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Satellite tracking immature loggerhead turtles in temperate and subarctic ocean habitats around the Sea of Japan*

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Abstract— The distribution limits of North Pacific loggerhead turtles, *Caretta caretta*, within the Sea of Japan are unknown, but are suspected to be linked to a decrease in winter sea surface temperature. Immature loggerheads in the Sea of Japan are thought to follow the prevailing current via a southern route, or to leave from the north with extensions of the warm current, or are unable to leave when winter approaches. Here, we investigated the migrations of 30 immature captive-reared turtles of 26.5 to 75.2 cm SCL at 2–6 years of age released off the central Sea of Japan in summer of 2011 using satellite telemetry to ascertain 1) the seasonal movements of immature loggerheads and 2) their behavior in the subarctic zone. Nineteen turtles successfully left the Sea of Japan, mainly via the Soya Strait traveling into the North Pacific; however, eleven did not leave and may have died due to stranding during the winter. Their excursion paths were similar to migrations of wild turtles. The presence of exit routes suggests that immature loggerheads entering the Sea of Japan can disperse successfully and contribute to the North Pacific subpopulation. During the summer of 2011, the turtles that left the Sea of Japan experienced water temperatures that were relatively wide ranging and lower than turtles that stayed in Sea of Japan. The sea surface temperatures (SSTs) experienced by the turtles that left the Sea of Japan were significantly different from those of the time percent temperatures (TPTs) (range: 17–35 °C vs. 5–35 °C, mode: 23–25 °C vs. 10–15 °C). The relatively lower TPTs may be due to their active diving behaviors. In contrast, the SSTs and TPTs (range: 10–35 °C, mode: 21–23 °C) experienced by the turtles that stayed in the Sea of Japan were almost identical. Success in leaving the Sea of Japan could be related to a higher frequency of dives, although further research is required to confirm this.

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Introduction

Loggerhead turtles, *Caretta caretta*, are a threatened species listed as "Vulnerable" under the IUCN Red List categories (Casale & Tucker 2015) and require a global conservation effort. Loggerhead turtles nest from temperate to sub-tropical areas, with the North Pacific subpopulation of loggerheads utilizing the southern Japanese Archipelago coast as their only reproductive area (Kamezaki et al. 2003). Turtle nesting beaches occur on both the Pacific and Sea of Japan coasts of Japan. The region from the Yaeyama Group located in southwestern Japan to the western North Pacific coast of Yamamoto-cho, Miyagi Prefecture, and the Sea of Japan coast of Ishikawa Prefecture in the northern Noto Peninsula are known recent nesting areas of loggerhead turtles. However, substantial nestings of Japanese loggerhead turtles also occur along the Pacific coast (Kamezaki et al. 2003; Figure 1).

Loggerhead turtles are known to often strand along the Sea of Japan coast due to cold stun (Nishimura 1967); however, their numbers have not been quantified. Cold stun is a phenomenon in which sea turtles can not regulate buoyancy as the water temperature decreases and passively float on the sea surface. It is difficult to study mortality rates of loggerhead turtles resulting from cold stun. Epperly et al. (1996) estimated the mortality of sea turtles, mainly loggerhead turtles, in winter along the northern coast of North Carolina from at-sea monitoring and beach stranding records. The proportion of deaths from bycatch in the winter trawl fishery was estimated to be 7–13%, with the majority estimated to be due to other factors. In the Atlantic, there are reports of cold stun on the US East Coast (e.g. Meylan & Sadove 1986; Morreale et al. 1992; Still et al. 2005; McMichael et al. 2008; Anderson et al. 2011) and Spain (Bellido et al. 2010). Kuramoto & Ishii (2003) reported the passive drifting of five species of sea turtles including loggerheads in Fukuoka Prefecture, near the west entrance of the Sea of Japan. Ichisawa et al. (2014) recorded two stranded and one bycaught loggerhead turtles near the coasts of Tottori Prefecture. Honma et al. (2010) recorded more than 70 loggerheads stranded along the coasts of Niigata Prefecture and Sado Island after 1830. Furthermore, Kharin (2008) mentioned finding sea turtles, including loggerheads, in the Sea of Japan's Russian waters. Recently, Ishihara et al. (2017) found 119 post-hatchling loggerhead turtles, approximately 10 cm in Standard Carapace Length (SCL), washed ashore or obtained as bycatch in the Sea of Japan from September 2012 to April 2013. Mixed stock analysis demonstrated that their natal orgins were mainly southern Japan, including Okinawa Islands, Okinoerabu Island, and Yakushima Island. Furthermore, tagged loggerhead turtles, 1 to 2 years of age, released offshore of Okinawa Island were recaptured in the Sea of Japan (Uchida & Teruya 1991). This also shows that loggerhead turtles from distant places, like Okinawa Island, can enter the Sea of Japan.

Nishimura (1969) stated that the most significant factors controlling animal distribution in the Sea of Japan were the strong influx of the Tsushima Warm Current from the south in the summer to autumn and the winter thermohaline convection and southward drift current induced by the cold and dry northwest monsoon. Moreover, the periodic winter wind in this area is closely related to severe water temperature decreases. Many sea turtles that were carried to the Sea of Japan by the Tsushima Warm Current might not be able to endure the decreased water temperature during winter, weaken, and drift ashore to die (Nishimura 1967). Some hatchlings born at the nests that are established over a wide area from further south, including these sites, enter into the Sea of Japan with the Tsushima Warm Current and might not be dispersed effectively.

Previous studies regarding seasonal migration of loggerhead turtles have suggested that they migrate in response to a drop in sea surface temperature (SST) (Polovina et al. 2006, Kobayashi et al. 2008, Mansfield et al. 2009, Arendt et al. 2012, Saito et al. 2015). Polovina et al. (2000, 2004, 2006) identified that immature and adult loggerhead turtles in the North Pacific Ocean occupied specific areas of the pelagic environment, which is possibly related to SSTs and/or mechanisms of ocean productivity and retention of zooplankton prey. Similarly, the movement of turtles in the Sea of Japan may involve cues from such hydrographic conditions in these regions.

