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Decrease in Body Size of Loggerhead Turtles, *Caretta caretta*, Nesting at Yakushima Island, Japan

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Abstract: We investigated temporal changes in the body size of loggerhead turtles, *Caretta caretta*, nesting on Yakushima Island, Japan, and examined whether body size varied during the nesting season. Our results showed that the straight carapace length (SCL) of females nesting between 1999 and 2005 was significantly smaller than that of females nesting between 1985 and 1991, and the overall size distribution shifted toward a greater proportion of smaller individuals and a marked decrease in larger individuals. Analyses of the lower and upper tails of the SCL distribution also indicated significant reductions in both extremes. In the later period, several size classes exhibited higher nesting frequency than the earlier period, suggesting that nutritional conditions in foraging grounds may have improved, potentially contributing to higher nesting frequency. Smaller individuals tended to nest later in the season in both study periods, with first nesting dates significantly delayed for females within the lower tail. This seasonal tendency may be influenced by differences in migration distance between large females using neritic foraging grounds in the East China Sea and small females relying on pelagic foraging grounds in the North Pacific. Taken together, our findings indicate substantial temporal changes in the size structure of the Yakushima nesting population. In addition, consistent seasonal patterns in nesting timing were observed.

Key words: Body size; *Caretta caretta*; Nesting; Sea turtle; Yakushima

Introduction

In amphibians and reptiles, larger females have been reported to exhibit increased clutch size (Congdon and van Loben Sels, 1991; Hays and Speakman, 1991; Hays et al., 1993; Wallis et al., 1999; Broderick et al., 2003; Price et al., 2004; Roitberg et al., 2013; Gatto et al., 2020; Silva et al., 2020; Guo et al., 2022; Hobel et al., 2022), clutch mass (Guo et al., 2022; Petrov et al., 2024), egg size (Congdon and Tinkle, 1982; Guo et al., 2022), annual egg production (Wallis et al., 1999), and number of hatchlings (Gatto et al., 2020). Consequently,

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there is concern that a reduction in body size may lead to decreased reproductive output (Le Gouvello et al., 2020). Therefore, monitoring changes in body size is crucial for understanding population dynamics.

Loggerhead turtles, *Caretta caretta*, are distributed from warm oceanic regions to subtropical and tropical regions (Dodd, 1988). In these regions, Japan is the only country with nesting areas in the North Pacific Ocean (Kamezaki et al., 2003). Yakushima Island accounts for nearly half of all loggerhead turtle nesting in Japan (Watanabe et al., 2011). After nesting, adult females typically migrate to distant foraging grounds (Hatase et al., 2002b; Okuyama et al., 2022) before returning to the same beach in subsequent years, demonstrating strong site fidelity (Hatase et al., 2002a). The foraging areas of female loggerhead turtles nesting on Yakushima Island are thought to vary, with approximately 80% foraging in the East China Sea, while the remaining individuals forage in the Pacific Ocean and along the coast of the Sea of Japan (Hatase et al., 2002b). The body size of females foraging in the nutrient-rich East China Sea is larger than that of females foraging in the Pacific Ocean (Hatase et al., 2002b; Hatase et al., 2013).

In recent years, a decrease in body size has been reported in sea turtles at several nesting sites around the world (Le Gouvello et al., 2020; Phillips et al., 2021; Mortimer et al., 2022; Pereira et al., 2023; Evans et al., 2024; Hays et al., 2025). For example, in hawksbill turtles, *Eretmochelys imbricata*, Evans et al. (2024) reported a decline in mean curved carapace length (CCL) of approximately 0.05 cm per year between 1974 and 2022. Similarly, Hays et al. (2025) documented a decrease of about 4 cm in mean CCL between 2005 and 2022. Potential factors contributing to this decline include changes in population structure due to anthropogenic conservation efforts (Evans et al., 2024; Hays et al., 2025), which may have increased the proportion of newly recruited, smaller individuals, thereby reducing mean body size. Fisheries-related pressures (Peckham et al., 2007; Wallace et al., 2008) may also have selectively removed larger individuals from the population. In addition, alterations in growth conditions, thought to be driven by changes in the quantity and quality of food resources resulting from climate change and oceanic environmental fluctuations (Bjorndal et al., 2000; Weber et al., 2014; Le Gouvello et al., 2020; Phillips et al., 2021; Hays et al., 2025), may affect growth rates and size at maturity, leading to smaller adult body size. Importantly, recent studies have emphasized that a decline in body size does not necessarily indicate population deterioration, but may instead reflect increased recruitment of small neophyte individuals associated with successful conservation (Hays et al., 2025).

