



Latitudinal cline in the foraging dichotomy of loggerhead sea turtles reveals the importance of East China Sea for priority conservation

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Abstract

Aim: Quantifying the importance of habitat areas for conservation of highly migratory marine species with complex life histories can be challenging. For example loggerhead turtles (*Caretta caretta*) nesting in Japan forage both oceanically and neritically after their reproductive period. Here, we aimed to quantify the proportions of turtles using these two contrasting habitats (foraging dichotomy) to suggest priority conservation areas.

Location: North Pacific Ocean.

Methods: We examined the occurrence of foraging dichotomy at three nesting sites (Ishigaki, Okinoerabu Islands and Ichinomiya) based on stable isotope analysis of the egg yolks for 82 turtles and satellite tracking of post-nesting migration for 12 turtles. Moreover, we used the data of three other sites from previous studies (Yakushima Island, Minabe and Omaezaki).

Results: Two neritic foraging grounds (East China Sea and the coastal area of the Japanese archipelago), and an oceanic ground (North Pacific Ocean) were identified. We found a latitudinal cline with respect to the occurrence of foraging dichotomy; >84% of the females nesting at southern sites (Ishigaki and Okinoerabu Islands), 73% at middle sites (Yakushima Island and Minabe) and <46% at northern sites (Omaezaki and Ichinomiya) were neritic foragers; the proportion of oceanic foragers increased at northern sites. Based on the annual number of nests in the entire nesting region of Japan, satellite tracking and the latitudinal cline of foraging dichotomy, we estimated that 70% and 9% of annual nesting females in Japan utilize the neritic foraging habitat in the East China Sea and the coastal area of the Japanese archipelago, respectively, and that and 22% utilize the oceanic habitat of the North Pacific Ocean.

Main conclusions: The East China Sea represents a critical foraging habitat for the North Pacific populations of endangered loggerhead sea turtles. Our findings emphasize the need for international management to ensure their protection.

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KEYWORDS

Caretta caretta, East China Sea, foraging hotspots, international management, polymorphism, priority conservation area, satellite tracking, sea turtle, stable isotope analysis

1 | INTRODUCTION

The conservation of large marine vertebrates is challenging because they are typically slow-growing and late maturing, and mortality as a result of human actions can severely and rapidly deplete their populations [e.g. whales (Whitehead et al., 1997) and seabirds (Croxall et al., 2012)]. In addition, large marine vertebrates are usually wide-ranging and highly migratory. Therefore, they potentially face significant threats across their distributional range that may span multiple nations, which makes the implementation of measures to conserve them particularly challenging. Detailed knowledge of the distribution, range and habitats of these species is key to generate effective conservation approaches (Gerber & Heppell, 2004; Hamann et al., 2010; Rees et al., 2016). To manage migratory species with complex life histories effectively, it is essential to understand their ecology and life history and identify priority conservation areas with high ecological importance throughout their life history (Scales et al., 2014; Webster et al., 2002).

When designating a priority area for a specific population of threatened species and evaluating the impact of conservation measures, it is essential to assess the number of individuals in a population utilizing that area. However, quantifying such information for marine migratory species presents unique challenges because it is generally difficult to investigate their distribution, range, migration route and connectivity between distant populations (e.g. between reproductive and foraging sites) due to their complex life histories (Scales et al., 2014; Webster et al., 2002). However, exciting advances in satellite telemetry, genetic and stable isotope analyses, and combinations of these techniques have enabled researchers to investigate the population and geographical range as well as connectivity among distant populations of individual marine animals (Ceriani et al., 2012; Hobson, 1999; Pajuelo et al., 2012; Rundel et al., 2013; Webster et al., 2002). Indeed, the application of these techniques has already enabled the identification of priority conservation areas for marine migratory animals [e.g. seabirds (Arcos et al., 2012), sea turtles (Pajuelo et al., 2012; Tomaszewicz et al., 2015) and whales (de Castro et al., 2014)].

Sea turtles are an example of megafauna that exhibit complex life histories with ontogenetic shifts across a wide variety of habitat uses (Lutz & Musick, 1997). Understanding the complicated relationships between nesting sites, nurseries and foraging areas is crucial for quantifying the impacts of anthropogenic threats at the population level as well as for designing effective conservation responses to these threats (Hamann et al., 2010; Wallace et al., 2010). In particular, some sea turtle species exhibit polymorphisms with respect to foraging habitats; turtles from a single nesting population utilize multiple separate foraging sites, but an individual turtle uses exclusively one of the multiple sites, although the populations

using these habitats are genetically similar (e.g. Ceriani et al., 2012; Dutton et al., 2007; Eder et al., 2012; Hatase et al., 2002b; Hawkes et al., 2006; Rees et al., 2010; Seminoff et al., 2012; Watanabe et al., 2011; Zbinden et al., 2011). This polymorphism complicates the understanding of ecologically important areas and the establishment of priority areas for their conservation and management.

Loggerhead turtles (*Caretta caretta*) are endangered worldwide and are listed as vulnerable in the IUCN Red List, as only 10 populations exist globally (Casale & Tucker, 2017). Pacific loggerheads are genetically isolated from loggerheads in other ocean basins (Bowen, 2003). In addition, there is a genetic discontinuity between North Pacific loggerheads that nest in Japan and South Pacific loggerheads that nest primarily in Australia and New Caledonia (Bowen, 2003; Bowen et al., 1995; Boyle et al., 2009; Hatase et al., 2002a; Matsuzawa et al., 2016; Nishizawa et al., 2014; Watanabe et al., 2011). In the North Pacific population, loggerhead turtles nest exclusively in Japan (Kamezaki et al., 2003) and can be classified into three genetic management units: the Japanese archipelago, Yakushima and Okinawa (Matsuzawa et al., 2016). Over the last three decades, loggerhead nesting populations in Japan have shown a rapid decline in the 1990s, followed by a trend of gradual recovery (Biodiversity Center of Japan & Ministry of the Environment, 2016; Kamezaki et al., 2003). Casale and Matsuzawa (2015) estimated that the number of adult females was approximately 8,100 in the North Pacific populations based on nest count data from 2009 to 2013. Since 2013, however, it has drastically reduced again with several nesting beaches attaining the lowest numbers of nesting individuals in 2019 (Biodiversity Center of Japan & Ministry of the Environment, 2016, 2020), such as Omaezaki (Omaezaki city, 2020), Yakushima (Martin et al., 2020), Okinoerabu (Y. Yamashita personal communication) and Ishigaki Islands (Okuyama et al., 2020). Therefore, immediate conservation action for nesting populations is needed for the sustainable management of the North Pacific population.

Hatase et al. (2002b) first reported the foraging dichotomy in loggerhead females nesting in Japan. They found that small-sized females migrated to the North Pacific Ocean (NPO) after the reproductive period and mainly foraged on nutrient-poor planktonic prey in oceanic habitats, whereas larger females mainly migrated to the East China Sea (ECS) and foraged on nutrient-rich benthic prey in neritic habitats (Hatase et al., 2002b, 2007, 2013). This foraging dichotomy was verified in the nesting populations of Minabe and Yakushima Island (Hatase et al., 2002b, 2013) and Omaezaki (Minami et al., 2008) in Japan. However, the occurrence of dichotomy (neritic benthivore vs. oceanic planktivore) differed depending on the nesting beaches. Therefore, the proportion of individuals using neritic habitats and those using oceanic habitats remains unclear, thereby hindering the effective conservation and management of the North Pacific loggerhead population. Here, we examined the occurrence of foraging dichotomy

by stable isotope analysis and determined the foraging habitat after the reproductive period by satellite tracking of loggerhead females nesting at three beaches which geographically represent the nesting areas in Japan. Additionally, we combined these new data with existing data to estimate the proportion of the entire nesting population in the North Pacific utilizing either neritic or oceanic habitats and determined the foraging areas with high priority that need to be protected to safeguard this endangered species.

2 | METHODS

2.1 | Nesting survey

In previous studies, the foraging dichotomy of loggerhead turtles and its relationship to their body size were investigated at three major nesting beaches in Japan [Minabe, Yakushima Island (Hatase et al., 2002b, 2013), and Omaezaki (Minami et al., 2008)]. Therefore, to assess the trend of foraging dichotomy in the entire nesting area of Japan, we chose three other nesting sites in this study to represent the geographic nesting regions of Japan; Ishigaki Island, Okinoerabu Island and Ichinomiya (Figure 1a). Ishigaki Island is the geographic southern limit of nesting sites in the North Pacific loggerhead population (Okuyama et al., 2020), while Ichinomiya is the northern limit. Okinoerabu Island is located between the Yakushima and Ishigaki Islands. In addition to these six nesting sites, data on the straight carapace length (SCL) of females in Miyazaki are also available (Kamezaki et al., 1995). Since the SCL of females is related to the type of foraging dichotomy (Hatase et al., 2002b, 2013), we compared the SCL among seven sites including Miyazaki to estimate the trend of dichotomy in terms of body size. In this study, Ichinomiya and Omaezaki are termed as the two northern nesting sites, while Okinoerabu and Ishigaki Islands are the southern ones. Minabe, Miyazaki and Yakushima Island are the middle sites (Figure 1a). The annual number of nests, in the order of north to south, in Ichinomiya, Omaezaki, Minabe, Yakushima Island, Okinoerabu Island and Ishigaki Island account for 0.3%, 1.1%, 1.7%, 50.1%, 2.1% and 0.3% of the annual nests in all nesting sites respectively (Kamezaki, 2012).

On the southernmost site Ishigaki Island, regular surveys for nesting have been conducted since 1993 (Okuyama et al., 2020). For isotope analysis, one egg sample was collected from each nest during 2015–2018. Unfortunately, the nesting events of loggerhead turtles were rarely seen on Ishigaki Island because of the very small nesting population (the range of annual number of nests: 5–12, Okuyama et al., 2020). Thus, we collected the eggs only from the nests that occurred within 8 days on a beach in each year to avoid sampling the eggs from the same female, based on the fact that the inter-nesting interval of females varied between 9 and 14 days on Ishigaki Island (Okuyama et al., 2020). The data on SCL of nesting females were obtained from the results of a previous nesting survey during 2003–2013 (Okuyama et al., 2020).

