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Male-Biased Sex Ratio of Adult-Sized Loggerhead Turtles (*Caretta caretta*) Migrating to High-Latitude Summer-Restricted Foraging Grounds in the Northwest Pacific¹

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Abstract: Although part of the life history of loggerhead turtles (*Caretta caretta*) in the northwest Pacific population has been documented, there is still a paucity of data regarding their spatiotemporal ecology at the local level. The Sanriku Coast is known to be the high-latitude foraging grounds (39° N) for loggerhead turtles of the northwest Pacific population. This site is located far north from the northernmost loggerhead rookeries (>400 km) and more than 10 years of surveys have found that loggerhead turtles migrate there only in the summer. To better understand the spatiotemporal ecology of this population along the Sanriku Coast, the present study investigated the sex of 164 loggerhead turtles captured as bycatch along the Sanriku Coast between 2013 and 2017 by measuring the external morphology and serum testosterone concentrations. These analyses suggested that most of the adult-sized turtles in the Sanriku foraging grounds were males (few females), whereas both sexes of immature-sized turtles migrated to this Coast. This is possibly because migration to the Sanriku Coast is restricted to summer due to the seasonal sea surface temperature shift, and this period overlaps with the nesting period. Therefore, only immature turtles and adult males may be able to migrate. Understanding sex differences in spatiotemporal ecology should contribute to conservation practice in this population, where global warming, together with the turtle's temperature-dependent sex determination, can be expected to reduce the proportion of male hatchlings in the future.

Keywords: *Caretta caretta*, global warming, morphology, sea surface temperature, sex difference, spatiotemporal ecology, testosterone

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THE LOGGERHEAD TURTLE (*Caretta caretta*) is a sea turtle species distributed in temperate, subtropical, and tropical waters (Dodd 1988). Hatchlings of this species disperse from terrestrial beaches through nearshore to off-shore waters, and reenter their natal area for subsequent growth at the larger immature

stage and for reproduction when they reach sexual maturity (Ishihara 2012). Japanese waters are important foraging grounds, and the southern coasts of Japan (from Nansei Shoto Archipelago to Kanto District: Kamezaki et al. 2003; Figure 1) are the only breeding grounds for loggerhead turtles of the