Currently, there are no published reports tracking body size trends in sea turtles nesting in Japan, making it difficult to assess the environmental impacts on these populations or determine whether they are facing critical threats. To address this gap, the present study investigates changes in body size of loggerhead turtles, the species with the highest number of nesting records in Japan (Biodiversity Center of Japan, Ministry of the Environment, 2020), focusing on individuals nesting at Yakushima Island, the largest nesting site in the country. Additionally, to further understand body size variation, we examined whether seasonal differences exist in the body size of nesting individuals.

Materials and Methods

Sample collection

We analyzed nesting females from two survey periods: 1985–1991 (hereafter the earlier period) and 1999–2005 (hereafter the later period). From April 1 to August 31 in the both earlier and later periods, loggerhead turtle nesting was surveyed nightly from dusk until 0400 h along the coastline of Nagatahama Beach (30.2° N, 130.3° E), located in the northwest of Yakushima Island, Kagoshima Prefecture, Japan (Fig. 1). Nagatahama is a white sand beach composed of sediments derived from the weathering of granite, and it

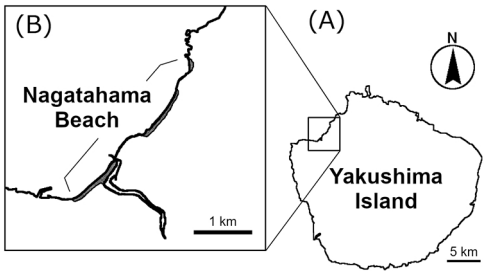

FIG. 1. Location of the study site on Yakushima Island (A). The shaded area within the rectangle indicates Nagatahama Beach (B), where loggerhead turtle nesting was recorded.

extends across approximately 3 kilometers of coastal stretch. The straight carapace length (SCL) and width of females were measured using calipers and individually marked for individual identification during their nesting visits. Individuals that arrived at the nesting site after 0400 h were only counted but not identified. Field research was conducted with permission from Yakushima Town, Kagoshima Prefecture (Table S1).

Data analysis

To study changes in the body size of nesting females over long periods, Welch's t-tests (unequal variances) were used to compare SCL between turtles nesting in the earlier period and those nesting in the later period. Furthermore, F-tests were also used to examine differences in SCL distribution between the two periods.

To examine whether the smallest size class differed between the two periods, the lower tail of the SCL distribution was operationally defined as the range from the smallest individual to the SD-based boundary (SCL≤[mean–2SD]) for each period, following Stewart et al. (2007), and SCL was compared within this interval between periods (Mann–Whitney U test, two-sided). This SD-based depiction of the lower extreme follows the recommendation to characterize mature size ranges using mean±2SD rather than single-minimum cutoffs (Stewart et al., 2007). Furthermore, following Phillips et al. (2021), who assessed changes in population structure by analyzing individuals exceeding the SD-based upper boundary (SCL≥[mean+2SD]), we also compared the SCL of individuals larger than this threshold as the upper tail of the SCL distribution between the same periods (Mann–Whitney U test, two-sided). This aligns with the use of 2SD boundaries to track structural changes in size distributions (Phillips et al., 2021).

For the comparison of the two periods, we analyzed data based on individual identification rather than counting multiple nesting events by the same turtle. For females nesting more than once per season, only the earliest SCL measurement was included.

To evaluate temporal changes in seasonal clutch frequency, we analyzed differences in the proportion of females nesting at high frequency between the earlier and later periods. Nesting females were grouped into four size classes based on SCL, which were 70 to <80 cm, 80 to <90 cm, 90 to <100 cm, and 100 to <110 cm. For each size class, we created a two-by-two contingency table using the numbers of females that began nesting in April or May and that were categorized as either high-frequency nesters, defined as four or five clutches per season, or other nesters, defined as one to three clutches per season. Because smaller females often show lower clutch frequencies (Raposo et al., 2025), we also repeated the test for the 70 to <80 cm class after redefining high frequency nesting as three to five clutches per season. To evaluate differences in the proportion of high-frequency nesters between the two periods, we performed a two-sample Z-test for equality of proportions for each size class. In these tests, pooled proportions were calculated from the combined high-frequency nesting rates in the two periods, and Z values and P values were obtained from the associated standard errors.