On the southern Okinoerabu Island, a nesting survey was conducted on three beaches (Okidomari, Wanjo and Yowa) during the main nesting season (from the end of May to the middle of June)

from 2015 to 2018. If turtles were encountered during the night survey, the SCLs of nesting individuals were measured. They were then tagged externally using metal and plastic tags on both hind flippers. These procedures took place after the turtles completed laying eggs in their nests. A single egg was collected from each female during oviposition.

The northernmost site Ichinomiya occupies a 20-km-long beach where sea turtles nest. Daily and nightly nesting surveys were conducted from 2015 to 2018. Similar to Ishigaki Island, Ichinomiya also has an extremely low density of nesting populations because it lies at the northern limit of the loggerhead nesting area. Therefore, nesting events were rarely seen. However, if a female was encountered, we tagged and measured its SCLs. The eggs were sampled from all nests that occurred during 2016–2018 because we could not identify the individual females due to the lack of nesting interval data. Only one egg sample was collected from each nest.

2.2 | Satellite tracking

Argos satellite-linked transmitters (Satellite Relay Data Logger (SRDL), SMRU Instrumentations, UK or TAM-4410-3, Telonics, Inc.) were deployed on 12 turtles (Table 1). Of these turtles tracked, egg samples for the isotope analysis were obtained from 10 turtles (Table 1). Unfortunately, the egg samples from the remaining two were not obtained because they did not lay eggs when the transmitter was deployed. Eight transmitters were deployed on the southern Okinoerabu Island and four transmitters were deployed at the northernmost site Ichinomiya (Table 1). No turtles were satellite-tagged on the southernmost Ishigaki Island because none were encountered during the research period. The transmitter was deployed on the carapace using epoxy putty, two-component epoxy resin and a glass fibre cloth (Konishi Co., Ltd.) after the physical measurements and conventional tag attachment.

To plot the migration trajectories, we used the location data with Argos location classes (B, A, 0, 1, 2, 3). The first two classes have no accuracy information assigned by Argos, and the remaining classes have reported accuracies of >1,500, 500–1,500, 250–500 and <250 m respectively. However, location error has been measured on marine mammals as 10.3 and 6.2 km for class B and A respectively (Costa et al., 2010). Location data with excessive speed (>5 km h⁻¹) were omitted (Luschi et al., 1998). An anomalous movement pattern of tracked turtles based on location and dive data was regarded as a mortality event (Schofield et al., 2020). The SRDL provided a temperature-depth profile while tracking the turtles. Sea surface temperature (SST) was defined as the temperature at 5-m depth, which was the shallowest point of the temperature-depth profile.

2.3 | Stable isotope analysis

The stable isotope values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of nesting turtles were investigated to determine the occurrence of foraging dichotomy in the

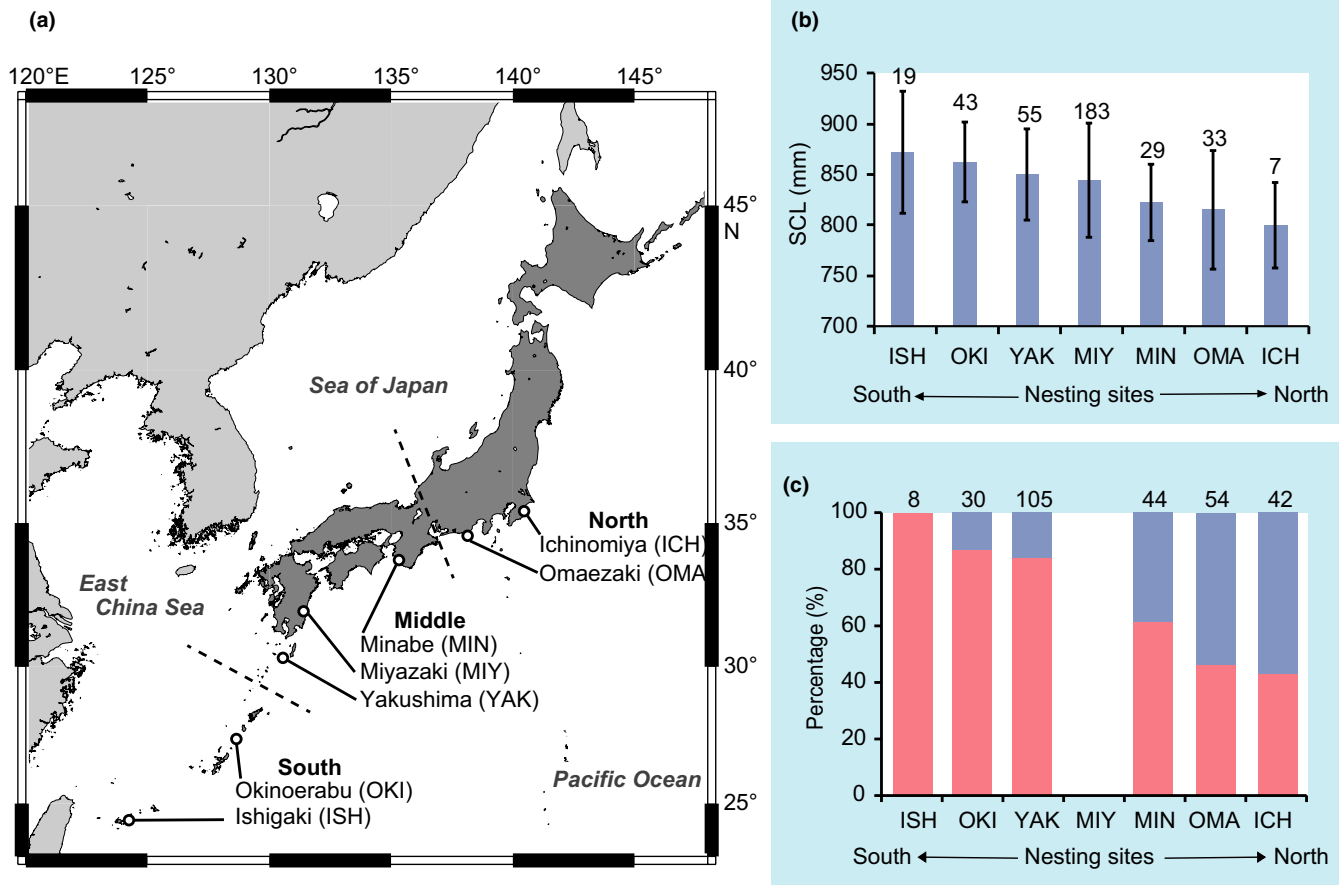


FIGURE 1 (a) A map showing the nesting locations of loggerhead turtles in Japan where surveys were conducted either in this study or in previous studies. Dashed lines represent the segments of nesting areas between north, middle and south. (b) A comparison of the straight carapace length (SCL) of nesting loggerhead turtles among the nesting sites. Vertical bars represent the standard deviations. The numbers above the columns represent the sample size for each site. (c) A comparison of the proportion of foraging types of nesting loggerhead turtles among the nesting sites. Red represents neritic foraging benthivores, while blue represents oceanic planktivores. Note that the proportion of foraging types in Ichinomiya (ICH) was estimated from the stable isotope ratios of egg yolk for all nests made during the research period and clutch frequency of nesting season of oceanic and neritic females (see Methods)

southernmost Ishigaki Island, the southern Okinoerabu Island and the northernmost site Ichinomiya. Furthermore, they were also used to examine the link between the isotope values from satellite-tracked turtles and their post-nesting foraging habitat. In accordance with previous studies (Hatase et al., 2002b, 2013), an egg yolk was used as the material for stable isotope analysis to compare the occurrence of foraging dichotomy in the current study with that reported in previous studies. An egg yolk was also chosen, since the nesting females were rarely seen in Ishigaki Island and Ichinomiya, and it could be sampled after females finished nesting and returned to the sea. All whole egg samples were frozen at -20°C until analytical preparation. Following this, the egg yolk samples were dried at 60°C for 72–96 h. Lipids were removed using a chloroform-methanol (2:1) solution and then ground to a fine powder. The carbon and nitrogen stable isotope ratios in the egg yolks were measured as per the methods described by Hatase et al. (2002b). Isotope ratios in lipid-free powdered yolks (~2 mg) were determined at the Atmosphere and Ocean Research Institute, University of Tokyo, using a mass spectrometer (IsoPrime100) interfaced with an elemental analyser (Vario Micro Cube). The $\delta^{13}\text{C}$ and

$\delta^{15}\text{N}$ were expressed as deviations from the standard (Vienna Pee Dee Belemnite and N_2 in air for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ respectively), as defined by the following equation: $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1,000(\text{‰})$, where R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. The isotopic composition was calibrated against a commercial standard (L-Alanine AZ101-SS13, $\delta^{13}\text{C} = -19.6\text{‰}$ and $\delta^{15}\text{N} = 13.7\text{‰}$, Shoko Science). The analytical precision was estimated to be 0.2‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ based on repeated analyses ($n = 5$) of in-house standard (mussel tissue standard for trace elements, SRM 2976, National Institute of Standards and Technology) of which CN ratio is similar to egg yolk.

For the turtles for which the post-nesting foraging types (neritic benthivore vs. oceanic planktivore) were unknown, we conducted a quadratic discriminant analysis based on the stable isotope ratios of the egg yolks to categorize them into each of the two types (Ceriani et al., 2012; Pajuelo et al., 2012). First, we created a prediction model of a quadratic discriminant function using the stable isotope ratios of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in 10 turtles for which the post-nesting foraging regions were determined by satellite tracking (Table 1). The accuracy (the probability of correct assignment) and error rate of the prediction

TABLE 1 Physical information and tracking summary of nesting loggerhead turtles in this study

ID	Release date	Nesting site	SCL (mm)	Destination	Days tracked (d)	PTT	Foraging type
Oki-1	2016/6/17	Okinoerabu	785	North Pacific	58	SRDL	Oceanic
Oki-2	2016/6/25	Okinoerabu	798	North Pacific	543	SRDL	Oceanic
Oki-3	2016/6/27	Okinoerabu	915	East China Sea	516	SRDL	Neritic
Oki-4	2016/6/29	Okinoerabu	862	The Japanese archipelago	139	SRDL	Neritic
Oki-5	2017/6/4	Okinoerabu	876	East China Sea	39	SRDL	Neritic
Oki-6	2017/6/7	Okinoerabu	818	East China Sea	215	SRDL	Neritic
Oki-7	2017/6/19	Okinoerabu	843	East China Sea	219	SRDL	Neritic
Oki-8	2018/6/5	Okinoerabu	804	East China Sea	218	SRDL	Neritic
Ich-1	2015/7/26	Ichinomiya	768	East China Sea	338	TAM-4410-3	-
Ich-2	2016/6/22	Ichinomiya	784	North Pacific	111	SRDL	Oceanic
Ich-3	2016/7/30	Ichinomiya	801	North Pacific	93	TAM-4410-3	Oceanic
Ich-4	2017/8/27	Ichinomiya	870	The Japanese archipelago	114	SRDL	-

Note: Foraging type was determined by the isotope ratios of egg yolk.