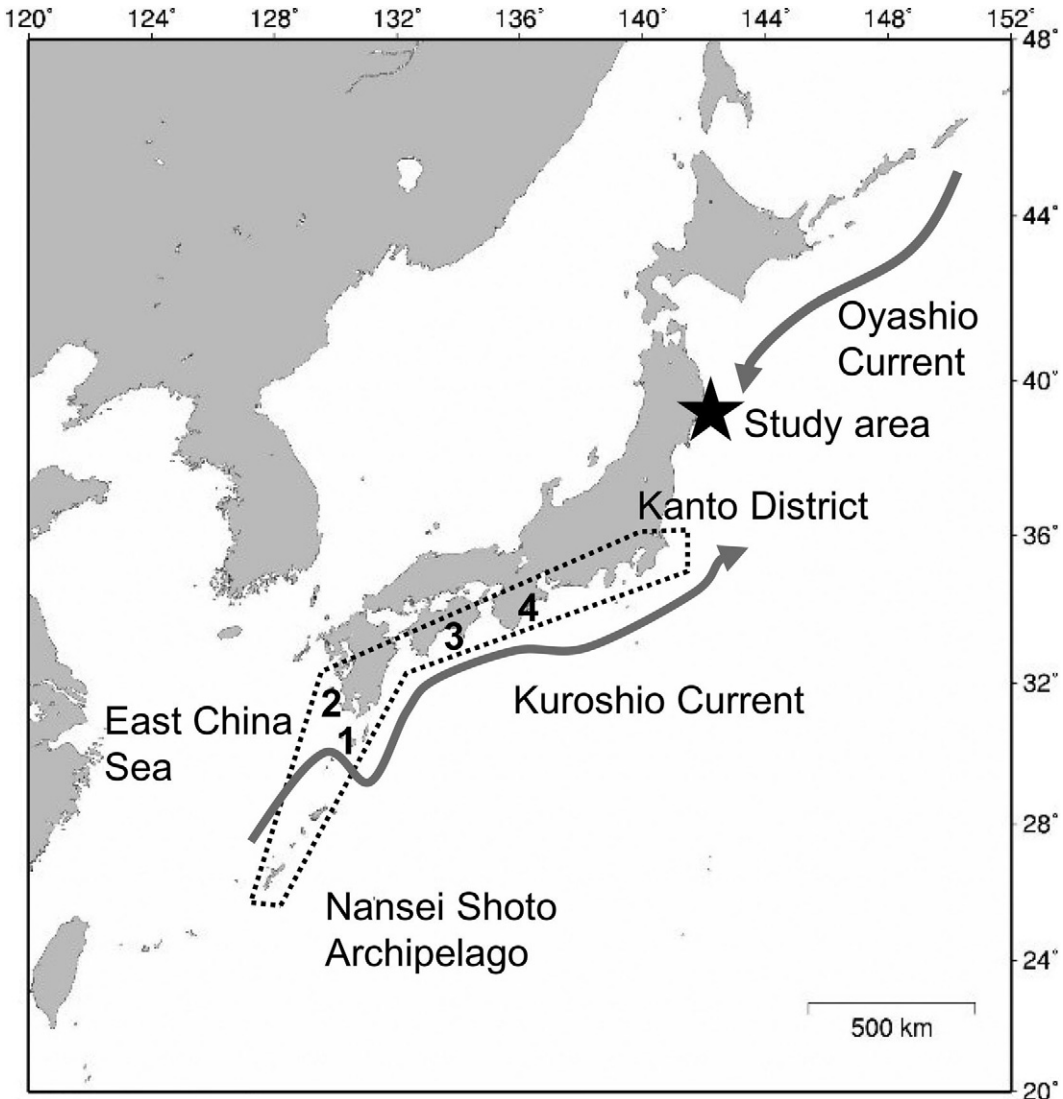


FIGURE 1. Map of Japanese waters showing loggerhead nesting and foraging grounds. The star indicates the Sanriku Coast (study area). The coastal area enclosed by the dotted line shows the main nesting area of loggerhead turtles in the northwest Pacific (Kamezaki et al. 2003). The wavy arrow indicates the direction of the Kuroshio Current and the Oyashio Current. Numbers indicate the locations noted in the article (1: Yakushima; 2: Satsuma Peninsula; 3: Kochi Prefecture; 4: Mie Prefecture).

north Pacific population (Hatase et al. 2002a). Analysis of mitochondrial DNA suggested that hatchlings from Japanese rookeries disperse eastward, transported by the Kuroshio Current and Kuroshio extension, with some reaching Baja California (Bowen et al. 1995, Hatase 2012). After reentering Japanese waters and upon reaching sexual maturity, they breed, and females lay eggs in their natal rookeries from April to August (Miyawaki 1981, Uchida and Nishiwaki 1982). Their migration after reentry to Japanese waters has been documented by some satellite tracking studies. For example, a study found that juveniles exhibit seasonal migration associated with shifts in sea surface temperature (SST) (Narazaki et al. 2015). Other studies on females nesting in the Yakushima rookery reported that post-nesting females migrated to either the East China Sea close to the rookery or along the warm Kuroshio extension to the open Pacific (Hatase et al. 2002b, 2007; Figure 1). Saito et al. (2015) showed that males released from the coastal waters of the Satsuma Peninsula, south western Japan, remained along the coast, or migrated to the East China Sea (Figure 1). Although some of their life history have been documented as described above, there is still a paucity of data regarding the spatiotemporal ecology of male and female loggerhead turtles at local level. This is particularly important because the loggerhead turtle is a species of conservation concern (Ministry of the Environment 2019), and better information is vital for effective conservation management.

