MtDNA Analysis Suggests Local Origin of Pelagic-Stage Juvenile Green Turtles Collected in Japanese Coastal Waters[1]

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Abstract: Understanding the distribution range across the life history of endangered animals is crucial for effective conservation and management planning. However, endangered migratory green turtles with straight carapace lengths (SCLs) of <35 cm have been rarely observed in the northwestern Pacific. Information on wild green turtles with an SCL of <35 cm in this region is therefore scarce. Historically, four individuals with an SCL of <35 cm from the Japanese coasts and an oceanic area in Japan have been reported. From 2011 to 2013, we collected nine turtles with an SCL of <35 cm from Japanese coasts and coastal waters. We reviewed the existing literature and compiled records of newly collected individuals and their mitochondrial deoxyribonucleic acid haplotypes. The combined total of 13 turtles had SCLs ranging from 6.2 to 28.0 cm. Molecular analyses of nine newly collected turtles indicated that most individuals had hatched at green turtle nesting sites on the Ogasawara Islands and islands in the Ryukyu Archipelago. These results suggest that early juvenile green turtles inhabit Japanese waters, and some turtles with an SCL of <35 cm appear to have remained in Japanese waters after leaving their natal beaches in Japan without drifting with the prevailing oceanic currents to central north or eastern Pacific regions. Although the sample size in the present study was small, this is a first step in constructing comprehensive conservation and management plans for green turtles in the northwestern Pacific.

The green turtle (*Chelonia mydas*) belongs to a group of chelonians with a worldwide tropical/temperate distribution and has been classified as globally endangered on the International Union for Conservation of Nature (IUCN) Red List since 1986 (IUCN 2014). It is the largest of all hard-shelled sea turtles; although the hatchlings have carapace lengths (CLs) of only approximately 5 cm, adults reach a CL of 1 m (Hirth 1980). Adult female turtles lay their eggs (80–130 per clutch) on sandy beaches, usually during the summer months (Miller 1997). About 2 months after oviposition, hatchlings emerge from their nests and immediately move toward the sea, swimming actively offshore

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when they reach the water (Musick and Limpus 1997). They are thought to disperse widely in oceanic water and exist as omnivores in pelagic habitats (pelagic stage) (Bolten 2003). Many juvenile green turtles subsequently shift habitat to neritic waters (neritic stage) with a concomitant dietary shift to primarily herbivory (Bolten 2003) at a CL of 20–35 cm in the Atlantic (Meylan et al. 2011) and 35–40 cm in the Pacific (Limpus et al. 2005). Like most marine turtle species, the distribution and ecology of pelagic-stage green turtles are the least well-characterized parts of their life history because of the poor accessibility of widely dispersed small animals in the vast ocean. This life stage is therefore termed the "lost years." Recent technological advances have enabled direct observation of the initial migration routes of early juvenile marine turtles (Mansfield et al. 2014), assessment of the dietary shift (e.g., Arthur et al. 2008), and simulation of possible offshore dispersal pathways (e.g., Putman and Naro-Maciel 2013, Scott et al. 2014), and the duration of the pelagic stage is now estimated to be 3–5 yr for green turtles in the Bahamas (Reich et al. 2007). However, our knowledge of the ecology of green turtles in the pelagic stage is still insufficient compared with that of the neritic-stage turtles and the most accessible nesting females. Lacking basic information regarding their early life stages impedes comprehensive conservation and estimation of the anthropogenic impact on these animals in the early stages of development. Filling the gap in our knowledge of their life history is significant not only from the viewpoint of biological interest, but also for conservation and management.

Green turtle nesting sites on North Pacific shores of Japan are located on the Ogasawara Islands (Nishizawa et al. 2013) and the Ryukyu Archipelago (Nishizawa et al. 2011, Hamabata et al. 2014) (Figure 1). They occupy the coasts of the Japanese main islands and Ryukyu Archipelago, where sea grass and algae are distributed (Nishizawa et al. 2013, 2014; Hamabata et al. 2015). Turtle sizes at recruitment to Japanese neritic foraging grounds range from 35 to 40 cm in straight carapace length (SCL) (e.g., Okamoto et al. 2011, Hamabata et al. 2015) and are similar to neritic recruitment sizes in other Pacific sites. The pelagic period, during which green turtles grow to a juvenile size of approximately 35 cm SCL after hatching on Japanese beaches, is referred to as the "lost years" for Japanese green turtles. The Japanese literature lists a collection of four green turtles with SCLs ≤16.5 cm found at the coasts and an oceanic area of Ryukyu Archipelago (Hirate and Kimura 1996, Shima 1999, Kameda et al. 2013). More recently, nine small green turtles with SCLs ≤28.0 cm were collected off Japanese coasts. These records may contribute to future studies of offshore dispersal and the growth rates of wild green turtle hatchlings in the northwestern (NW) Pacific and are also expected to contribute to the comprehensive conservation of green turtles in this region. We herein report the sizes and geographical locations of small turtles found along Japanese coasts and coastal waters and present a review of the available Japanese literature. We also infer the possible natal regions of green turtles based on their mitochondrial deoxyribonucleic acid (mtDNA) haplotypes. We discuss green turtle offshore dispersal in comparison with the loggerhead turtle (*Caretta caretta*), which also hatches on Japanese coasts.

