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Summer migration to temperate foraging habitats and active winter diving of juvenile loggerhead turtles *Caretta caretta* in the western North Pacific

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Abstract Endangered loggerhead turtles (*Caretta caretta*) are highly migratory marine reptiles that spend extended maturation periods at sea. Although an understanding of the biology and ecology of juveniles is essential for effective conservation of this species, such information is still limited, especially for the North Pacific population. The first quantitative bycatch survey in northern Japan revealed that the Sanriku coastal area served as an important summer foraging habitat for large juvenile loggerhead turtles in the western North Pacific. To examine their year-round distribution and diving behaviour, we deployed satellite-relayed data loggers on six turtles (mean SCLn–t $\pm$ SD = 69.2 $\pm$ 9.2 cm, range = 58.3–82.5 cm). While turtles predominantly utilize the Sanriku coastal area and surrounding oceanic waters during summer, all turtles spent most of their time travelling in oceanic waters (>200 m) several kilometres east of Japan and sometimes in association with the Kuroshio Extension Current during winter. Although water temperature experienced by turtles significantly decreased during winter, they predominantly stayed in water >15 °C. There was no strong seasonal pattern in diving behaviour, and daily average dive duration was 20.9 $\pm$ 11.6 min regardless of summer or winter. In addition, turtles sporadically performed deep dives, including the deepest dive (>340 m) ever recorded for this species, during winter. These results suggest that juveniles remained active and possibly foraging in oceanic habitats throughout the winter rather than adopting the quiescent overwintering strategy (i.e. undertaking prolonged dives lasting >300 min) previously reported in adult females.

Introduction

While knowledge of distribution, habitat range and behaviour is essential for designing effective conservation management for threatened species (Parrish 2005; Hamann et al. 2010), such information is often deficient for animals inhabiting the marine realm (Norse and Crowder 2005). Endangered loggerhead turtles, *Caretta caretta* (Linnaeus 1758), are highly migratory animals that travel between breeding and foraging habitats (Musick and Limpus 1997). Although modern telemetry studies have identified important foraging habitats (Polovina et al. 2006; Casale et al. 2012) and seasonal migration patterns (e.g. Mansfield et al. 2009) for some populations, our knowledge beyond the breeding habitats is still limited. As sea turtles are slow growing and late maturing, understanding their biology during extended maturation periods at sea is particularly important for their conservation.

In the North Pacific, the south-west coast of the Japanese Archipelago hosts the largest loggerhead turtle nesting habitats with >90 % of the North Pacific population (Bowen et al. 1995). Immediately after hatching, turtles disperse

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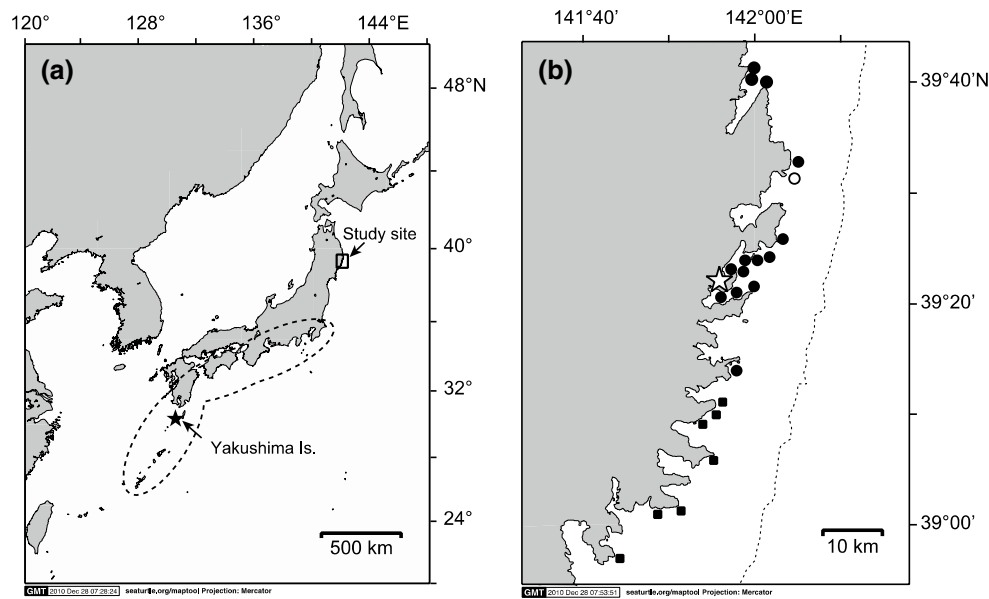
Fig. 1 Maps of the study site. **a** Japanese archipelago showing the location of the study site. Coastal area encircled by a *dashed line* indicates the geographic range of nesting sites of North Pacific loggerhead turtles based on information by Kamezaki et al. (2003). The *black star* indicates Yakushima Island, the largest nesting site in North Pacific. **b** Map of the study site indicating set net locations where turtles were collected since 2005 (*open dot*), 2006 (*closed dots*) and 2008 (*closed squares*). The *open star* indicates the location of the International Coastal Research Center. The *dashed line* represents 200-m-depth contour

into the ocean undertaking a mostly passive migration transported by oceanic gyre systems, such as the Kuroshio and North Pacific Currents, and some turtles reach Baja California in the eastern Pacific (Bowen et al. 1995). After several years, large juveniles return and recruit to foraging habitats around Japan. Upon maturity, adult females undertake seasonal breeding migration between foraging habitats and specific nesting beaches every few years (Plotkin 2003). Flipper tag recovery and satellite tracking studies suggest that adult females nested in Japan migrate to either the East China Sea or the Pacific Ocean along the Kuroshio Current (Kamezaki et al. 1997; Hatase et al. 2002b, 2007). In addition, bycatch surveys reported aggregations of large juveniles and adults in the Japanese coastal areas in the vicinity of their nesting beaches (Ishihara and Kamezaki 2011; Ishihara et al. 2011). However, there is a paucity of data regarding how large juveniles returning from the eastern Pacific utilize potential foraging habitats around Japan until they reach sexual maturity.