The Sanriku Coast, Iwate Prefecture, Japan (Figure 1) was reported as a study area for sea turtles in the northwest Pacific (Narazaki et al. 2009, 2013, 2015, Nishizawa et al. 2014, Fukuoka et al. 2015, 2016, 2019, Sato et al. 2016, Kinoshita et al. 2018). This study area is located in the warm Kuroshio and cool Oyashio transition area; its high productivity makes it the primary fishing grounds for the region (Sugimoto and Tameishi 1992, Tsuda et al. 2004). Although this study area is located far north from the northernmost loggerhead turtle rookeries (>400 km), more than 10 years of year-round bycatch survey at this site revealed that the

turtles were incidentally captured by commercial set nets as bycatch only in summer (predominantly from July to August) (Narazaki et al. 2015: SST ranging from 12 °C to 23 °C, mean SST when turtles were captured was 18 °C). Furthermore, a satellite tracking study found that all tracked turtles ($n=9$) left the study area toward southern warmer areas after the summer season (Narazaki et al. 2015). This indicates that the Sanriku Coast is summer-restricted foraging grounds for loggerhead turtles of the northwest Pacific population (Narazaki et al. 2015).

To better understand the spatiotemporal ecology of the loggerhead turtles of the northwest Pacific Population in their high-latitude summer-restricted foraging grounds, the present study investigated the sex of the loggerhead turtles migrating to the Sanriku Coast by measuring their external morphology (straight carapace length notch-to-tip: SCLn-t; tail length: TL) and serum testosterone (T) concentrations, which were used to estimate the sex of the sea turtles (e.g., Owen 1997, Ishihara and Kamezaki 2011). Since sea turtles possess temperature-dependent sex determination, with warmer incubation temperature producing more females (Yntema and Mrosovsky 1980), the sex ratio will be increasingly biased by global warming (Hawkes et al. 2007a, Witt et al. 2010, Fuentes et al. 2011, Patino-Martinez et al. 2012, Laloë et al. 2014, Jensen et al. 2018). Therefore, understanding the sex difference in spatiotemporal ecology should be fundamental for future conservation practices in the northwest Pacific population, especially if there is differential human exploitation of the sexes through spatiotemporally focused fisheries (Wearmouth and Sims 2008).

MATERIALS AND METHODS

Sampling Procedure

We conducted a daily survey of the bycatch in the Sanriku Coast, Iwate Prefecture, Japan, from the end of June to the beginning of October in 2014 and 2016, and from July to the beginning of October in 2013, 2015, and 2017. We received

loggerhead turtles when fishermen incidentally captured them in commercial set nets between Kamaishi City and Miyako City in the Sanriku Coast (39° 16'–39° 40' N, 141° 53'–142° 05' E; [Figure 1](#)), and measured the SST when the turtles were captured. In cases where temperature was not documented, the mean daily temperature of the bay at the nearest observation point was used for analysis (Iwate Fisheries Information Report System; www.suigi.pref.iwate.jp). After we received them, these turtles were immediately transferred to tanks at the International Coastal Research Center, Atmosphere and Ocean Research Institute, the University of Tokyo (39° 21' 05" N, 141° 56' 04" E) within 2 h. Their external morphology was measured by means of SCLn-t and TL. The SCLn-t was measured from the anterior point at the midline (nuchal scute) to the posterior tip of the supracaudals, and the TL was measured from the end of the plastron to the center of the cloaca as described previously ([Bolten 1999](#), [Ishihara and Kamezaki 2011](#)). Blood samples were collected from the dorsal cervical sinus of all turtles using a 5-ml syringe with 20 G needle (Terumo Corporation, Tokyo, Japan), poured into a 2 ml microtube or a 15-ml centrifuge tube, and centrifuged for 5 min at $3320 \times g$. The serum was collected and stored at -30°C until T concentrations were measured. The measurement of the external morphology and collection of blood were mostly completed within 1 h of transference.