MATERIALS AND METHODS

In total, 13 green turtles were found in Japanese waters from 1996 to 2013. SCLs of all individuals were measured. Four turtles were from historical collections described in the literature, and tissue samples were not preserved (Table 1). Muscle samples were taken from eight green turtle carcasses from 2011 to 2013 (identification numbers [IDs]: 5, 6, and 8–13) (Table 2) and preserved in 99% ethanol at room temperature. Blood was taken from one cold-stunned turtle in 2012 (ID: 7) (Table 2) after an 8-month rehabilitation period in the Oga Aquarium. The blood was anticoagulated with heparin and frozen until laboratory analysis. We isolated tissue DNA using a DNeasy Blood and Tissue Kit (Qiagen). Polymerase chain reaction amplification and sequencing were performed using the primers LCM15382 and H950 (Abreu-Grobois et al.

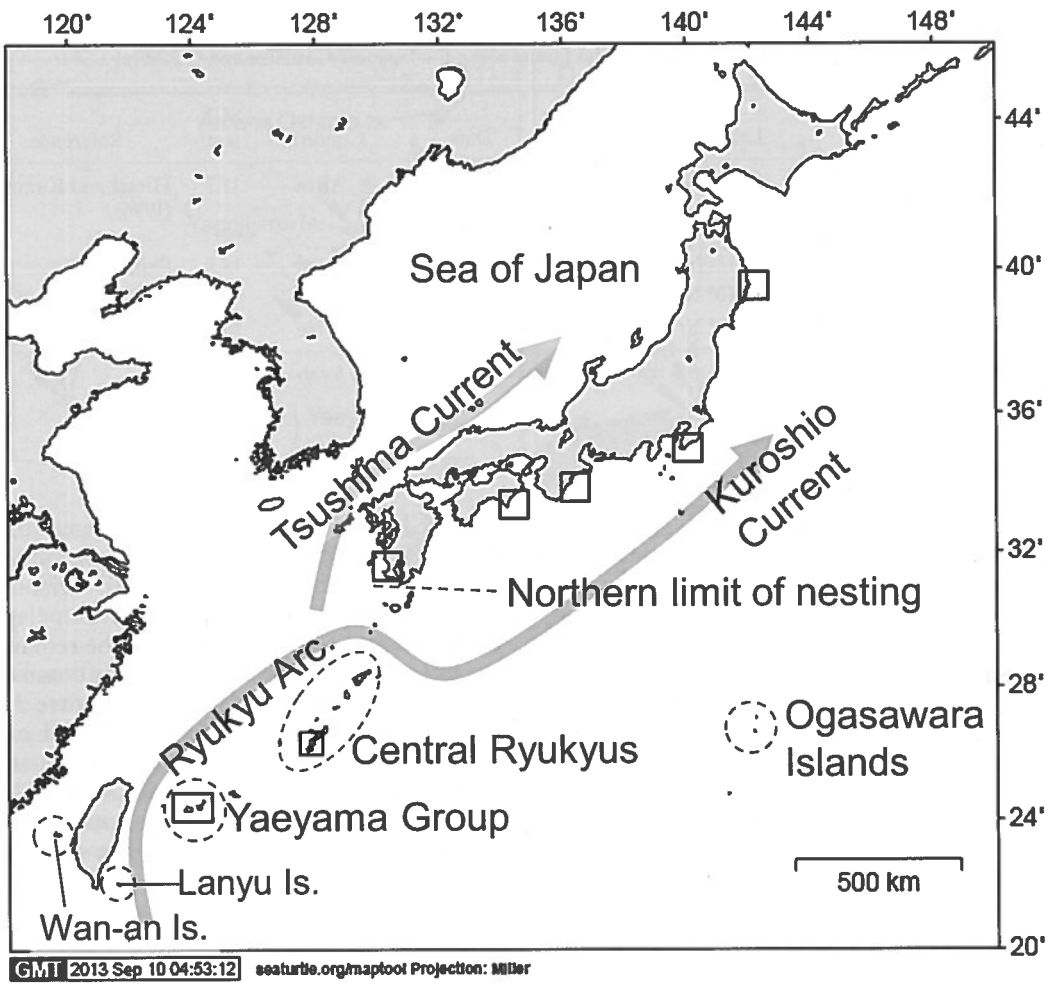

FIGURE 1. Locations of green turtle nesting sites in Japan and Taiwan (dashed circles). The northern limit of nesting is indicated by the dashed line. Gray lines represent the typical year-round tracks of the Kuroshio and Tsushima Currents; arrows indicate directions of current flow. Squares indicate the foraging grounds, which were genetically confirmed as foraging aggregates by neritic-stage green turtles sourced from Japanese rookeries (Hamabata et al. 2009, 2015; Nishizawa et al. 2013, 2014).