Foraging habitats for large juvenile loggerhead turtles have been better documented for North Atlantic populations. For example, large juvenile loggerhead turtles are widely found in the lagoons, estuaries and coastal waters in the eastern USA from Florida to Long Island in New York (Mendoca and Ehrhart 1982; Dodd 1988). The major developmental foraging habitats for North Atlantic populations are located in temperate coastal waters of Virginia and Chesapeake Bay where a number of large juveniles show strong seasonal philopatry during summer (Lutcavage and Musick 1985; Musick and Limpus 1997; Mansfield et al. 2009). In the western North Pacific, Sanriku coastal area is located at similar latitudes as Chesapeake Bay (39°N). The Sanriku coastal area is located at 'Kuroshio–Oyashio confluence zone' where dynamic physical processes derived by coexistence of warm Kuroshio-derived water and nutrient-rich cold Oyashio water result in high productivity (Lohrenz and Castro 2006). Although it is located >500 km north from the major Japanese nesting beaches (Fig. 1), there are anecdotal records of sea turtle bycatch in the commercial set nets fishery in this area. Thus, it is highly possible that this area hosts summer foraging habitats for North Pacific loggerhead turtles.

As a strategy, seasonal migration enables animals to exploit seasonal peaks of food resources and/or to avoid the physiological stresses of unfavourable climates (Alerstam et al. 2003; Ultsch 2006). While migration to higher latitudes allows turtles to exploit profitable foraging habitats in temperate water, distribution of turtles is also restricted by thermal conditions of the environment (e.g. Coles and Musick 2000; Mansfield et al. 2009; Hawkes et al. 2011) because their body temperatures are only a few degrees above the ambient temperature and their physiology and behaviour are profoundly influenced by decreasing temperature (Lutz et al. 1989; Sato et al. 1994; Hochscheid et al. 2004; Sato 2014). Due to large seasonal variations, thermal conditions at temperate foraging habitats may not

be favourable for turtles during the winter (Morreale et al. 1992; Mansfield et al. 2009). Some turtles avoid cold winter temperatures by migrating into lower latitudes and/or warmer waters (Hawkes et al. 2007; Mansfield et al. 2009; Hawkes et al. 2011). Yet, not all sea turtles seem to adopt this strategy; at least some turtles may enter a state of hibernation, potentially having reduced metabolic rates in response to decreased ambient temperature. Carr et al. (1980–1981) documented that an aggregation of loggerhead turtles captured by shrimp trawlers during winter in Florida was lethargic and often covered in mud, suggesting that they were hibernating in the mud at the sea bottom. More recently, Hochscheid et al. (2005) showed using satellite-relayed data loggers (SRDLs) that a loggerhead turtle made long resting dives lasting up to 6.8 h during winter when water temperature fell <15 °C. Such prolonged winter dives (>5 h) have been reported in the Mediterranean (Hochscheid et al. 2005; Broderick et al. 2007; Hochscheid et al. 2007), North Atlantic (Hawkes et al. 2007) and North Pacific populations (Hatase et al. 2007), albeit with small sample sizes.

Like many other populations, the North Pacific population of loggerhead turtles is of profound conservation concern. The number of nesting female decreased >80 % over the past three decades (Kamezaki et al. 2003) most likely as a result of anthropogenic threats including fisheries bycatch (Hatase et al. 2002a; Lewison et al. 2004). Understanding year-round distribution and behaviour of this species at the population level is essential for the application of efficient mitigation measures. However, such information is critically deficient in the North Pacific population compared with the North Atlantic and Mediterranean. Thus, we first set out to quantitatively describe seasonal occurrence and size distribution of turtles at temperate habitats in the western North Pacific by conducting bycatch survey at the potential foraging habitats in northern Japan (Sanriku coastal area). Due to large seasonal temperature variations, it is expected that turtles in Sanriku coastal area migrate to warmer water and/or reduce activity during winter. Using satellite tracking, the aims of this study were to examine year-round movements of large juveniles in the North Pacific and to discuss their overwintering strategy by comparing seasonal distributions and diving behaviours.

Materials and methods

Bycatch survey

We collected loggerhead turtles (*Caretta caretta*) between 2005 and 2010, which were incidentally captured by commercial set nets at the Sanriku coastal area (Iwate Prefecture, Japan, Fig. 1). All turtles were promptly transferred to the outdoor flow-through saltwater tanks of the International Coastal Research Center, Atmosphere and Ocean Research Institute, the University of Tokyo (39°21′05N, 141°56′04E), where they were retained for 1 day to up to 3 months. The turtles were fed on soft tissues of Japanese common squid (*Todarodes pacificus*) to keep them healthy. Following the definition by Bolten (1999), we measured straight carapace length notch to tip (SCLn–t), total tail length (TTL) and body mass (BM). Sex was not determined unless an obvious extension of tail (TTL > 30 cm) was observed in a large turtle (SCLn–t > 70 cm), which is a secondary sexual characteristic of males. As this study was conducted as part of a tag and release program, all turtles were released from the study area after applying plastic and metal ID tags issued by the Sea Turtle Association of Japan (Non-Profit Organization; http://www.umigame.org/).

Satellite tracking

In 2009 and 2010, satellite-relayed data loggers (SRDL; Sea Mammal Research Unit, St. Andrews, UK) were deployed on nine turtles that were collected during the bycatch survey (Table 1). After the SRDLs were glued on

Table 1 Summary of satellite tagged loggerhead turtles

Turtle ID	SCLn–t (cm)	Sex	Release date (year/month/day)	Tracking duration (days)	Experienced temperature range* (°C)
L0941	78.5	Male	2009/08/17	17	19.4–24.9
L0905	88.4	Male	2009/08/20	22	16.9–21.1
L0707	65.0	Unknown	2009/08/17	133	17.2–24.1
L0910	58.3	Unknown	2009/08/20	239	10.3–25.4
L0912	63.3	Unknown	2009/08/20	403	13.1–28.6
L0956	68.4	Unknown	2009/09/25	111	13.2–26.3
L1002	63.8	Unknown	2010/07/21	94	16.3–26.3
L1004	77.8	Male	2010/07/23	311	17.7–26.1
L1005	82.5	Male	2010/07/23	255	15.5–26.8