Testosterone Measurement

Testosterone was extracted from serum using diethyl ether, and the concentrations of T in this blood serum were measured in samples from 2013, 2015, 2016, and 2017 by double-antibody radioimmunoassay (RIA) using ^{125}I -labelled radioligands as described previously ([Taya et al. 1985](#)). Because a tracer for RIA was not available in 2014, concentrations of T in the unextracted blood serum were measured alternatively by time-resolved fluoroimmunoassay (TR-FIA) using a DELFIA® Testosterone Kit (PerkinElmer, Waltham, MA, USA), according to the manufacturer's protocol. To confirm the

compatibility of the different assay systems, several samples measured by RIA were subjected to TR-FIA, and the concentration showed similarities between the assays, allowing us to use TR-FIA results without correction. Serum samples assayed at different doses showed parallelism with the standard curves, and the intra-assay coefficients of variations were 6.0% and 4.7% for RIA and TR-FIA, respectively. The inter-assay coefficient of variation was 6.6% for RIA. Because samples in TR-FIA were measured using one assay, the inter-assay coefficients of variation were not calculated.

Sex Estimation of Turtles

Since the TL of males elongates during maturation, we can identify males based on the external morphology of the loggerhead turtle in the north Pacific according to [Ishihara and Kamezaki \(2011\)](#); the turtles with relative TL ($r\text{TL} = \text{TL}/\text{SCLn-t}$) > 0.277 , or those with $r\text{TL} > 0.228$ and $\text{SCLn-t} < 73.8$ cm were classified as male. However, this method cannot distinguish between immature males and females. To estimate the sex of the other turtles, the blood T concentration was analyzed. It should be noted that, although male sea turtles generally have higher T concentrations than females (e.g., [Owen 1997](#)), T concentration can vary due to various factors such as SST at the time of capture ([Braun-McNeill et al. 2007](#), [Hawkes et al. 2013](#)), capture stress ([Gregory and Schmid 2001](#)), reproductive status ([Wibbels et al. 1990](#), [Rostal et al. 1998](#)), and assay system ([Cocci et al. 2014](#)). Thus, we could not adopt threshold sexing T concentrations of loggerhead turtles as reported previously (e.g., [Braun-McNeill et al. 2007, 2016](#), [Arendt et al. 2012a](#), [Cocci et al. 2014](#)). Alternatively, since males show relatively higher T concentrations than females (i.e., females show lower T concentration) even considering the SST at capturing turtle ([Braun-McNeill et al. 2007](#)) and capture stress ([Gregory and Schmid 2001](#)), we compared the T concentration of males sexed by external morphologies with that of other sex unknown turtles to attempt

to estimate the sex of turtles migrating to the Sanriku Coast.

Statistics

A chi-square test was used to analyze the sex ratio. The correlation between T concentration and SST at the time of capture was tested by the Spearman rank correlation test. Statistical analysis was performed using Graph Pad Prism5 (San Diego, CA, USA). A P -value $< 5\%$ was considered significant.

RESULTS

Loggerhead Turtles at High-Latitude Foraging Grounds in the Northwest Pacific

During the study period, we collected 164 loggerhead turtles (2013: $n = 44$; 2014: $n = 53$; 2015: $n = 5$; 2016: $n = 30$; 2017: $n = 32$). The SCLn-t was 72.7 ± 7.5 cm (mean \pm SD) (range: 52.7–92.0 cm) and rTL was 0.249 ± 0.094 (mean \pm SD) (range: 0.112–0.508). Turtles began to be captured around the Sanriku Coast in late June, when the SST