Abbreviations: SCL, straight carapace length; PTT, platform terminal transmitter; SRDL, satellite relay data logger.

model of discriminant function were 80% and 20%, respectively, which were determined by leave-one-out cross-validation. In this method, data from a single turtle are removed from the overall data and classified into a foraging region by the functions derived from all turtles other than the excluded turtle, with the process being repeated for each remaining turtle. We then applied the prediction model of a quadratic discriminant function to assign the turtles for which the post-nesting foraging region was unknown, to either neritic benthivore or oceanic planktivore foraging type. We used only assignment data of foraging types with $\geq 80\%$ of a posterior probability (Pajuelo et al., 2012), to calculate the proportions of foraging types in each nesting site. The quadratic discriminant analysis was conducted using the statistical program R and MASS package (R Development Core Team, 2021).

As for the egg samples collected at the northernmost site Ichinomiya, we could not identify individual females. Thus, the stable isotope ratios of egg yolk for all nests made during the research period (2016–2018) were measured. To estimate the proportion of foraging dichotomy of females nesting at Ichinomiya, we used the data of clutch frequency per nesting season of oceanic and neritic females (3.6 and 4.3 respectively) obtained at Yakushima Island (Hatase et al., 2013) and calculated the estimated number of individual females of each foraging type in each year in Ichinomiya using the following equation:

$$\text{Indiv}_{\text{Neritic}} = \frac{\text{Nest}_{\text{Neritic}}}{4.3} \quad (1)$$

$$\text{Indiv}_{\text{Oceanic}} = \frac{\text{Nest}_{\text{Oceanic}}}{3.6} \quad (2)$$

where, $\text{Indiv}_{\text{Neritic}}$ and $\text{Indiv}_{\text{Oceanic}}$ are the estimated numbers of neritic and oceanic females respectively. $\text{Nest}_{\text{Neritic}}$ and $\text{Nest}_{\text{Oceanic}}$ represent the number of nests built by neritic and oceanic females

respectively. Thus, we calculated the proportion of foraging dichotomy from the estimated numbers of neritic and oceanic females for each year and then averaged it across the 3 years of the research period (2016–2018).

2.4 | Estimating the proportion of foraging dichotomy in the entire nesting population

In Japan, there are more than 300 beaches where loggerhead turtles nest. Six nesting sites in this study—with the exception of Miyazaki where the foraging dichotomy was not examined—correspond to only 55.7% of the annual number of nests in the entire nesting population of Japan (Kamezaki, 2012). To estimate the proportion of foraging dichotomy in the entire nesting population in Japan, we divided all nesting sites in Japan into six regions (Figure 4). This segmentation was based on the geographical locations of the six nesting sites investigated in the current and previous studies (Ichinomiya, Omaezaki, Minabe, Yakushima Island, Okinoerabu Island, Ishigaki Island) to cover all the nesting sites in Japan. We then assumed that the characteristics of foraging dichotomy in each of the six regions (I to VI from the northernmost site) were represented by six nesting sites investigated in this study (from north to south, Ichinomiya, Omaezaki, Minabe, Yakushima Island, Okinoerabu Island and Ishigaki Island) based on the latitudinal cline of the proportion of foraging dichotomy (see the Results). The six regions (I to VI) comprise 0.3%, 13.7%, 74.1%, 4.9%, 6.6% and 0.5% of the annual number of nests in the entirety of Japan respectively (Kamezaki, 2012). Furthermore, we assumed that the clutch frequencies per nesting season of oceanic and neritic females were 3.6 and 4.3 respectively (Hatase et al., 2013). Thus, the number of individuals of neritic and oceanic females in the entire nesting population was estimated using the following equations:

$$\text{Indiv}_{\text{Region, Neritic}} \times 4.3 + \text{Indiv}_{\text{Region, Oceanic}} \times 3.4 = \text{Proportion}_{\text{Region}} \quad (3)$$

$$\text{Indiv}_{\text{Region, Neritic}} : \text{Indiv}_{\text{Region, Oceanic}} = \text{Ratio}_{\text{Region, Neritic}} : \text{Ratio}_{\text{Region, Oceanic}} \quad (4)$$

where, Region represents each of six regions (I to VI); Proportion and Ratio represent the proportion of annual number of nests at a given region to those in all nesting regions and the ratio of foraging dichotomy (neritic benthivore or oceanic planktivore) at a given region respectively. Solving these equations for each of the six regions provided the numbers of individuals of neritic and oceanic turtles in the six nesting regions. The number of individuals of neritic ($\text{Indiv}_{\text{Entire, Neritic}}$) and oceanic turtles ($\text{Indiv}_{\text{Entire, Oceanic}}$) in the entire nesting population was arrived at by adding the numbers of individuals from the six nesting regions. According to the summary of satellite tracking experiments which have been conducted since 1992 (Table 2), the neritic foraging type consists of the turtles utilizing the ECS and the coastal area of the Japanese archipelago. Following this, the numbers of individuals of neritic turtles utilizing the ECS ($\text{Indiv}_{\text{Region, ECS}}$) and the coastal area of the Japanese archipelago ($\text{Indiv}_{\text{Region, JA}}$) for each nesting region were calculated based on the tracking summary (Table 2) using the following equations:

$$\text{Indiv}_{\text{Region, ECS}} = \text{Indiv}_{\text{Region, Neritic}} \times 0.89 \quad (5)$$

$$\text{Indiv}_{\text{Region, JA}} = \text{Indiv}_{\text{Region, Neritic}} \times 0.11 \quad (6)$$

3 | RESULTS

3.1 | Straight carapace length

Our nesting survey showed that the mean SCLs (\pm SD) of females nesting on the southernmost Ishigaki Island, the southern Okinoerabu Island and the northernmost site Ichinomiya were 872 ± 60 mm ($n = 19$), 862 ± 40 mm ($n = 43$) and 800 ± 42 mm ($n = 7$) respectively

(Figure 1b). There was a significant difference in the SCL among the three sites [One-way analysis of variance (ANOVA), $F_{2,66} = 6.5$, $p < .01$]. To offset the difference in sample size, we conducted a sensitivity analysis 20 times to examine the difference among the three sites, with seven samples randomly selected for each site. However, there were no significant differences in any of the comparisons. Including the SCL data obtained at Yakushima Island ($n = 55$, Hatase et al., 2002b), Miyazaki ($n = 183$, Kamezaki et al., 1995), Minabe ($n = 29$, Hatase et al., 2002b) and Omaezaki ($n = 33$, Nobetsu et al., 2004), the SCL of nesting females declined in the turtles from the nesting sites in the south to the north (the southern two sites: 867 mm, the middle three sites: 839 mm and the northern two sites: 807 mm on average, Figure 1b).

3.2 | Post-nesting migration destinations

In total, eight females nesting on Okinoerabu Island were tracked for 243 ± 190 days after their reproductive period, while four turtles from Ichinomiya were tracked for 164 ± 116 days (Table 1). For detailed descriptions on the individual movement of tracked turtles, see Appendix S1. In brief, five of the eight turtles nesting on Okinoerabu Island migrated to the East China Sea (ECS) and stayed within a narrow area, except for Oki-3 and Oki-8 which showed seasonal migration (Figure 2a,b). The other two turtles (Oki-1 and Oki-2) migrated eastward along the Kuroshio Current, and then reached the oceanic area of the North Pacific Ocean (NPO) (Figure 2a). The last of the eight turtles (Oki-4) undertook post-nesting migration to the coastal area of the Japanese archipelago and stayed in the area for approximately 4 months (Figure 2a,c). After that, she probably died because her location data moved to the open ocean, while her dive data showed that she always stayed at the surface.

Two of the four females tagged at Ichinomiya (Ich-2 and Ich-3) migrated eastward and reached the NPO (Figure 2a). Another

TABLE 2 Summary of post-nesting foraging sites of loggerhead females in Japan

Sources	Place where turtles were released	Numbers tracked	ECS	The Japanese archipelago	NPO	Unidentified
Baba et al. (1992)	Omaezaki	3	0	1	1	1
Baba et al. (1993)	Omaezaki	2	0	0	2	0
Sakamoto et al. (1997)	Minabe	2	2	0	0	0
Japan Fisheries Resource Conservation Association (1999)	Yakushima Is.	23	20	1	2	0
Hatase et al. (2002b)	Minabe	5	3	0	2	0
Nobetsu et al. (2003)	Omaezaki	2	0	0	2	0
Nobetsu et al. (2004)	Omaezaki	7	3	1	3	0
Hatase et al. (2007)	Yakushima Is.	2	1	0	1	0
Oki et al. (2019)	Amami Oshima Is.	5	5	0	0	0
Present study	Okinoerabu Is. & Ichinomiya	12	6	2	4	0

Abbreviations: JFRCA, Japan Fisheries Resource Conservation Association; ECS, East China Sea; NPO, North Pacific Ocean.