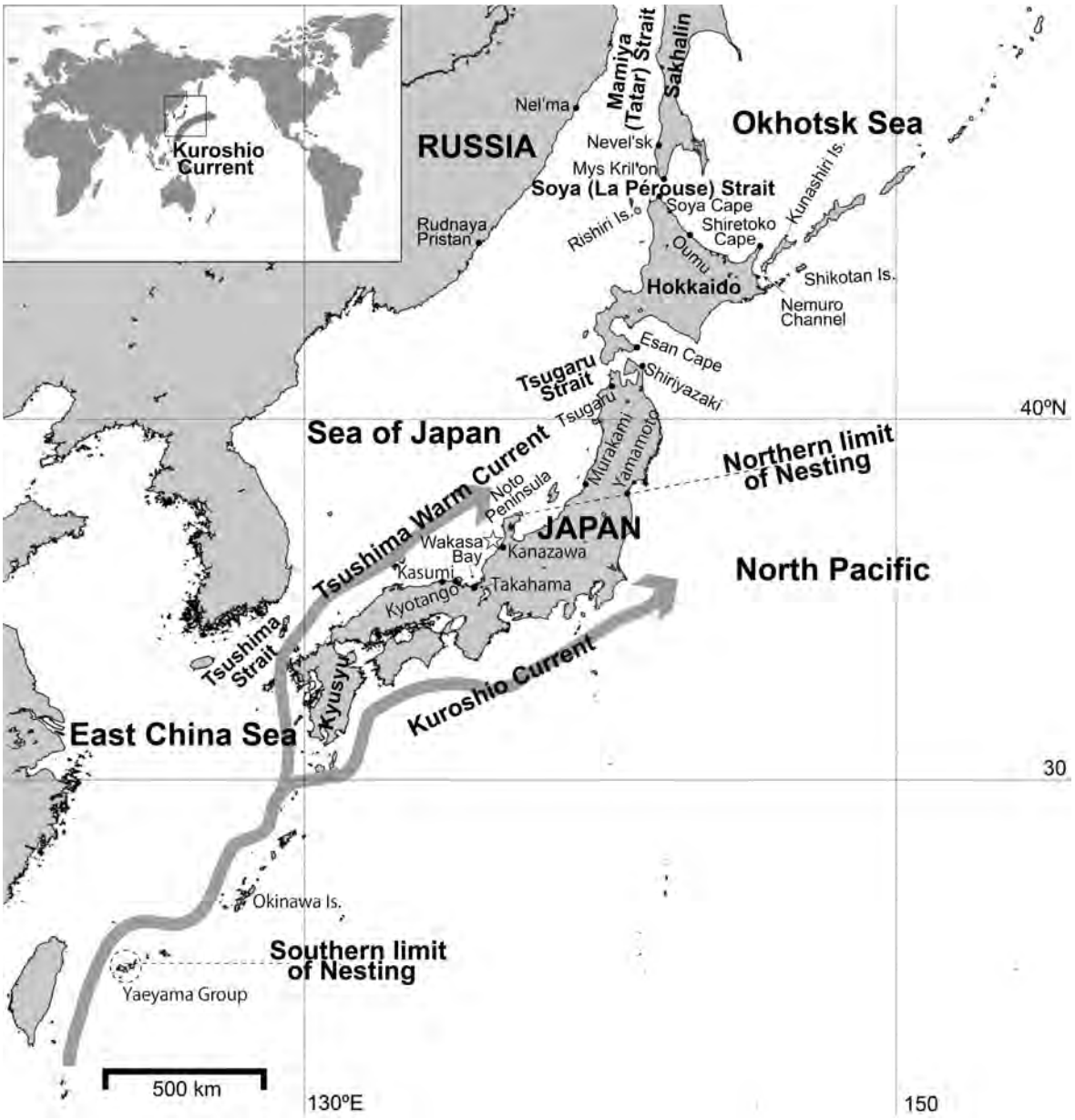

Figure 1. Map of study sites. Location of release and recapture sites of the loggerhead turtles. Dashed lines: northern and southern limits of turtle nesting. Gray lines and arrows: typical year-round tracks of the Kuroshio and Tsushima Warm Currents with directions of current flow. Open star: release site.

Satellite telemetry has made it possible to monitor the movements of turtles over large areas, which can assist in researching their life history in more detail. Extensive research has been performed on hundreds of loggerhead turtles raised by the Port of Nagoya Public Aquarium (PNPA), that were released and tracked in pelagic waters on the Pacific east coast of Japan (Polovina et al. 2006, Kobayashi et al. 2008). In contrast, no satellite tracking studies have been conducted on loggerhead turtles along the western Japan coast and within the Sea of Japan. In the present study, 30 immature loggerheads were tracked in the Sea of Japan using satellite telemetry. This study is unique, because it involved the release of immature loggerheads with Argos-linked transmitters that were smaller and younger than turtles caught using longlines. The only way to obtain such very young turtles for the present study was to use captive-reared turtles (Parker et al. 2005).

It is unknown whether nesting in this region and the initial influx of hatchlings into the Sea of Japan contributes to the North Pacific subpopulation of loggerheads or if they die due to low water temperature in winter. There are three possible outcomes for loggerheads in the Sea of Japan: 1) Leave the Sea of Japan via a southern route to the Pacific Ocean; 2) Follow the Tsushima Warm Current and exit the Sea of Japan to the North; or 3) Remain in the Sea of Japan and suffer the consequences of lethal low temperatures. The aims of the present study were to acertain the seasonal migratory route of immature Japanese loggerheads from the Sea of Japan to the western North Pacific Ocean and clarify how they behave in the temperate to subarctic habitat zone.

Materials and Methods

TURTLE INFORMATION

A total of 24 immature loggerhead turtles <50 cm SCL (range: 26.5 to 37.7 cm SCL) at 2 years of age and six turtles >50 cm SCL (range: 57.7 to 75.2 cm SCL) at 3–6 years of age were used (Tables 1, 2). These turtles were obtained from the PNPA captive breeding and rearing program. All turtles were healthy and vigorous when released. Prior to release, the SCL and body mass (BM) of each turtle were measured to the nearest 0.1 cm and 0.1 kg, respectively. It was not possible to identify the sex of immature turtles at this stage based on external morphology (i.e., tail length or presence of claws on the front flippers; Limpus & Limpus 2003).

SATELLITE TAG ATTACHMENT

The transmitters were the smallest available for diving animals and, hence, the minimum size possible to track our loggerheads was 26.5 cm in straight carapace length (SCL). Small-sized satellite tags for hatchings are not yet readily available; therefore, we tracked what we could by including size-appropriate turtles for the small transmitters available. The devices utilized to collect SSTs and time percent temperatures (TPTs) data included TAM-2639 (size: 3.2 x 6.6 x 3.0 cm, weight in air: 90 g) and TAM-4510 (size: 15.0 x 7.3 x 3.9 cm,weight in air: 435 g; Telonics, Inc., Mesa, AZ, USA), and SPOT5 (size: 8.0 x 5.0 x 2.0 cm, weight in air: 59 g; Wildlife Computers Inc., Redmond, WA, USA) platform terminal transmitters (Tables 1, 2). All SSTs were obtained via satellite when the turtles broke the surface. Temperatures experienced by each turtle during the study were calculated as daily or ten-day mean SSTs and sorted with a resolution of 0.1 °C. The TPTs during the study were calculated as the daily (24 h) percent time at water temperatures experienced by each turtle against the total time and sorted into bins from −40 °C or more and less than 0 °C and following as: −40–0, 0–5, 5–10, 10–15, 15–17, 17–19, 19–21, 21–23, 23–25, 25–35, 35–55, 55–60 °C.

These devices were attached to the carapace of each turtle with polyester resin and fiberglass cloth after the carapace had been carefully cleaned of grease and debris (Balazs et al. 1996). After attachment of the transmitters with resin had completely dried, turtles were individually maintained and fed in cages placed inside a tank in the PNPA until their release. Approximately one week later after tag attachment, the turtles were transported gently by a truck and a fishing boat. To assist in the collection of recapture information, we distributed posters and fliers indicating the procedure

undertaken to organizations such as prefectural offices and institutes of fisheries and aquariums located near the predicted routes of the turtles.

INFORMATION COLLECTED FROM SATELLITE TAGS

All turtles were released at the same time from the coastal waters off Kanazawa-shi, central Sea of Japan on July 15, 2011 (Figure 1, Tables 1, 2). The SST upon release was 26.5 °C. The locations of the turtles were obtained via the Argos satellite system that classified six location classes (LC) of decreasing accuracy (LC 3–1: 1 km, LC 0, LC A, and LC B; LC Z were not used). We utilized LC 3–1, 0, A and B fixes that provided reliable information regarding migration paths (Figures 2–4). When more than one location was obtained within a day, the earliest and most accurate location class was selected based on the CLS/Argos hierarchy of accuracy. Consecutive geolocations requiring a travel speed of more than 5 km h^{-1} were eliminated (Luschi et al. 1998). The total distances traveled by the turtles were defined as the sum of the shortest distances between successive locations. The minimum average travel speed for each segment of track was calculated.

The numbers of days in the Sea of Japan or the North Pacific waters were calculated using location and time data. The boundary between the Sea of Japan and the North Pacific Ocean through the Soya Strait was fixed between Mys Kril'on, Sakhalin and Soya Cape, northern Hokkaido, and that of Tsugaru Strait was fixed between Esan Cape, southern Hokkaido and Shiriyazaki, Aomori Prefecture (Figure 1). Summer and winter seasons were defined as the periods from May 1 to October 31 and November 1 to April 30, respectively.

DATA FOR OCEANOGRAPHIC MAPS

Daily, 25 km SST maps were produced from January 1, 2011 to December 31, 2013 using GHRSST Level 4 AVHRR Optimum Interpolation Global Blended Sea Surface Temperature (coastwatch.pfeg.noaa.gov) (Figures 5, 6). SST maps of the averaged daily images for summer (May–October) and winter (November–April) for the Sea of Japan and western North Pacific were generated.

