship between the decrease in nest numbers and SST at Kuroshima Island. A recent study on Mediterranean loggerhead populations reported the northward expansion of their nesting distribution and associated it with higher SSTs (Maffucci et al. 2016). Therefore, there

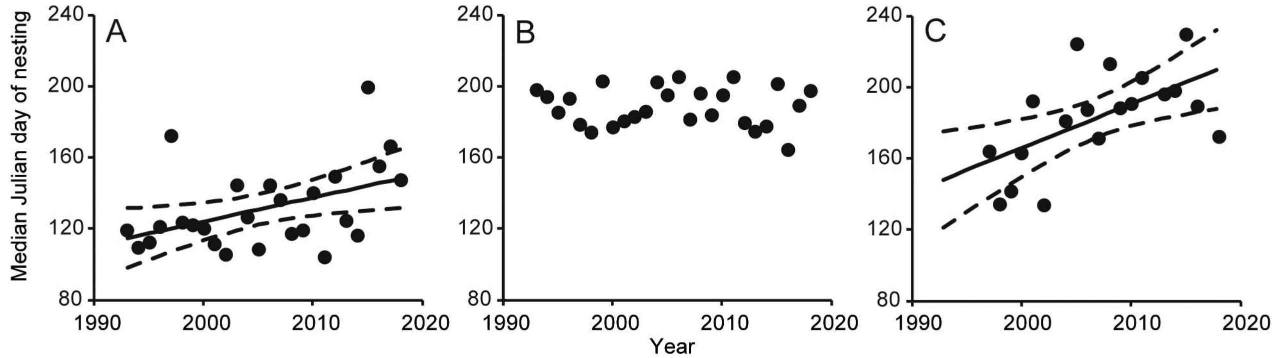

Figure 6. Median of the nesting date (Julian day) in each year for (A) loggerhead, (B) green, and (C) hawksbill turtles. Solid lines and dashed lines represent the linear regression and 95% confidence interval, respectively.

is also the possibility that loggerheads previously nesting at Ishigakijima Island shifted their reproductive sites northward.

Brothers and Lohmann (2015) reported that the nest density of the north Atlantic loggerhead population varied with changes in the geomagnetic field because sea turtles locate their nesting beaches by using geomagnetic cues. In the case of Ishigakijima Island, all of the geomagnetic field components in the area changed subtly over the decades. However, all of the inclination and intensity isolines near Ishigakijima Island showed a southward shift. This geomagnetic shift direction was inverse to the shift of the nesting distribution of sea turtles, which followed a northward direction. Thus, the decline of the loggerhead nesting population at Ishigakijima Island was not likely due to the geomagnetic field shift.

The clutch size and emergence ratio did not change throughout the 26-yr period. Moreover, those values were within the general range of reproductive performance (Van Buskirk and Crowder 1994). The estimated incubation temperature in the clutches at Ishigakijima Island indicates that it would have probably produced a considerably female skewed sex ratio of hatchlings over the past 3 decades (according to the pivotal temperature of sex determination [28.6°C–29.7°C; Mrosovsky 1994]). Meanwhile, the incubation temperature has not yet reached lethal levels (31.6°C at the inflection point of survival rate; Matsuzawa et al. 2002); it has, however, been recently getting near the lethal line, although lethal incubation temperatures are quite different among nesting populations (Weber et al. 2011). Thus, further temperature increases may have a crucial impact on the nesting population of loggerhead turtles at Ishigakijima Island in the near future.

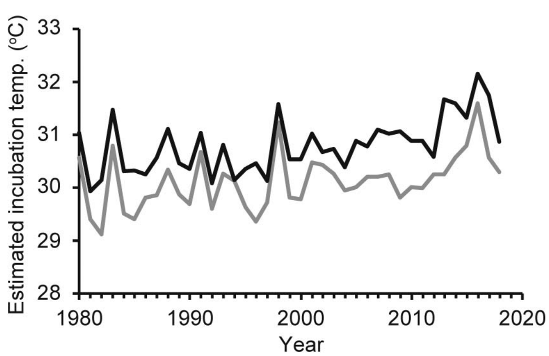

Figure 7. Estimated annual incubation temperature in the clutch at Ishigaki Island. Gray and black lines represent the estimated mean temperature during the incubation period for loggerhead (April–August) and for green (May–October) turtles. For calculation of estimated incubation temperature, see the text.