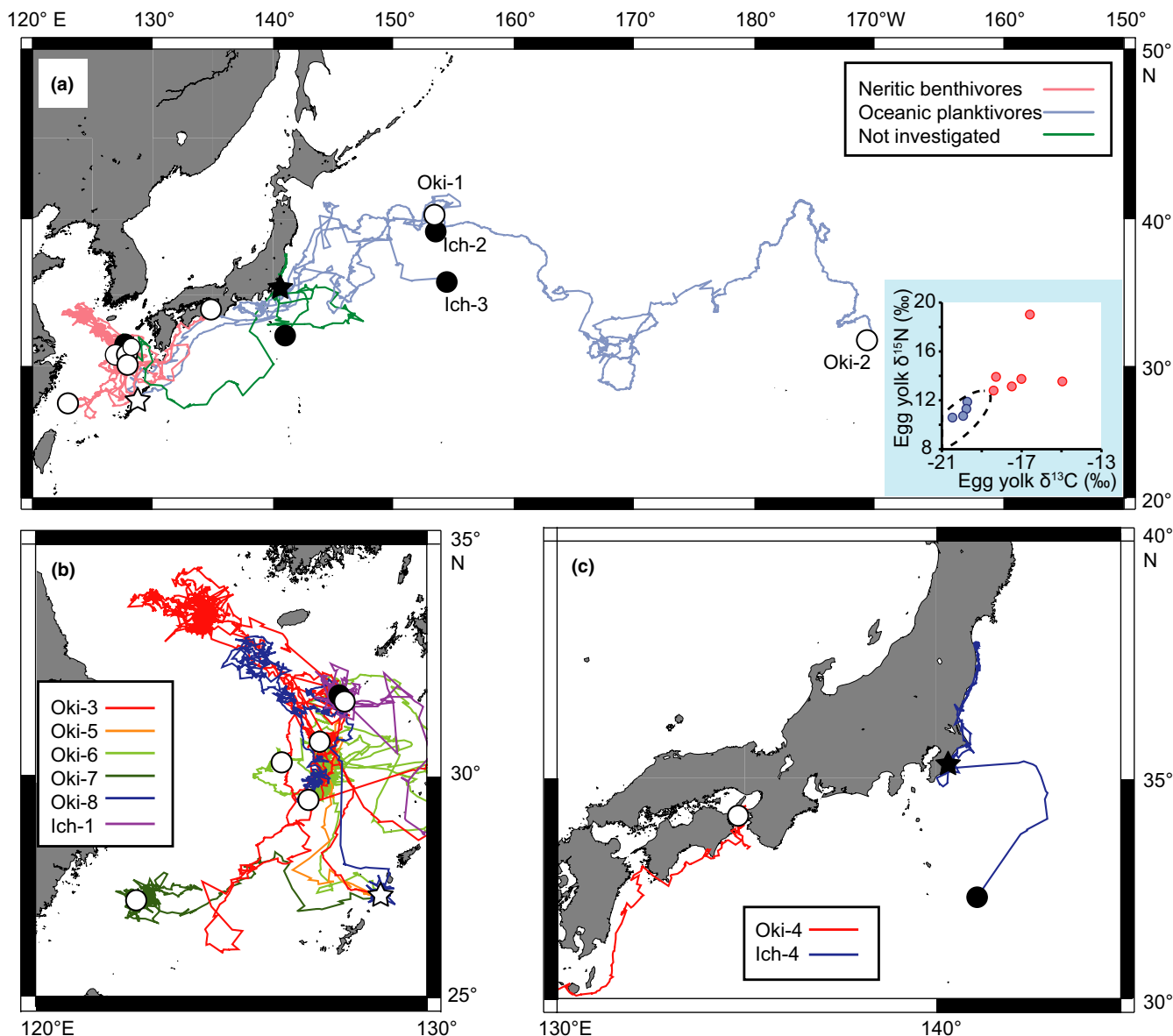


FIGURE 2 (a) Post-nesting migration of 12 female loggerhead turtles nesting at Okinoerabu Island (open star) and Ichinomiya (filled star). End points of the migration routes of the turtles nesting at Okinoerabu Island and Ichinomiya are represented by open and filled circles respectively. Red trajectories represent the migration routes of neritic foraging benthivores determined by isotope analysis (see the blue-boxed graph), while blue trajectories represent those of oceanic planktivores. Green trajectories show the migration routes of nesting turtles whose foraging type was not investigated because the egg samples were not collected. The graph in the blue-boxed graph illustrates the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in yolks from eggs laid by loggerhead turtles whose post-nesting migration routes were tracked. Red dots represent turtles migrating to the neritic regions (East China Sea and the coastal area of the Japanese archipelago), while blue dots represent those migrating to the oceanic region in the North Pacific Ocean. The dashed line represents the partition between oceanic and neritic foraging types determined by a quadratic discriminant analysis (see main text). Post-nesting migration routes and utilized areas of nesting loggerhead turtles are shown in (b) the East China Sea and (c) the coastal area of the Japanese archipelago. Each individual is represented by a colour. Note that (b) and (c) show the migration routes only for turtles utilizing the East China Sea and coastal area of the Japanese archipelago respectively

(Ich-1) headed westward and reached the middle part of the ECS (Figure 2a,b). The last of the four turtles (Ich-4) stayed in the coastal area with seasonal migration in the eastern part of the mainland of the Japanese archipelago for approximately 4 months (September–December) (Figure 2c). She then left the coastal area and headed southward to the open ocean. Unfortunately, the transmission terminated soon after she left the coastal area.

3.3 | Stable isotope ratio analysis and proportion of foraging types

Stable isotope ratios in egg yolks from a total of 82 females were analysed. The mean $\delta^{13}\text{C}$ values ($\pm\text{SD}$) of the egg yolk collected from Ishigaki Island (in 2015: $n = 4$, 2016: $n = 2$, 2017: $n = 3$), Okinoerabu Island (in 2016: $n = 10$, 2017: $n = 12$, 2018: $n = 8$) and Ichinomiya (in

2016: $n = 19$, 2017: $n = 21$, 2018: $n = 3$) were -17.4 ± 1.1 , -17.9 ± 1.1 and $-18.7 \pm 1.3\text{‰}$, while the $\delta^{15}\text{N}$ values were 13.8 ± 1.1 , 13.8 ± 1.5 and $12.5 \pm 2.0\text{‰}$ respectively (Figure 3). There were significant differences in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between the three nesting sites (one-way ANOVA, $F_{2,79} = 6.90$, $p < .05$ for $\delta^{13}\text{C}$, $F_{2,79} = 5.80$, $p < .05$ for $\delta^{15}\text{N}$).

The isotopic ratios in the egg yolk laid by 10 of the 12 females tracked during the post-nesting migration indicated that the females migrating to the ECS and the coastal area of the Japanese archipelago could be classified as neritic benthivores ($n = 6$, -18.5‰ to -15.0‰ for $\delta^{13}\text{C}$, 12.8‰ to 19.0‰ for $\delta^{15}\text{N}$, Figure 2a), while those moving to oceanic areas in the NPO could be classed as oceanic planktivores ($n = 4$, -20.5‰ to -19.7‰ for $\delta^{13}\text{C}$, 10.6‰ to 11.9‰ for $\delta^{15}\text{N}$). Moreover, for the 10 turtles for which the post-nesting foraging regions were determined by satellite tracking, there was a significant difference in combined $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between neritic and oceanic foraging types [Multivariate analysis of variance (MANOVA), $F_{2,7} = 8.13$, $p < .05$]. Of the neritic foragers, the turtle migrating to the Japanese archipelago (Oki-4) had higher $\delta^{15}\text{N}$ values than those in the ECS. A comparison of the body sizes of turtles between oceanic and neritic areas (ECS and coastal area of the Japanese archipelago) revealed that oceanic foraging females (792 ± 9 mm, $n = 4$) were significantly smaller than neritic females (853 ± 40 mm, $n = 6$, t test, $t = 2.9$, $p < .05$).

The stable isotope analysis by the current and previous studies revealed that the proportions of foraging types in the nesting

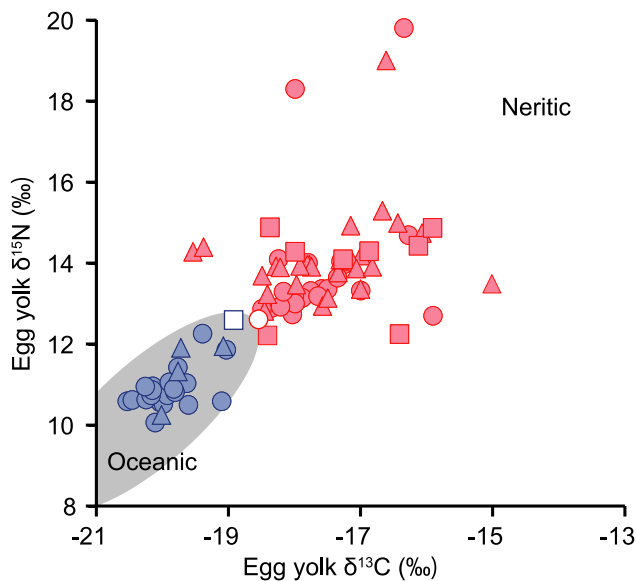


FIGURE 3 A plot of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in yolks from eggs that were laid by loggerhead turtles in Ishigaki (squares, $n = 9$) and Okinoerabu Islands (triangles, $n = 30$), and Ichinomiya (circles, $n = 43$). Red represents neritic foraging benthivores, while blue represents oceanic planktivores. The grey area represents the partition between oceanic and neritic foraging types determined by a quadratic discriminant analysis. Turtles assigned with $\geq 80\%$ of a posterior probability are shown as filled symbols ($n = 80$), while open symbols represent the turtles assigned with $< 80\%$ of a posterior probability ($n = 2$)

sites in Japan showed a geographic gradient similar to that in SCL, in which the neritic type increased as the latitude decreased (in more southern sites) (Figure 1c). A quadratic discriminant analysis showed that 98% (80 out of 82) of the turtles were assigned to one of the foraging types (neritic benthivore vs. oceanic planktivore) with $\geq 80\%$ of a posterior probability (Figure 3). The remaining two turtles with $< 80\%$ of a posterior probability were from Ishigaki Island and Ichinomiya respectively. Thus, these two turtles were omitted from the following calculation on the proportion of foraging types. The proportions of foraging types (neritic vs. oceanic) at each nesting site were 100.0:0.0 on the southernmost Ishigaki Island ($n = 8$), 86.7:13.3 on the southern Okinoerabu Island ($n = 30$) and 43.4:56.6 at the northernmost site Ichinomiya ($n = 42$). Previous studies have reported that the proportions of foraging types at the middle sites Yakushima Island, Minabe (Hatase et al., 2002b) and the northern Omaezaki (Minami et al., 2008) were 84.0:16.0, 61.4:38.6 and 46.3:53.7 based on stable isotope analysis of the egg yolks (Minabe: $n = 44$, Yakushima: $n = 105$) or of the blood cell and plasma (Omaezaki: $n = 54$) respectively.

