Chelonian Conservation and Biology, 2019, 18(1): 000–000
doi:10.2744/CCB-1337.1

Inferred Adult Foraging Grounds of Two Marine Turtle Species Nesting at Amami-Oshima, Japan

KATSUKI OKI[1], TOMOKO HAMABATA[2,*], TOSHIMITSU ARATA[3], DENISE M. PARKER[4], CONNIE KA YAN NG[5], AND GEORGE H. BALAZS[6]

[1]*Amami Marine Life Association, 99-1 Nase-Hiramatsucho, Amami, Kagoshima, 894-0045, Japan [okika@po.synapse.ne.jp];*
[2]*Graduate School of Life Science, Tohoku University, 6-3 Aramaki Aza Aoba, Aoba-ku, Sendai 980-8578, Japan [tmk.hamabata@gmail.com];*
[3]*Doren Camp-site, 2887-9 Ankyaba, Tatsugo-cho, Amami, Kagoshima, 894-0323, Japan [doren-camp@po2.synapse.ne.jp];*
[4]*Newport, Oregon USA [Denise.M.Parker@outlook.com];*
[5]*Department of Chemistry and State Key Laboratory in Marine Pollution, City University of Hong Kong, Hong Kong Special Administrative Region, People's Republic of China [kayan.ng.connie@gmail.com];*
[6]*Golden Honu Services of Oceania, 992 Awaawaanoa Place, Honolulu, Hawaii 96825 USA [itsahonuworldinhawaii@hotmail.com]*
**Corresponding author*

ABSTRACT. – **During late June and July in 2015, we tracked the postnesting migrations of 5 loggerhead turtles (*Caretta caretta*) and 5 green turtles (*Chelonia mydas*) from a beach on Amami-Oshima Island (Amami) in the Ryukyu Archipelago, Japan, to identify the potential adult foraging grounds of these 2 species of marine turtle. All 5 loggerheads utilized the East China Sea, but 4 took direct paths there while 1 turtle first traveled to and stayed within the Sea of Japan until the water temperature in the area dropped to around 13°C before moving into the East China Sea. In contrast, 3 of the 5 green turtles moved to the coasts of Japan's main islands, 1 green turtle moved to the southwest of the Amami, and 1 green turtle stayed around the Amami throughout the tracking period.**

要旨

2015年**6**月下旬から**7**月にかけて、琉球列島に位置する奄美大島の砂浜で産卵した**2**種のウミガメ類、アカウミガメ**(*Caretta caretta*)**および、アオウミガメ**(*Chelonia mydas*)**について、成熟個体の摂餌域を探索するため、各５個体の産卵後の移動を追跡した。アカウミガメは全ての個体が東シナ海に向けて移動を開始した。その後、４個体はそのまま東シナ海に留まったが、１個体は日本海へ向けてさらに移動を続け、冬季まで日本海に留まった後、日本海の水温がおよそ**13**℃に低下すると東シナ海に南下した。一方、アオウミガメは、５個体中３個体が日本の本州・九州沿岸まで移動し、１個体は奄美大島から南西に向けて移動し、１個体は奄美大島に沿岸に留まった。

摘要

在**2015**年**6**月下旬及**7**月，為確定於日本琉球群島奄美大島海灘上產卵的成年赤蠵龜**(*Caretta caretta*)**及綠海龜**(*Chelonia mydas*)**的潛在覓食地，我們在該處追踪了各五隻赤蠵龜及綠海龜母龜的產後遷徙。全部赤蠵龜均進入東海**:** 其中四隻直接到達東海，另一隻先移至並逗留日本海，直到該區水溫下降至**13 °C**，才進入東海。 相反，在整個追踪期間，其中三隻綠海龜遷移到日本主要島嶼的海岸，一隻遷移到奄美市西南部，另一隻則棲息於奄美海岸一帶。

Mature female marine turtles have site fidelity and strong natal philopatry to their nesting beach (Jensen et al. 2013). Ecological studies have revealed the high fidelity of breeding females to their foraging grounds as well as to their nesting beaches (Limpus et al. 1992; Balazs et al. 2017). In addition, marine turtles can be reproductively active for decades (Balazs et al. 2015). Beaches have been prioritized for marine turtle conservation because adult females and hatchlings are found there and, thus, conservation of beaches protects both life stages. Such programs on beaches have provided good results in many regions and populations; e.g., Chaloupka et al. (2008) for green turtles (*Chelonia mydas*) worldwide, Stewart et al. (2011) for leatherback turtles (*Dermochelys coriacea*) in Florida, Richardson et al. (2006) and Beggs et al. (2007) for hawksbill turtles (*Eretmochelys imbricata*) in the Caribbean region, and Florida Fish and Wildlife Conservation Commission (2017) for loggerhead turtles (*Caretta caretta*) in Florida. The 7 extant species of marine turtles overall show positive trends in abundance (Mazaris et al. 2017). However, some species and populations show limited or no recovery; e.g., Fonseca et al. (2009) for olive ridley turtles (*Lepidochelys olivacea*) in Costa Rica and Tapilatu et al. (2013) for leatherbacks in the western Pacific. Marine turtles that inhabit various ecosystems throughout their life stages face multiple threats (Bolten et al. 2011). Understanding the adult habitat range of each breeding stock is therefore necessary to identify the potential threats and to achieve more-effective management and conservation.