2006), which were designed targeting 820 bp in a partial sequence of tRNA-Pro and the 5′ end of the mtDNA control region. Polymerase chain reaction and cycle sequencing were performed as described previously (Hamabata et al. 2015). Haplotypes of mtDNA were determined by comparing results with previous genetic studies on nesting populations of western Pacific green turtles (Dethmers et al. 2006; Cheng et al. 2008; Nishizawa et al. 2011, 2013; Hamabata et al. 2014; Ng et al. 2014*a*).

We estimated approximate ages of wild turtles using growth records for captive hatchlings in Ogasawara (Kurata et al. 1984), when turtles possessed the haplotype found in rookeries of the NW Pacific. However, the growth rates of captive animals are not readily applicable to wild animals because captive turtles likely grow more quickly due to their generous diet (Bjorndal 1985). On average, the captive green turtles on Ogasawara reached an SCL of 15.2 cm in 6 months and 16.4 cm

TABLE 1

Historical Records of Green Turtles Found along the Japanese Coastline and Offshore

ID	Locality	Latitude/Longitude	Date	Condition	SCL (cm)	Reference
1	Between Miyakojima and Okinawajima islands	25.84° N/126.75° E	15 March 1996	Alive	15.7	Hirate and Kimura (1996)
2	Iriomotejima Island	24.32° N/123.68° E	13 June 1999	Dead	15.0	Shima (1999)
3	Iriomotejima Island	24.40° N/123.83° E	28 October 2010	Alive	6.2	Kameda et al. (2013)
4	Iriomotejima Island	24.42° N/123.80° E	2 April 2011	Alive	16.5	Kameda et al. (2013)

Notes: No genetic data were provided with these records. Ages were not estimated for these specimens.

in 9 months (Kurata et al. 1984). These growth rates were therefore used to establish the maximum possible rates for wild conspecifics, and rough age estimates for wild animals were obtained. The nesting and hatchling periods vary with latitude. Therefore, we did not estimate the ages of four turtles described in the literature, the origins of which were unknown, because a lack of information on hatching season increases uncertainty in age estimations. We followed the terminology proposed by Musick and Limpus (1997) to describe the life stages of the sea turtles.

RESULTS

The SCLs of the 13 green turtles ranged from 6.2 to 28.0 cm (Tables 1 and 2). Eight turtles were found along the coast and offshore among islands of the Ryukyu Archipelago (IDs: 1–6 and 11–12) (Figure 2*a*); the remaining five turtles were found along the coasts of the Sea of Japan (IDs: 7–10, 13) (Figure 2*b*). Four turtles were alive when found. The circumstances of discovery for one of the live turtles (ID: 1) were recorded in detail. This turtle was captured at sea (location: 25° 50′ 08″ N, 126° 45′ 07″ E) with floating sea algae

TABLE 2

Records of the Green Turtles Found in Japanese Waters from 2011 to 2013

ID	Locality	Latitude/Longitude	Date	Condition	SCL (cm)	Sex	Haplotype
Individuals at 5–7 months old							
5	Okinawajima Island	26.63° N/128.07° E	25 December 2011	Dead	9.4	—	CmP39.1
6	Yagajijima Island	26.65° N/128.02° E	29 December 2011	Dead	7.7	—	CmP39.1
7	Akita Prefecture	40.00° N/139.88° E	22 December 2012	Alive	11.7	—	CmP50.1
8	Fukui Prefecture	36.15° N/136.08° E	29 January 2013	Dead	10.1	—	CmP50.1
9	Fukui Prefecture	35.60° N/135.85° E	1 February 2013	Dead	12.2	—	CmP50.1
10	Fukui Prefecture	35.93° N/135.98° E	11 February 2013	Dead	12.2	—	CmP54.1
Individuals turtles at ≥1 yr old							
11	Amami Oshima Island	28.38° N/129.48° E	9 January 2012	Dead	28.0	M	CmP39.1
12	Amami Oshima Island	28.40° N/129.45° E	6 February 2013	Dead	22.8	—	CmP50.1
13	Akita Prefecture	40.03° N/139.92° E	6 March 2013	Dead	27.5	M	CmP49.1

Note: Sex was known for only two of the turtles (IDs 11 and 13).