3.4 | The proportion of foraging dichotomy in the entire nesting population

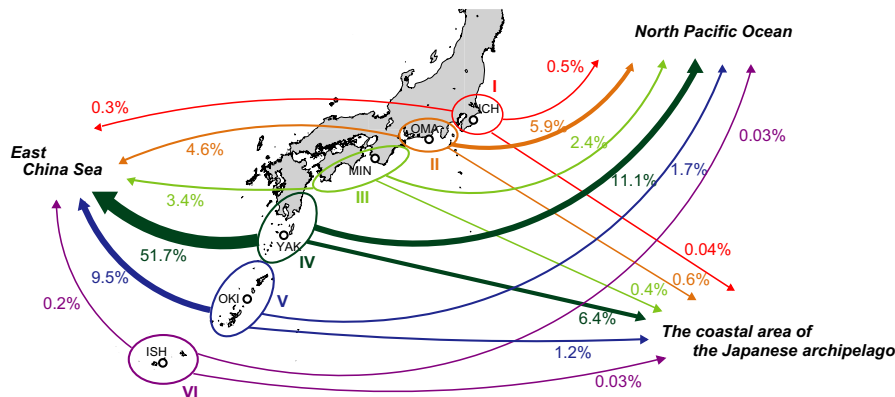
Based on the data on the proportion of foraging dichotomy (neritic vs. oceanic) in the six nesting beaches (Figure 1c), the annual number of nests in the entire nesting region of Japan (Kamezaki, 2012) and the satellite tracking experiments (Table 2), we estimated that 70% and 9% of annually nesting females were neritic foragers that utilized the ECS and the coastal area of the Japanese archipelago, respectively, and that 22% were oceanic foragers that utilized the NPO as their foraging habitat after their reproductive period (Figure 4).

4 | DISCUSSION

4.1 | Foraging dichotomy in the North Pacific loggerhead nesting population

Stable isotope analysis of egg yolks demonstrated that loggerhead females nesting at three nesting beaches (the southernmost Ishigaki Island, the southern Okinoerabu Island and the northernmost site Ichinomiya) in the North Pacific exhibited foraging dichotomy (neritic benthivore vs. oceanic planktivore), although the turtles at the southernmost site, Ishigaki Island, were 100% neritic benthivores. The results of assignment to two foraging types by a quadratic discriminant analysis in this study were similar to those by assignment based on the criteria of Hatase et al. (2013); only two individuals were classified to different foraging types based on the two methods. Although only 12 females were satellite-tracked in our study, the results revealed that most females nesting on Okinoerabu Island (the southern site) and Ichinomiya (the northernmost site) migrated to the ECS and the NPO after their nesting

FIGURE 4 A schematic showing the estimated proportions of individuals of annually nesting loggerhead turtles utilizing three foraging habitats from six regions (I to VI) of the nesting area of Japan. Colours represent each of the six regions in the nesting area. ICH, Ichinomiya; OMA, Omaezaki; MIN, Minabe; YAK, Yakushima Island; OKI, Okinoerabu Island; ISH, Ishigaki Island



period. These areas corresponded with the destinations of post-nesting migration of 51 turtles in six other nesting sites that were not sampled in this study (Table 2). Therefore, the ECS and NPO are essential foraging grounds for North Pacific loggerhead populations. On the other hand, this study found that two of 12 females stayed in the coastal area of the Japanese archipelago for a considerable length of time after their nesting period. In particular, the turtle tracked from the northernmost site Ichinomiya (Ich-4) utilized the coastal area of the Japanese archipelago during the warmer period after nesting, left the coastal area before the onset of winter, and headed for the open ocean. This movement pattern is similar to the seasonal foraging migration of large juvenile loggerhead turtles which utilized the coastal area during summer and migrated to oceanic warmer waters during fall, winter and spring (Narazaki et al., 2015). Moreover, previous satellite tracking studies have demonstrated that three of 51 females nesting in Japan exhibited post-nesting migration to the coastal area of the Japanese archipelago (Table 2). Another turtle that was tracked from the southern site Okinoerabu (Oki-4) to the coastal area of the Japanese archipelago exhibited higher $\delta^{15}\text{N}$ values ($>18\text{‰}$) than the neritic turtles in the ECS. In this study, such a high value ($>18\text{‰}$) of $\delta^{15}\text{N}$ was recorded in three of the 57 neritic turtles. Hatase et al. (2013) also reported one turtle with $>18\text{‰}$ of $\delta^{15}\text{N}$ in their 304 samples of neritic turtles, although this turtle was not satellite-tracked to determine its post-nesting foraging habitat.

The benthic animals inhabiting the urban coastal areas of the Japanese archipelago were reported to have a high $\delta^{15}\text{N}$ value (about 15‰) due to the eutrophication of the coastal waters (Kobayashi et al., 2019; Watanabe et al., 2009; Xue et al., 2009). This fact was also true for the coastal area to which the Oki-4 migrated (Doiuchi et al., 2011; Murai et al., 2008). Meanwhile, the $\delta^{15}\text{N}$ value of the benthic animals in the ECS ranged between 10‰ to 12‰ (Chang et al., 2014; Hatase et al., 2002). Animal $\delta^{15}\text{N}$ is enriched ca. 3‰ to 4‰ relative to the diet $\delta^{15}\text{N}$ (DeNiro & Epstein, 1978; Minagawa & Wada, 1984). Therefore, our results suggest that the neritic loggerhead females with $\delta^{15}\text{N}$ values ranging between 10.2‰ and 19.8‰ are possibly utilizing the coastal area of the Japanese archipelago and the ECS as a foraging ground, although the proportion of the turtle population using the coastal area of the Japanese archipelago is comparatively low.

4.2 | Latitudinal cline in the proportion of foraging dichotomy

This study demonstrated a latitudinal cline of the 'neritic benthivore versus oceanic planktivore' foraging dichotomy. This fact mirrors a latitudinal cline in the average size of nesting turtles because the neritic turtles are larger than the oceanic turtles (Hatase et al., 2002b, 2013), that is the increase in the proportion of neritic foragers results in an increase in body size. Although the foraging dichotomy of females nesting in Miyazaki—located between Minabe and Yakushima Island—was not examined, the body size of these turtles was intermediate between Minabe and Yakushima Island, indicating that the nesting population in Miyazaki also follows the latitudinal cline with respect to foraging dichotomy. However, the isotope ratios and the turtle size for each nesting site were collected in different years (e.g. the data for Minabe were obtained in 1998–1999, while data for Okinoerabu Island were obtained in 2015–2018). Hatase et al. (2013) reported the foraging dichotomy and the turtle size of each foraging type in three discrete years (1999, 2008 and 2011) on Yakushima Island, showing the approximate trend in foraging dichotomy and the turtle sizes did not change among the years. Therefore, we strongly believe that there is a temporal consistency in the latitudinal cline of the foraging dichotomy throughout the years.

The reason behind the occurrence of such a latitudinal cline in the foraging dichotomy will be discussed in this section. A similar but inverse latitudinal cline, in which the body size increased with higher latitude, was recorded in the Mediterranean loggerhead population (Schofield et al., 2013). Moreover, a similar trend was confirmed for the foraging-site polymorphism in the Northwest Atlantic loggerhead nesting populations, however, all the turtles were neritic benthivores (Pfaller et al., 2020). Furthermore, similar latitudinal clines in life-history polymorphisms have been reported in marine migratory species, including three species of eels [river, estuary and marine types (Daverat et al., 2006; Tsukamoto et al., 2009)] and Salmonidae species [migrants to the sea vs. resident in freshwater (Kato, 1991; McDowall, 1997)]. These clines in eels and salmon could be explained by the increase in food abundance between freshwater and marine habitats at different latitudes; the productivity of marine habitats is much higher than that of freshwater

in the northern regions, whereas freshwater habitats have greater productivity in the southern regions (Daverat et al., 2006; Kato, 1991; Tsukamoto et al., 2009). The difference in food abundance might be a reason for triggering the foraging dichotomy in loggerhead turtles as well. Hatase et al. (2002b) suggested that differences in the habitats of immature turtles cause differences in habitat selection between neritic and oceanic habitats after sexual maturity. Indeed, Lagrangian numerical simulation based on a high-resolution ocean circulation model indicated that the dispersal processes of post-hatchling turtles in the North Pacific differed between nesting sites (Okuyama et al., 2011). Therefore, the latitudinal cline of the foraging dichotomy might be caused by differences in the dispersal process and habitat selection of the turtles born in either northern or southern nesting sites (Hays et al., 2010). However, further studies are needed to reveal the mechanisms behind foraging dichotomy or polymorphism in loggerhead turtles.

Hatase et al. (2004) suggested that adult females do not change habitat with age after the establishment of their foraging type during the immature stage of their life history, indicating that the selection of foraging habitats (neritic vs. oceanic) does not depend on the geographical distance between a nesting site and a foraging habitat, but instead depends on foraging type. For example some females nesting at the southern sites utilize the NPO as a foraging habitat (e.g. Oki-1 and Oki-2) despite the ECS being located close to their nesting sites. Similarly, some females nesting at the northern sites utilize a distant foraging habitat at the ECS (e.g. Ich-1).

4.3 | Implications for conservation management of North Pacific loggerhead population

Our results demonstrated that a substantial proportion of annually nesting females are neritic foragers that utilize the ECS as their foraging habitat after their reproductive period, whereas the proportions of neritic type foragers in the coastal area of the Japanese archipelago and oceanic type in the NPO were relatively small. These facts indicate that the ECS is critically important as a foraging site for nesting females of loggerhead turtles, and that it is a priority conservation area for North Pacific loggerheads. Previous studies have also indicated the importance of the ECS for nesting females of loggerhead turtles (Hatase et al., 2002b), as well as for males and subadults (Kobayashi et al., 2011; Saito et al., 2015). Most loggerheads, particularly those migrating to the southern ECS, showed site fidelity towards narrow foraging areas and did not change locations throughout the tracking period (Hatase et al., 2007; Japan Fisheries Resource Conservation Association, 1999; Oki et al., 2019; Saito et al., 2015; present study). Moreover, the turtle Oki-3, showed site fidelity towards her summer foraging spot across the years. Similar site fidelity over multiple years has been reported in the Mediterranean (Broderick et al., 2007).

The duration of the adult stage (post-maturation longevity) of loggerhead turtles has been estimated to be 19 years on average (Avens et al., 2015). Therefore, each female would utilize the ECS

for more than two decades in her life history, including the subadult stage. These facts further enhance the indispensability of the ECS as a foraging habitat of North Pacific loggerheads. Moreover, neritic foraging turtles have a 2.4-fold greater reproductive output than oceanic foraging turtles (Hatase et al., 2013). These facts further highlight the necessity of habitat protection and risk assessment in the ECS for conservation management of the entire North Pacific loggerhead population because the conservation of mature females is directly linked to the recovery of reproductive output (the number of nesting events).