The Japanese Archipelago consists of nearly 6900 islands, 450 of which are human-settled islands (Fig. 1). Three of the seven marine turtle species—loggerheads, greens, and hawksbills—nest in Japan (Kamezaki 1989; Matsuzawa et al. 2016; Kondo et al. 2017). All 3 species are now protected on nesting beaches by regulations set by local prefecture governments. Nesting sites of hawksbills are mostly limited to the islands of the southern Ryukyu Archipelago (Ryukyus), and the population trend of this species is not well understood. On the other hand, loggerheads, which nest on the beaches both in the Japanese main islands and in the Ryukyus, and the green turtle, which nests in the Ogasawara Islands and in the Ryukyus, have wider distributions of nesting sites compared with the hawksbill turtle.

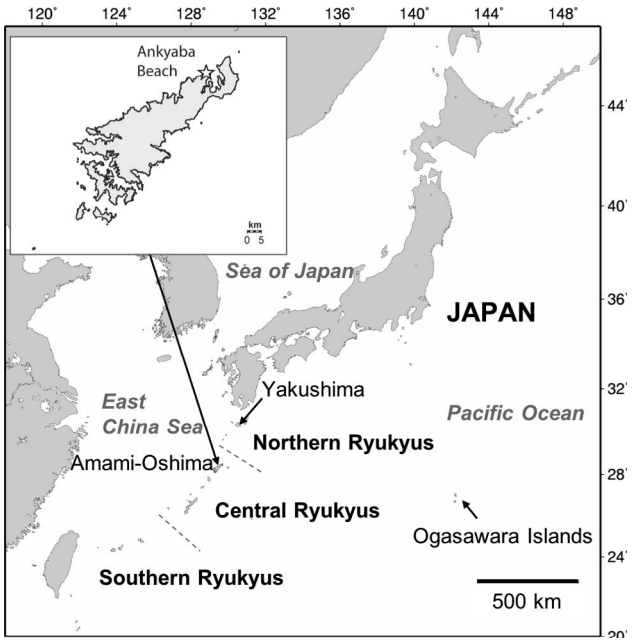

Figure 1. Map of the Japanese Archipelago and the locations of the northern, central, and southern Ryukyu Archipelago (Ryukyus), Amami-Oshima Island, Yakushima, and Ogasawara. Star in the inset map represents the Ankyaba Beach where we conducted this study.

To date, postnesting migrations of loggerhead turtles nesting on the beaches of Japan have been investigated by mark–recapture (Kamezaki et al. 1997) and satellite tracking (Hatase et al. 2002, 2007; Nobetsu et al. 2003). These studies have identified coastal waters in Japan's main islands, the South and East China Seas, and the pelagic Pacific as important foraging grounds for adult female Japanese loggerheads. However, most turtles in these previous studies were tracked from Yakushima in the northern Ryukyus and the Japanese main islands. Only one loggerhead was found along the coast of Vietnam 405 d after it nested in the Miyakojima Islands in the southern Ryukyus (Kamezaki et al. 1997). Little is known about the potential foraging grounds of loggerheads of the central and southern Ryukyus. Similarly, postnesting migrations of green turtles in Ogasawara have revealed that the coasts of Japan's main islands are major foraging sites for green turtles (Hatase et al. 2006). Mixed stock analysis (MSA) based on mitochondrial DNA markers suggested that the coasts of Japan's main islands may also serve as foraging habitat for green turtles from the Ryukyus (Nishizawa et al. 2013). Indeed, size-specific MSA suggested that some Japanese green turtles moved from the Ryukyus to the coasts of Japan's main islands to settle in their adult foraging grounds (Hamabata et al. 2015, 2018). However, green turtle breeding stocks in Japan share many haplotypes among regions, especially between Ogasawara and the central Ryukyus (Hamabata et al. 2014), although they are significantly differentiated by frequency. Thus, there are no direct observations that the coasts of Japan's main islands actually serve as adult foraging grounds for green turtles from the central Ryukyus. Tracking the postnesting migration of green turtles can offer insight into adult habitats of green turtles from the central Ryukyus.

In the present study, the postnesting movements of loggerhead and green turtles nesting on the beaches of Amami-Oshima Island (hereafter referred to as Amami), located on the central Ryukyus, were satellite tracked to identify their potential foraging areas. To our knowledge, this is the first study that resulted in successful satellite tracking of 2 species of marine turtles, loggerheads and greens, nesting on the same beach of the central Ryukyus.

Methods. — Amami-Oshima Island is located in the central Ryukyus (Kizaki 1986; Fig. 1). Nesting surveys of marine turtles covering all the beaches in Amami were first conducted in 2012. In total, 1081 nests were found: 605 nests of loggerhead turtles, 327 nests of green turtles, and 149 nests of unknown species in that year (Oki and Mizuno 2013). Although the number of nests fluctuated from year to year, both loggerhead and green turtles nest on the beaches in Amami every year (K.O., unpubl. data, 2018).