The increase in SSTs around the nesting beaches is reported to have caused the north Atlantic population of loggerheads to shift their nesting season a bit earlier to a more temperate period (Weishampel et al. 2004; Hawkes et al. 2007). The phenological shift of this species seems to be a reasonable response to climate change. However, our results showed a counterresponse in loggerhead turtles: the median nesting date moved roughly 20–30 d later and shifted to warmer dates over a quarter-century period. It is unknown why such a phenological shift occurred in loggerhead turtles. Further monitoring of nesting populations on Ishigakijima Island may help us understand the mechanism behind the delay in the nesting dates.

Green Turtles. — In green turtles, there was no relationship between the annual number of nests and SST, unlike in loggerheads. The northern (high-latitude) limit of the nesting distribution of green turtles is a bit to the north of Ishigakijima Island (Biodiversity Center of Japan 2016). Thus, the water temperature around Ishigakijima Island was not likely cold enough to regulate the nesting distribution for green turtles.

The global population of nesting green turtles increased over the past 2–3 decades (Chaloupka et al. 2008a). Moreover, a recent increment in the nesting population of green turtles was also reported for the entire Japanese population (Biodiversity Center of Japan 2016; Kondo et al. 2017) and Lanyu Island, Taiwan, which is close to Ishigakijima Island (Cheng et al. 2018) (Fig. 1). At Ishigakijima Island, nesting green turtles showed natal philopatry (Nishizawa et al. 2011). Based on the assumption that age at maturity in green turtles is 30–40 yrs (Seminoff 2004), many green turtles born at Ishigakijima Island in the 1970s–1980s may have been recently recruited, thus contributing to the increase of the recent nesting population. Another possible reason for the recent increment is that some migrant turtles from the neighboring nesting populations might establish Ishigakijima Island as their nesting place. However, it should be noted that further warming beyond the lethal incubation temperature (31°C–33°C; Weber et al. 2011) may cause considerable reductions in hatchling emergence. We did not detect a nesting date shift in green turtles as in loggerheads. This may be because green turtle nesting sites may remain relatively fixed with regard to nesting beach temperatures even in a warming environment (Pike 2009).

GPS tracking and 2 reports of tag recapture indicate that the waters around Okinawajima Island may be one of the main foraging grounds for green turtles nesting at Ishigakijima Island. Indeed, coastal waters around Okinawajima provide several foraging grounds (Hayashi and Nishizawa 2015); the clutch frequency is slightly higher (2.93 ± 0.28 clutches/season; Van Buskirk and Crowder 1994), while the remigration interval is a bit lengthier than in other nesting populations (2.86 ± 0.23 yrs; Van Buskirk and Crowder 1994) but within the usual range (Mortimer and Carr 1987; Broderick et al. 2002).

Hawksbill Turtles. — The time-series nesting data did not show a significant trend for hawksbill turtles. We detected their nests nearly every year in Ishigakijima Island, but the annual nest number was small. However, these nests tended to occur not at the same beach but sporadically at several beaches. This fact may indicate that hawksbill turtles on Ishigakijima Island did not have strong nest site fidelity based on the knowledge that they generally lay multiple egg clutches within a season (2.74 ± 0.22 clutches/season; Van Buskirk and Crowder 1994) and with strong site fidelity for nesting places (Kamel and Mrosovsky 2005). Ishigakijima Island is on the northern (high-latitude) peripheral nesting distribution of the northwestern Pacific population. The nests on this island could have been used not by hawksbill turtles returning to their natal home but by turtles migrating from neighboring sites (e.g., the Philippines) because of the lack of their orientation ability to find their natal beach. However, further studies may improve our understanding of the nest site selection of the peripheral population of hawksbill turtles.

To our knowledge, there have been no studies on the postnesting migration and potential foraging habitat of peripheral hawksbill turtle populations in the northern (high-latitude) nesting limit of the northwestern Pacific. Similarly, genetic characteristics of nesting hawksbills on Ishigakijima Island did not show a clear connectivity to potential foraging habitats (Nishizawa et al. 2012). Moreover, genetic diversity and a complex pattern of phylogeography of hawksbill turtles in the Indo-Pacific region made it difficult for researchers to understand how hawksbills expand their nesting distribution in the western Pacific and how they finally reach Ishigakijima Island (Okayama et al. 1999; Nishizawa et al. 2010, 2012; Vargas et al. 2015). Therefore, additional genetic and tracking studies may elucidate the linkage between Ishigakijima Island and neighbor nesting rookeries and the connection to potential foraging habitats.