In the ECS, fisheries bycatch is the main cause of mortality (Chan et al., 2007), and this is the case throughout the North Pacific Ocean (Casale & Matsuzawa, 2015). Indeed, bycatches of loggerhead turtle nesting in Japan have been reported in the ECS mainly as caused by bottom trawl fisheries (Iwamoto et al., 1985; Kamezaki et al., 1997; Nishimura & Nakahigashi, 1990). However, to the best of our knowledge, no scientific information on the mortality and bycatch rates of loggerhead turtles in the ECS is available, although there are some reports available in other foraging regions [e.g. the coastal waters of Japan (Ishihara et al., 2014), North Pacific (Martin et al., 2020), Baja California and Mexico (Seminoff et al., 2014)]. This lack of data emphasizes the urgent need for a quantitative assessment of the threats to sea turtles around the ECS and the effects on their mortality. Moreover, regarding the cross-border conservation of the North Pacific loggerhead populations, there is now a tri-national recovery team that brings together policymakers from Japan, Mexico and the United States to manage a multinational conservation action plan (Seminoff et al., 2018). Our results emphasize that this multinational conservation management should include more countries surrounding the ECS, such as China, Taiwan and the Republic of Korea. Wildlife conservation efforts are often most effective when focused on habitats where there is a large impact on the population's survival rate and reproductive success. Therefore, the ECS foraging ground represents critical habitat for the endangered North Pacific population of loggerhead turtles, and ongoing international management is necessary to ensure their recovery.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Satellite tracking data and data of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of nesting loggerhead turtles are available from the Movebank at <https://doi.org/10.5441/001/1.m3c90703> and the Dryad Digital Repository at <https://doi.org/10.5061/dryad.gmsbcc2nj>.

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REFERENCES

- Arcos, J. M., Bécarea, J., Villero, D., Brotons, L., Rodríguez, B., & Ruiz, A. (2012). Assessing the location and stability of foraging hotspots for pelagic seabirds: an approach to identify marine Important Bird Areas (IBAs) in Spain. *Biological Conservation*, 156, 30–42. <https://doi.org/10.1016/j.biocon.2011.12.011>
- Avens, L., Goshe, L. R., Coggins, L., Snover, M. L., Pajuelo, M., Bjørndal, K. A., & Bolten, A. B. (2015). Age and size at maturation and adult stage duration for loggerhead sea turtles in the western North Atlantic. *Marine Biology*, 162, 1749–1767. <https://doi.org/10.1007/s00227-015-2705-x>
- Baba, N., Kiyota, M., Suganuma, H., & Tachikawa, H. (1992). *Research on migratory routes of loggerhead turtles and green turtles by the Argos system. In Report on commissioned project for data analysis by scientific observers aboard fishing vessels in 1991* (pp. 89–99). Fisheries Agency of Japan. (in Japanese)
- Baba, N., Kiyota, M., Suganuma, H., & Tachikawa, H. (1993). *Research on migratory routes of loggerhead turtles and green turtles by the Argos system. In Report on commissioned project for data analysis by scientific observers aboard fishing vessels in 1992* (pp. 86–99). Fisheries Agency of Japan. (in Japanese)
- Biodiversity Center of Japan, Ministry of the Environment (2016). *Annual report of Sea turtles Survey on Monitoring sites 1000 project in FY2015*. Biodiversity Center of Japan, Ministry of the Environment. (In Japanese with English abstract).
- Biodiversity Center of Japan, Ministry of the Environment (2020). *Annual report of Sea turtles Survey on Monitoring sites 1000 project in FY2019*. Biodiversity Center of Japan, Ministry of the Environment. (In Japanese with English abstract).
- Bowen, B. (2003). What is a loggerhead turtle? The genetic perspective. In A. B. Bolten, & B. E. Witherington (Eds.), *Loggerhead sea turtles* (pp. 7–27). Smithsonian Institution Press.
- Bowen, B. W., Abreu-Grobois, F. A., Balazs, G. H., Kamezaki, N., Limpus, C., & Ferl, R. J. (1995). Trans-Pacific migrations of the loggerhead turtle (*Caretta caretta*) demonstrated with mitochondrial DNA markers. *Proceedings of the National Academy of Sciences of the United States of America*, 92, 3731–3734. <https://doi.org/10.1073/pnas.92.9.3731>
- Boyle, M. C., FitzSimmons, N. N., Limpus, C. J., Kelez, S., Velez-Zuazo, X., & Waycott, M. (2009). Evidence for transoceanic migrations by loggerhead sea turtles in the southern Pacific Ocean. *Proceedings of the Royal Society B: Biological Sciences*, 276, 1993–1999. <https://doi.org/10.1098/rspb.2008.1931>
- Broderick, A. C., Coyne, M. S., Fuller, W. J., Glen, F., & Godley, B. J. (2007). Fidelity and over-wintering of sea turtles. *Proceedings of the Royal Society B: Biological Sciences*, 274, 1533–1539. <https://doi.org/10.1098/rspb.2007.0211>
- Casale, P., & Matsuzawa, Y. (2015). *Caretta caretta* (North Pacific sub-population). The IUCN Red List of Threatened Species 2015: e.T83652278A83652322. Gland, Switzerland: IUCN.
- Casale, P., & Tucker, A. D. (2017). *Caretta caretta* (amended version of 2015 assessment). The IUCN Red List of Threatened Species 2017: e.T3897A119333622. Gland, Switzerland: IUCN.
- Ceriani, S. A., Roth, J. D., Evans, D. R., Weishampel, J. F., & Ehrhart, L. M. (2012). Inferring foraging areas of nesting loggerhead turtles using satellite telemetry and stable isotopes. *PLoS One*, 7, e45335. <https://doi.org/10.1371/journal.pone.0045335>
- Chan, S. K. F., Cheng, I. J., Zhou, T., Wang, H. J., Gu, H. X., & Song, X. J. (2007). A comprehensive overview of the population and conservation status of sea turtles in China. *Chelonian Conservation and Biology*, 6, 185–198.
- Chang, N. N., Shiao, J. C., Gong, G. C., Kao, S. J., & Hsieh, C. H. (2014). Stable isotope ratios reveal food source of benthic fish and crustaceans along a gradient of trophic status in the East China Sea. *Continental Shelf Research*, 34, 23–34. <https://doi.org/10.1016/j.csr.2014.04.021>
- Costa, D. P., Robinson, P. W., Arnould, J. P. Y., Harrison, A.-L., Simmons, S. E., Hassrick, J. L., Hoskins, A. J., Kirkman, S. P., Oosthuizen, H., Villegas-Amtmann, S., & Crocker, D. E. (2010). Accuracy of ARGOS locations of pinnipeds at-sea estimated using Fastloc GPS. *PLoS One*, 5(1), e8677. <https://doi.org/10.1371/journal.pone.0008677>
- Croxall, J. P., Butchart, S. H., Lascelles, B. E. N., Stattersfield, A. J., Sullivan, B. E. N., Symes, A., & Taylor, P. H. I. L. (2012). Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International*, 22, 1–34. <https://doi.org/10.1017/S0959270912000020>
- Daverat, F., Limburg, K. E., Thibault, I., Shiao, J. C., Dodson, J. J., Caron, F., Tzeng, W. N., Iizuka, Y., & Wickström, H. (2006). Phenotypic plasticity of habitat use by three temperate eel species, *Anguilla anguilla*, *A. japonica* and *A. rostrata*. *Marine Ecology Progress Series*, 308, 231–241. <https://doi.org/10.3354/meps308231>
- de Castro, F. R., Mamede, N., Danilewicz, D., Geyer, Y., Pizzorno, J. L. A., Zerbini, A. N., & Andriolo, A. (2014). Are marine protected areas and priority areas for conservation representative of humpback whale breeding habitats in the western South Atlantic? *Biological Conservation*, 179, 106–114. <https://doi.org/10.1016/j.biocon.2014.09.013>
- DeNiro, M. J., & Epstein, S. (1978). Influence of diet on the distribution of carbon isotopes in animals. *Geochimica Et Cosmochimica Acta*, 42, 495–506. [https://doi.org/10.1016/0016-7037\(78\)90199-0](https://doi.org/10.1016/0016-7037(78)90199-0)
- Doiuchi, R., Yasue, N., Takeuchi, T., Yamauchi, M., Okuyama, Y., Suwa, T., Mukaino, M., Kokubo, T., & Haya, H. (2011). Comparison of carbon sources for *Trichiurus japonicus* and other benthic fishes in the Kii Channel, Japan, based on carbon and nitrogen stable isotope ratios. *Nippon Suisan Gakkaishi*, 77, 205–214. <https://doi.org/10.2331/suisan.77.205> (in Japanese with English abstract)
- Dutton, P. H., Hitipeuw, C., Zein, M., Benson, S. R., Petro, G., Pita, J., Rei, V., Ambio, L., & Bakarbesy, J. (2007). Status and genetic structure of nesting populations of leatherback turtles (*Dermodochelys coriacea*) in the western Pacific. *Chelonian Conservation and Biology*, 6, 47–53.
- Eder, E., Ceballos, A., Martins, S., Pérez-García, H., Marín, I., Marco, A., & Cardona, L. (2012). Foraging dichotomy in loggerhead sea turtles *Caretta caretta* off northwestern Africa. *Marine Ecology Progress Series*, 470, 113–122. <https://doi.org/10.3354/meps10018>
- Gerber, L. R., & Heppell, S. S. (2004). The use of demographic sensitivity analysis in marine species conservation planning.