STATISTICAL ANALYSIS

To test the differences in the frequency distributions of SSTs and TPTs, the daily TPTs data and the daily mean SSTs data were summarized during the same periods (Figures 8, 9). In this analysis SSTs data were sorted and organized in the same way as the TPTs bins. The frequency distributions of SSTs and/or TPTs were compared using chi-square tests performed with BellCurve Excel Statistics for Windows (SSRI, Tokyo, Japan). Statistical significance was assumed if $P < 0.05$.

Results

SATELLITE TRACKING OF IMMATURE TURTLES <50 CM SCL FROM THE SEA OF JAPAN

Seventeen of the 24 satellite tagged turtles left the Sea of Japan and were tracked for an average of 232 days and an averate distance of 5,291.7 km (Tables 1, 3). Sixteen of these left the Sea of Japan via the Soya Strait between August 12 and October 11, 2011 and reached the Okhotsk Sea after having traveled north in the Tsushima Warm Current and its extended Soya Current (Figure 2A–C). One turtle (ID 57144, 36.4 cm SCL) went through the Tsugaru Strait on July 29, 2011, when the SST was 19.6 °C (Figures 2B, 5A). After passing the Soya Strait, those turtles moved southeast along the northeast coast of Hokkaido (Figures 2A–C, 3A–C, 5A, B). Two of these turtles were captured in salmon set nets (Table 4); however, the remainder reached the southeastern sea region of Hokkaido. Seven turtles (IDs 22270, 23537, 25695, 42712, 50135, 57144 and 65426, 30.7–37.7 cm SCL) reached the central North Pacific Ocean after being tracked for an average of 413 days over a total mean distance of 9,068.3 km.

Seven turtles did not leave the Sea of Japan and were tracked for 70 days on average with total distance traveled of 1,653.9 km on average (Table 3, Figures 3A–C, 5C, D).

Table 1. Data from satellite-tagged loggerhead turtles <50 cm SCL released into the Sea of Japan. *: 'T' means a device was attached to record the time percent temperature (TPT) data experienced by turtles

Argos ID	Date of emergence (UTC)	SCL (cm)	BM (kg)	Year class	Device	Duty cycle (hours on / off) *	Tracking duration (days)	Distance traveled (km)	Experienced temperature (℃)	Travel speed ($km \cdot hr^{-1}$)	Date of exited from the Sea of Japan	Strait passed	Terminal site
Left the Sea of Japan													
8552	14-Aug-09	26.5	4.9	2	SPOT5	4/44	78	1775	13.5-35.5	0.9	12-Aug-11	Soya Strait	off Oumu-cho, Hokkaido/Okhotsk Sea
22270	14-Aug-09	35.4	6.7	2	SPOT5	4/92	752	15730	9.7-30.9	0.9	22-Aug-11	Soya Strait	central North Pacific
22275	14-Aug-09	31.7	5.7	2	SPOT5	4/44T	84	2255	13.1-32.1	1.1	17-Sep-11	Soya Strait	off Shiretoko Cape/Okhotsk Sea
23537	14-Aug-09	30.7	4.2	2	SPOT5	4/44T	212	5256	8.8-31.3	1.0	21-Sep-11	Soya Strait	central North Pacific
25359	14-Aug-09	36.2	7.7	2	SPOT5	4/92T	131	2986.	8.3-24.8	0.9	19-Aug-11	Soya Strait	400 km ESE of Shiretoko Cape/W North Pacific
25695	14-Aug-09	32.2	5.6	2	SPOT5	4/92	729	13913	9.0-37.1	0.8	18-Aug-11	Soya Strait	central North Pacific
40470	14-Aug-09	35.0	7.1	2	SPOT5	4/44T	136	2594	1.6-30.6	0.8	20-Aug-11	Soya Strait	near Shiretoko Cape/Okhotsk Sea
40605	14-Aug-09	32.9	5.8	2	SPOT5	4/92T	71	1929	18.7-28.8	1.1	20-Sep-11	Soya Strait	near Shiretoko Cape/Okhotsk Sea
42712	14-Aug-09	37.5	9.2	2	SPOT5	4/44	432	10439	5.8-39.9	1.0	18-Aug-11	Soya Strait	central North Pacific
50135	14-Aug-09	37.7	8.2	2	SPOT5	4/44	324	5459.	7.1-34.2	0.7	18-Aug-11	Soya Strait	central North Pacific
50144	14-Aug-09	34.9	7.4	2	SPOT5	4/92T	94	2213	12.0-28.4	1.0	18-Aug-11	Soya Strait	NE of Kunashiri Is./Okhotsk Sea
57144	14-Aug-09	36.4	7.2	2	SPOT5	4/92T	166	4639	3.5-24.5	1.2	29-Jul-11	Tsugaru Strait	central North Pacific
57148	14-Aug-09	32.1	5.2	2	SPOT5	4/92	96	2077.0	12.8-30.3	0.9	11-Oct-11	Soya Strait	Nemuro Channel/Okhotsk Sea
57152	14-Aug-09	34.9	7.2	2	SPOT5	4/44	105	-	10.1-38.2	-	26-Aug-11	Soya Strait	SW Nemuro Channel/Okhotsk Sea
65426	14-Aug-09	33.4	6.5	2	SPOT5	4/44T	278	8042	10.3-28.6	1.2	24-Aug-11	Soya Strait	central North Pacific
65435	14-Aug-09	36.6	7.1	2	SPOT5	4/92	139	2590	5.2-27.2	0.8	19-Aug-11	Soya Strait	near Shikotan Is./W North Pacific
88060	14-Aug-09	32.3	5.0	2	SPOT5	4/44T	118	2770	11.5-33.1	1.0	01-Sep-11	Soya Strait	near Shiretoko Cape/Okhotsk Sea
Stayed in the Sea of Japan													
19593	14-Aug-09	33.0	5.4	2	SPOT5	4/44	152	3035	3.7-33.8	0.8	-	-	140 km W of Tsugaru Strait
29060	14-Aug-09	31.2	5.4	2	SPOT5	4/92	91	2101	12.0-31.6	0.9	-	-	off Nevel'sk, Sakhalin Oblast
50151	14-Aug-09	33.1	6.0	2	SPOT5	4/44	84	2068	12.8-30.8	1.0	-	-	50 km W of Mys Kril'on, Sakhalin Oblast
53771	14-Aug-09	34.6	6.8	2	SPOT5	4/92T	94	2246	-	1.0	-	-	Mamiya (Tatar) Strait
57151	14-Aug-09	35.4	6.7	2	SPOT5	4/92	4	179	15.4-31.3	2.9	-	-	near Noto Peninsula
65424	14-Aug-09	33.1	8.2	2	SPOT5	4/44T	28	1101	20.9-28.2	1.6	-	-	near Rishiri Is., Hokkaido
71916	14-Aug-09	30.4	5.1	2	SPOT5	4/44	42	847	20.5-26.4	0.8	-	-	100 km off Rudnaya Pristan, Russian Maritime Provinces

Table 2. Data from satellite-tagged loggerhead turtles >50 cm SCL released into the Sea of Japan

Argos ID	Date of emergence (UTC)	SCL (cm)	BM (kg)	Year class	Device	Duty cycle (hours on / off)	Tracking duration (days)	Distance traveled (km)	Travel speed (km•hr^{-1})	Date left the Sea of Japan	Strait passed	Terminal site
Left the Sea of Japan												
53759	18-Aug-07	61.9	34.2	4	TAM-2639	6/48	327	10492	1.3	26-Sep-11	Tsugaru Strait	central North Pacific
52695	24-Aug-08	57.7	27.2	3	TAM-2639	6/48	158	2840	0.7	26-Sep-11	Soya Strait	290 km SE of Shiretoko Cape/W North Pacific
Stayed in the Sea of Japan												
23513	06-Jun-05	75.2	53.9	6	TAM-4510	6/48	138	2777	0.8	-	-	off Kyotango-shi, Tango Peninsula, Kyoto-fu
23542	19-Aug-06	69.5	44.3	5	TAM-4510	6/48	136	1423	0.4	-	-	off Tsugaru-shi, Aomori Prefecture
53758	19-Aug-06	67.9	44.5	5	TAM-2639	6/48	226	4340	0.8	-	-	off Takahama-cho, Fukui Prefecture, Wakasa Bay
71916	14-Aug-09	66.5	41.5	4	TAM-2639	6/48	22	622	1.2	-	-	off Murakami-shi, Niigata Prefecture