To examine seasonal changes in body size, the SCL of nesting females was analyzed monthly from April to August. Data were divided into two periods, excluding months with fewer than 20 observations (April and

August in the earlier period and August in the later period). Next, differences in SCL among months within each period were tested separately using ANOVA. If ANOVA indicated significance, the Tukey-Kramer method was used to test whether differences in SCL were observed between different months.

We examined whether the proportion of smaller and larger individuals varied among months. To do this, we divided the data into two periods and calculated, for each period, the values 2SD below and above the period-specific mean SCL for nesting females. Using a chi-square test, we then assessed whether the monthly proportions of individuals with SCL≤ (mean–2SD) and those with SCL≥(mean+2SD) differed significantly. When significant differences were detected, pairwise comparisons were performed using a Z-test for proportions to identify which months differed. P values for these pairwise tests were adjusted using the Holm method. In the analysis of body size changes during the nesting season, we allowed repeated measurements of the same individuals within the same month to capture the relative abundance of different size classes arriving to nest each month. We provided additional visualizations, including kernel density estimation (KDE) curves, as Supplementary Materials.

To evaluate whether smaller individuals initiate nesting later in the season, we compared first nesting dates between females within the lower tail (SCL≤[mean–2SD]) and all others using the Wilcoxon rank-sum test and reported Hodges–Lehmann estimates of the median difference. Because smaller females use pelagic foraging grounds and return later (Hatase et al., 2002b; Okuyama et al., 2022), we applied a one-sided Wilcoxon test assuming delayed nesting. We also visualized the distribution of first nesting dates across SCL size classes.

Results

Temporal comparison

For the earlier period, 2,853 emergences and 2,430 nesting events were recorded when repeated nesting was considered. For the later period, only the number of nesting events was available, and 5,243 nesting events were recorded due to incomplete records of emergences. A total of 2,612 and 4,711 SCL measurements were obtained for the two periods, respectively. For analyses based on individual identification, 1,199 females were recorded in the earlier period and 1,804 in the later period, with SCL data available for 1,107 and 1,704 individuals, respectively. Year-specific counts and data availability that underlie these totals are reported in Table S2. Females nesting in the earlier period had significantly larger SCL (89.7±5.3 cm) than those nesting in the later period (84.7±4.7 cm) (t-test, $P<0.001$; Table 1). F-tests indicated that variance in SCL differed significantly between the two periods ($P<0.001$). Individuals with SCL of 70–75 cm were rarely observed during the earlier period, whereas individuals larger than 100 cm became extremely rare during the later period. The lower tail of the SCL distribution was 74.0–79.1 cm SCL in the earlier period and 70.1–75.4 cm SCL in the later period, while the upper tail of the SCL distribution was 100.4–110.0 cm in the earlier period and 94.1–97.8 cm SCL in the later period (Fig. 2). Both the lower and upper tail of the SCL distribution of nesting females were significantly larger in the earlier period than in the later period (Mann–Whitney U test, $P<0.001$). These shifts in distribution are also evident in the kernel density estimation (KDE) curves provided in Fig. S1, which visualize the leftward shift and changes in the tails across periods.

For females in the 80 to <90 cm class and the 90 to <100 cm class, the proportion of individuals exhibiting high frequency nesting (4 or 5 clutches per season) was significantly higher in the later period than the earlier period (Z-test, $P<0.001$; Fig. 3). In contrast, no significant difference was detected for the 70 to <80 cm class when high frequency nesting was defined as 4 or 5 clutches per season (Z-test, $P>0.05$). However, when high frequency nesting for this size class was defined as 3 to 5 clutches per season, the proportion of high frequency nesters was significantly higher in the

TABLE 1. Period comparison of straight carapace length (SCL) between 1985–1991 (earlier period) and 1999–2005 (later period).
Comparison targeted: between-period difference in mean SCL (rows=periods; test=Welch's t-test, unequal variances).
Unit of analysis: individual-identified dataset—for females nesting more than once, the earliest SCL per individual across the study period was used.
Reporting: mean±SD; two-sided P-value.