Although Ishigakijima Island is on the northern peripheral nesting distribution, nesting performance characteristics, such as the number of eggs and hatchling emergence success, were similar to those reported in previous studies (Van Buskirk and Crowder 1994). Therefore, the beach conditions at Ishigakijima Island could be suitable for nesting hawksbill turtles. The hawksbill turtles showed the phenological shift of nesting date to a later period, as did loggerheads. It is unknown why such a phenological shift occurred in loggerhead and hawksbill but not green turtles. Further monitoring of nesting populations in Ishigakijima Island may help us understand the mechanism behind the delay in the nesting dates.

CONCLUSIONS

Our long-term nesting survey indicates the significance of the continuous monitoring of local populations incorporating the margin of nesting distribution over the decades. Although the dynamics of nesting sea turtle populations are affected by many factors, climate change is considered a major hazard in their future (Chaloupka et al. 2008b). Our results demonstrated the different trends in the nesting populations of 3 sea turtle species at Ishigakijima Island, which were probably caused by different reasons. However, warming temperature seems to be one of the reasons behind the reduction of the loggerhead turtle population. If the local nesting population of loggerhead turtles at Ishigakijima Island goes extinct in the near future, this means that the southern limit of their nesting distribution may shift northward. Such empirical data indicating ecological shifts in distribution and dominant species could essentially contribute to the prediction of population dynamics and changes in the distribution of sea turtles as well as the development of appropriate conservation measures.

ACKNOWLEDGMENTS

Our nesting survey was supported by many volunteers: H. Abe, Y. Dosei, Y. Funakura, K. Hanashiro, H. Hayakawa, K. Hirate, T. Katsumi, K. Kawamura, A. Kobayashi, M. Kobayashi, M. Kobayashi, Y. Naito, Y. Okamura, N. Saito, K. Sano, Y. Tanizaki, Y. Tazawa, S. Yasumura, H. Yamagata, M. Yamasaki, S. Maekawa, T. Sagawa, and the staff of WWF Shiraho Coral Reef Conservation and Research Center. This study was also supported by faculty and graduate students of Kyoto University (N. Arai, T. Yasuda, K. Ichikawa, Y. Kawabata, T. Yokota, H. Watanabe, T. Koizumi, A. Nakabayashi, K. Nakajima, A. Wada, and Y. Obe) and undergraduate students of Kindai University (D. Imakita, K. Watajima, and T. Mogi). Data analysis was supported by Y. Fujikura. This study was conducted with the permissions by the Fisheries Adjustment Commission of

Okinawa Prefecture (13-31, 14-27, 15-32, 16-20, 17-30, 18-45, 19-37, 20-40, 23-40, 24-13, 25-25, 26-25, 27-31, 28-24, 29-29, 30-15) and the Ministry of the Environment, Japan (071011001, 080616001, 090721001, 10063001, 110713002, 1407042, 1506163, 1606063, 1706023, 1806115). The research protocol, including the deployment of a satellite transmitter in this study, was approved by the Animal Experimentation Committees of Kyoto University (Inf-K25-4, Inf-K14006, Inf-K15006) and the Seikai National Fisheries Institute (2015-05, 2016-03, 2017-03, 2018-003). A part of this study was financially supported by WWF Japan and Grant-in-Aid for JSPS Research Activity Start-Up (J.O. no. 19880017), Young Scientists B (J.O. no. 22710236), and Young Scientists A (J.O. no. 15H05584).

LITERATURE CITED

ABE, O., SHIBUNO, T., TAKADA, Y., HASHIMOTO, K., TANIZAKI, S., ISHII, H., FUNAKURA, Y., SANO, K., AND OKAMURA, Y. 2004. Nesting populations of sea turtle in Ishigaki Island, Okinawa. In: Arai, N. (Ed.). Proceedings of 4th SEASTAR2000 Workshop. Kyoto: Kyoto University, pp. 40–43.

BIODIVERSITY CENTER OF JAPAN. 2016. Report of sea turtle research in 2015, Monitoring Sites 1000 Project. www.biodic.go.jp/moni1000/findings/reports/pdf/h27_seaturtles.pdf (26 November 2019). (In Japanese.)