While the nesting season of loggerheads usually starts at the beginning of May and ends in the middle of July, the nesting season of green turtles starts in June and lasts through July, hence the temporal overlap of these sympatric species. During late June and July in 2015, at the Ankyaba beach, northern Amami (Fig. 1), 10 Argos-linked satellite transmitters (TAM2639, Telonics, Inc., USA) were deployed on 5 nesting females of each species (Tables 1 and 2). While females were laying eggs, their straight carapace lengths (SCL) and straight carapace widths (SCW) were measured with a slide caliper. All turtles were marked with flipper tags. We monitored the nesting and emergence activities on the same beach and selected individuals that were expected to be near the end of their reproductive period to avoid the track internesting movements. The transmitters were attached to the carapace of each turtle with fiberglass cloth and polyester resin following the procedure by Balazs et al. (1996).

Location data received from Argos Service were filtered based on the location accuracy. Duty cycles of tags were 6 hrs on, 24 hrs off for all transmitters. We used the data with location class (LC) 3–1, predicting the locations from the animal's actual position within 1000 m, and the other data with LC A, B, and 0 were discarded. The locations of foraging grounds were compared between the present nesting populations and other nesting populations in Japan to determine whether the foraging grounds of two species nesting in the central Ryukyus overlap those of different populations or whether there are unidentified foraging grounds for the 2 species in Japan.

Results. — The loggerhead turtles were tracked for 127–346 d (Table 1). All 5 turtles migrated to the East China Sea (Fig. 2A–E). Although 2 of 5 loggerheads were tracked until or over the winter, they did not exhibit large movements, suggesting site fidelity to their chosen foraging area even in the winter season (Fig. 2C–D).

Table 1. Detailed satellite track records of the postnesting migrations of the loggerhead turtles nesting at the Ankyaba Beach in Amami-Oshima Island in 2015 and estimated locations of their foraging grounds. SCL = straight carapace length; SCW = straight carapace width; FG = foraging ground.

Turtle ID	SCL (cm)	SCW (cm)	Date tagged	Last transmission	No. of days tracked	Location of FG
53766	85.6	67.5	23 Jun 2015	22 Nov 2015	152	East China Sea
53749	85.7	69.7	2 Jul 2015	1 Jan 2016	183	East China Sea
57147	85.5	66.4	3 Jul 2015	7 Nov 2015	127	East China Sea
71916	88.7	69.2	8 Jul 2015	18 Jun 2016	346	East China Sea
50148	102.0	74.0	18 Jul 2015	23 Apr 2016	280	Sea of Japan and East China Sea
Average	89.5	69.4	—	—	218	—

The sea surface temperatures (SSTs) at the locations in the East China Sea where these 2 turtles stayed were higher than 20°C even in winter (Daily SSTs database of Japan Meteorological Agency, https://www.data.jma.go.jp/kaiyou/data/db/kaikyo/daily/sst_HQ.html?areano=3). One turtle (ID 50148) migrated farther to the northeast and entered the Sea of Japan through the Tsushima Strait between the Tsushima and Kyushu islands (Fig. 2E). This turtle stayed off the north side of the coastal waters of the Kyushu Island in the Sea of Japan. However, it started moving south in the winter as temperatures in the area started to decrease, and fully moved out of the Sea of Japan when the SST around there dropped to around 13°C in December 2015, into the East China Sea and recruited to the offshore area of the other 4 loggerheads tracked in this study. Thereafter, it moved back north toward the Sea of Japan but, unfortunately, transmissions stopped on 23 April 2016 without an observation of whether it entered the Sea of Japan again. All 5 turtles, including turtle ID 50148, stayed at sea over the continental shelf (shallower than 200 m) of the Eurasian Continent in the East China Sea for most of their tracking periods.

The green turtles were tracked for 33–64 d. One turtle (ID 42712) stayed around the northern Amami Island during the 43-d tracking period (Fig. 3A). Two turtles (ID 53747 and ID 41457) moved along the Pacific coasts of Japanese main islands. Turtle ID 53747 reached the Miyakejima Island of the Izu islands after 33 d of tracking (Fig. 3B). The other green turtle (ID 41457) reached Tanabe Bay, located in the middle part of the Japanese main islands, after 46 d of tracking (Fig. 3C). Turtle ID 65422 moved northward from Amami and entered the Yatsushiro Sea, which is a shallow, semienclosed inland sea located at the west coast of the Kyushu Island, after passing nearby to Yakushima Island and the south coast of the Kyushu Island (Fig. 3D). Only 1 turtle, ID 40605, moved to the south out to sea to the northwest of Okinawa after nesting (Fig. 3E). However, this individual transmitted very infrequently with poor or no positions and tracking unfortunately stopped without further transmission.

Discussion. — The present study constitutes the postnesting tracking of loggerhead and green turtles nesting at the northern Amami Island, located in the central Ryukyus. We identify the foraging areas that loggerheads nesting in the central Ryukyus use and show evidence that the green turtles nesting in the central Ryukyus could migrate to the coasts of main islands in Japan.