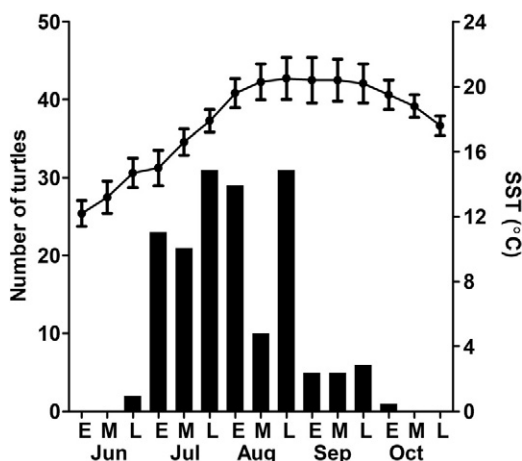


FIGURE 2. Cumulative numbers of loggerhead turtles captured over five years from 2013 to 2017 (bars) in set nests in the Sanriku Coast. E, M, and L indicate early, mid, and late period of each month, respectively. The study period was from the end of June to the beginning of October in 2014 and 2016, and from July to beginning of October in 2013, 2015, and 2017. Mean sea surface temperature (SST) (Kamaishi Bay; <http://www.suigi.pref.iwate.jp/teichi>) is shown as filled circles with error bars (standard deviation) on the right axis.

was around 14°C . Most of captures occurred during early July to late August, when the SST was increasing toward its highest point (from 15°C to 21°C ; Figure 2). The turtle bycatch then decreased in September when the SST began to decrease (Figure 2).

Identification of Sex Based on their External Morphology

Fifty-four of 164 turtles were identified as males based on their external morphology (Figure 3, Table 1). In the larger turtles (SCLn-t > 80 cm, $n = 29$), the minimum percentage of male (MPM) was significantly different from 1:1 ($p = 0.04$). The MPM did not differ significantly between years ($p = 0.79$) or between months ($p = 0.64$).

Serum Testosterone Concentrations

The T concentrations in the serum ranged from undetectable to 6910 pg ml^{-1} ($n = 164$). The T concentrations were significantly and positively correlated with SST at the time of capture (Spearman $r = 0.25$, $p = 0.002$:

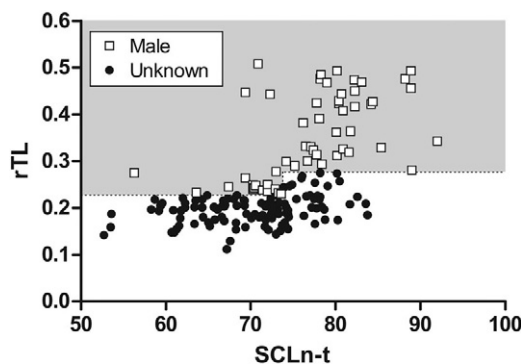


FIGURE 3. Scatter plot showing the relationship between straight carapace length notch-to-tip (SCLn-t) and relative straight tail length (rTL) for loggerhead turtles captured in the present study. Open squares indicate males identified based on the external morphology of the loggerhead turtle in the north Pacific according to Ishihara and Kamezaki (2011); the turtles with $rTL > 0.277$, or those with $rTL > 0.228$ and $SCLn-t < 73.8$ cm (gray area) were classified as male. Filled circles indicate turtles with unknown sex. Dotted line indicates the threshold values of SCLn-t and rTL used to identify the males.

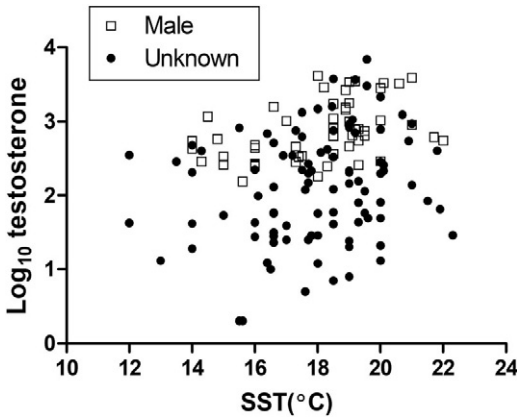


FIGURE 4. Scatter plot showing the relationship between sea surface temperature at the time of turtle capture and \log_{10} transformed testosterone concentration for loggerhead turtles captured in the present study. Open squares indicate males identified based on external morphology. Filled circles indicate turtles with unknown sex. The testosterone concentrations were significantly and positively correlated with SST at the time of capture (Spearman $r = 0.25$, $p = 0.002$).