BIODIVERSITY CENTER OF JAPAN. 2019. Report of sea turtle research in 2017 and 2018, Monitoring Sites 1000 Project. www.biodic.go.jp/moni1000/findings/reports/pdf/h30_seaturtles.pdf (26 November 2019). (In Japanese.)

BOWEN, B.W., KAMEZAKI, N., LIMPUS, C.J., HUGHES, G.R., MEYLAN, A.B., AND AVISE, J.C. 1994. Global phylogeography of the loggerhead turtle (*Caretta caretta*) as indicated by mitochondrial DNA haplotypes. Evolution 48:1820–1828.

BRODERICK, A.C., GLEN, F., GODLEY, B.J., AND HAYS, G.C. 2002. Estimating the number of green and loggerhead turtles nesting annually in the Mediterranean. Oryx 36:227–235.

BROTHERS, J.R. AND LOHMANN, K.J. 2015. Evidence for geomagnetic imprinting and magnetic navigation in the natal homing of sea turtles. Current Biology 25:392–396.

CHALOUPKA, M., BJORNDAL, K.A., BALAZS, G.H., BOLTEN, A.B., EHRHART, L.M., LIMPUS, C.J., SUGANUMA, H., TROËNG, S., AND YAMAGUCHI M. 2008a. Encouraging outlook for recovery of a once severely exploited marine megaherbivore. Global Ecology and Biogeography 17:297–304.

CHALOUPKA, M., KAMEZAKI, N., AND LIMPUS, C. 2008b. Is climate change affecting the population dynamics of the endangered Pacific loggerhead sea turtle? Journal of Experimental Marine Biology and Ecology 356:136–143.

CHENG, I.J., CHENG, W.H., AND CHAN, Y.T. 2018. Geographically closed, yet so different: contrasting long-term trends at two adjacent sea turtle nesting populations in Taiwan due to different anthropogenic effects. PLoS ONE 13:e0200063.

HAMPE, A. AND PETIT, R.J. 2005. Conserving biodiversity under climate change: the rear edge matters. Ecology Letters 8:461–467.

HATASE, H., OMUTA, K., AND TSUKAMOTO, K. 2007. Bottom or midwater: alternative foraging behaviours in adult female loggerhead sea turtles. Journal of Zoology 273:46–55.

HATASE, H., OMUTA, K., AND TSUKAMOTO, K. 2013. A mechanism that maintains alternative life histories in a loggerhead sea turtle population. Ecology 94:2583–2594.

HATASE, H., TAKAI, N., MATSUZAWA, Y., SAKAMOTO, W., OMUTA, K., GOTO, K., ARAI, N., AND FUJIWARA, T. 2002. Size-related differences in feeding habitat use of adult female loggerhead turtles *Caretta caretta* around Japan determined by stable isotope analyses and satellite telemetry. Marine Ecology Progress Series 233:273–281.

HAWKES, L.A., BRODERICK, A.C., GODFREY, M.H., AND GODLEY, B.J. 2007. Investigating the potential impacts of climate change on a marine turtle population. Global Change Biology 13:923–932.

HAWKES, L.A., BRODERICK, A.C., GODFREY, M.H., AND GODLEY, B.J. 2009. Climate change and marine turtles. Endangered Species Research 7:137–154.

HAYASHI, R. AND NISHIZAWA, H. 2015. Body size distribution demonstrates flexible habitat shift of green turtle (*Chelonia mydas*). Global Ecology and Conservation 3:115–120.

JENSEN, M.P., ALLEN, C.D., EGUCHI, T., BELL, I.P., LACASELLA, E.L., HILTON, W.A., HOFF, C.A.M., AND DUTTON, P.H. 2018. Environmental warming and feminization of one of the largest sea turtle populations in the world. Current Biology 28:154–159.

KAMEDA, K., WAKATSUKI, M., SHIMA, T., NARUSE, T., AND KODERA, M. 2007. Census report on sea turtles in Nishinohama-Beach, Kuroshima Island, Yaeyama-Group (2001–2006) and the trend from 1978. Umigame Newsletter of Japan 72:4–11. (In Japanese.)