- Biological Conservation*, 120, 121–128. <https://doi.org/10.1016/j.biocon.2004.01.029>
- Hatase, H., Kinoshita, M., Bando, T., Kamezaki, N., Sato, K., Matsuzawa, Y., Goto, K., Omuta, K., Nakashima, Y., Takeshita, H., & Sakamoto, W. (2002a). Population structure of loggerhead turtles, *Caretta caretta*, nesting in Japan: bottlenecks on the Pacific population. *Marine Biology*, 141, 299–305. <https://doi.org/10.1007/s00227-002-0819-4>
- Hamann, M., Godfrey, M. H., Seminoff, J. A., Arthur, K., Barata, P., Bjorndal, K. A., Bolten, A. B., Broderick, A. C., Campbell, L. M., Carreras, C., Casale, P., Chaloupka, M., Chan, S., Coyne, M. S., Crowder, L. B., Diez, C. E., Dutton, P. H., Epperly, S. P., FitzSimmons, N. N., ... Godley, B. J. (2010). Global research priorities for sea turtles: informing management and conservation in the 21st century. *Endangered Species Research*, 11(3), 245–269. <https://doi.org/10.3354/esr00279>
- Hatase, H., Matsuzawa, Y., Sato, K., Bando, T., & Goto, K. (2004). Remigration and growth of loggerhead turtles (*Caretta caretta*) nesting on Senri Beach in Minabe, Japan: life-history polymorphism in a sea turtle population. *Marine Biology*, 144, 807–811. <https://doi.org/10.1007/s00227-003-1232-3>
- Hatase, H., Omuta, K., & Tsukamoto, K. (2007). Bottom or midwater: alternative foraging behaviours in adult female loggerhead sea turtles. *Journal of Zoology*, 273, 46–55. <https://doi.org/10.1111/j.1469-7998.2007.00298.x>
- Hatase, H., Omuta, K., & Tsukamoto, K. (2010). Oceanic residents, neritic migrants: a possible mechanism underlying foraging dichotomy in adult female loggerhead turtles (*Caretta caretta*). *Marine Biology*, 157, 1337–1342. <https://doi.org/10.1007/s00227-010-1413-9>
- Hatase, H., Omuta, K., & Tsukamoto, K. (2013). A mechanism that maintains alternative life histories in a loggerhead sea turtle population. *Ecology*, 94, 2583–2594. <https://doi.org/10.1890/12-1588.1>
- Hatase, H., Takai, N., Matsuzawa, Y., Sakamoto, W., Omuta, K., Goto, K., Arai, N., & Fujiwara, T. (2002b). 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. <https://doi.org/10.3354/meps233273>
- Hawkes, L. A., Broderick, A. C., Coyne, M. S., Godfrey, M. H., Lopez-Jurado, L.-F., Lopez-Suarez, P., Merino, S. E., Varo-Cruz, N., & Godley, B. J. (2006). Phenotypically linked dichotomy in sea turtle foraging requires multiple conservation approaches. *Current Biology*, 16, 990–995. <https://doi.org/10.1016/j.cub.2006.03.063>
- Hays, G. C., Fossette, S., Katselidis, K. A., Mariani, P., & Schofield, G. (2010). Ontogenetic development of migration: Lagrangian drift trajectories suggest a new paradigm for sea turtles. *Journal of the Royal Society Interface*, 7, 1319–1327. <https://doi.org/10.1098/rsif.2010.00>
- Hobson, K. A. (1999). Tracing origins and migration of wildlife using stable isotopes: A review. *Oecologia*, 120, 314–326. <https://doi.org/10.1007/s004420050865>
- Ishihara, T., Kamezaki, N., Matsuzawa, Y., & Ishizaki, A. (2014). Assessing the status of Japanese coastal fisheries and sea turtle bycatch. *Wildlife and Human Society*, 2, 23–35. https://doi.org/10.20798/awhswhs.2.1_23 (in Japanese with English abstract).
- Iwamoto, T., Ishii, M., Nakashima, Y., Takeshita, H., & Itoh, A. (1985). Nesting cycles and migrations of the loggerhead sea turtle in Miyazaki, Japan. *Japanese Journal of Ecology*, 35, 505–511. https://doi.org/10.18960/seitai.35.4_505
- Japan Fisheries Resource Conservation Association (1999). *Research on migratory routes and diving ecology of sea turtles. General report on commissioned project for conservation research of aquatic animals in 1994–1998* (pp. 1–90). Fisheries Resource Conservation Association. (in Japanese)
- Kamezaki, N. (2012). Loggerhead turtles in Japan: ecology and conservation. In N. Kamezaki (Ed.), *Natural history of sea turtles in Japan* (pp. 281–301). Tokyoku University Press. (in Japanese).
- Kamezaki, N., Goto, K., Matsuzawa, Y., Nakajima, Y., Oomuta, K., & Sato, K. (1995). Carapace length and width of the loggerhead turtle, *Caretta caretta* nested in the coast of Japan. *Umigame Newsletter of Japan*, 26, 12–13. (in Japanese).
- Kamezaki, N., Matsuzawa, Y., Abe, O., Asakawa, H., Fujii, T., Goto, K., & Wakabayashi, I. (2003). Loggerhead turtles nesting in Japan. In A. B. Bolten, & B. E. Witherington (Eds.), *Loggerhead sea turtles* (pp. 210–217). Smithsonian Institution Press.
- Kamezaki, N., Miyawaki, I., Suganuma, H., Omuta, K., Nakajima, Y., Goto, K., & Iwamoto, T. (1997). Post-nesting migration of Japanese loggerhead turtle, *Caretta caretta*. *Wildlife Conservation Japan*, 3, 29–39. (in Japanese with English abstract).
- Kato, F. (1991). Life histories of masu and amago salmon (*Oncorhynchus masou* and *Oncorhynchus rhodurus*). In C. Groot, & L. Margolis (Eds.), *Pacific salmon life histories* (pp. 447–520). University of British Columbia.
- Kobayashi, D. R., Cheng, I. J., Parker, D. M., Polovina, J. J., Kamezaki, N., & Balazs, G. H. (2011). Loggerhead turtle (*Caretta caretta*) movement off the coast of Taiwan: characterization of a hotspot in the East China Sea and investigation of mesoscale eddies. *ICES Journal of Marine Science*, 68, 707–718. <https://doi.org/10.1093/icesjms/fsq185>
- Kobayashi, J., Yoshimoto, M., Yamada, K., Okamura, K., & Sakurai, T. (2019). Comparison of trophic magnification factors of PCBs and PBDEs in Tokyo Bay based on nitrogen isotope ratios in bulk nitrogen and amino acids. *Chemosphere*, 226, 220–228. <https://doi.org/10.1016/j.chemosphere.2019.03.133>
- Luschi, P., Hays, G. C., Del Seppia, C., Marsh, R., & Papi, F. (1998). The navigational feats of green sea turtles migrating from Ascension Island investigated by satellite telemetry. *Proceedings of the Royal Society B: Biological Sciences*, 265, 2279–2284. <https://doi.org/10.1098/rspb.1998.0571>
- Lutz, P. L., & Musick, J. A. (1997). *Biology of sea turtle* (pp. 446). CRC Press.
- Martin, S. L., Siders, Z., Eguchi, T., Langseth, B., Yau, A., Baker, J., & Jones, T. T. (2020). Assessing the population-level impacts of North Pacific loggerhead and western Pacific leatherback turtle interactions in the Hawaii-based shallow-set longline fishery. U.S. Dept. of Commerce, NOAA Technical Memorandum NOAA-TM-NMFS-PIFSC-95, 183 p. <https://doi.org/10.25923/ydp1-f891>
- Matsuzawa, Y., Kamezaki, N., Ishihara, T., Omuta, K., Takeshita, H., Goto, K., Arata, T., Honda, H., Kameda, K., Kashima, Y., Kayo, M., Kawazu, I., Kodama, J., Kumazawa, Y., Kuroyanagi, K., Mizobuchi, K., Mizuno, K., Oki, K., Watanabe, K. K., ... Dutton, P. H. (2016). Fine-scale genetic population structure of loggerhead turtles in the Northwest Pacific. *Endangered Species Research*, 30, 83–93. <https://doi.org/10.3354/esr00724>
- McDowall, R. M. (1997). The evolution of diadromy in fishes (revisited) and its place in phylogenetic analysis. *Reviews in Fish Biology and Fisheries*, 7, 443–462. <https://doi.org/10.1023/A:1018404331601>
- Minagawa, M., & Wada, E. (1984). Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochimica Et Cosmochimica Acta*, 48, 1135–1140. [https://doi.org/10.1016/0016-7037\(84\)90204-7](https://doi.org/10.1016/0016-7037(84)90204-7)
- Minami, H., Kiyota, M., & Miyamoto, N. (2008). Feeding ecology and habitat use of seabirds and sea turtles. In O. Tominaga, & N. Takai (Eds.), *Discoveries in aquatic animal ecology presented by stable isotope scope, Bivalve to Whale* (pp. 137–152). Koseisha Koseikaku. (in Japanese).
- Murai, R., Sugimoto, A., Tanabe, S., & Takeuchi, I. (2008). Biomagnification profiles of tributyltin (TBT) and triphenyltin (TPT) in Japanese coastal food webs elucidated by stable nitrogen isotope ratios. *Chemosphere*, 73, 1749–1756. <https://doi.org/10.1016/j.chemosphere.2008.09.004>
- Narazaki, T., Sato, K., & 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. <https://doi.org/10.1007/s00227-015-2666-0>
- Nishimura, W., & Nakahigashi, S. (1990). Incidental capture of sea turtles by Japanese research and training vessels: results of a questionnaire. *Marine Turtle Newsletters*, 51, 4.
- Nishizawa, H., Narazaki, T., Fukuoka, T., Sato, K., Hamabata, T., Kinoshita, M., & Arai, N. (2014). Genetic composition of loggerhead turtle feeding aggregations: Migration patterns in the North Pacific. *Endangered Species Research*, 24, 85–93. <https://doi.org/10.3354/esr00588>
- Nobetsu, T., Minami, H., Kiyota, M., Shiode, D., Matsunaga, H., Okazaki, M., & Nakano, H. (2003). Oceanic migration of post-nesting loggerhead turtles (*Caretta caretta*) in the northwestern North Pacific tracked by satellite telemetry. In N. Arai (Ed.), *Proc 4th SEASTAR2000 Workshop* (pp. 28–31). Kyoto University.
- Nobetsu, T., Minami, H., Matsunaga, H., Kiyota, M., & Yokota, K. (2004). Nesting and post-nesting studies of loggerhead turtles (*Caretta caretta*) at Omaezaki, Japan. In N. Arai (Ed.), *Proc 5th SEASTAR2000 Workshop* (pp. 30–33). Kyoto University.
- Oki, K., Hamabata, T., Arata, T., Parker, D. M., Ng, C. K. Y., & Balazs, G. H. (2019). Inferred adult foraging grounds of two marine turtle species nesting at Amami-Oshima, Japan. *Chelonian Conservation and Biology*, 18, 91–97. <https://doi.org/10.2744/CCB-1337.1>
- Okuyama, J., Ishii, H., Tanizaki, S., Suzuki, T., Abe, O., Nishizawa, H., Yano, A., Tsujimura, M., Ishigaki, T., Ishigaki, T., Kobayashi, M., & Yanagida, H. (2020). Quarter-century (1993–2018) nesting trends in the peripheral populations of three sea turtle species at Ishigakijima Island, Japan. *Chelonian Conservation and Biology*, 19(1), 101–110. <https://doi.org/10.2744/CCB-1428.1>
- Okuyama, J., Kitagawa, T., Zenimoto, K., Kimura, S., Arai, N., Sasai, Y., & Sasaki, H. (2011). Trans-Pacific dispersal of loggerhead turtle hatchlings inferred from numerical simulation modeling. *Marine Biology*, 158, 2055–2063. <https://doi.org/10.1007/s00227-011-1712-9>
- Omaezaki City. (2020). *The statuses of landing, nesting and hatching of loggerhead turtles in Omaezaki city*. Accessed May 26, 2020. <https://www.city.omaezaki.shizuoka.jp/soshiki/shakaikyoiku/bunka/omaezakinoumigame/umigametoukeishiryo/jorikusanranhuka.html> (in Japanese)
- Pajuelo, M., Bjorndal, K. A., Reich, K. J., Vander Zanden, H. B., Hawkes, L. A., & Bolten, A. B. (2012). Assignment of nesting loggerhead turtles to their foraging areas in the Northwest Atlantic using stable isotopes. *Ecosphere*, 3, 1–18. <https://doi.org/10.1890/ES12-00220.1>
- Pfaller, J. B., Pajuelo, M., Vander Zanden, H. B., Andrews, K. M., Dodd, M. G., Godfrey, M. H., Griffin, D. B. B., Ondich, B. L., Pate, S. M., Williams, K. L., Shamblin, B. M., Nairn, C. J., Bolten, A. B., & Bjorndal, K. A. (2020). Identifying patterns in foraging-area origins in breeding aggregations of migratory species: Loggerhead turtles in the Northwest Atlantic. *PLoS One*, 15(4), e0231325. <https://doi.org/10.1371/journal.pone.0231325>
- R Development Core Team (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Rees, A. F., Al Saady, S., Broderick, A. C., Coyne, M. S., Papatanasopoulou, N., & Godley, B. J. (2010). Behavioural polymorphism in one of the world's largest populations of loggerhead sea turtles *Caretta caretta*. *Marine Ecology Progress Series*, 418, 201–212. <https://doi.org/10.3354/meps08767>
- Rees, A. F., Alfaro-Shigueto, J., Barata, P. C. R., Bjorndal, K. A., Bolten, A. B., Bourjea, J., & Godley, B. J. (2016). Are we working towards global research priorities for management and conservation of sea turtles? *Endangered Species Research*, 31, 337–382. <https://doi.org/10.3354/esr00801>
- Rundel, C. W., Wunder, M. B., Alvarado, A. H., Ruegg, K. C., Harrigan, R., Schuh, A., Kelly, J. F., Siegel, R. B., DeSante, D. F., Smith, T. B., & Novembre, J. (2013). Novel statistical methods for integrating genetic and stable isotope data to infer individual-level migratory connectivity. *Molecular Ecology*, 22(16), 4163–4176. <https://doi.org/10.1111/mec.12393>
- Saito, T., Kurita, M., Okamoto, H., Uchida, I., Parker, D., & Balazs, G. H. (2015). Tracking male loggerhead turtle migrations around southwestern Japan using satellite telemetry. *Chelonian Conservation and Biology*, 14, 82–87. <https://doi.org/10.2744/ccab-14-01-82-87.1>
- Sakamoto, W., Bando, T., Arai, N., & Baba, N. (1997). Migration paths of the adult female and male loggerhead turtles *Caretta caretta* determined through satellite telemetry. *Fisheries Science*, 63, 547–552. <https://doi.org/10.2331/fishsci.63.547>
- Scales, K. L., Miller, P. I., Hawkes, L. A., Ingram, S. N., Sims, D. W., & Votier, S. C. (2014). On the front line: Frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *Journal of Applied Ecology*, 51, 1575–1583. <https://doi.org/10.1111/1365-2664.12330>
- Schofield, G., Dimadi, A., Fossette, S., Katselidis, K. A., Koutsoubas, D., Lilley, M. K. S., Luckman, A., Pantis, J. D., Karagouni, A. D., & Hays, G. C. (2013). Satellite tracking large numbers of individuals to infer population level dispersal and core areas for the protection of an endangered species. *Diversity and Distributions*, 19, 834–844. <https://doi.org/10.1111/ddi.12077>
- Schofield, G., Klaassen, M., Papafitsoros, K., Lilley, M. K., Katselidis, K. A., & Hays, G. C. (2020). Long-term photo-id and satellite tracking reveal sex-biased survival linked to movements in an endangered species. *Ecology*, 101, e03027. <https://doi.org/10.1002/ECY.3027>
- Seminoff, J. A., Abreu-Grobois, F. A., Alfaro-Shigueto, J., Balazs, G. H., Hatase, H., Jones, T. T., & Matsuzawa, Y. (2018). The Pacific loggerhead, so excellent a connector. *SWOT Report*, 13, 12–17.
- Seminoff, J. A., Benson, S. R., Arthur, K. E., Eguchi, T., Dutton, P. H., Tapilatu, R. F., & Popp, B. N. (2012). Stable isotope tracking of endangered sea turtles: validation with satellite telemetry and $\delta^{15}N$ analysis of amino acids. *PLoS One*, 7, e37403. <https://doi.org/10.1371/journal.pone.0037403>
- Seminoff, J. A., Eguchi, T., Carretta, J., Allen, C. D., Prosperi, D., Rangel, R., Gilpatrick, J. W., Forney, K., & Peckham, S. H. (2014). Loggerhead sea turtle abundance at a foraging hotspot in the eastern Pacific Ocean: Implications for at-sea conservation. *Endangered Species Research*, 24, 207–220. <https://doi.org/10.3354/esr00601>
- Tsukamoto, K., Miller, M. J., Kotake, A., Aoyama, J., & Uchida, K. (2009). The origin of fish migration: The random escapement hypothesis. In A. Haro, K. L. Smith, R. A. Rulifson, C. M. Moffitt, R. J. Klauda, M. J. Dadswell, R. A. Cunjak, J. E. Cooper, K. L. Beal, & T. S. Avery (Eds.) *Challenges for diadromous fishes in a dynamic global environment*, *American Fisheries Society Symposium*, 69, 45–61. <https://doi.org/10.47886/9781934874080>
- Turner Tomaszewicz, C. N., Seminoff, J. A., Avens, L., Goshe, L. R., Peckham, S. H., Rguez-Baron, J. M., Bickerman, K., & Kurle, C. M. (2015). Age and residency duration of loggerhead turtles at a North Pacific bycatch hotspot using skeletochronology. *Biological Conservation*, 186, 134–142. <https://doi.org/10.1016/j.biocon.2015.03.015>
- Wallace, B. P., DiMatteo, A. D., Hurley, B. J., Finkbeiner, E. M., Bolten, A. B., Chaloupka, M. Y., Hutchinson, B. J., Abreu-Grobois, F. A., Amorocho, D., Bjorndal, K. A., Bourjea, J., Bowen, B. W., Dueñas, R. B., Casale, P., Choudhury, B. C., Costa, A., Dutton, P. H., Fallabrino, A., Girard, A., ... Mast, R. B. (2010). Regional management units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. *PLoS One*, 5(12), e15465. <https://doi.org/10.1371/journal.pone.0015465>
- Watanabe, K. K., Hatase, H., Kinoshita, M., Omuta, K., Bando, T., Kamezaki, N., Sato, K., Matsuzawa, Y., Goto, K., Nakashima, Y., Takeshita, H., Aoyama, J., & Tsukamoto, K. (2011). Population structure of the loggerhead turtle *Caretta caretta*, a large marine carnivore that exhibits alternative foraging behaviors. *Marine Ecology Progress Series*, 424, 273–283. <https://doi.org/10.3354/meps08989>