* Temperature ranges experienced by tracked turtles were recorded by SRDL at 2 m depth

the turtles' carapaces using epoxy resin (Loctite E-60 NC, Henkel, Düsseldorf, Germany), all turtles were released in Otsuchi Bay, Iwate, Japan (39°20′30N, 141°56′00E). The locations of SRDLs were determined using the ARGOS system, which assigns a quality index for each location. Accuracy of the location classes 3, 2 and 1 is <150 m, 350 m and 1 km, respectively, and there are no limits of accuracy for the remaining location classes 0, A, B and Z. But, maximum error of class 0 was estimated <19 km at coastal water of Japan (Baba et al., 2000). To reconstruct the migration track of each turtle, we used locations of classes 3, 2, 1 and 0. In addition, implausible locations having unnaturally high swim speeds (>9 km h^{-1}) were filtered out from the track (Hochscheid et al. 2007). We calculated daily median locations for each turtle based on the filtered track. Then, daily median locations of all turtles were tailed into hexagonal area bins using QGIS Geographic Information System (Open Source Geospatial Foundation Project, http://qgis.osgeo.org).

The SRDL was fitted with an internal clock, a depth sensor and a temperature sensor. The SRDL measured depth every 4 s and recorded individual dives when the turtle submerged to the depth below 3 m for more than 30 s. The configuration of SRDLs differed between the deployment years: the maximum depth ranges were 220 and 340 m in 2009 and 2010, respectively (see supplemental tables for the resolutions of dive parameters). Once a dive was completed, the raw dive data were processed on-board to determine the time and depth of the five most significant points of inflection, and the resulting dive profile data were stored in a buffer within the SRDL. Then, the data in the buffer were randomly transmitted via ARGOS system for the next 5 days, insuring that the transmitted dives were representative and not biased by the transmission schedule (Fedak et al. 2002). In addition, all dive data were summarized for 24-h periods and transmitted as daily summary that includes total number of dives, mean and maximum values for both dive depth and duration.

The SRDL also measured ambient temperatures every 4 s at a resolution of 0.1 °C, providing temperature profiles over the depth range used by the turtles. Of all temperatures measured, 12 depth–temperature points were selected based on the conventional broken-stick algorithm used for expendable bathythermographs. Then, the resulting data were stored in a buffer where it was made available for transmission for up to 5 days. Hereafter, we refer to water temperature as the temperature recorded at 2 m depth, the shallowest temperature obtained by SRDLs, as an approximate measure of sea surface temperature. In this study, we obtained water temperature data from SRDLs at intervals of 0.6 ± 0.8 days on average. However, temperature data were not available for up to 17 days because SRDLs were programmed to prioritize transmitting dive data over

temperature data. Therefore, daily median water temperature was calculated by linear interpolation.

The seasonal effect on water temperature experienced by turtles and diving behaviours were examined using generalized linear mixed models (GLMM) with a Gaussian distribution (identity link). Summer and winter seasons were defined as the periods between May 1 and October 31, and November 1 and April 30, respectively. As the SRDL deployed on three turtles (L0941, L0905 and L1002) ceased transmission before entering winter periods, these data were excluded from the statistical analysis. Turtle ID was included as random effects to account for pseudoreplication because data obtained from the same turtle were not independent. Dependent variables were daily water temperature and daily summary of diving behaviour (log-transformed maximum and average dive depth and duration). Explanatory variable was 'season' (summer or winter) for the water temperature model. For the diving behaviour models, explanatory variables were 'season' and 'daily water temperature'. For each dependent variable, the most parsimonious model was selected on the basis of AIC. The significance of the fixed effect of the selected model was tested using Wald's F test. All statistical analysis was performed using R (The R project for Statistical Computing, http://www.r-project.org).