Variable	Year	N	Mean±SD	P-value
SCL (cm)	1985–1991	1107	89.7±5.3	P<0.001
	1999–2005	1704	84.7±4.7	

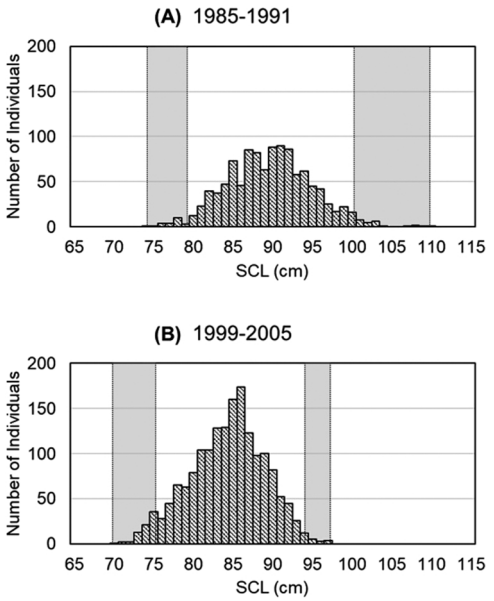

FIG. 2. Size distributions of nesting female loggerheads at Yakushima shown as absolute-count histograms for two study periods. Panels show (A) 1985–1991 (N=1,107) and (B) 1999–2005 (N=1,704). Shaded hatched bands indicate the lower and upper tails defined as mean±2SD, computed separately for each period.

later period than in the earlier period (Z-test, P<0.01). In the largest size class, corresponding to females with an SCL of 100 cm or greater and less than 110 cm, no individuals were observed in the later period, and temporal changes in this class could not be evaluated.

Seasonal variation

For females that nested in the earlier period, there was no significant difference in SCL for each month between May and July (ANOVA, P>0.05; Table 2). In contrast, in the later period, mean SCL differed significantly among months (ANOVA, P<0.001; Table 3), with females nesting in April (87.7±4.2 cm) and May (85.9±4.4 cm) being significantly larger than those in June (85.0±4.6 cm) and July (84.6±4.7 cm). The overall lower tail of the SCL distribution (mean SCL–2SD) without the data from the eliminated months was 74.0–79.4 cm for the earlier period and 70.1–75.9 cm for the later period. In both periods, the proportion of individuals within lower tails differed significantly among months (chi-square test; earlier period: P<0.01; later period: P<0.001; Fig. 4). The upper tail of the SCL distribution was 100.7–110.0 cm in the earlier period and 94.4–97.8 cm in the later period, and no significant differences were found among months (chi-square test; earlier period: P>0.05; later period: P>0.05). In the earlier period, the proportion of individuals in the lower tail was significantly higher in July than in June (Z-test, P<0.01), whereas in the later period, both June and July had significantly higher proportions than May (Z-test; May to June: P<0.05; May to July: P<0.001; Fig. 5). Small females (SCL≤[mean–2SD]) initiated nesting significantly later than the rest of the females in both periods (Wilcoxon one-sided tests; earlier period: P=0.029, 5 days later; later period: P<0.001, 7 days later; Table S3). For reference, the first nesting date of small females was May 19 in the earlier period and May 6 in the later period. Consistent with these findings, the size-class visualization (Fig. S2) suggests that individuals with smaller SCL tended to nest later in the season, although differences among size classes were not clearly defined.