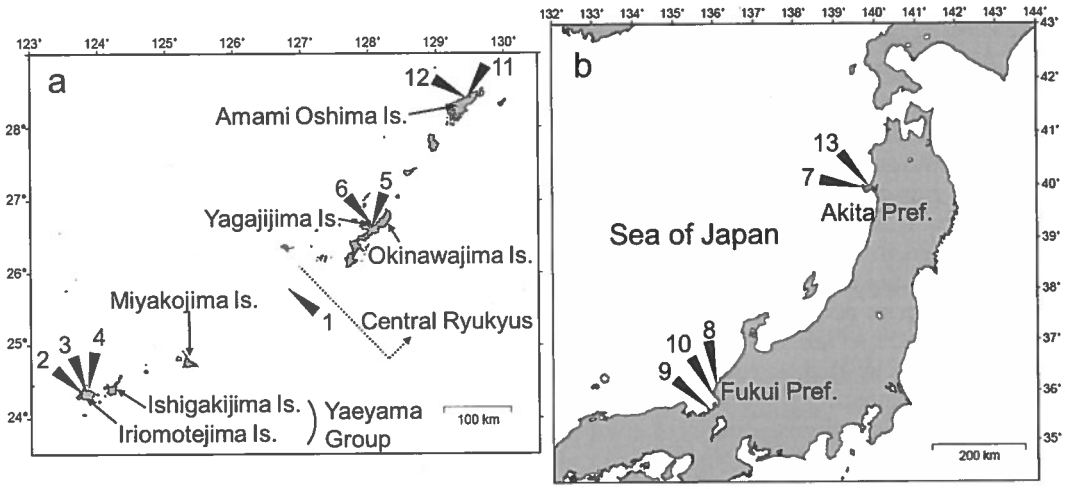

FIGURE 2. Extended maps of the islands in the Yaeyama Group and the central Ryukyus (Ryukyu Archipelago) (*a*) and the coastline of the Sea of Japan (*b*). Triangles represent locations where juvenile green turtles were found. Numbers refer to ID designations of individual in Tables 1 and 2.

and artifacts, and its diving behavior and active swimming in the tank were noted (Hirate and Kimura 1996). One turtle found in the coastal water of the Sea of Japan was cold-stunned and rescued in Oga Aquarium (ID: 7). The remaining two living individuals (IDs: 3 and 4) were found at the northern coast of Iriomotejima Island and released after rehabilitation (Kameda et al. 2013). Nine turtles were found dead as carcasses stranded on the coasts (IDs: 2, 5, 6, and 8–13).

We obtained molecular data for the nine newly collected turtles (IDs: 5–13) and identified four haplotypes among them. Four individuals possessed haplotype CmP50.1 (GenBank Accession no. AB819809), identified as CMJ25 in short 500-bp or 380-bp sequences. Three individuals possessed haplotype CmP39.1 (GenBank Accession no. AB819807), identified as CMJ18 in short 500-bp or 380-bp sequences. One individual each possessed haplotype CmP54.1 (GenBank Accession no. AB819811), identified as CMJ6 in short 500-bp or 380-bp sequences, and haplotype CmP49.1 (GenBank Accession no. AB819808), identified as CMJ30 in 500-bp and C3 in 380-bp sequences (Table 2).

Most green turtle nesting occurs in the period from mid-May to late July in the Ryukyu Archipelago and on the Ogasawara Islands (e.g., Abe 2000, Yamaguchi et al. 2005). Hatchlings emerge from late July to September in this region. Thus, wild individuals with an SCL of <12.2 cm (IDs: 5–10) were probably 5–7 months old and had likely hatched in the previous reproductive season on Japanese beaches. The wild turtles that were much larger than captive 9-month-old animals in Ogasawara (IDs: 11–13; 22.8–28.0 cm SCL) were all collected during the winter (January–March). Thus, they were not born in the previous reproductive season in Japan and were likely ≥1 year old.

DISCUSSION

In this study, we first analyzed the genetic haplotypes of early juvenile green turtles found in the coasts and coastal waters of Japan and successfully identified four haplotypes from nine individuals. The most frequent haplotype, CmP50.1, was found in the Ogasawara, central Ryukyu, and Yaeyama (Ishigakijima and Iriomotejima) nesting populations (Nishizawa et al. 2011, 2013; Hamabata et al. 2014). CmP39.1 identified from three individuals was found in the Ogasawara, central Ryukyu, and Ishigakijima in Yaeyama

nesting populations (Nishizawa et al. 2011, 2013; Hamabata et al. 2014). CmP54.1 identified from one individual was found in the Ogasawara and Yaeyama (Ishigakijima and Iriomotejima) nesting populations (Nishizawa et al. 2011, 2013). These three haplotypes have not been reported in rookeries outside of Japan. In contrast, haplotype CmP49.1, which was identified in one individual collected on the coast of Akita Prefecture, is widespread in diverse rookeries across the Indo-Pacific region (Dethmers et al. 2006, Dutton et al. 2014). In the NW Pacific, this haplotype has been found in nesting populations of Ogasawara, central Ryukyus, and at Lanyu in Taiwan (Cheng et al. 2008, Nishizawa et al. 2013, Hamabata et al. 2014). Thus, eight of the nine turtles had haplotypes endemic to Japanese rookeries and had probably hatched on Japanese beaches. Unfortunately, we could not infer the natal origins of four individuals reported in the literature, so their ages were not estimated. The SCL range of 6.2 to 28.0 cm is, however, distinctly in the pelagic stage. The fact that the early juvenile turtles, including several living turtles, were found in Japanese waters during the nonhatching season of Japanese rookeries strongly suggested that turtles at this stage do indeed inhabit Japanese waters, and some have their origin in Japanese rookeries.