Results

Bycatch survey

Between 2005 and 2010, a total of 152 loggerhead turtles were captured as bycatch in set nets. The number of turtles collected each year ranged from 6 to 55. However, inter-annual variation will not be discussed since the number of set nets increased over the study periods: one net in 2005, 15 nets in 2006–2007 and 22 nets in 2008–2010 (Fig. 1b). Only three out of 152 turtles were found dead during the study resulting in 2 % mortality rate. Bycatch incidents were reported from mid-June to late October (Fig. 2). Mean temperature, at which turtles were captured, was 18.5 ± 2.4 °C (±SD, range = 12.0–23.8 °C). Size of turtles ranged from 49.5 to 88.4 cm SCLn–t (mean ± SD = 70.8 ± 6.4 cm; Fig. 3a). However, the smallest turtle showed an apparent deformity having a concaved carapace. Excluding this malformed turtle, the SCLn–t of the smallest turtle in this study was 52.5 cm. Body mass ranged from 21.5 to 104.5 kg (55.5 ± 13.5 kg: Fig. 3b) and was positively correlated with SCLn–t (BM = 0.00109 × SCLn–t$^{2.54}$, R^2 = 0.90, $F_{1, 147}$ = 1264.0, $P < 0.01$: Fig. 3c). Distinctive elongation in the tail (TTL > 30 cm) was found in 17 turtles (mean SCLn–t ± SD = 79.3 ± 3.7 cm, range = 72.8–88.4 cm). None of the turtles were marked by the old ID tags at their
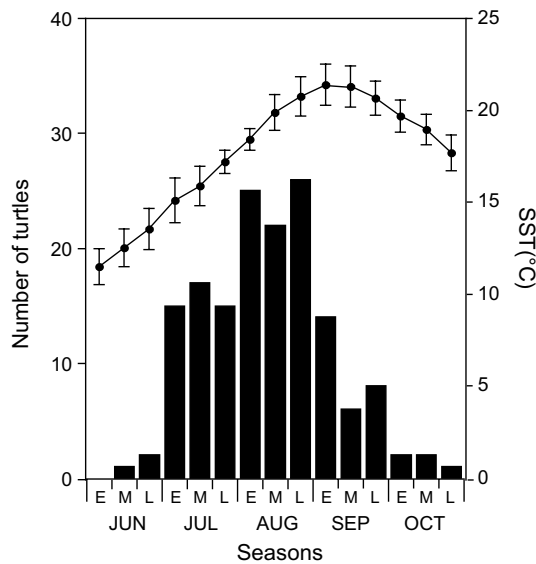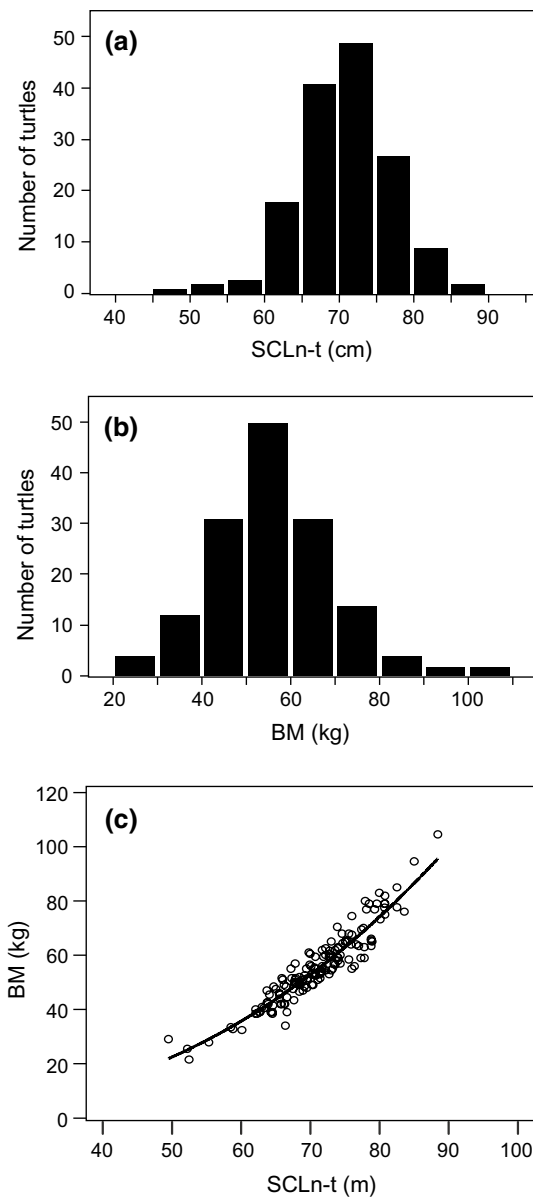
Fig. 2 Number of loggerhead turtles captured in the set nets. *E*, *M* and *L* represent the early, mid and late periods of each month. Average sea and standard deviation of surface temperature measured at the fixed observation point in the study site (at Kamaishi Bay; http://www.suigi.pref.iwate.jp/teichi) is showed on the right axis

initial capture at our study site. Thus, new ID tags were applied to all turtles before releasing from our study site. During the 6-year study period, four out of 149 tagged turtles were recaptured at the study site 1–3 years after the release. Annual growth rate of the three smaller turtles (SCLn–t range = 62.6–70.1 cm at the initial capture) was 1.2–1.6 cm year^{-1}, whereas that of the largest turtle (SCLn–t = 80.7 cm) was only 0.1 cm year^{-1}.

Satellite tracking and general movements

Nine turtles were tracked for an average of 176 ± 133 days (mean ± SD, range = 17–403 days; Table 1). The SRDLs deployed on three turtles (L0941, L0905 and L1002) worked for relatively short periods (17–94 days) and stopped transmitting data before the winter. During these periods, the three turtles showed similar patterns utilizing neritic water (<200 m): two males (L0941 and L0905) travelled southward along the coast of Honshu, while L1002 travelled northward up to 42°14′N in September 2010. After spending a few days in the coastal area of Hokkaido, it headed back southward along the coast until early October 2010. Then, L1002 travelled eastward staying in oceanic water (>200 m) until the transmission ceased in late October 2010. The remaining six turtles were tracked >100 days covering both summer and winter periods. After release from the Sanriku coastal area, all of these turtles concentrated their movements in waters off the eastern coast of Honshu (35–45°N, 140–145°E) during the


Fig. 3 Size distribution of loggerhead turtles captured at Sanriku coastal area: **a** frequency histogram of straight carapace length, **b** frequency histogram of body mass and **c** a relationship between body mass and straight carapace length. Equation for the regression *curve* is BM = 0.00109 × SCLn–t$^{2.54}$

summer, but some turtles continued eastward travelling as far as 170°E (Figs. 4a, 5a, b). During winter, the turtles predominantly stayed in oceanic waters (>200 m), travelling hundreds kilometres offshore east of Japan and within the Kuroshio Extension Current region (Figs. 4b, 5c, d).

Ambient temperature

Mean water temperature experienced by the nine turtles (i.e. recorded at 2 m depth) throughout the entire tracking