All 5 loggerheads moved to the East China Sea and spent their time there throughout the tracking period, except for 1 individual that entered the Sea of Japan for a period of time. Previous studies have shown that the East China Sea is the foraging ground inhabited by mature female loggerhead turtles nesting in the Yakushima and Japan's mainland (Hatase et al. 2002, 2007). Our present work indicates that some loggerheads nesting in the central Ryukyus located to the south of Yakushima also reside in the East China Sea.

One individual exhibited an exceptional movement that entered the southern part of the Sea of Japan through the straits of South Korea and Kyushu. Similar foraging tracks were reported in male loggerheads released from southwest coast of the Kyushu Island (Saito et al. 2015). A male turtle released from the Tanegashima Island was also tracked until the entrance of the Sea of Japan (Kume et al. 2017). Those loggerheads that were tracked during migration toward the Sea of Japan stayed around the strait

Table 2. Detailed satellite track records of the postnesting migrations of the green turtles nesting at the Ankyaba Beach in Amami-Oshima Island in 2015 and final locations where the transmission stopped. SCL = straight carapace length; SCW = straight carapace width; FG = foraging ground.

Turtle ID	SCL (cm)	SCW (cm)	Date tagged	Last transmission	No. of days tracked	Final location
42712	101.0	78.5	21 Jun 2015	28 Aug 2015	68	Amami-Oshima, Japan
53747	86.0	67.0	27 Jun 2015	30 Jul 2015	33	Miyakejima, Japan
40605	99.6	72.7	8 Jul 2015	20 Aug 2015	43	Okinawa, Japan
65422	90.4	67.0	8 Jul 2015	10 Sep 2015	64	Minamata, Japan
41457	92.0	71.5	17 Jul 2015	1 Sep 2015	46	Tanabe, Japan
Average	93.8	71.3	—	—	46	—

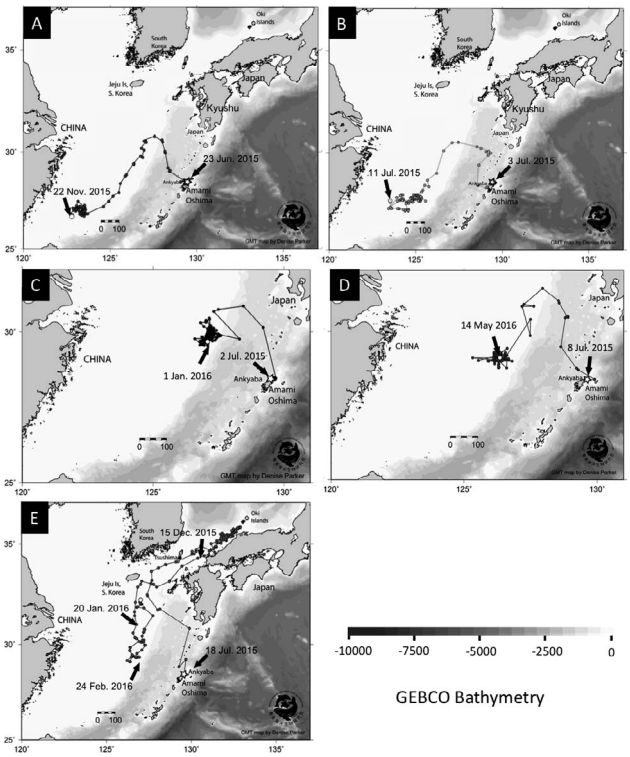

Figure 2. Movement of postnesting loggerhead turtles released from Ankyaba Beach, Amami-Oshima Island, Japan. The movements are of turtles ID 53766 (A), ID 57147 (B), ID 71916 (C), ID 53749 (D), and ID 50148 (E).

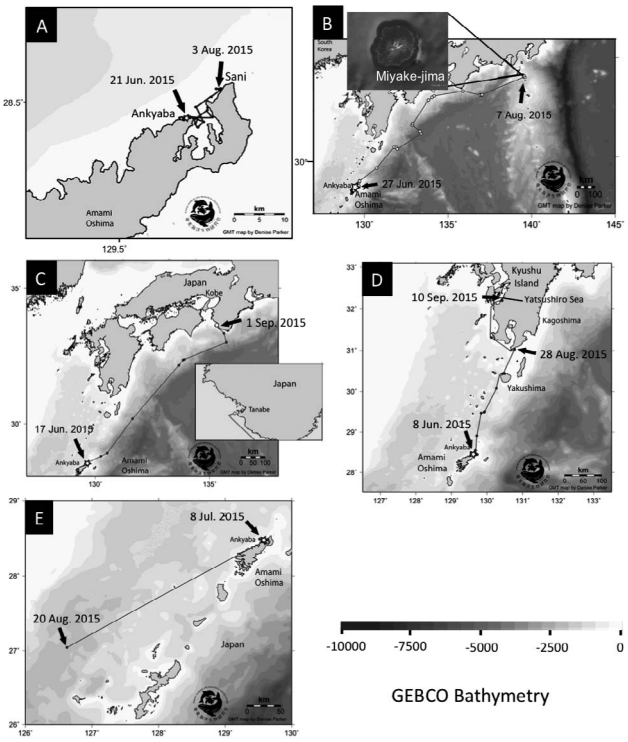

Figure 3. Movement of postnesting green turtles released from Ankyaba Beach, Amami-Oshima Island, Japan. The movements are of turtles ID 42712 (A), ID 53747 (B), ID 41457 (C), ID 65422 (D), and ID 40605 (E).