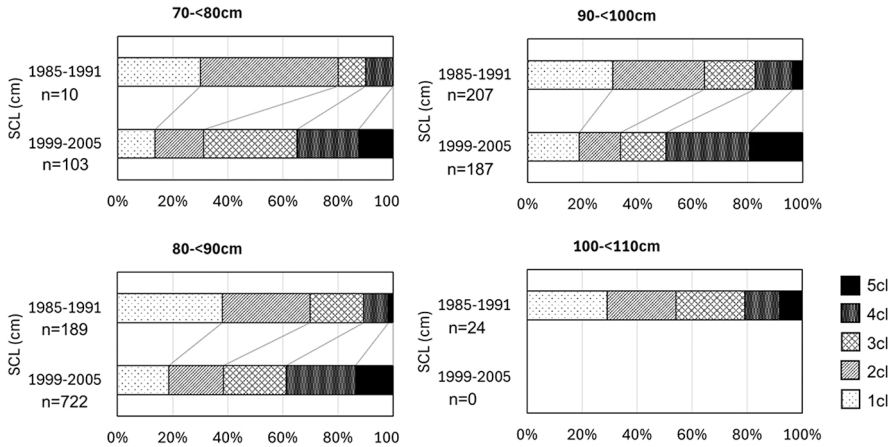

FIG. 3. Proportion of females in each SCL class that produced one to five clutches per season in April–May during 1985–1991 and 1999–2005. cl indicates the number of clutches per season.

TABLE 2. Monthly comparison of mean SCL for nesting females during 1985–1991 (May–July).
Comparison targeted: among-month differences within the earlier period (rows=months; test=one-way ANOVA on SCL).
Unit of analysis: event-based counts within month to represent within-season arrival structure; however, where individuals nested more than once within the same month, repeated SCL measurements for the same individual were not duplicated for mean estimation.
Reporting: mean±SD; overall ANOVA F and P-values shown. Months with N<20 (e.g., April, August) are reported but excluded from the ANOVA.

	Month	N	Mean±SD	F-value	P-value
SCL (cm)	April	0	—	—	—
	May	629	90.3±5.4	1.7	0.191
	June	1372	90.1±5.2		
	July	936	89.8±5.4		
	August	3	88.0±8.7	—	—

DISCUSSION

Temporal comparison

We detected a temporal decline in the body size of loggerhead turtles nesting on Yakushima Island. Compared with the earlier period (1985–1991), individuals nesting in the later period (1999–2005) were smaller, and the size distribution changed in shape, with individuals of 70–75 cm being almost absent during the earlier period, whereas individuals exceeding 100 cm became absent during the later period. The increase in smaller females may be explained by several factors, including resource competition associated with an increase in subadult numbers (Bjorndal et al., 2000), changes in growth patterns driven by climate-related shifts in food quantity and quality (Le Gouvello et al., 2020), recruitment of new individuals into the nesting population (Evans et al., 2024; Hays et al., 2025), and the inclusion of small nesting females within reproductive cohorts as documented elsewhere (Benscoter et al., 2022). Additionally, climate-induced feminization and earlier maturation, as well as the arrival of colonizers from regions

TABLE 3. Monthly comparison of mean SCL for nesting females during 1999–2005 (April–July), with post-hoc Tukey–Kramer tests.
Comparison targeted: among-month differences within the later period (rows=months; test=one-way ANOVA on SCL; post-hoc=Tukey–Kramer for pairwise month comparisons).
Unit of analysis: event-based counts within month to represent within-season arrival structure; handling of potential within-month repeated measurements follows Table 2.
Reporting: mean±SD; ANOVA F and P-values; post-hoc pairwise comparisons with adjusted P-values. Month with N<20 (e.g., August) is reported but excluded from the ANOVA and Tukey–Kramer tests.

	Month	N	Mean±SD	F-value	P-value	Multiple Comparison: P-value
SCL (cm)	April	21	87.7±4.2	20.2	P<0.001	June<April: P<0.05
	May	1241	85.9±4.4			July<April: P<0.05
	June	2114	85.0±4.6			June<May: P<0.001
	July	1330	84.6±4.7			July<May: P<0.001
	August	5	86.2±5.2	—	—	—

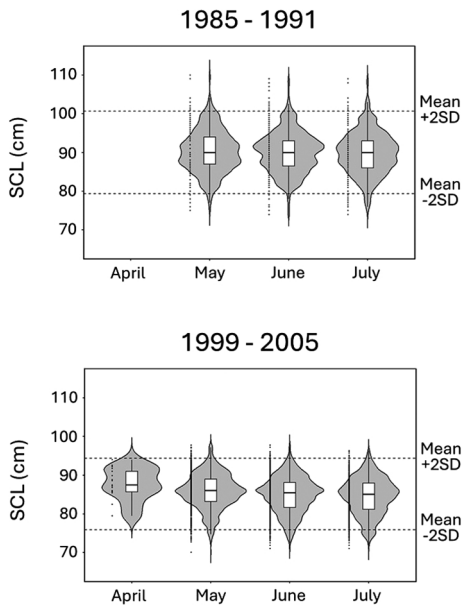

FIG. 4. Monthly distribution of nesting female SCL for the periods 1985–1991 and 1999–2005. Violin plots show the distribution of SCL. Boxplots indicate the median and interquartile range, and dots represent individual observations.