All turtles from Sea of Japan waters were collected from the eastern half of the coasts in winter, when the sea surface temperature (SST) had dropped below 12°C at each sample locality (Japan Meteorological Agency: http://www.data.jma.go.jp/kaiyou/data/db/kaikyo/daily/sst_HQ.html). Experiments showed that the swimming activity of green turtle hatchlings is reduced at such low temperatures (Tabata et al. 2014). Although the season when each early juvenile turtle entered the Sea of Japan was not known, it is likely that they became cold-stunned and stranded because their swimming performance declined with decreasing water temperature in winter. The surface water layer (<200 m depth) of the Sea of Japan is supplied all year round by the warm Tsushima Current sourced from the Kuroshio region and East China Sea (Isobe 1999). Whereas the coastal SST of the Sea of Japan falls to near or blow 10°C in winter, it remains at 12°C–15°C at the western half of coasts even in winter (Japan Meteorological Agency: http://www.data.jma.go.jp/kaiyou/data/db/kaikyo/daily/sst_HQ.html). Thus, the winter SST in the eastern half of the coast can cause cold-stunning and stranding of early juvenile turtles, leading to high mortality rates as in the turtles described herein. However, an SST of 12°C–15°C may not be always fatal for green turtles; turtles with an SCL of >35 cm are sometimes captured alive off the coast of Fukui Prefecture and to the west of the Sea of Japan in the period from summer to winter (Fukui Coastal Nature Center 2008, Hamabata et al. 2009). Pelagic-stage green turtles may also survive over winter in some parts of the Sea of Japan.

In the present study, estimates of the origins of early juvenile turtles were based on only nine individuals. Data from such a small sample size must be interpreted with caution. However, the retention of pelagic-stage green turtles in the local waters may explain the different patterns of offshore dispersal and subsequent habitat shift between loggerhead and green turtles hatched in Japan. Many loggerhead turtle hatchlings that emerge on Japanese beaches appear to be dispersed across the Pacific Ocean to eastern Pacific feeding grounds, where they grow to neritic juvenile stages (Bowen et al. 1995). Unlike loggerhead turtles, green turtles hatched in Japan are rarely found in the foraging grounds in Hawaii (a possible pathway to the eastern Pacific) and the eastern Pacific, and most turtles in these foraging grounds are derived from local nesting populations (Dutton et al. 2008, Amorocho et al. 2012). Whereas loggerhead turtles are recruited into the Japanese neritic habitats at an SCL of 56 to 75 cm (Ishihara et al. 2011), green turtles hatched in Japan are recruited at an SCL of 35 to 40 cm along the coasts of the Japanese main islands and Ryukyu Archipelago (Figure 1). These differences between species may be attributable to their respective juvenile behaviors. Neonate loggerhead turtles are largely inactive in their nursery habitats (Witherington 2002) and are transported to productive oceanic feeding grounds by major currents, if not entirely in a

passive manner (reviewed by Mansfield and Putman 2013). In contrast, green turtle hatchlings swim actively (Balazs 1980, Hirate and Kimura 1996, Wyneken 1997, Witherington et al. 2012) and may be able to disperse independent of prevailing surface currents (Balazs 1980). Early active behavior of green turtles is likely to contribute to avoidance of the prolonged current drift in the oceanic environment, consequently enabling them to be recruited to the neritic habitats at an earlier life stage than loggerhead turtles are. The behavioral differences in early stages between loggerhead and green turtles likely have effects on the differences in hatchling and juvenile distributions, enabling each species to reach optimal foraging sites with optimal timing. However, an alternative green turtle life history pattern has been suggested in which they remain longer in oceanic habitats up to subadult and adult stages in some locations (Hatase et al. 2006, Parker et al. 2011). Future studies based on larger sample sizes or with more sophisticated methods are needed to clarify the differences and adaptive evolution in offshore dispersal from Japan in these two species, which hatch on the same or nearby beaches at almost the same time. The present study provides evidence and supportive data for such future studies.