KAMEL, S.J. AND MROSOVSKY, N. 2005. Repeatability of nesting preferences in the hawksbill sea turtle, *Eretmochelys imbricata*, and their fitness consequences. Animal Behaviour 70: 819–828.

KAMEZAKI, N. 1991. A preliminary report on the distribution of nesting sites of sea turtles in the Ryukyu Archipelago, and their evaluation. The Biological Magazine Okinawa 29:29–35. (In Japanese.)

KAMEZAKI, N., MATSUZAWA, Y., ABE, O., ASAKAWA, H., FUJII, T., GOTO, K., HAGINO, S., HAYAMI, M., ISHII, M., IWAMOTO, T., KAMATA, T., KATO, H., KODAMA, J, KONDO, Y., MIYAWAKI, I., MIZOBUCHI, K., NAKAMURA, Y., NAKASHIMA, Y., NARUSE, H., OMUTA, K., SAMEJIMA, M., SUGANUMA, H., TAKESHITA, H., TANAKA, T., TOJI, T., UEMATSU, M., YAMAMOTO, A., YAMATO, T., AND WAKABAYASHI, I. 2003. Loggerhead turtle nesting in Japan. In: Bolten, A. and Witherington, B. (Eds.). Loggerhead Sea Turtles. Washington DC: Smithsonian Books, pp. 210–217.

KOBAYASHI, D.R., POLOVINA, J.J., PARKER, D.M., KAMEZAKI, N., CHENG, I.J., UCHIDA, I., DUTTON, P.H., AND BALAZS, G.H. 2008. Pelagic habitat characterization of loggerhead sea turtles, *Caretta caretta*, in the North Pacific Ocean (1997–2006): insights from satellite tag tracking and remotely sensed data. Journal of Experimental Marine Biology and Ecology 356:96–114.

KONDO, S., MORIMOTO, Y., SATO, T., AND SUGANUMA, H. 2017. Factors affecting the long-term population dynamics of green turtles (*Chelonia mydas*) in Ogasawara, Japan: influence of natural and artificial production of hatchlings and harvest pressure. Chelonian Conservation and Biology 16:83–92.

KONDO, T., KOTERA, Y., ASAI, Y., KUROYANAGI, K., NOMURA, K., MISAKI, H., HORI, M., IWASE, F., SATO, F., AND SHIGEI, A. 2000. Nesting status of sea turtles in the Nishi-no-hama beach, Kuroshima, Yaeyama Islands 1991–2000. Marine Parks Journal 129:3–7. (In Japanese.)

LALOË, J.O., COZENS, J., RENOM, B., TAXONERA, A., AND HAYS, G.C. 2014. Effects of rising temperature on the viability of an important sea turtle rookery. Nature Climate Change 4:513–518.

LALOË, J.O., COZENS, J., RENOM, B., TAXONERA, A., AND HAYS, G.C. 2017. Climate change and temperature–linked hatchling mortality at a globally important sea turtle nesting site. Global Change Biology 23:4922–4931.

LOHMANN, K.J., WITHERINGTON, B.W., LOHMANN, C.M.F., AND SALMON, M. 1997. Orientation, navigation, and natal beach homing in sea turtles. In: Lutz, P.L. and Musick, J.A. (Eds.). Biology of Sea Turtles. Volume 1. Boca Raton, FL: CRC Press, pp. 107–136.

MAFFUCCI, F., CORRADO, R., PALATELLA, L., BORRA, M., MARULLO, S., HOCHSCHEID, S., LACORATA, G., AND IUDICONE, D. 2016. Seasonal heterogeneity of ocean warming: a mortality sink for ectotherm colonizers. Scientific Reports 6:23983.

MATSUZAWA, Y., SATO, K., SAKAMOTO, W., AND BJORNDAL, K.A. 2002. Seasonal fluctuations in sand temperature: effects on the incubation period and mortality of loggerhead sea turtle (*Caretta caretta*) pre-emergent hatchlings in Minabe, Japan. Marine Biology 140:639–646.

MORTIMER, J.A. AND CARR, A. 1987. Reproduction and migrations of the Ascension Island green turtle (*Chelonia mydas*). Copeia 1987:103–113.

MROSOVSKY, N. 1994. Sex ratios of sea turtles. Journal of Experimental Zoology 270:16–27.