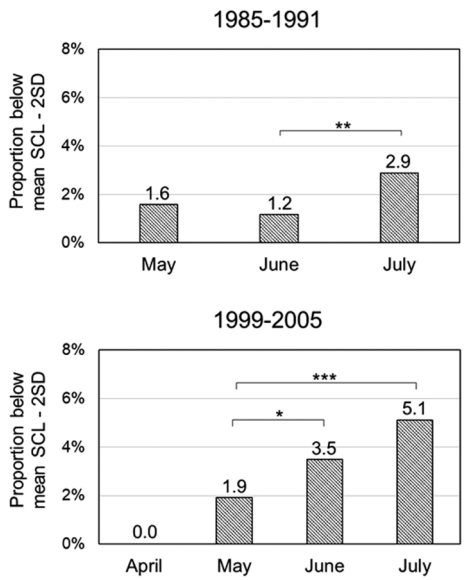

FIG. 5. Monthly proportions of nesting females with SCL smaller than the mean minus 2SD for the periods 1985–1991 and 1999–2005. Bars represent the proportion for each month, and asterisks indicate significant differences among months based on Z-tests (*: P<0.05, **: P<0.01, ***: P<0.001).

where turtles mature at smaller sizes (Luna-Ortiz et al., 2024), may further contribute to an increased proportion of small nesting females.

On the east coast of Florida, both mean SCL and the lower tail of the SCL distribution of nesting females have declined, likely due to an increased proportion of individuals originating from foraging areas where turtles are smaller

and to reduced food quality and quantity leading to slower growth and smaller size at maturity (Phillips et al., 2021). At Yakushima, both the mean SCL and the lower tail of the SCL distribution also showed a decreasing trend. However, this pattern is unlikely to have resulted from growth retardation or a reduction in size at maturity caused by declines in food resources. Larger females nesting on Yakushima are known to forage predominantly in the nutrient-rich waters of the East China Sea (Hatase, 2002b; Hatase et al., 2013). In the present study, the proportion of females exhibiting high nesting frequency (4 to 5 clutches per year) was higher in the later period than in the earlier period, across size classes. This pattern suggests that nesting females may have experienced improved nutritional conditions in their foraging grounds. Consistent with these patterns, loggerhead females that exploit higher quality neritic foraging habitats exhibit higher reproductive output, expressed as greater clutch frequency or shorter remigration intervals, than conspecifics using lower quality or more distant oceanic habitats (Hatase et al., 2013; Ceriani et al., 2015). The observation that even relatively small individuals (SCL 70–80 cm) exhibited high nesting frequency suggests that nutritional limitation was unlikely to have been a strong constraint for small females foraging in the North Pacific. This also suggests that the increase in small nesting females is unlikely to be explained by resource competition resulting from increased subadult abundance, because such competition would be expected to reduce nutritional condition and reproductive output. In light of this, the elevated nesting frequency across size classes likely indicates improved nutritional conditions at foraging grounds. Such conditions could enhance survival and recruitment, particularly among smaller individuals, and may have contributed to the increase in small nesting females.

However, this interpretation should be treated with caution, as our study does not provide direct evidence for changes in survival rates, remigration intervals, or individual body condition. Therefore, alternative explanations should also be considered. For example, the increase in smaller nesting females may reflect increased recruitment (Evans et al., 2024; Hays et al., 2025), immigration from other nesting regions (Bowen et al., 1995; Kobayashi et al., 2008; Peckham et al., 2011), or shifts in life-history traits such as earlier maturation and feminization (Luna-Ortiz et al., 2024). It has also been suggested that climate change may increase feminization and accelerate maturation, resulting in smaller maturation sizes and, consequently, a higher proportion of smaller females (Luna-Ortiz et al., 2024). Because sea turtles exhibit temperature-dependent sex determination, rising incubation temperatures can produce female-biased sex ratios, which may increase the number of breeding females and promote earlier maturation at smaller body sizes.