during the relatively warm season and migrated south with the decrease of the water temperature in winter. Such seasonal migration in response to the water temperature is observed in other loggerhead populations in the Mediterranean (Bentivegna 2002; Zbinden et al. 2008). However, the turtle ID 50148 in our study migrated farther north (300 km farther from the strait) and showed prolonged activity in the Sea of Japan, and the turtle eventually passed through the strait when the SST there dropped to around 13°C in winter. Marine turtles can maintain a higher body temperature than that of the ambient water according to the body size (Sato 2014). Turtle ID 50148 was the largest loggerhead specimen (SCL = 102 cm) in the present study and was larger than the male specimens that showed similar movement in the previous study (73.7 and 88.7 cm SCL in Saito et al. [2015]). Thus, the larger body size of the turtle in our study (ID 50148) might enable longer foraging activity in decreasing water temperature in the Sea of Japan. The depths of the locations where this female stayed in the Sea of Japan were similar to those of the locations where the other turtles stayed in East China Sea. Although little is known about the habitat utilization of marine turtles in the Sea of Japan, our present result suggested that the west part of the Sea of Japan might be an extension of foraging grounds of loggerheads serving adult female turtles from the central Ryukyus as seasonal habitats.

Furthermore, 2 species in our study are known to show foraging dichotomy within a stock where some turtles spend time in the pelagic Pacific of the south of Japan's main islands, even after they mature, without recruiting to coastal benthic or neritic areas (< 200 m) of the East China Sea (Hatase et al. 2002, 2006; Nobetsu et al. 2003). In particular, the nesting females from the Yakushima and mainland loggerhead nesting populations have been focused upon to study the size-related foraging dichotomy within a population, as smaller adult females forage in the pelagic Pacific and larger females forage in the neritic East China Sea (Hatase et al. 2002, 2007). All our loggerheads were larger than 85 cm SCL, and no turtles migrated to the pelagic Pacific in this study. Nesting females with SCL < 80 cm, which might be expected to forage in the pelagic Pacific, were often recorded at the Ankyaba beach (19% of the total recorded loggerhead turtles in 2012; T.A., unpubl. data, 2012). Some female loggerheads in the Ryukyu nesting population are therefore expected to use the pelagic Pacific environment as their adult foraging ground. Future tracking of postnesting movement in those smaller females is needed to clarify the foraging range of loggerhead turtles in the central Ryukyus.

In contrast to the loggerhead turtles, green turtles nesting in the Amami Island moved to a wider range of foraging locations from the east coast of the Japanese main islands southwest to the Amami Island. Probably, 1 turtle that stayed around Amami had not finished the nesting

period, and its internesting could be tracked because nests of green turtle were found on the Ankyaba beach and a beach in Sani around the days that the transmissions with the location accuracy of LC3 from this female were recorded (Fig. 3). This individual stayed around that area at least until the end of August and so may settle near the nesting beach. This may not be the exception in this species, as Taquet et al. (2006) reported a mature green turtle, whose foraging patterns at Mayotte Island were examined by acoustic transmitters, later nested on the beaches near the foraging site. It is difficult to predict the destination of 1 turtle that moved to the southwest, but this suggests the diversity of foraging grounds of green turtles nesting in Amami. Tracking duration of green turtles that moved to the coastal areas of the main islands was also relatively short because the transmission stopped just after they arrived there, likely owing to antenna damage resulting from foraging and resting in benthic (or bottom) habitat or to some accidents due to human interaction such as entanglement of fishing net/line, boat impact, or other risk that may have been introduced due to the tagging study (Jeffers and Godley 2016). It was not proven that each female settled in the area where the last location signal was transmitted, choosing those areas as their preferred foraging grounds. To date, a few studies suggested that the coasts of western Japanese main islands seem to be a multiple-coast foraging site based on the similarity in size distribution of green turtles among sites and the absence of genetic differentiation (Hamabata et al. 2015). Several reports that turtles recaptured within a few weeks among the different sites at the coasts of the main islands also support a multiple-coast foraging site around the main islands (e.g., Okamoto and Kamezaki 2014). This suggests that the foraging green turtles along the coasts of Japan's main islands might continue to move, depending on the habitat condition and season. While the present study did not identify the conclusive adult foraging grounds of green turtles nesting in the central Ryukyus, the locations where transmission stopped suggest that green turtles from the central Ryukyus also inhabit various coastal areas of the Japanese main islands, a finding which previously was only estimated from simulations of MSA using genetic data.

Impact of Fisheries. — Previous studies showed that the East China Sea is also inhabited by immature loggerhead subadults caught as bycatch in the coasts of Taiwan (Kobayashi et al. 2011), southwest of the Kyushu Island (Saito et al. 2015), and the Tanegashima Island (Kume et al. 2017). This area is one of the foraging hotspots for both adult and immature loggerhead turtles in the North Pacific (Kobayashi et al. 2011). In addition, this area is a common fishing ground of Japan, China, and Korea, and fisheries such as trawling and large- and medium-scale purse seine fisheries are active (Japan Fisheries Research and Education Agency 2013). The number of nests of the North Pacific loggerhead turtle does not necessarily increase in spite of the protection on the nesting beaches. Fisheries are now considered as one of the biggest threats against the population recovery of this species (Ministry of the Environment Japan 2014). However, the impact of fisheries activity upon loggerhead turtles in the East China Sea has not been evaluated. It is important how often turtles were captured by fisheries nets in the East China Sea and their resulting mortality. Hazards and impacts in this area affect both immature and adult loggerhead turtles.