Fig. 4 Spatial use and movements of loggerhead turtles equipped with SRDLs during **a** summer (817 track days by nine turtles) and **b** winter (810 track days by six turtles). *Colour* denotes the number of days turtles were recorded in each hexagon. The area of each hexagon is 2282 km² on average. The *star* represents the release site. The *dashed line* represents 200-m-depth contour. *Open circles* indicate locations where deep dives (>200 m) were recorded
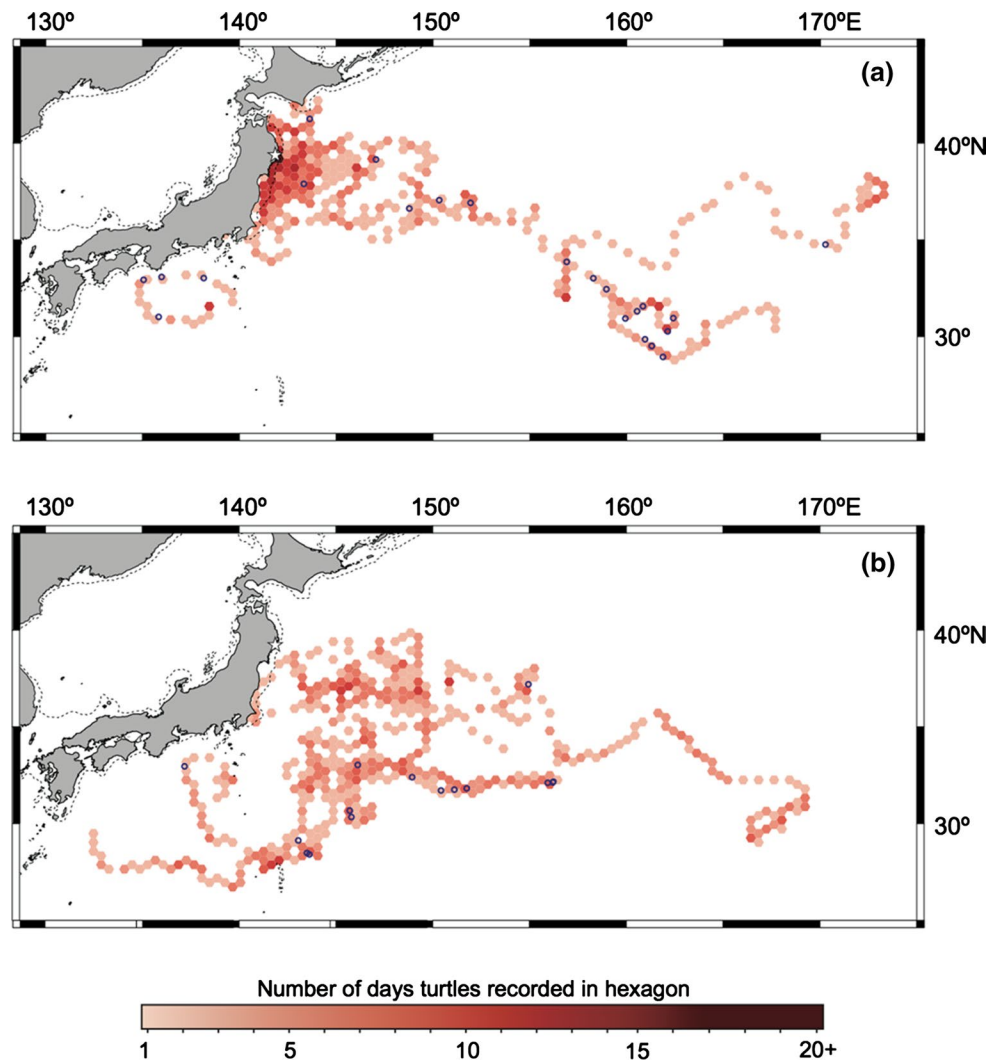
periods ranged from 19.4 to 22.7 °C. Six turtles (L0707, L0910, L0912, L0956, L1004 and L1005) were successfully tracked during both summer and winter periods. For the six turtles, water temperature significantly varied between summer and winter ($F_{1,\ 1349.2} = 568.6$, $P < 0.01$; Fig. 6): the turtles experienced warmer water during summer (mean $\pm$ SD = 22.2 $\pm$ 2.6 °C, $N = 621$ days) than winter periods (19.3 $\pm$ 2.5 °C, $N = 733$ days). Three turtles (L0910, L0912 and L0956) experienced sea surface temperatures <15 °C during winter (Fig. 7). L0956 briefly stayed in cold water (i.e. <15 °C at 2 m depth) for 2 days in the end of November, whereas L0910 and L0912 moved to cold water several times spending up to 10 and 18 days in the water <15 °C, respectively. The lowest temperature of 10.3 °C was recorded by L0910 in 2 April 2010. Although this lowest temperature was recorded 9 days before the SRDL ceased transmitting temperature data, it is less likely that the turtle was dead or cold-stunned because the SRDL continued transmitting dive data until 25 May 2010.