To further evaluate changes in population composition between the two study periods, we examined individual overlap based on tagging data. Only a small number of individuals (n=9) were recorded in both periods, whereas the vast majority of individuals observed in the later period (n=1,795) had not been recorded in the earlier period. This high turnover indicates that the nesting population in the later period was largely composed of previously unrecorded individuals. Such a pattern is consistent with demographic changes such as increased recruitment, but may also reflect incomplete detection or differences in sampling effort.

We next consider mechanisms that could reduce the proportion of large females, while acknowledging that these mechanisms do not necessarily explain the overall increase in sample size in the later period. Larger females nesting on Yakushima typically forage in the nutrient-rich waters of the East China Sea (Hatase et al., 2002b; Hatase et al., 2013), whereas others forage in the North Pacific or along the Japanese coast (Okuyama et al., 2022). Within these focal foraging regions, incidental capture of loggerhead turtles in large set nets and bottom trawl fisheries occurs frequently, and have been reported (Ishihara et al.,

2014; Ishihara et al., 2024; Song et al., 2025). Loggerheads' strong swimming ability increases stress and injury when entangled, and gillnets or bottom trawls pose a high risk of suffocation or drowning (FAO, 2010). Bycatch risks differ among foraging areas, with larger females mainly exposed to set nets and trawls in the East China Sea, and smaller females potentially interacting with longline fisheries in the pelagic North Pacific. Susceptibility to capture varies by gear type; demersal longlines and bottom trawls used in coastal areas tend to capture larger individuals (Casale, 2008). Thus, bycatch and capture could have contributed to the decline of large females. However, because large turtles are often released immediately after capture and their post-capture mortality is reportedly low, this factor alone is unlikely to explain the observed decline (Ishihara et al., 2014).

Sea turtles have historically been harvested for food in many regions (Campbell, 2003), and such practices persist along the Chinese coast (Chan et al., 2007). Intentional harvesting may therefore have contributed to the decline of large individuals. The Chinese coast is a major foraging area for many Yakushima females (Okuyama et al., 2022). Although official records of sea turtle harvesting in the East China Sea are lacking, media reports have documented illegal trade that appear to include loggerhead turtles (Sina News, 2018), some of which may originate from Yakushima. Along the Shandong coast of China, SCL of loggerhead turtles decreased from approximately 90 cm in the early 1960s to about 50–80 cm in the 1980s, a trend attributed to age-structure shifts caused by excessive harvesting (Wang et al., 1980, as cited in Chan et al., 2007). This indicates that one plausible explanation for the SCL decline in our study area may be age-structure shifts linked to intentional harvesting, as has been suggested for the Shandong coast. Further research should assess bycatch and harvest pressure, identify foraging areas and their use, evaluate changes in food quality and quantity, examine shifts in age structure and growth patterns, and determine the influence of immigration from other foraging areas to clarify the drivers of the body size reduction in nesting loggerhead turtles.

Seasonal variation

No significant monthly differences in mean SCL were detected among nesting females during the earlier period. In contrast, during the later period, mean SCL was significantly greater in June and July than in May. Despite this difference, in both periods the fraction of smaller females increased toward the later part of the nesting season, indicating that the proportion of small-bodied individuals tends to rise as the season progresses. This tendency is also visible when treating SCL as a continuous variable: the first nesting date shifts to later in the season at smaller sizes (Fig. S2). The statistical comparison of first nesting dates also supported this pattern, with smaller females nesting significantly later than other females in both periods (Table S3), indicating that delayed nesting initiation is consistently associated with smaller body size. This seasonal shift toward smaller sizes is consistent with patterns reported in the eastern Atlantic, where smaller females have been observed to nest later in the season, although the underlying cause remains unclear (Martins et al., 2022).