The coasts along Japan's main islands are also active fisheries grounds. Although mortality is high in some kinds of set nets, such as set nets with a bag net at medium depth or at the bottom of coastal fisheries (Tamura et al. 2014), many large set nets, which most frequently take sea turtles as bycatch, are designed to open the ceiling at the sea surface. Thus, turtles can come up to the surface to breathe (Ishihara et al. 2014). Not only green turtles but also loggerheads are captured by those coastal fisheries' nets, and most of them are released alive (Ishihara et al. 2011). Consistent increases in green turtle nesting populations in Japan suggest the coastal set net fisheries may not be a serious threat, at least to the Japanese green turtle populations. This also suggests that the loggerheads may probably face threats in the different areas and emphasizes the importance of risk assessment in the East China Sea for the North Pacific loggerhead populations.

Acknowledgments. — This study was conducted under the permission from Tatsugo Town of the Amami-Oshima, Kagoshima Prefecture (Permission No. 93 from the Environmental Division). All appropriate animal use and care protocols were followed to ensure humane treatment of the sea turtles. We extend our appreciation to the people of Amami-Oshima for their helpfulness and consistent good cheer. This study could not have been accomplished without their support. We acknowledge and express gratitude to Dr Yoshimasa Matsuzawa and the Sea Turtle Association of Japan for their assistance in the successful conduction of this study. We thank the National Oceanic and Atmospheric Administration (NOAA) Pacific Islands Fisheries Science Center in Hawaii for supplying the Telonics satellite tags and Argos satellite services used in this study.

謝辞

本研究は、鹿児島県奄美大島龍郷町のウミガメ捕獲等許可（龍生第 93 号）のもと行いました。ウミガメへの発信機の装着は、個体の倫理的取扱いおよび適切な手順を遵守して行いました。安木屋場浜での調査や研究は、周辺住民の方々に多くのご協力や励ましを頂きながら行いました。そのようなご理解、ご協力なしに本研究は行うことはできませんでした。皆様のご支援に心から感謝申し上げます。また、本研究が成功するようサポートをしてくれた松沢慶将博士および日本ウミガメ協議会にも感謝申し上げます。本研究で用いた Telonics 社の衛星タグの提供及び、アルゴス衛星サービスの利用を支援してくださった米国立海洋大気庁 (NOAA) 在ハワイ Pacific Islands Fisheries Science Center に感謝申し上げます。

LITERATURE CITED

BALAZS, G.H., MIYA, R.K., AND BEAVER, S.C. 1996. Procedures to attach a satellite transmitter to the carapace of an adult green turtle, *Chelonia mydas*. In: Keinath, J.A., Barnard, D.E., Musick, J.A., and Bell, B.A. (Eds.). Proceedings of the 15th Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memor. NMFS-SEFSC-387, pp. 21–26.

BALAZS, G.H., PARKER, D.M., AND RICE, M.R. 2017. Ocean pathways and residential foraging locations for satellite tracked green turtles breeding at French Frigate Shoals in the Hawaiian Islands. Micronesica 4:1–19.

BALAZS, G.H., VAN HOUTAN, K.S., HARGROVE, S.A., BRUNSON, S.M., AND MURAKAWA, S.K.K. 2015. A review of the demographic features of Hawaiian green turtles (*Chelonia mydas*). Chelonian Conservation and Biology 14:119–129.

BEGGS, J.A., HORROCKS, J.A., AND KRUEGER, B.H. 2007. Increase in hawksbill sea turtle *Eretmochelys imbricata* nesting in Barbados, West Indies. Endangered Species Research 3:159–168.

BENTIVEGNA, F. 2002. Intra-Mediterranean migrations of loggerhead sea turtles (*Caretta caretta*) monitored by satellite telemetry. Marine Biology 141:795–800. doi:10.1007/s00227-002-0856-z.

BOLTEN, A.B., CROWDER, L.B., DODD, M.G., MACPHERSON, S.L., MUSICK, J.A., SCHROEDER, B.A., WITHERINGTON, B.E., LONG, K.J., AND SNOVER, M.L. 2011. Quantifying multiple threats to endangered species: an example from loggerhead sea turtles. Frontiers in Ecology and the Environment 9:295–301. doi:10.1890/090126.

CHALOUPKA, M., BJORNDAL, K.A., BALAZS, G.H., BOLTEN, A.B., EHRHART, L.M., LIMPUS, C.J., SUGANUMA, H., TROËNG, S., AND YAMAGUCHI, M. 2008. Encouraging outlook for recovery of a once severely exploited marine megaherbivore. Global Ecology and Biogeography 17:297–304. doi:10.1111/j.1466-8238.2007.00367.x.