Diving behaviour

Daily dive summary data showed that turtles generally undertook shallow dives (range of medians of daily average dive depth = 6–24 m, $N = 6$ turtles), but occasionally performed deep dives (range of medians of daily maximum dive depth = 20–65 m). Five turtles in this study performed dives beyond the maximum depth range of SRDLs (i.e. >220 m for L0910 and L0912; >340 m for L1004, L1005 and L1002). The GLMM analysis showed that daily average dive depth was influenced by both season and water temperature: daily average depth increased during summer (mean $\pm$ SD = 17.5 $\pm$ 9.2 m, range = 3.0–50.0 m, $N = 621$ days for summer, 14.8 $\pm$ 10.4 m, 3.0–72.5 m, $N = 733$ days for winter; $F_{1,\ 1347.5} = 30.61$, $P < 0.01$) and with increasing water temperature ($F_{1,\ 1349.1} = 73.86$, $P < 0.01$). Daily maximum dive depth was also positively related to water temperature ($F_{1,\ 1350.2} = 329.84$, $P < 0.01$). However, there was no significant seasonal effect on
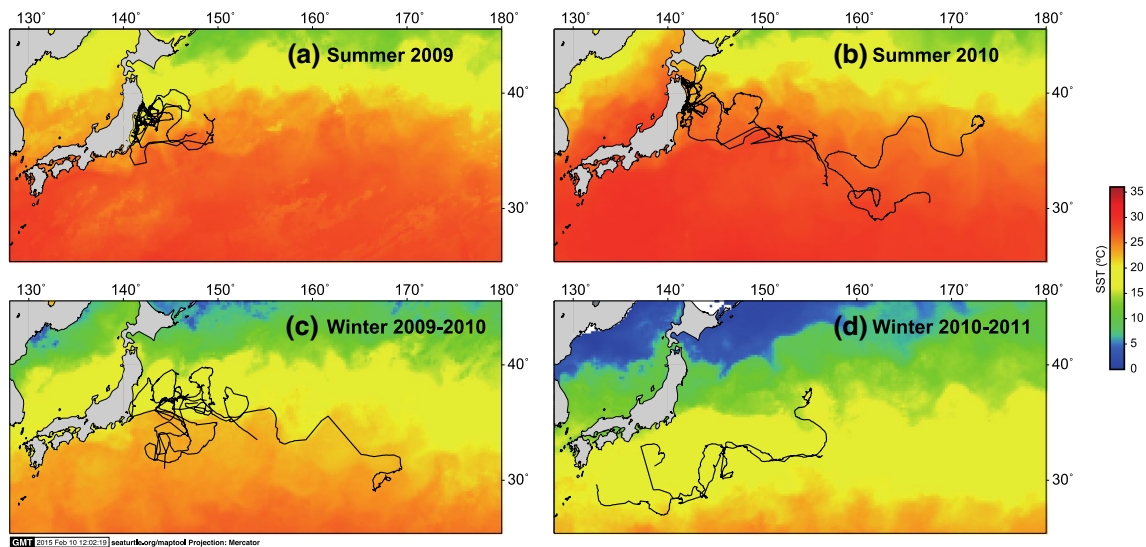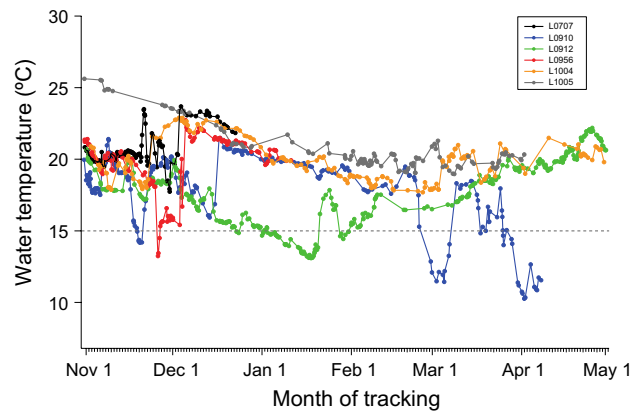
Fig. 5 Satellite tracks of loggerhead turtles and sea surface temperature (SST) in the western North Pacific. **a** Tracks of L0707, L0905, L0910, L0912, L0956 and L0941 during August and October 2009 (*black lines*). *Coloured background shading* shows mean SST for September 2009. **b** Tracks of L0912, L1002, L1004 and L1005 during May and October 2010 overlaid onto mean SST for September 2010. **c** Tracks of L0707, L0910, L0912 and L0956 during November 2009 and April 2010 overlaid onto mean SST for December 2009. **d** Tracks of L1004 and L105 during November 2010 and April 2011 overlaid onto mean SST for January 2011. For the monthly mean SST, NOAA's AVHRR Oceans Pathfinder SST (http://podaac.jp.asa.gov) was used
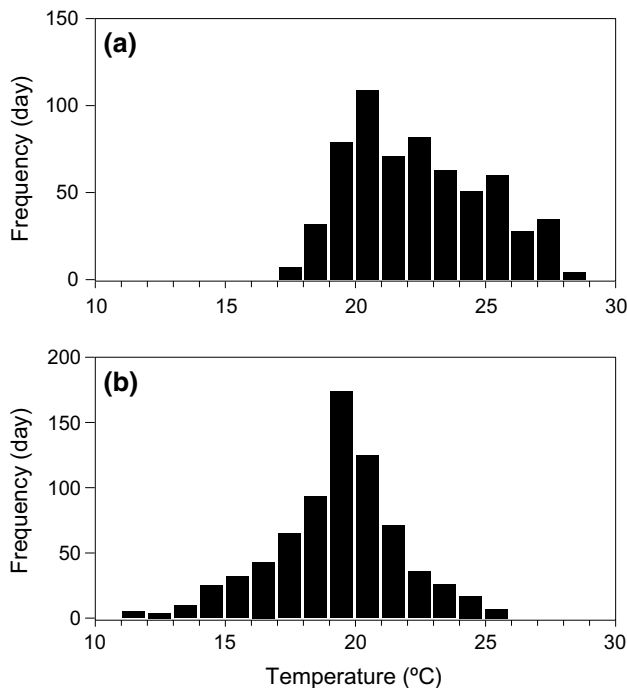
Fig. 6 Frequency histogram of daily water temperature at 2 m depth recorded by SRDLs of six turtles during **a** summer and **b** winter

Fig. 7 Temporal variations in water temperature at 2 m depth measured by SRDLs during winter months. Note that three turtles experienced low temperatures below 15 °C (*dashed line*) for more than a few days

daily maximum dive depth (57.6 ± 47.6 m, 4.0–340.0 m, $N = 1354$ days), and all six turtles undertook deep dives (>100 m) during winter, including the deepest dives (>340 m) by L1004 and L1005 (Table 2). The GLMM analysis for daily dive duration showed that both maximum and average duration were not significantly affected by temperature. Moreover, there was no significant seasonal difference in daily average dive duration (20.9 ± 11.6 min, 0.7–80.0 min, $N = 1354$ days). Daily maximum dive duration was significantly longer during the winter (67.9 ± 32.0 min, 0.7–200.0 min, $N = 733$ days) than the summer (51.5 ± 22.5 min, 12.0–140.0 min, $N = 621$ days; $F_{1, 1348.5} = 94.16$, $P < 0.01$). The longest dive recorded in this study was 200 min, which was performed by L1005

Table 2 Descriptive dive statistics during summer and winter

ID	Summer					Winter				
	No. of dives	Duration (min) [$Q_1 - Q_3$]	Depth (m) [$Q_1 - Q_3$]	Max duration (min)	Max depth (m)	No. of dives	Duration (min) [$Q_1 - Q_3$]	Depth (m) [$Q_1 - Q_3$]	Max duration (min)	Max depth (m)
L0707	1124	7.0 [1.3–24.0]	8.0 [4.0–16.0]	90	180	762	10.0 [1.3–24.0]	8.0 [4.0–16.0]	100	120
L0910	1159	7.0 [1.3–18.0]	8.0 [5.0–22.0]	75	>220	1302	4.0 [2.0–30.0]	8.0 [5.0–20.0]	140	200
L0912	3086	16.0 [1.7–35.0]*	8.0 [4.0–24.0]*	115	>220	2069	2.0 [0.8–30.0]	3.0 [3.0–6.0]	130	160
L0956	673	9.0 [1.3–22.0]*	8.0 [5.0–20.0]*	80	120	801	2.0 [0.8–10.0]	6.0 [4.0–14.0]	115	140
L1004	2304	18.0 [5.0–28.0]	19.0 [7.0–37.5]*	75	>340	2681	20.0 [2.3–35.0]*	12.0 [5.0–32.5]	150	>340
L1005	1665	10.0 [1.3–30.0]	7.0 [4.0–16.0]	140	160	1962	16.0 [4.0–30.0]*	10.0 [5.0–17.0]*	200	>340

Median dive duration and depth are provided with 25 % (Q_1) and 75 % (Q_3) quintiles

Seasonal differences in dive duration and depth were examined for each turtle, and significantly larger value was marked with an asterisk (* $P < 0.05$, Wilcoxon's rank test)

in January 2011 (daily water temperature = 21.1 °C). We obtained a total of 19,588 dive profiles (10,011 and 9577 dives during summer and winter, respectively) from six turtles. Descriptive statistics of these dives are summarized in Table 2.