Our discovery of small turtles was in large part attributable to the increased attention and efforts by local people and professional researchers in Japan now being focused on marine turtles. Notably, however, local children sometimes take hatchlings from beaches (e.g., Iriomotejima Island, Yaeyama Group) and keep them as pets for a short while before releasing them (Kameda et al. 2013), so it is possible that the small turtles we collected and reviewed in this study had been kept previously as pets (Kameda et al. 2013). Turtles that hatch on beaches immediately enter a frenzy period when they move quickly to the water and swim rapidly offshore. The intensity of this behavior is markedly reduced in hatchlings kept briefly as pets; these turtles disperse over much shorter distances out to sea (Okuyama et al. 2009) and may easily drift back and become stranded on shore. We do not have evidence to show that all small turtles collected in waters off the Japanese coast had previously been kept in captive environments, but it is important to realize that anthropogenic effects may influence the migratory patterns of these animals.

The results of the present study must be interpreted with caution. However, this study represents a first step in constructing comprehensive conservation and management plans for green turtles in the NW Pacific. Green turtle nesting populations in the NW Pacific region include a genetically endemic lineage and have evolutionary significance (Hamabata et al. 2014). Fortunately, recovering trends in the number of nesting females have been reported (Chaloupka et al. 2008). However, the population sizes in this region are relatively small due to their northern limit distribution range (the annual number of clutches is a few thousand at most in regional total), and therefore they are vulnerable. Although conservation efforts in the nesting sites seem to have been successful, threats and dangers faced by local early juvenile turtles in the oceanic environment and coastal waters have not been assessed (however, see Ng et al. 2014*b*). This study represents a starting point to gain an understanding of the ecology and threats to green turtles in the "lost years" stage in the NW Pacific.

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Literature Cited

Abe, O. 2000. Nesting activity of sea turtles in Ishigaki Island, Yaeyama Group. Study report of 1999. Available from the HP of

the Seikai National Fisheries Research Institute. [In Japanese.] http://snf.fra.affrc.go.jp/seika/snf99/snf99004.htm.

Abreu-Grobois, F. A., J. A. Horrocks, B. Krueger, A. Formia, and J. Beggs. 2006. New mtDNA dloop primers which work for a variety of marine turtle species may increase the resolution of mixed stock analyses. Book of abstracts from the 26th Annual Symposium on Sea Turtle Biology and Conservation. International Sea Turtle Society 179. ISBN: 9608792614. International Sea Turtle Society, La Jolla, California.

Amorocho, D. F., F. A. Abreu-Grobois, P. H. Dutton, and R. D. Reina. 2012. Multiple distant origins for green sea turtles aggregating off Gorgona Island in the Colombian Eastern Pacific. PLoS ONE 7 (2): e31486. doi:10.1371/journal.pone.0031486.

Arthur, K. E., M. C. Boyle, and C. J. Limpus. 2008. Ontogenetic changes in diet and habitat use in green sea turtle (*Chelonia mydas*) life history. Mar. Ecol. Prog. Ser. Vol. 362:303–311.

Balazs, G. H. 1980. Synopsis of biological data on the green turtle in the Hawaiian Island. National Oceanic and Atmospheric Administration, Southwest Fisheries Center Administrative Report H-79-24-C. NOAA Fisheries, Southwest Fisheries Science Center, La Jolla, California.

Bjorndal, K. A. 1985. Nutritional ecology of sea turtles. Copeia 3:736–751.

Bolten, A. B. 2003. Variation in sea turtle life history patterns: Neritic vs. oceanic developmental stages. Pages 243–257 *in* P. L. Lutz, J. A. Musick, and J. Wyneken, eds. The biology of sea turtles. Vol. 2. CRC Press, Boca Raton, Florida.

Bowen, B. W., F. A. Abreu-Grobois, G. H. Balazs, N. Kamezaki, C. J. Limpus, and R. J. Ferl. 1995. Trans-Pacific migrations of the loggerhead turtle (*Caretta caretta*) demonstrated with mitochondrial DNA markers. Proc. Natl. Acad. Sci. U.S.A. 92: 3731–3734.

Chaloupka, M., K. A. Bjorndal, G. H. Balazs, A. B. Bolten, L. M. Ehrhart, C. J. Limpus, H. Suganuma, S. Troëng, and M. Yamaguchi. 2008. Encouraging outlook for recovery of a once severely exploited marine megaherbivore. Glob. Ecol. Biogeogr. 17: 297–304.

Cheng, I.-J., P. H. Dutton, C.-L. Chen, H.-C. Chen, Y.-H. Chen, and J.-W. Shea. 2008. Comparison of the genetics and nesting ecology of two green turtle rookeries. J. Zool. Lond. 276:375–384.

Dethmers, K. E. M., D. Broderick, C. Moritz, N. N. Fitzsimmons, C. J. Limpus, S. Lavery, S. Whiting, M. Guinea, R. I. T Prince, and R. Kennett. 2006. The genetic structure of Australasian green turtles (*Chelonia mydas*): Exploring the geographical scale of genetic exchange. Mol. Ecol. 15:3931–3946.