Table 3. Summary of satellite-tagged loggerhead turtles released into the Sea of Japan

Category	N	SCL (cm)		BM (kg)		Tracking duration (days)		Distance traveled (km)		Temperature (°C)	Travel speed (km•hr^{-1})	Date left Sea of Japan	Strait passed
		mean ± SD	range	mean ± SD	range	mean	range	mean	range	range	range		
left the Sea of Japan <50 cm SCL	17	33.9 ± 2.9	26.5-37.7	6.5 ± 1.3	4.2-9.2	232.1	78-752	5291.7	1775-15730	1.6-39.9	0.7-1.2	29 July - 11 Oct. 2011	Soya Strait (except one passed Tsugaru Strait)
stayed in the Sea of Japan <50 cm SCL	7	33.0 ± 1.7	30.4-35.4	6.2 ± 1.1	5.1-8.2	70.7	4-152	1653.9	179-3035	3.7-33.8	0.8-2.9	-	-
left the Sea of Japan >50 cm SCL	2	59.8 ± 3.0	57.7-61.9	30.7 ± 4.9	27.2-34.2	242.5	158-327	6666.0	2840-10492	-	0.7-1.3	26 Sep. 2011	Soya Strait (except one passed Tsugaru Strait)
stayed in the Sea of Japan >50 cm SCL	4	69.8 ± 3.8	66.5-75.2	46.1 ± 5.4	41.5-53.9	130.5	22-138	2290.5	622-4340	-	0.8-1.2	-	-

Table 4. Records of recaptured turtles in the present study following their release on 15 July, 2011.

Argos ID	Date terminated	Final location	Remarks
<50 cm SCL			
57152	28-Oct-11 captured	captured site 43°44'N 145°07'E	Captured live by a salmon set net near Shiretoko Cape, E of Hokkaido on 28 Oct. 2011, held at the Shibetsu Salmon Museum (36.1 cm SCL, 8.4 kg BM) and returned to PNPA.
71916	26-Aug-11	Last signal 43°56'N 135°45'E	Possibly captured. Stopped on 26 Aug. 2011 near Vladamir Bay, Russia. Restarted on land, remote coastline of Russia on 1 Mar. 2012, 10 km S of Rudyana Pristan.
88060	10-Nov-11	Last signal 44°11'N 145°21'E	Captured by a salmon set net around Shiretoko Cape, E of Hokkaido, on PM of 19 Nov. 2011. This turtle was already dead and sent to PNPA.
>50 cm SCL			
23513	30-Nov-11	Last Signal 35°46'N 135°09'E	Captured by a set net around Kasumi-cho, Hyogo Prefecture on the morning of 9 Aug. 2011. This turtle was sent to Kasumi Fishing Port and released on that PM from off Kasumi Fishing Port, but ended near shore.
23542	28-Nov-11	Last Signal 35°07'N 136°44'E	Captured by a set net around Tsunegami Point, Fukui Prefecture, Wakasa Bay on PM 1st Aug. 2011. This turtle was sent to Hiruga Fishing Port and released immediately on that evening from off Hiruga Fishing Port, but died and stranded on the Shichiri Nagahama-Beach, Tsugaru-shi, Aomori Prefecture, on PM of 20 Nov. 2011.

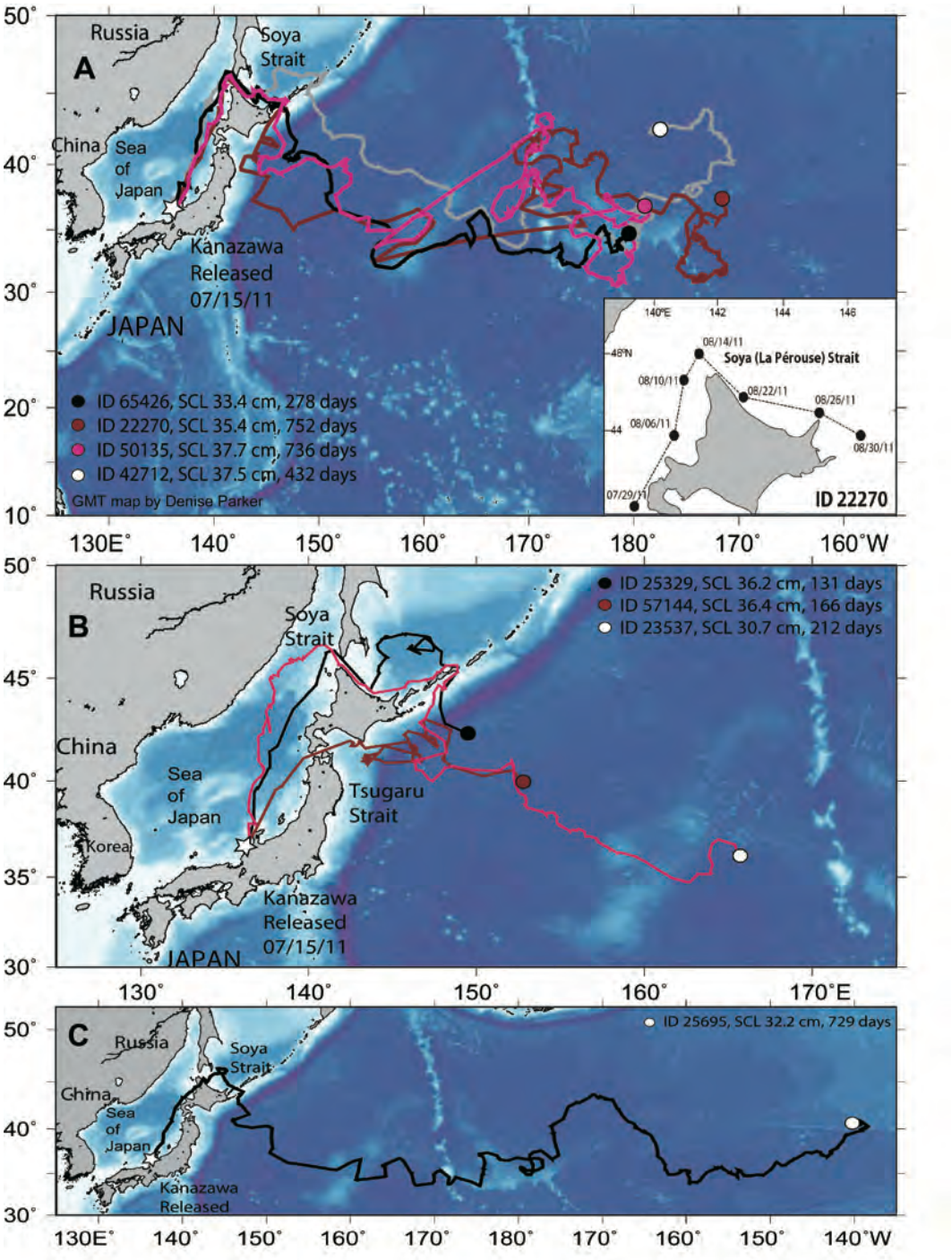

Figure 2. Movement route maps of satellite-tagged loggerhead turtles <50 cm straight carapace length (SCL) after their release off Kanazawa-shi, Sea of Japan, on July 15, 2011. Circles: final positions. Open star: start position. (A) Tracks of turtle IDs 22270, 42712, 50135 and 65426. Inlet: track of turtle ID 22270 leaving the Sea of Japan on August 22, 2011 through the Soya Strait. (B) Tracks of turtle IDs 23537, 25329 and 57144. (C) Track of turtle ID 25695.