Discussion

Highly migratory loggerhead turtles are the most temperate species of hard-shelled marine turtles. Combining bycatch survey and satellite tracking, our study highlighted that loggerhead turtles in the western North Pacific utilized temperate habitats on a seasonal basis, as previously reported in the North Atlantic and Mediterranean populations (e.g. Hawkes et al. 2007; Zbinden et al. 2008; Mansfield et al. 2009). Our study provided the first quantitative report of the seasonal occurrence of loggerhead turtles in the Sanriku coastal area. The Sanriku coastal area is known for highly productive fishery grounds in Japan due to complex oceanographic structures caused by mixing of nutrient-rich Oyashio and warm Kuroshio-derived waters. Tens of turtles were incidentally captured by coastal set nets annually during June and October, which coincided with the period when the effect of the Kuroshio-derived water increases (Hanawa and Mitsudera, 1987). Satellite tracking also showed that turtles frequently used the Sanriku coastal area and adjacent oceanic areas during the summer (Fig. 4a). Recent population genetic analysis revealed that individuals in feeding aggregations from Sanriku mainly originated from southern rookeries in Japan, especially from Yakushima Island (Nishizawa et al. 2014). Some turtles seasonally migrate with warm Kuroshio-derived water to capitalize on the highly productive Sanriku coastal area although it is located > 1400 km from their major natal sites (i.e. Yakushima Island, see Fig. 1a).

In the North Pacific, juvenile loggerhead turtles undertake transoceanic migration from their juvenile nursery habitats in the eastern Pacific (Bowen et al. 1995). Ishihara et al. (2011) estimated the size of loggerhead turtles re-entering Japanese water at 56.0–74.9 cm by examining the size distribution of turtles captured off Cape Muroto in Japan (33°15′N, 134°11′E) which is approximately 950 km south-west from our study site. The size distribution of Sanriku and Muroto aggregations largely overlaps. However, it is interesting to note that turtles captured in Sanriku (mean ± SD = 70.8 ± 6.4 cm, range = 52.5–88.4 cm) were slightly smaller than that in Muroto (75.7 ± 6.7 cm, 56.3–105.0 cm). It might be possible that the Sanriku coastal area provides seasonal foraging habitat for younger juveniles, including the ones that just completed their trans-pacific migration from their nursery habitats in the eastern Pacific (Nishizawa et al. 2014).

It is generally challenging to determine the degree of maturity of living sea turtles without using an endoscope. However, we speculate that turtles migrating to the Sanriku coastal area were predominantly juveniles because of the small body sizes. Based on the anatomical examination of >100 bycatch individuals in Japan, the size at maturity (where 50 % of turtles had fully developed gonads or genital duct) for North Pacific loggerhead turtles was estimated at 82.1 cm in SCLn–t for both sexes (Ishihara and Kamezaki 2011). The smallest mature turtle reported in their study was 73.8 and 77.8 cm for females and males, respectively, which coincided with the smallest nesting females recorded in their major nesting ground (i.e. 73.5 cm in Yakushima Island; Kamezaki 2003). Only 33 % of turtles captured in Sanriku were larger than 73.5 cm and 3 % were larger than 82.1 cm, inferring that most of them had not reached sexual maturity. Furthermore, no old tags were attached on any of the turtles when they were first captured

at the study site although standardized tags have been affixed to nesting females in Japan since 1990 (Suganuma and Kamezaki 1991). For example, a total of 2219 adult females were tagged at 16 major nesting beaches in Japan during 1991 and 1995 (Kamezaki et al. 1997). Given that similar efforts have been made until recently, the absence of old tags infers that most of turtles captured at Sanriku have not reached reproductive maturity. It is possible some adult males migrated to Sanriku coastal water as 11 % of turtles showed the secondary characteristics of males, having a distinctively long tail (SCLn–t = 72.8–88.4 cm). Yet, whether these males reached maturity remains uncertain because tail elongation appears to begin before reaching sexual maturity (Ishihara and Kamezaki 2011).

Although the Sanriku coastal area provides favourable foraging habitat for juvenile loggerhead turtles during summer, it is subject to large seasonal variation in water temperature. In the later autumn through the spring, sea surface temperature progressively decreases as low as 4 °C (Takasugi 1992; Sato et al. 2007). The lethal temperature of loggerhead turtles would be just below 10 °C at which turtles become lethargic and float due to physiological failure (Milton and Lutz 2003), and cold-stunning events were widely reported at <8 °C (e.g. Witherington and Ehrhart 1989). Therefore, turtles in Sanriku should migrate to warmer water to avoid lethally cold temperature. This hypothesis was supported by the fact that bycatch incidents were limited during June and October while sea surface temperatures were ≥12 °C (Fig. 2). Satellite tracking of six overwintering turtles showed that they predominantly travelled in the north-west Pacific off east Japan (Fig. 4b). One of the key features characterizing oceanographic condition in this region is Kuroshio Extension Current, a strong warm eastward-flowing inertial jet accompanied by large-amplitude meanders (Qiu 2002). During the winters in 2009–2011, the mean axis of the Kuroshio Extension Current was located around 35°N latitude in the region between 142° and 155°E longitude (Seo et al. 2014). Movements of the overwintering turtles seemed to be associated with the northern and southern edges of the Kuroshio Extension Current, which is recognized for its high eddy kinetic energy and high phytoplankton and zooplankton productivity (Kimura et al. 2000; Qiu 2002). Movements associated with meso-scale eddies are not uncommon in loggerhead turtles, potentially taking advantage of eddy-induced aggregation of prey (Polovina et al. 2004, 2006; Mansfield et al. 2009). A large satellite tracking dataset of juvenile loggerhead turtles in the central and eastern North Pacific identified some important oceanic foraging habitats, such as the Kuroshio Extension Bifurcation Region (30°–40°N, 155°–180°E; Polovina et al. 2006) and the Transition Zone Chlorophyll Front in the central North Pacific (Polovina et al. 2000). The size of turtles tracked in the central North