Figure 4). The relationship between T concentrations and their external morphologies are shown in Figure 5a and b. Turtles with larger rTL had higher T concentrations while turtles with smaller rTL showed a wide range of T concentrations (Figure 5a). The T concentrations in males identified by external morphologies were high in each SCLn-t size

TABLE 1
Number and Minimum Percentage of Male in Different Size Classes Determined by Measuring External Morphology

SCLn-t (cm)	Male	Unknown	Min. Male (%)
>50–55	0	3	0
>55–60	1	5	17
>60–65	1	18	5
>65–70	3	23	12
>70–75	14	35	29
>75–80	13	19	41
>80–85	16	7	70
>85–90	5	0	100
>90–95	1	0	100

SCLn-t: straight carapace length notch to tip.

class (Figure 5b). Therefore, we considered that the T concentrations of these males were male level T concentrations, while T concentrations below this level were considered to be female level. The lowest T concentration in males sexed by external morphology was 154 pg ml^{-1} . Using this concentration as a threshold T concentration for sexing, the male sex ratio in the larger turtle (SCLn-t > 80 cm) was estimated to be 90% and that in smaller turtles was 57%. The estimated sex ratio was significantly different from 1:1 in larger turtles

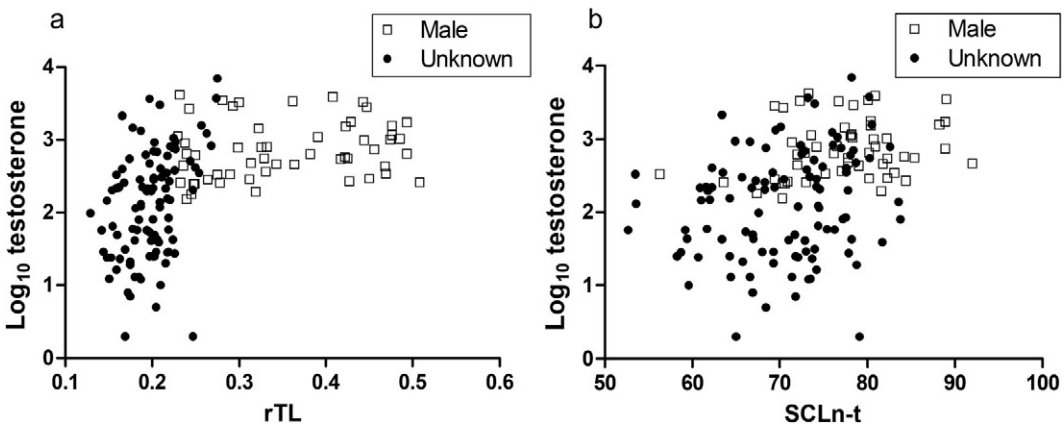


FIGURE 5. Scatter plot showing the relationship between external morphology (a: relative tail length; b: straight carapace notch to tip) and \log_{10} transformed testosterone concentration of loggerhead turtles captured in the present study. Open squares indicate males identified based on external morphology. Filled circles indicate turtles with unknown sex. Dotted lines indicate the threshold values of SCLn-t and rTL used to identify the males.

($p = 0.0009$) but not in smaller turtles ($p = 0.24$). The sex ratio estimated by T concentration did not differ significantly between years ($p = 0.80$) or between months ($p = 0.72$).

DISCUSSION

In the present study, to estimate the sex of loggerhead turtles migrating to the summer-restricted high-latitude foraging area in the northwest Pacific (Sanriku Coast), we measured their external morphology and serum T concentrations. Analysis of external morphology showed that the MPM of larger turtles (SCLn-t > 80 cm) was significantly male-biased, with only males confirmed to have SCLn-t > 85 cm (Table 1). Ishihara and Kamezaki (2011) revealed that size at maturity is not different between the sexes, and a size of SCLn-t > 80 cm is the general adult size for loggerhead turtles in the north Pacific population. Therefore, this indicates that most adult-sized loggerhead turtles migrating to the Sanriku Coast are males.