Dutton, P. H., G. H. Balazs, R. A. LeRoux, Sh. K. K. Murakawa, P. Zarate, and L. S. Martines. 2008. Composition of Hawaiian green turtle foraging aggregations: mtDNA evidence for a distinct regional population. Endanger. Species Res. 5:37–44.

Dutton, P. H., M. P. Jensen, K. Frutchey, A. Frey, E. LaCasella, G. H. Balazs, J. Cruce, A. Tagarino, R. Farman, and M. Tatarata. 2014. Genetic stock structure of green turtle (*Chelonia mydas*) nesting populations across the Pacific Islands. Pac. Sci. 68: 451–464.

Fukui Coastal Nature Center. 2008. Survey report of marine turtles at the fisheries associations of Fukui. 3. Surveys of the coastal sea area of Shikimi beach. [In Japanese.] http://www.fcnc.jp/banner/summery.html.

Hamabata, T., T. Hikida, K. Okamoto, S. Watanabe, and N. Kamezaki. 2015. Ontogenetic habitat shifts of green turtles (*Chelonia mydas*) suggested by the size modality in foraging aggregations along the coasts of the western Japanese main islands. J. Exp. Mar. Biol. Ecol. 463:181–188.

Hamabata, T., N. Kamezaki, and T. Hikida. 2014. Genetic structure of green turtle (*Chelonia mydas*) peripheral populations nesting in the northwestern Pacific rookeries: Evidence for northern refugia and postglacial colonization. Mar. Biol. 161: 495–507.

Hamabata, T., S. Nishida, N. Kamezaki, and H. Koike. 2009. Genetic structure of populations of the green turtle (*Chelonia mydas*)

in Japan using mtDNA control region sequences. Bull. Grad. School. Soc. Cult. Stud. Kyushu Univ. 15:35–50.

Hatase, H., K. Sato, M. Yamaguchi, K. Takahashi, and K. Tsukamoto. 2006. Individual variation in feeding habitat use by adult female green sea turtles (*Chelonia mydas*): Are they obligate neritic herbivores? Oecologia (Berl.) 149:52–64.

Hirate, K., and M. Kimura. 1996. Rapid communication: A capture of the young green turtle in the drifting phase (lost aged phase) from the adjacent water of the Ryukyu Archipelago. [In Japanese.] Umigame News Lett. 29:10–11.

Hirth, H. 1980. Some aspects of the nesting behavior and reproductive biology of sea turtles. Am. Zool. 20 (3): 507–523.

International Union for Conservation of Nature. 2014. The IUCN Red List of Threatened Species. Version 2014.3. Accessed 10 April 2015. www.iucnredlist.org.

Ishihara, T., N. Kamezaki, Y. Mztsuzawa, F. Iwamoto, T. Oshika, Y. Miyagata, C. Ebisui, and S. Yamashita. 2011. Reentery of Juvenile and sub-adult loggerhead turtles into natal waters of Japan. Curr. Herpetol. 30: 63–68.

Isobe, A. 1999. On the origin of the Tsushima Warm Current and its seasonality. Cont. Shelf Res. 19 (1): 117–133.

Kameda, K., Y. Asari, K. Sugitani, and M. Wakatsuki. 2013. Stranding status of sea turtles at Iriomote Island, Okinawa Prefecture, Japan. [In Japanese.] Umigame News Lett. 96:2–8.

Kurata, Y., Y. Aoki, and J. Kimura. 1984. Study on bioresources of immature green turtles. [In Japanese.] Res. Rep. Tokyo Metrop. Fish. Exp. Station 186:25–31.

Limpus, C. J., D. J. Limpus, K. E. Arther, and C. J. Parmenter. 2005. Monitoring green turtle population dynamics in Shoalwater Bay: 2000–2004. Queensland Environmental Protection Agency and the Great Barrier Reef Marine Park Authority, Queensland, Australia.

Mansfield, K. L., and N. F. Putman. 2013. Oceanic habits and habitats: *Caretta caretta*. Pages 189–210 *in* J. Wyneken, K. L. Lohmann, and J. A. Musick, eds. The Biology of Sea Turtles. Vol. 3. CRC Press, Boca Raton, Florida.

Mansfield, K. L., J. Wyneken, W. P. Porter, and J. Luo. 2014. First satellite tracks of neonate sea turtles redefine the "lost years" oceanic niche. Proc. R. Soc. B 281:20133039. http://dx.doi.org/10.1098/rspb.2013.3039.

Meylan, P. A., A. B. Meylan, and J. A. Grey. 2011. The ecology and migrations of sea turtles 8: Tests of the developmental habitat hypothesis. Bull. Am. Mus. Nat. Hist. 357:1–70.

Miller, J. D. 1997. Reproduction in sea turtles. Pages 51–81 *in* P. Lutz and J. Musick, eds. The biology of sea turtles. CRC Press, Boca Raton, Florida.