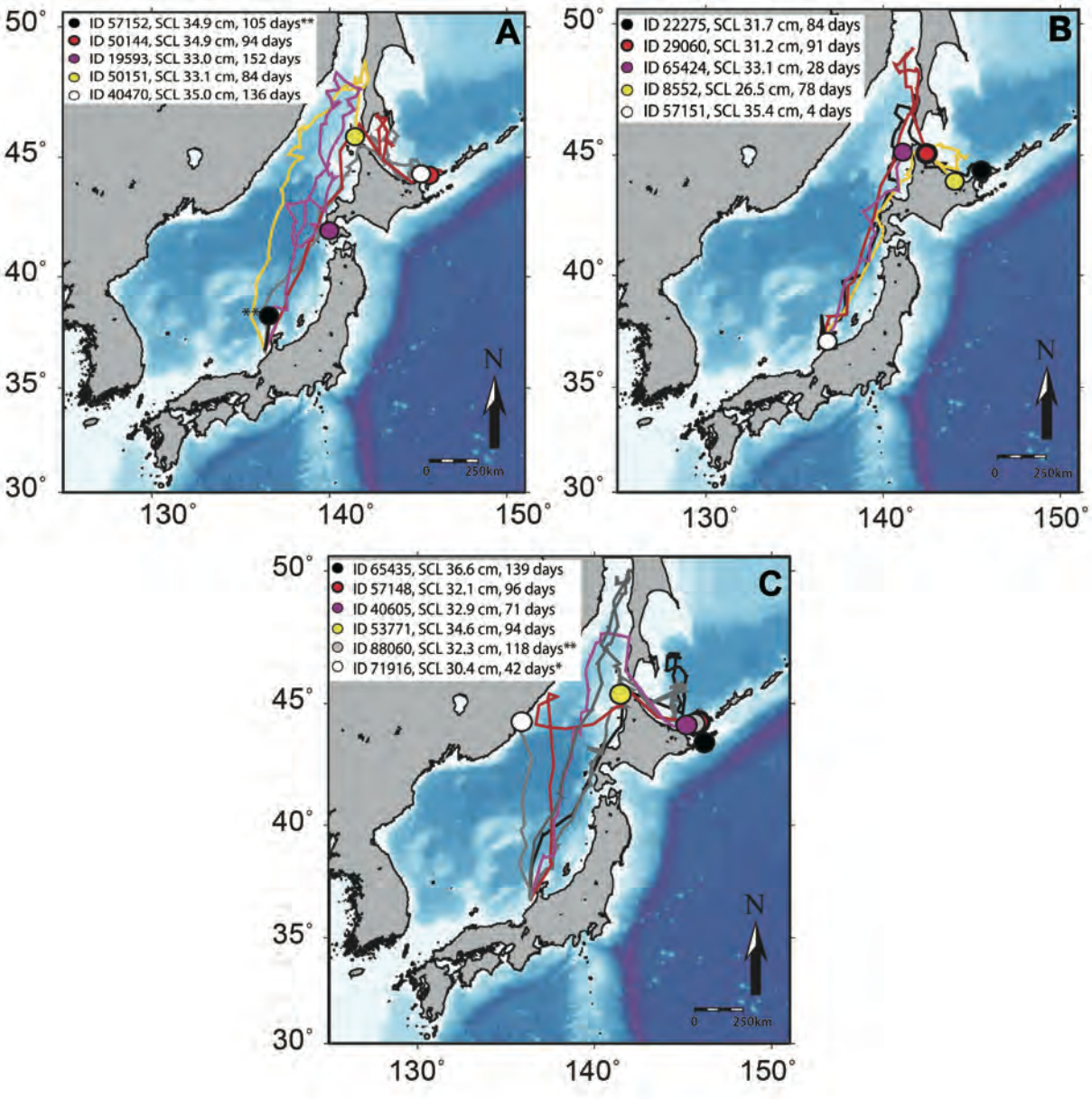

Figure 3. Movement route maps of satellite-tagged loggerhead turtles <50 cm straight carapace length (SCL) after their release off Kanazawa-shi, Sea of Japan, on July 15, 2011. Circles: final positions. *: likely stranded. **: recaptured. (A) Tracks of turtle IDs 19593, 40470, 50144, 50152 and 57152. (B) Tracks of turtle IDs 8552, 22275, 29060, 65424 and 57151. (C) Tracks of turtle IDs 40605, 53771, 57148, 65435, 71916 and 88060.

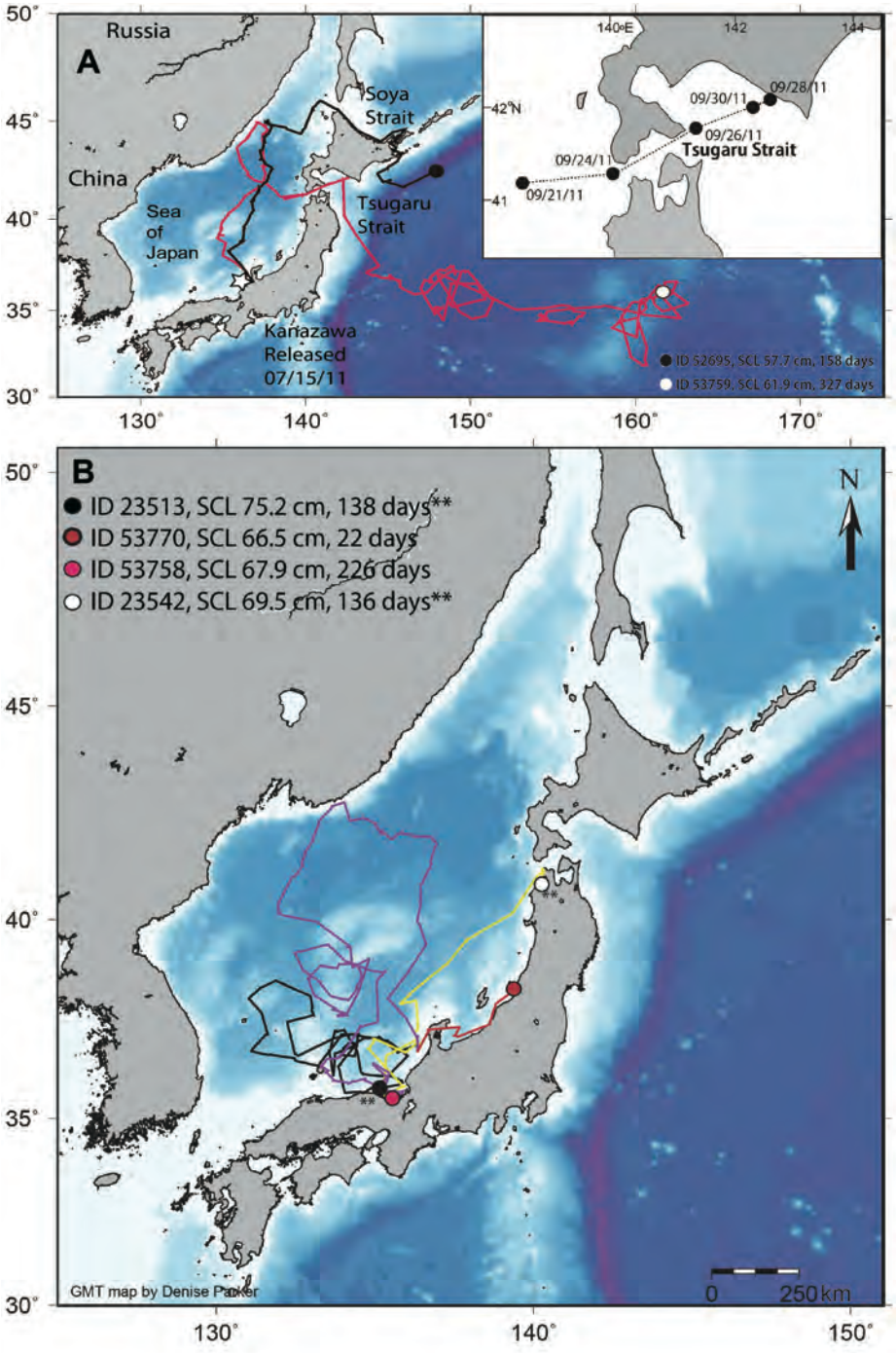

Figure 4. Movement route maps of satellite-tagged loggerhead turtles >50 cm SCL after their release off Kanazawa-shi, Sea of Japan, on July 15, 2011. Circles: final positions. Open star: start position. **: recaptured. (A) Tracks of turtle IDs 52695 and 53759. Inlet: track of turtle ID 53759 leaving the Sea of Japan on September 26, 2011 through the Tsugaru Strait. (B) Tracks of turtle IDs 23513, 23542, 53770 and 53758.