In the smaller turtles (SCLn-t ≤ 80 cm: presumably immature), the sex of many turtles could not be identified by measuring only external morphology. To estimate the sex of these turtles, we measured the serum T concentrations. We acknowledge the limitation of this method as the T concentration is affected by some factors such as SST at the time of capturing a turtle (Braun-McNeill et al. 2007) and capture stress (Gregory and Schmid 2001), which will affect correct sexing. Our study also confirmed the positive correlation between SST and T concentration (Figure 4), possibly resulting from the suppression of T concentrations by low SST. Despite this, we found that T concentrations of males identified by external morphology were consistently higher, whereas those of sex unknown turtles varied (Figure 5), suggesting that most of the turtles with higher T level (>154 pg ml⁻¹) could be male, and those with T concentrations below this level (<154 pg ml⁻¹) could be female. It should be noted that turtles with SCLn-t ≤ 80 cm might include smaller adult females, and that reproductively active female sea turtles have been known to show high

concentrations of T before mating (Wibbels et al. 1990, Rostal et al. 1998). This may cause misidentification of their sex. However, sampling was undertaken during the post-mating period (mating period is likely to occur around March to June in the northwest Pacific), when their T concentrations are expected to be as low as those of reproductively inactive individuals (Wibbels et al. 1990, Rostal et al. 1998, Yanagisawa 2012). Hence, sexual maturity should not affect their sex estimation by our sexing method. The estimated sex ratio in the smaller turtles is not clearly different from 1:1 (57% males), especially considering uncertainties due to the effect of SST and capture stress on T concentration. To obtain more robust conclusion, laparoscopic examination to study their gonads will be needed for more accurate sexing of smaller turtles. Despite this, given that many turtles with SCLn-t ≤ 80 cm showed much lower T concentrations compared with the males sexed by their morphology (Figure 5b), we could consider that smaller turtles of both sexes migrated to the Sanriku Coast, whereas the larger turtles were male-biased. Consequently, measuring both their external morphology and T concentrations suggests that the sex ratio of loggerhead turtles at the Sanriku Coast differs between size classes.

One possible explanation for the male-biased sex ratio of adult-sized turtles migrating to the Sanriku Coast is that all turtles in the present study were derived from male-producing rookeries. If so, all SCLn-t size classes should be male-biased. However, our results suggest that the sex ratios differ between the size classes, as discussed above, indicating that this possibility is unlikely. Another possibility is that adult males are more likely to be captured in the set nets than females, resulting in the male-biased sex ratio for the adult size class. However, the method to capture the turtles in our study was identical to that of previous studies examining the sex ratio in the northwest Pacific (female-biased: Ishihara and Kamezaki 2011, unbiased: Kawazu et al. 2013), which indicates that such an assumption is also unlikely. Thus, there must be another reason for the

male-biased sex ratio of adult-sized turtles migrating to the Sanriku coast.

A previous study showed a male-biased sex ratio at adult-sized class in the foraging grounds for loggerhead turtles during the nesting period in one particular area of Amvrakikos Gulf, Mediterranean Sea (Rees et al. 2013), whereas the Mediterranean population showed a mostly female-biased hatchling production (Witt et al. 2010). Because turtles migrating to the Sanriku Coast which is far from their rookery also occurred during the nesting period in the northwest Pacific (April to August: Uchida and Nishiwaki 1982), this suggests that “foraging ground” and “nesting period” could be key factors to understand the male-biased sex ratio of adult-sized loggerhead turtles in our study site. Considering this, we propose a potential mechanism underlying the sex ratio in the Sanriku Coast, focusing on the relationship between foraging migration timing from breeding ground and SST.