Musick, J. A., and C. J. Limpus. 1997. Habitat utilization and migration in juvenile sea turtles. Pages 137–163 in P. Lutz and J. Musick, eds. The biology of sea turtles. CRC Press, Boca Raton, Florida.

Ng, C. K., P. H. Dutton, S. K. Chan, K. Cheung, J. Qiu, and Y. Sun. 2014*a*. Characterization and conservation concerns of green turtles (*Chelonia mydas*) nesting in Hong Kong, China Pac. Sci. 68 (2): 231–243.

Ng, C. K., C. Tien-His Chen, and G. H. Balazs. 2014*b*. Flying fish egg harvest off Keelung, Taiwan uncovers occurrence of pelagic-phase green turtles. Mar. Turtle Newslett. 143:14–15.

Nishizawa, H, O. Abe, J. Okuyama, M. Kobayashi, and N. Arai. 2011. Population genetic structure and implications for natal philopatry of nesting green turtles *Chelonia mydas* in the Yaeyama Islands, Japan. Endanger. Species Res. 14:141–148.

Nishizawa, H., Y. Naito, H. Suganuma, O. Abe, J. Okuyama, K. Hirate, S. Tanaka, E. Inoguchi, K. Narushima, K. Kobayashi, H. Ishii, S. Tanizaki, M. Kobayashi, A. Goto, and N. Arai. 2013. Composition of green turtle feeding aggregations along the Japanese archipelago: Implications for changes in composition with current flow. Mar. Biol. 160:2671–2685.

Nishizawa, H., T. Narazaki, T. Fukuoka, K. Sato, T. Hamabata, M. Kinoshita, and N. Arai. 2014. Juvenile green turtles on the northern edge of their range: mtDNA

evidence of long-distance westward dispersals in the northern Pacific Ocean. Endanger. Species Res. 24:171–179.

Okamoto, K., T. Ishihara, M. Taniguchi, N. Yamashita, and N. Kamezaki. 2011. Occurrence of the sea turtles at the coastal water of Kumanonada. [In Japanese.] Umigame News Lett. 88:13–17.

Okuyama, J., O. Abe, H. Nishizawa, M. Kobayashi, K. Yoseda, and N. Arai. 2009. Ontogeny of the dispersal migration of green turtle (*Chelonia mydas*) hatchlings. J. Exp. Mar. Biol. Ecol. 379:43–50.

Parker, D. M., P. H. Dutton, and G. H. Balazs. 2011. Oceanic diet and distribution of haplotypes for the green turtle, *Chelonia mydas*, in the Central North Pacific. Pac. Sci. 65:419–431.

Putman, N. F., and E. Naro-Maciel. 2013. Finding the "lost years" in green turtles: Insights from ocean circulation models and genetic analysis. Proc. R. Soc. B 280:20131468. http://dx.doi.org/10.1098/rspb.2013.1468.

Reich, K. J., K. A. Bjorndal, and A. B. Bolten. 2007. The "lost years" of green turtles: Using stable isotopes to study cryptic lifestages. Biol. Lett. 3:712–714.

Scott, R., A. Biastoch, C. Roder, V. A. Stiebens, and C. Eizaguirre. 2014. Nanotags for neonates and ocean-mediated swimming behaviours linked to rapid dispersal of hatchling sea turtles. Proc. R. Soc. B 281:20141209. http://dx.doi.org/10.1098/rspb.2014.1209.

Shima, T. 1999. Rapid communication: Stranding of a young green turtle at the Amitori Bay, Iriomote Is. [In Japanese.] Umigame News Lett. 41:13.

Tabata, R., A. Wada, J. Okuyama, K. Nakajima, M. Kobayashi, and N. Arai. 2014. Difference in activity corresponding to changing water temperature among juvenile green sea turtles. Proc. Des. Symp. Conserv. Ecosyst. 13th SEASTAR2000 Workshop 2:66–69.

Witherington, B. E. 2002. Ecology of neonate loggerhead turtles inhabiting lines of downwelling near a Gulf Stream front. Mar. Biol. 140:843–853.

Witherington, B. E., S. Hirama, and R. Hardy. 2012. Young sea turtles of the pelagic sargassum-dominated drift community: Habitat use, population density, and threats. Mar. Ecol. Prog. Ser. 463:1–22.

Wyneken, J. 1997. Sea turtle locomotion: Mechanisms, behavior, and energetics. Pages 165–198 *in* P. L. Lutz and J. A. Musik, eds. The biology of sea turtles. CRC Press, Boca Raton, Florida.

Yamaguchi, M., H. Suganuma, and K. Narushima. 2005. Nesting status of green turtles (*Chelonia mydas*) in Chichijima Islands, Ogasawara in 2005 and a nesting trend over the last 27 years. [In Japanese.] Unigame News Lett. 66:2–6.