- Watanabe, S., Kodama, M., & Fukuda, M. (2009). Nitrogen stable isotope ratio in the manila clam, *Ruditapes philippinarum*, reflects eutrophication levels in tidal flats. *Marine Pollution Bulletin*, 58, 1447–1453. <https://doi.org/10.1016/j.marpolbul.2009.06.018>
- Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S., & Holmes, R. T. (2002). Links between worlds: Unraveling migratory connectivity. *Trends in Ecology & Evolution*, 17, 76–83. [https://doi.org/10.1016/S0169-5347\(01\)02380-1](https://doi.org/10.1016/S0169-5347(01)02380-1)
- Whitehead, H., Christal, J., & Dufault, S. (1997). Past and distant whaling and the rapid decline of sperm whales off the Galápagos Islands. *Conservation Biology*, 11, 1387–1396. <https://doi.org/10.1046/j.1523-1739.1997.96246.x>
- Xue, D., Botte, J., De Baets, B., Accoe, F., Nestler, A., Taylor, P., Van Cleemput, O., Berglund, M., & Boeckx, P. (2009). Present limitations and future prospects of stable isotope methods for nitrate source identification in surface-and groundwater. *Water Research*, 43, 1159–1170. <https://doi.org/10.1016/j.watres.2008.12.048>
- Zbinden, J. A., Bearhop, S., Bradshaw, P., Gill, B., Margaritoulis, D., Newton, J., & Godley, B. J. (2011). Migratory dichotomy and associated phenotypic variation in marine turtles revealed by satellite tracking and stable isotope analysis. *Marine Ecology Progress Series*, 421, 291–302. <https://doi.org/10.3354/meps08871>

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BIOSKETCH

The research team includes a broad group comprised of academic and agency scientists and local research groups in various regions in Japan. The main focuses of our team are the monitoring of long-term nesting trend of threatened sea turtles in Japan, and the ecology, specifically distribution, movement of post-nesting turtles and identification of important areas to assist management and conservation.

Author contributions: J.O. conceived and designed the study. K.T., K.S. and N.S. performed the isotope analysis. J.O., A.W., S.T., M.A., K.F., H.N. and T.N. conducted the field research and data collection. Y.Y. and K.K. supported the field research. J.O. drafted the manuscript. K.T., K.S. and H.N. revised the manuscript. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.