FLORIDA FISH AND WILDLIFE CONSERVATION COMMISSION. 2017. Index Nesting Beach Survey Totals (1989–2017). http://myfwc.com/research/wildlife/sea-turtles/nesting/beach-survey-totals/ (18 May 2018).

FONSECA, L.G., MURILLO, G.A., GUADAMÚZ, L., SPÍNOLA, R.M., AND VALVERDE, R.A. 2009. Downward but stable trend in the abundance of arribada olive ridley sea turtles (*Lepidochelys olivacea*) at Nancite Beach, Costa Rica (1971–2007). Chelonian Conservation and Biology 8:19–27.

HAMABATA, T., HIKIDA, T., OKAMOTO, K., WATANABE, S., AND KAMEZAKI, N. 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. Journal of Experimental Marine Biology and Ecology 463:181–188. doi:10.1016/j.jembe.2014.12.007.

HAMABATA, T., KAMEZAKI, N., AND HIKIDA, T. 2014. Genetic structure of green turtle (*Chelonia mydas*) peripheral populations nesting in the northwestern Pacific rookeries: evidence for northern refugia and postglacial colonization. Marine Biology 161:495–507. doi:10.1007/s00227-013-2352-z.

HAMABATA, T., NISHIZAWA, H., KAWAZU, I., KAMEDA, K., KAMEZAKI, N., AND HIKIDA, T. 2018. Stock composition of green turtles *Chelonia mydas* foraging in the Ryukyu Archipelago differs with size class. Marine Ecology Progress Series 600:151–163. doi:https://doi.org/10.3354/meps12657.

HATASE, H., OMUTA, K., AND TSUKAMOTO, K. 2007. Bottom or midwater: alternative foraging behaviours in adult female loggerhead sea turtles. Journal of Zoology 273:46–55. doi:10.1111/j.1469-7998.2007.00298.x.

HATASE, H., SATO, K., YAMAGUCHI, M., TAKAHASHI, K., AND TSUKAMOTO, K. 2006. Individual variation in feeding habitat use by adult female green sea turtles (*Chelonia mydas*): are they obligately neritic herbivores? Oecologia 149:52–64. doi:10.1007/s00442-006-0431-2.

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

ISHIHARA, T., KAMEZAKI, N., MATSUZAWA, Y., AND ISHIZAKI, A. 2014. Assessing the status of Japanese coastal fisheries and sea turtle bycatch. Wildlife and Human Society 2:23–35.

ISHIHARA, T., KAMEZAKI, N., MATSUZAWA, Y., IWAMOTO, F., OSHIKA, T., MIYAGATA, Y., EBISUI, C., AND YAMASHITA S. 2011. Reentery of juvenile and sub-adult loggerhead turtles into natal waters of Japan. Current Herpetology 30:63–68.

JAPAN FISHERIES RESEARCH AND EDUCATION AGENCY. 2013. Fishery resources in the East China Sea and the Yellow Sea (Review).

JEFFERS, V.F. AND GODLEY, B.J. 2016. Satellite tracking in sea turtles: how do we find our way to the conservation dividends? Biological Conservation 199:172–184. doi:10.1016/J.BIOCON.2016.04.032.

JENSEN, M.P., FITZSIMMONS, N.N., AND DUTTON, P.H. 2013. Molecular genetics of sea turtles. Chapter 6. In: Wyneken, J., Lohmann, K.J., and Musick, J.A. (Eds.). The Biology of Sea Turtles. Volume III. Boca Raton, FL: CRC Press, pp. 135–161.

KAMEZAKI, N. 1989. The nesting sites of sea turtles in the Ryukyu Archipelago and Taiwan. In: Current Herpetology in East Asia. Kyoto: Herpetological Society of Japan, pp. 342–348.

KAMEZAKI, N., MIYAWAKI, I., SUGANUMA, H., OMUTA, K., NAKAJIMA, Y., GOTO, K., SATO, K., MATSUZAWA, Y., SAMEJIMA, M., ISHII, M., AND IWAMOTO, T. 1997. Post-nesting migration of Japanese loggerhead turtle, *Caretta caretta*. Widlife Conservation Japan 3:29–39. (In Japanese with English abstract.)

KIZAKI, K. 1986. Geology and tectonics of the Ryukyu Islands. Tectonophysics 125:193–207.

KOBAYASHI, D.R., CHENG, I.-J., PARKER, D.M., POLOVINA, J.J., KAMEZAKI, N., AND 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.

KONDO, S., MORIMOTO, Y., SATO, T., AND SUGANUMA, H. 2017. Factors affecting the long-term population dynamics of green turtles (*Chelonia mydas*) in Ogasawara, Japan: influence of natural and artificial production of hatchlings and harvest pressure. Chelonian Conservation and Biology 16:83–92. doi:10.2744/CCB-1222.1.

KUME, M., ISHIHARA, T., PARKER, D.M., AND BALAZS, G.H. 2017. Habitat use of sea turtles in the coastal waters around Tanegashima Island, Kagoshima Prefecture. Umigame Newsletter 105:2–10. (In Japanese with English abstract.)