A plausible explanation for this seasonal shift toward smaller females is that smaller females disproportionately forage in the pelagic North Pacific, whereas larger females more often use neritic habitats such as the East China Sea. This size-linked foraging dichotomy has been documented around Japan (Hatase et al., 2002b; Okuyama et al., 2022). Because pelagic foragers returning from the North Pacific must traverse far greater distances than neritic foragers in the East China Sea, their inbound migration can take much longer, in some cases approaching several months for pelagic routes, whereas East China Sea foragers returning to Yakushima may require only a matter of days (Okuyama et al., 2022). This difference in travel time can delay the initiation of nesting by smaller females that rely on pelagic foraging. In addition, variation in water

temperature among foraging regions may also contribute to this pattern. Individuals foraging in pelagic habitats of the North Pacific experience lower temperatures than those in the East China Sea, which may influence physiological processes related to reproduction and delay the initiation of migration. Recent satellite tracking analyses support this mechanism by showing distinct post nesting destinations and movement modes, with pelagic foragers drifting eastward in the oceanic North Pacific and neritic foragers undertaking shorter returns that are oriented toward benthic feeding within the East China Sea (Fujita et al., 2023). Taken together, differences in distance and travel time between foraging and nesting areas provide a likely explanation for the later seasonal appearance of smaller females in our data. Although large females appeared mainly in the early season, there were no significant monthly differences in the proportion of individuals in the upper tail (SCL≥[mean+2SD]), suggesting that large females did not necessarily terminate nesting earlier than smaller females. In addition, although relatively few larger females were observed nesting multiple times, some individuals were recorded nesting from May to July in both study periods (n=3 in the earlier period; n=9 in the later period), suggesting that large females may continue nesting throughout a substantial portion of the season rather than terminating early. However, this inference should be interpreted with caution due to limited sample size. Furthermore, individual identification data showed no evidence that large females nested less frequently than smaller females, suggesting that the seasonal pattern is unlikely to be explained by differences in nesting frequency among size classes.

A different hypothesis, commonly invoked for other reptiles and amphibians, is that smaller individuals delay reproduction due to a trade-off between growth and reproductive investment. In amphibians and reptiles other than sea turtles, larger individuals often initiate reproduction earlier than smaller ones (Bauwens and Verheyen, 1985; Tejedo, 1992). This pattern reflects a trade-off in energy allocation between growth and reproduction; smaller individuals invest energy in both processes, whereas larger individuals allocate a greater proportion of energy to reproduction, leading to earlier reproductive onset (Bauwens and Verheyen, 1985; Tejedo, 1992). However, post-maturity growth in sea turtles is minimal (Hatase et al., 2004; Ishihara and Kamezaki, 2011), making this trade-off unlikely to explain the delayed onset of nesting observed in smaller individuals in the present study.

Conclusion

The body size of female loggerhead turtles nesting on Yakushima Island was smaller in the later period than in the earlier period, and the overall size distribution also changed. In the later period, the nesting group contained a larger number of small individuals and fewer large individuals, which resulted in a shift toward smaller sizes at the population level. Although earlier studies have suggested many ecological and human related processes that may influence long term changes in sea turtle body size, the data in the present study do not allow us to determine the specific reasons for the increase in small individuals or for the decrease in large individuals. The increased nesting frequency observed across size classes in the later period may reflect improved nutritional conditions in foraging grounds; however, this interpretation remains tentative due to limited direct evidence. Other possible explanations, including differences in the use of feeding areas, long-term changes in population structure, and pressures such as bycatch or harvest, remain unconfirmed and require further examination. We also found that smaller females began nesting later in the season in both study periods. This repeated seasonal pattern suggests a consistent relationship between body size and the timing of nesting. Differences in migration routes or feeding conditions before nesting may be involved, but the underlying mechanism remains unclear. Taken together, our findings indicate that the nesting population on Yakushima has undergone marked changes in size structure over the past

several decades. Continued monitoring of body size, the timing of nesting, and feeding ecology, combined with assessments of changes in population structure and external pressures, will be important for understanding how these processes influence population trends and for guiding conservation efforts.

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Data Availability

Supplementary materials are available from Figshare under the following DOIs: Table S1: https://doi.org/10.6084/m9.figshare.32787804; Table S2: https://doi.org/10.6084/m9.figshare.31832806; Table S3: https://doi.org/10.6084/m9.figshare.31832908; Fig. S1: https://doi.org/10.6084/m9.figshare.31832884; and Fig. S2: https://doi.org/10.6084/m9.figshare.31832932.

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