Foraging migration to high-latitude areas far from their rookeries was reported not only in the northwest Pacific (Sato et al. 2016) but also in other loggerhead turtle populations (Hawkes et al. 2007b, 2011, Mansfield et al. 2009, Arendt et al. 2012b, Schofield et al. 2013). Northern migration in the Northern Hemisphere is associated with increasing SST (Mansfield et al. 2009). Similarly, most turtles were found to migrate while the SST increased (July and August), and only a few migrants were confirmed following the point of highest SST (late August) in the present study area (September: Figure 2). This indicates that seasonal northern migration of loggerhead turtles in the northwest Pacific is also associated with increasing SST as seen in the other populations. Notably, immature turtles naturally undergo such seasonal northern migration, whereas adults are likely to face constraints, namely reproduction, for their migration. Given that the onset of egg-laying occurs approximately 1 month after mating in breeding adults (Kobayashi 2012), calculations from the peak nesting season suggests that their main mating season occurs around March to June in the northwest Pacific (Oki 2001, Kawazu et al. 2013). The end of the

mating season is equivalent to the SST increasing timing (Figure 2), and adult males are able to migrate from breeding (mating) areas to high-latitude foraging areas, seeking high productivity waters for the summer. However, for breeding females, the nesting activity ends around August (Uchida and Nishiwaki 1982). Therefore, even if these post-nesting females start to migrate northward during the post-nesting period, they would experience no further rise in SST on their way to high-latitude foraging grounds, and consequently change their direction of migration. This suggests that post-nesting females generally migrate to low-latitude foraging grounds closer to the nesting area or along warm sea currents, as confirmed by the satellite tracking study (Hatase et al. 2002b, 2007). This theory is also supported by comparing the sex ratios of adult-sized turtles in the high-latitude foraging grounds far from loggerhead turtle rookeries (present study: male-biased) and the low-latitude foraging grounds located in the vicinity of the rookeries (Kochi and Mie prefecture, Ishihara and Kamezaki 2011: female-biased) (Figure 1).

It should be noted that most adult females do not breed annually (e.g., Hatase et al. 2013, Hays et al. 2014); therefore, nonbreeding adult females may be expected to migrate to high-latitude areas in nonbreeding years. However, studies tracking loggerhead turtles through two complete successive years in the northwest Atlantic and Mediterranean Sea showed that they repeatedly use the same seasonal foraging site (Broderick et al. 2007, Hawkes et al. 2011; but see Dujon et al. 2018, some turtles used multiple foraging sites). This indicates the possibility that in the summer most nonbreeding females in the northwest Pacific would also, either remain in the low-latitude foraging grounds located in the vicinity of the rookeries or migrate along warm sea currents, rather than migrate to the high latitude foraging grounds (i.e., Sanriku Coast).

In summary, both sexes of immature-size northwest Pacific loggerhead turtles migrated to the summer-restricted high-latitude foraging grounds, whereas most of the migrating adult-size turtles were males (i.e., few

females). We suggest that the male-biased sex ratio of adult-sized loggerhead turtle migrating to the Sanriku Coast is due to the seasonal SST shift, which suppresses the northern migration of adult females during the post-nesting period in the northwest Pacific. Due to the seasonal SST, migration to this Coast is restricted to summer, and because this period overlaps with the nesting period, only immature turtles and adult males may be able to migrate. The identification of adult sex at other summer-restricted high-latitude foraging grounds which is far from their rookery for loggerhead turtles (e.g., the waters of Nova Scotia in the northwest Atlantic: Ceriani et al. 2017) could support this possibility. Since complete feminization which leads to the extinction of the sea turtle population is possible associated with global warming (Jensen et al. 2018), the findings of the present study can contribute to the effective conservation of sea turtle species; the protection of areas where males are likely to occur, thereby reducing their mortality risk, will be a crucial mitigation practice against sex ratio feminization.

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P17-1). This study was conducted as part of a tag and release program in which turtles caught by set nets as bycatch in the Sanriku Coast, were turned over by fishermen to researchers.

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