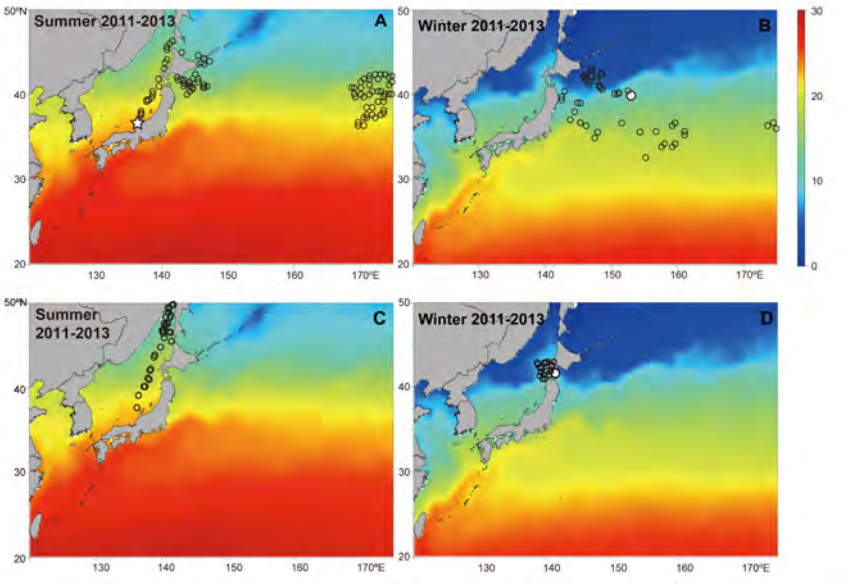

Figure 5. Sea surface temperature (SST) in the Sea of Japan and western North Pacific and positions of satellite-tagged loggerhead turtles <50 cm straight carapace length (SCL). Open star: start position, circles: positions. (A) Positions of turtle IDs 22270, 25695, 42712, 50135, 57144 and 65426 leaving the Sea of Japan at summer 2011–2013. (B) Positions of turtle IDs 22270, 25695, 42712, 50135, 57144 and 65426 leaving the Sea of Japan at winter 2011–2013. (C) Positions of turtle IDs 19593 and 53771 that stayed in the Sea of Japan at summer 2011–2013. (D) Positions of turtle ID 19593 that stayed in the Sea of Japan at winter 2011–2013.

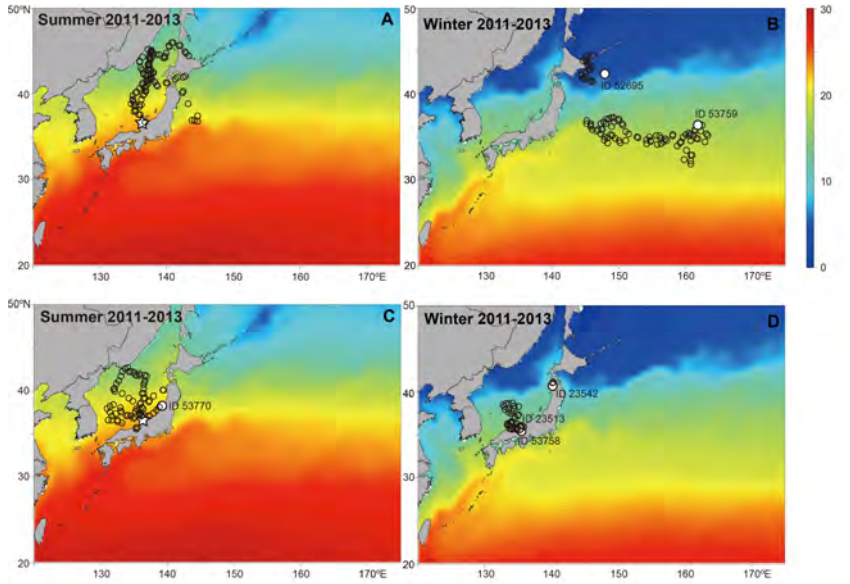

Figure 6. Sea surface temperature (SST) in the Sea of Japan and western North Pacific and positions of satellite-tagged loggerhead turtles >50 cm straight carapace length (SCL). Circles: positions, open star: start position. (A) Positions of turtle IDs 52695 and 53759 that left the Sea of Japan at summer 2011–2013. (B) Positions of turtle IDs 52695 and 53759 that left the Sea of Japan at winter 2011–2013. (C) Positions of turtle IDs 23513, 23542, 53758 and 53770 that stayed in the Sea of Japan at summer 2011–2013. (D) Positions of turtle IDs 23513, 23542 and 53758 that stayed in the Sea of Japan at winter 2011–2013.

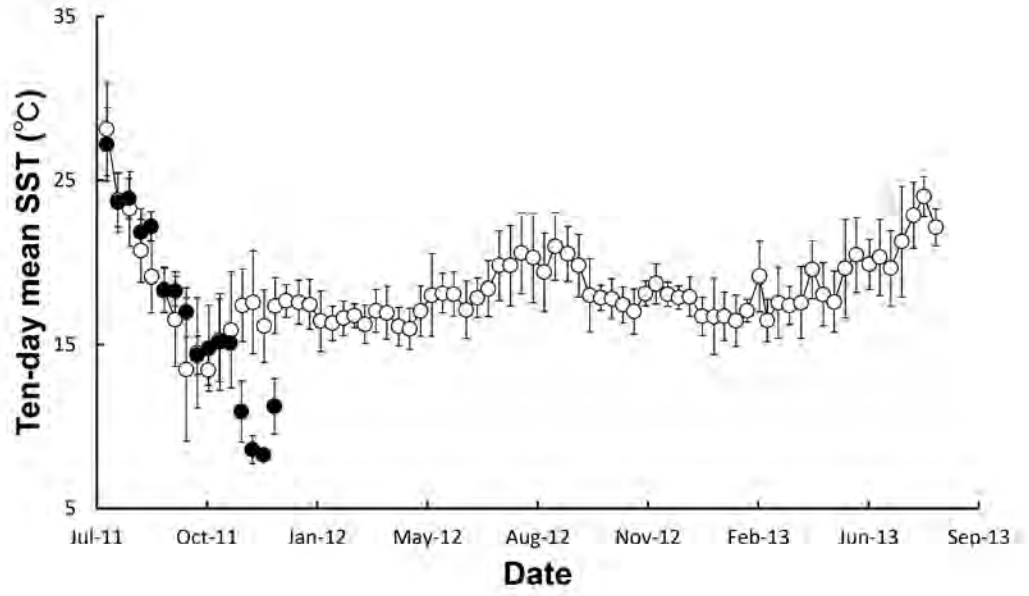

Figure 7. Ten-day mean (± SD) sea surface temperatures (SSTs) experienced by satellite-tagged loggerhead turtles <50 cm straight carapace length (SCL). Filled circles: six turtles staying in the Sea of Japan, open circles: three turtles leaving the Sea of Japan.