NARAZAKI, T., SATO, K., AND MIYAZAKI, N. 2015. Summer migration to temperate foraging habitats and active winter diving of juvenile loggerhead turtles *Caretta caretta* in the western North Pacific. Marine Biology 162:1251–1263.

NISHIZAWA, H., ABE, O., OKUYAMA, J., KOBAYASHI, M., AND ARAI, N. 2011. Population genetic structure and implications for natal philopatry of nesting green turtles *Chelonia mydas* in the Yaeyama Islands, Japan. Endangered Species Research 14: 141–148.

NISHIZAWA, H., OKUYAMA, J., ABE, O., KOBAYASHI, M., AND ARAI, N. 2012. Mitochondrial DNA variation in hawksbill turtles (*Eretmochelys imbricata*) nesting on Ishigaki Island, Japan. Marine Turtle Newsletter 132:1–2.

NISHIZAWA, H., OKUYAMA, J., KOBAYASHI, M., ABE, O., AND ARAI, N. 2010. Comparative phylogeny and historical perspectives on population genetics of the Pacific hawksbill (*Eretmochelys imbricata*) and green turtles (*Chelonia mydas*), inferred from feeding populations in the Yaeyama Islands, Japan. Zoological Science 27:14–18.

OKAYAMA, T., DIAZ-FERNANDEZ, R., BABA, Y., HALIM, M., ABE, O., AZENO, N., AND KOIKE, H. 1999. Genetic diversity of the hawksbill turtle in the Indo-Pacific and Caribbean regions. Chelonian Conservation and Biology 3:362–367.

PIKE, D.A. 2009. Do green turtles modify their nesting seasons in response to environmental temperatures? Chelonian Conservation and Biology 8:43–47.

POLOVINA, J.J., BALAZS, G.H., HOWELL, E.A., PARKER, D.M., SEKI, M.P., AND DUTTON, P.H. 2004. Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. Fisheries Oceanography 13:36–51.

R DEVELOPMENT CORE TEAM. 2018. R: A Language and Environment for Statistical Computing. Version 3.52. Vienna: R Foundation for Statistical Computing.

SEMINOFF, J.A. 2004. *Chelonia mydas*. The IUCN Red List of Threatened Species 2004. e.T4615A11037468. http://dx.doi.org/10.2305/IUCN.UK.2004.RLTS.T4615A11037468.en (26 November 2019).

SOLOW, A.R., BJORNDAL, K.A., AND BOLTEN, A.B. 2002. Annual variation in nesting numbers of marine turtles: the effect of sea surface temperature on re-migration intervals. Ecology Letters 5:742–746.

SPOTILA, J.R., O'CONNOR, M.P., AND PALADINO, F.V. 1997. Thermal biology. In: Lutz, P.L. and Musick, J.A. (Eds.). Biology of Sea Turtles. Volume 1. Boca Raton, FL: CRC Press, pp. 297–314.

UCHIDA, I. AND NISHIWAKI, M. 1982. Sea turtles in the waters adjacent to Japan. In: Bjorndal, K. (Ed.). Biology and Conservation of Sea Turtles. Washington, DC: Smithsonian Institution Press, pp. 317–319.

VAN BUSKIRK, J. AND CROWDER, L.B. 1994. Life-history variation in marine turtles. Copeia 1994:66–81.

VARGAS, S.M., JENSEN, M.P., HO, S.Y., MOBARAKI, A., BRODERICK, D., MORTIMER, J.A., WHITING, S.D., MILLER, J., PRINCE, R.I.T., BELL, I.P., HOENNER, X., LIMPUS, C.J., SANTOS, F.R., AND FITZSIMMONS, N.N. 2015. Phylogeography, genetic diversity, and management units of hawksbill turtles in the Indo-Pacific. Journal of Heredity 107:199–213.

WEBER, S.B., BRODERICK, A.C., GROOTHUIS, T.G.G., ELLICK, J., GODLEY, B.J., AND BLOUNT, J.D. 2011. Fine-scale adaptation in green turtle nesting population. Proceedings of the Royal Society of London B 279:1077–1084.

WEISHAMPEL, J.F., BAGLEY, D.A., AND EHRHART, L.M. 2004. Earlier nesting by loggerhead sea turtles following sea surface warming. Global Change Biology 10:1424–1427.

Received: 9 December 2019
Revised and Accepted: 27 March 2020
Published Online: 16 June 2020
Handling Editor: Jeffrey A. Seminoff