LIMPUS, C.J., MILLER, J.D., PARAMENTER, C., REIMER, D., MCLACHLAN, N., AND WEBB, R. 1992. Migration of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles to and from eastern Australian rookeries. Wildlife Research 19:347. doi:10.1071/WR9920347.

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., KATSUKI, O., WATANABE, K.K., YAMAMOTO, A., YAMASHITA, Y.,

YAMATO, Y., HAMABATA, T., ISHIZAKI, A., AND DUTTON, P.H. 2016. Fine-scale genetic population structure of loggerhead turtles in the Northwest Pacific. Endangered Species Research 30:83–93. doi:10.3354/esr00724.

MAZARIS, A.D., SCHOFIELD, G., GKAZINOU, C., ALMPANIDOU, V., AND HAYS, G.C. 2017. Global sea turtle conservation successes. Science Advances 3:1–7. doi:10.1126/sciadv.1600730.

MINISTRY OF THE ENVIRONMENT JAPAN. 2014. 3: Reptiles and amphibians. In: Biodiversity Center of Japan (Ed.). Threatened Wildlife of Japan. Red Data Book 2014. Fourth version. Tokyo: Ministry of the Environment Japan.

NISHIZAWA, H., NAITO, Y., SUGANUMA, H., ABE, O., OKUYAMA, J., HIRATE, K., TANAKA, S., INOGUCHI, E., NARUSHIMA, K., KOBAYASHI, K., ISHII, H., TANIZAKI, S., KOBAYASHI, M., GOTO, A., AND ARAI, N. 2013. Composition of green turtle feeding aggregations along the Japanese archipelago: implications for changes in composition with current flow. Marine Biology 160:2671–2685. doi:10.1007/s00227-013-2261-1.

NOBETSU, T., MINAMI, H., KIYOTA, M., SHIODE, D., MATSUNAGA, H., OKAZAKI, M., AND NAKANO, H. 2003. Oceanic migration of post-nesting loggerhead sea turtles (*Caretta caretta*) in the northwestern North Pacific tracked by satellite telemetry. In: Proceedings of the 4th SEASTAR2000 Workshop, pp. 28–31.

OKAMOTO, K. AND KAMEZAKI, N. 2014. Morphological variation in *Chelonia mydas* (Linnaeus, 1758) from the coastal waters of Japan, with special reference to the turtles allied to *Chelonia mydas agassizii* Bocourt, 1868. Current Herpetology 33:46–56. doi:10.5358/hsj.33.46.

OKI, K. AND MIZUNO, K. 2013. Report on sea turtle nesting on Amami-Oshima and nearby islands in 2012. Umigame News Letter 96:9–13. (In Japanese.)

RICHARDSON, J.I., HALL, D.B., MASON, P.A., ANDREWS, K.M., BJORKLAND, R., CAI, Y., AND BELL, R. 2006. Eighteen years of saturation tagging data reveal a significant increase in nesting hawksbill sea turtles (*Eretmochelys imbricata*) on Long Island, Antigua. Animal Conservation 9:302–307.

SAITO, T., KURITA, M., OKAMOTO, H., UCHIDA, I., PARKER, D., AND BALAZS, G.H. 2015. Tracking male loggerhead turtle migrations around southwestern Japan using satellite telemetry. Chelonian Conservation and Biology 14:82–87.

SATO, K. 2014. Body temperature stability achieved by the large body mass of sea turtles. Journal of Experimenal Biology 217:3607–3614. doi:10.1242/jeb.109470.

STEWART, K., SIMS, M., MEYLAN, A., WITHERINGTON, B., BROST, B., AND CROWDER, L.B. 2011. Leatherback nests increasing significantly in Florida, USA; trends assessed over 30 years using multilevel modeling. Ecological Applications 21:263–273.

TAMURA, R., SHIODE, D., KANEKO, Y., FU, F., TOKAI, T., KOBAYASHI, M., AND ABE, O. 2014. Behavior of sea turtles to a turtle releasing device (TED) for set nets of the mid-water and sea-bottom bagnet type. Nippon Suisan Gakkaishi 80:900–907.

TAPILATU, R.F., DUTTON, P.H., TIWARI, M., WIBBELS, T., FERDINANDUS, H.V., IWANGGIN, W.G., AND NUGROHO, H.B. 2013. Long-term decline of the western Pacific leatherback, *Dermochelys coriacea*: a globally important sea turtle population. Ecosphere 4:art25. doi:10.1890/ES12-00348.1.

TAQUET, C., TAQUET, M., DEMPSTER, T., SORIA, M., CICCIONE, S., AND ROOS, D. 2006. Foraging of the green sea turtle *Chelonia mydas* on seagrass beds at Mayotte Island (Indian Ocean), determined by acoustic transmitters. Marine Ecology Progress Series 306:295–302.

ZBINDEN, J.A., AEBISCHER, A., MARGARITOULIS, D., AND ARLETTAZ, R. 2008. Important areas at sea for adult loggerhead sea turtles in the Mediterranean Sea: satellite tracking corroborates findings from potentially biased sources. Marine Biology 153:899–906. doi:10.1007/s00227-007-0862-2.

Received: 2 July 2018
Revised and Accepted: 4 December 2018
Published Online: 6 June 2019
Handling Editor: Jeffrey A. Seminoff