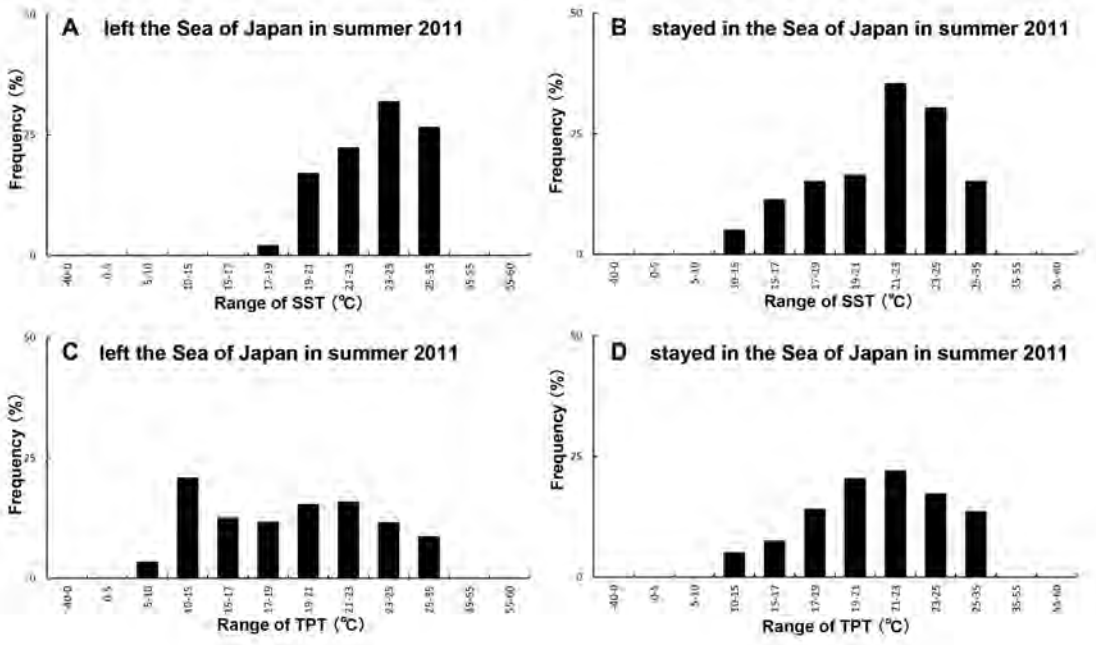

Figure 8. Comparison of frequency distributions between sea surface temperatures (SSTs) and time percent temperatures (TPTs) experienced by satellite-tagged loggerhead turtles <50 cm straight carapace length (SCL) during summer 2011. (A) SSTs collected for locations of eight turtles leaving the Sea of Japan. (B) SSTs collected for locations of seven turtles staying in the Sea of Japan. (C) TPTs collected for locations of eight turtles leaving the Sea of Japan. (D) TPTs collected for locations of three turtles staying in the Sea of Japan.

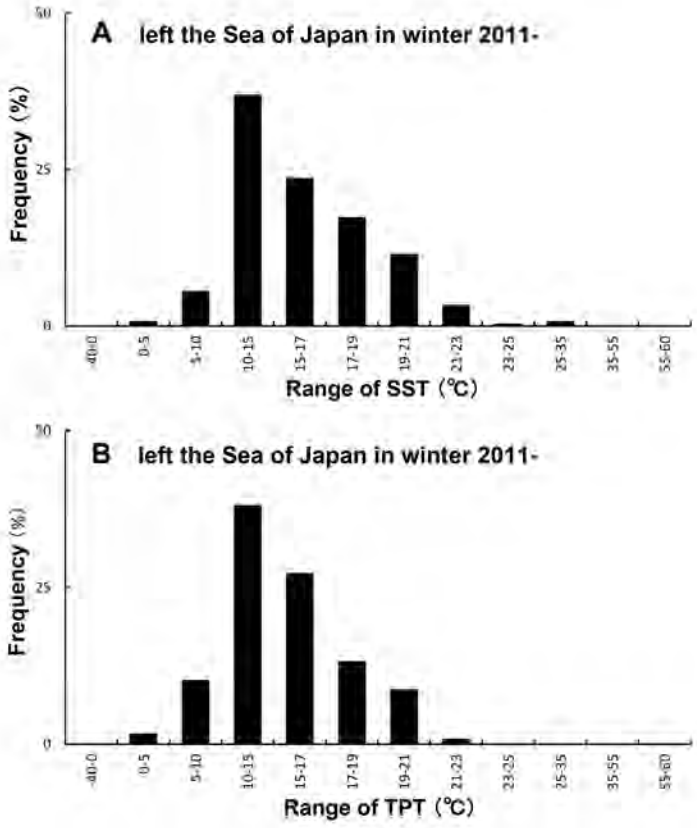

Figure 9. Comparison of frequency distributions between sea surface temperatures (SSTs) and time percent temperatures (TPTs) experienced by satellite-tagged loggerhead turtles <50 cm straight carapace length (SCL) after winter 2011. (A) SSTs collected for locations of eight turtles leaving the Sea of Japan. (B) TPTs collected for locations of eight turtles leaving the Sea of Japan.

SATELLITE TRACKING OF TURTLES >50 CM SCL FROM THE SEA OF JAPAN

Two smaller turtles (IDs 52695 and 53759, 57.7 cm and 61.9 cm SCL) of 3 and 4 years old, respectively, exited via the Soya or Tsugaru Straits on September 26, 2011 and reached the western North Pacific Ocean after moving north in the Tsushima Warm Current and its extensions (Figures 4A, 6A, B, Tables 2, 3). They were tracked for 58 and 327 days with total distances of 28,400 and 10.492 km, respectively (Table 3).

Four turtles did not leave the Sea of Japan and tracked for 130 days on average with total distance traveled of 2290.5 km on average (Table 3, Figures 4B, 6C, D).

SSTS AND TPTS EXPERIENCED BY TURTLES <50 CM SCL

Ten-day mean SSTs for turtles <50 cm SCL ranged from 8.3 to 28.1 °C between 2011 and 2013 (Figure 7). In summer 2011, the turtles that did not leave the Sea of Japan experienced SSTs ranging from 8.3 to 27.2 °C with mean (±SD) SSTs of 16.8 ± 3.4 °C; however, the turtles that left the Sea of Japan experienced a higher range from 13.4 to 28.1 °C with mean (±SD) SSTs of 18.1 ± 6.5 °C. Both groups of turtles demonstrated the same tendency in SSTs during summer 2011 (until mid-October); however, the former group experienced an extreme drop of SSTs to <10 °C, whereas the latter group

experienced a minimum SST of 13.4 °C. Thereafter, they showed a year-round migration pattern corresponding to the fluctuation of SSTs with a slight fall and rise of SSTs between 16.1 and 24.0 °C in the North Pacific Ocean.

The frequency distributions of SSTs and TPTs during the study period for the three turtles that left the Sea of Japan and the six that stayed in the Sea of Japan were compared (Figure 8A–D). During summer 2011, the three turtles that left the Sea of Japan (IDs 22270, 25695 and 42712) experienced SSTs with a range of 17–35 °C and a mode of 23–25 °C (mean ± SD = 18.5 ± 4.7 °C, N = 1113; Figure 8A), which were significantly different to the TPTs that had a range of 5–35 °C and a mode of 10–15 °C (χ^2-test, χ^2 = 120.17, P <0.001; Figure 8C). The six turtles that stayed in the Sea of Japan (IDs 19593, 29060, 50151, 57151, 65424 and 71916) experienced SSTs with a range of 10–35 °C and a mode of 21–23 °C (20.8 ± 4.0 °C, N = 162; Figure 8B), and the TPTs had a range of 10–35 °C and a mode of 21–23 °C (Figure 8D), which were not significantly different from each other (χ^2-test, χ^2 = 9.76, P >0.05).

The SSTs in summer 2011 between the turtles that left (Figure 8A) and those that stayed in the Sea of Japan (Figure 8B) were significantly different (χ^2-test, χ^2 = 44.71, P <0.001), and the SSTs of the former group were distributed in a narrower range. Similarly, the TPTs between the two groups were significantly different (χ^2-test, χ^2 = 1152.59, P <0.001), with the turtles in the group that left the Sea of Japan experiencing lower temperatures more frequently than the other group.

During winter 2011, the mean SSTs (16.7 ± 1.8, N = 3161) of the turtles that left the Sea of Japan ranged 0–35 °C with a mode of 10–15 °C (Figure 9A). The TPTs ranged 0–23 °C with a mode of 10–15 °C (Figure 9B). There was no significant difference between SSTs and TPTs (χ^2-test, χ^2 = 10.12, P >0.05).

RECAPTURED TURTLES

Three turtles that failed to pass through either strait by winter and two turtles that reached the western North Pacific Ocean were recaptured in set nets or were stranded in the Sea of Japan or around the Okhotsk Sea. One turtle (ID 57152) was recaptured alive on October 28, 2011, returned to the PNPA, and measured 11 days later. This turtle, which was 34.9 cm SCL and 7.2 kg BM at release, had grown to 36.1 cm SCL and 8.4 kg BM when it was recapture 3 months later (Table 4).

Discussion

The satellite tracking devices placed on the immature loggerhead turtles allowed us to follow some of the turtles in excess of a full year. After their exit from the Sea of Japan, they moved directly to the central North Pacific Ocean, which is an important nursery ground (Polovina et al. 2006, Narazaki et al. 2015). This pattern was traced well by the movements of two turtles (IDs 22270 and 53759) that were tracked for 752 and 327 days, respectively. Besides that, when we summarized the sites where the loggerhead turtles had drifted ashore or by-caught (Kuramoto and Ishii, 2003; Honma et al., 2010; Ichisawa et al., 2013; Usui et al., 2014; Ishihara et al., 2017), these tracked courses were considered similar to the migrations of wild loggerheads that depend on the Tsushima Warm Current and its extensions. The presence of exit routes suggests that the immature loggerheads entering into the Sea of Japan are able to disperse successfully and contributed to the North Pacific Ocean subpopulation.

Nineteen of all immature turtles continued traveling northeastward and exited the Sea of Japan, while the rest remained in the Sea of Japan until the transmitters stopped sending signals. The turtles that passed through the Soya Strait after leaving the Sea of Japan continued traveling southeastward along the northeast coast of Hokkaido in the Okhotsk Sea. Then, these turtles and those that passed through the Tsugaru Strait continued traveling eastward more than 180 °E and remained in oceanic waters traveling hundreds of kilometers offshore east of Japan and within the Kuroshio Extension Current region (Figures 2A–C, 4A, 5A, B, 6A, B). Differences in movement patterns were seen between larger and smaller turtles. After release, four of six turtles >50 cm SCL moved around and

stayed more to the south of the Sea of Japan. The rest of the larger turtles ($N = 2$) and all turtles <50 cm SCL headed north and never went southwestward close to the Tsushima Strait. In addition, all but five of the smaller turtles tried to leave the Sea of Japan via the Soya Strait, while the turtles >50 cm SCL utilized both straits. Moreover, if the smaller turtles were navigating only by the ocean current, it was strange that the smaller turtles were more biased to pass Soya Strait than Tsugaru Strait. In the Sea of Japan, 50–70% of the current moves through the Tsugaru Strait to the North Pacific (Hata 1962), and the rest moves north along the west Hokkaido coast, entering from the Soya Strait to the Okhotsk Sea (Leonov 1960). Smaller turtles may not drift passively only depending on ocean current. Briscoe et al. (2016) supported the current theories on active dispersal by young oceanic-stage sea turtles showing that the distribution of simulated turtles driven by currents significantly differed from that of the 1–3 year old loggerhead turtles. Although the warmer waters distributed uniformly higher near the Tsugaru Strait, it could be seen that there was an influence of cold water from the north near the Soya Strait (Figure 5). Such cold water masses may be another factor changing the migration routes for loggerheads which drift passively within warm current.

During the summer of 2011, turtles that left the Sea of Japan experienced a relatively wider range and lower water temperatures than those that stayed in the Sea of Japan. The SSTs experienced by three turtles that left the Sea of Japan were significantly different from those of the TPTs (range: 17–35 °C vs. 5–35 °C, mode: 23–25 °C vs. 10–15 °C; Figure 8A, C). In general, even in the northern Sea of Japan no SSTs ranged 5–10 °C were recorded during summer (Ogawa 1983). The relatively lower TPTs must have resulted from their active diving behaviors. In contrast, the six turtles that stayed in the Sea of Japan experienced relatively lower SSTs (range: 10–35 °C, mode: 21–23 °C, Figure 8B), with almost identical TPTs. These turtles likely did not dive often; however, in the present study, we could not record their diving behavior and so we cannot know if they were diving or not. Narazaki et al. (2015) reported that immature loggerheads performed deep dives (deepest dive at >340 m), although the SCLs were greater than those in the present study. In the present study, the turtles that left the Sea of Japan possibly dove to a water temperature of 5–10 °C. This temperature range is recorded in 150–200 m depth at 36°10′ N, 135°50′ E during a typical summer and autumn in the Sea of Japan (Naganuma 2000). The success in leaving the Sea of Japan is likely related to a higher frequency of dives, although further research is required to confirm this theory.

The turtles that left the Sea of Japan experienced lower TPTs than those that stayed during the summer of 2011. High frequency diving might have contributed to the success of leaving the Sea of Japan. The fastest turtle was able to leave the Sea of Japan after two weeks and even the slowest turtle left within three months after release (Table 1). Within two months after release, 13 out of the 19 turtles that left the Sea of Japan had already exited. Among the turtles that stayed, seven out of the 11 turtles survived more than two months after their release and might have managed to reach the Tsushima Warm Current. However, there is no way to confirm this.

Conversely, after winter 2011, no significant differences were reported between the frequency distribution of SSTs and TPTs in turtles that left the Sea of Japan (Figure 9A, B). In the open ocean, dense aggregations of gelatinous zooplankton can form around physical discontinuities such as fronts (Graham et al. 2001), which might provide a substantial food resource for loggerhead turtles (Parker et al. 2005). Narazaki et al. (2015) observed that overwintering turtles moved in relatively shallow water dives (i.e., daily mean depth = 14.8 m) and turtles during the winter of the present study might be able to feed on such mesopelagic prey without deeper exploratory dives.

Several of the immature turtles were unable to reach the North Pacific Ocean before experiencing remarkable temperature drops under the influence of the periodic wind and cold current. A few of the immature turtles traveled to the Soya Strait but nearly all of the tracks ended either at or before Shiretoko Cape or Kunashiri Island (or the Archipelago near this island). Almost all records of strandings were concentrated during late November to early April (Ishihara et al. 2017). The lethal temperature for loggerheads is <10 °C, where turtles become lethargic and float due to physiological failure, with cold-stunning events widely reported at <8 °C (Witherington & Ehrhart 1989).

Recapturing the majority of turtles was impossible as very few turtles were ever recovered after their release. Fortunately, turtle ID 57152 was recaptured alive on October 28, 2011, and was returned to the PNPA within a week and measured 11 days after recapture. The growth rate of this turtle during the period from release to recapture three months later was 0.12 mm day^{-1}. This was higher than the previously reported growth rate (0.08 mm day^{-1}) from a turtle released off Niigata-shi to recapture at Esashi-cho tracked for 61 days (Usui et al. 2014). The present result is one rare example of the advantage of careful measurement and weighing by the same person before and after recapture.

The results of the present study advance our knowledge of the movement habitats of immature loggerheads in the Sea of Japan and the oceanic North Pacific. In addition, bycatch in the subarctic zone, which has been thought to be outside their distribution, should also be investigated to clarify how many younger turtles are caught. In the future, this knowledge should be applied to conservation and management measures. Such applications would include reducing incidental loggerhead mortality by recognizing intersections of their distribution with fishing activities, developing the methods and technology to reduce bycatch, or enhancing national and internatinal efforts to identify and develop a new effective protected area during their migration periods.

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