Pacific was smaller (41.0–81.0 cm in SCL; Polovina et al. 2000, 2006) but partly overlapped with that of turtles in Sanriku coastal area (52.5–88.4 cm). In this study, one turtle (L0912) migrated eastward as far as 170°E. It is possible that some turtles in Sanriku coastal area might migrate further east to use oceanic foraging habitats in the central North Pacific.
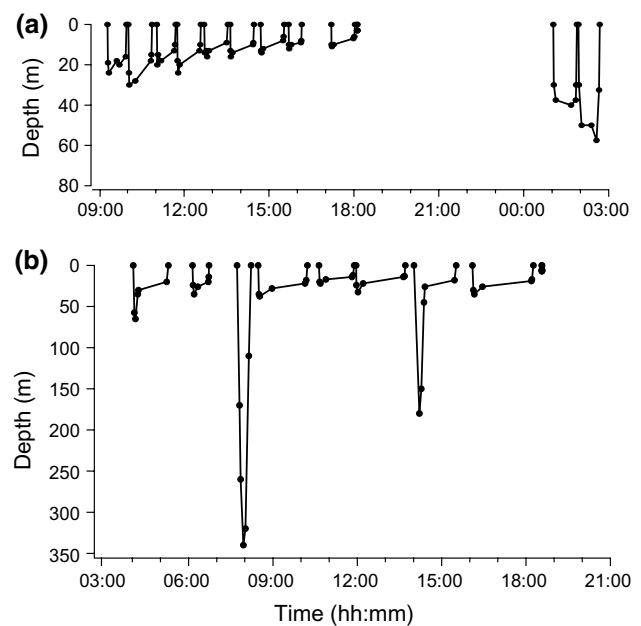
There are only a few reports about the diving behaviour of overwintering loggerhead turtles, all of which showed significant increases in dive duration during the winter associated with decreasing water temperatures (Hochscheid et al. 2005; Broderick et al. 2007; Hatase et al. 2007; Hawkes et al. 2007; Hochscheid et al. 2007). For example, dive duration of an adult female recorded in the coldest months in the Mediterranean Sea (i.e. mean ± SD = 307 ± 127 min, max = 614 min) was more than tenfold longer than summer dives (Broderick et al. 2007). In our study, however, there was no significant seasonal effect on dive duration. Furthermore, maximum dive duration recorded in this study was much shorter than previous studies (Fig. 8), inferring that turtles in this study retained more active throughout the winter although minimum water temperature was as low as 10.3 °C. Prolonged winter dives (>5 h) previously reported were typically characterized by repeated U-shaped dives to similar depth, suggesting that turtles remained quiescent, or potentially hibernating, on the sea bottom (Hochscheid et al. 2005, 2007; Broderick et al. 2007) or mid-water (Hatase et al. 2007; Hawkes et al. 2007). In contrast, our turtles performed various types of dives during winter, including some V-shaped dives to deep depths (>200 m) during the winter (Fig. 9). Some dives were deeper than 340 m although the exact dive depths were not recorded because it was outside of the range of the tags' depth sensors. Nevertheless, this is a new record for loggerhead turtles as previously the maximum dive depth recorded was 233 m (Sakamoto et al. 1990). It is estimated that adult loggerhead turtles become neutrally buoyant at depths near 14 m (Minamikawa et al. 2000). Thus, these deep dives can be considered as active dives because turtles need to stroke hard to compensate for negative buoyancy while ascending from the deep depth (Watanabe et al. 2006). In this study, overwintering turtles generally undertook relatively shallow dives (i.e. daily average depth = 14.8 ± 10.4 m), perhaps foraging on gelatinous prey while travelling at relatively shallow depths where they can attain near neutral buoyancy (Narazaki et al. 2013). In the open ocean, dense aggregations of gelatinous zooplankton can be formed around physical discontinuities such as fronts (Graham et al. 2001). Despite its low caloric value (Doyle et al. 2007), dense aggregation of gelatinous prey may offer substantial food resource for loggerhead turtles in the open ocean. It has been reported that loggerhead turtles consume various types of gelatinous prey, such as scyphozoan, urochordates (e.g. salps, pyrosomes)
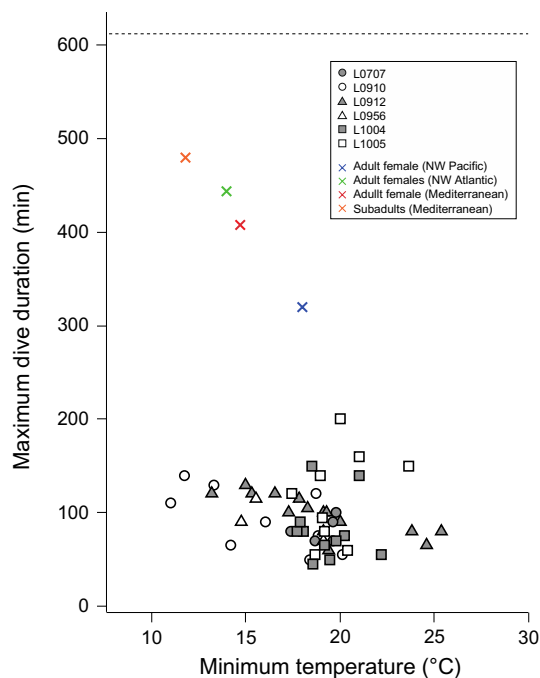
Fig. 8 Relationship between monthly maximum dive duration and monthly minimum water temperature. Maximum dive duration and the lowest temperature previously reported in an adult in North Pacific (Hatase et al. 2007), adults in North Atlantic (Hawkes et al. 2007), an adult and subadults in Mediterranean (Hochscheid et al. 2005, 2007) are added for comparative purposes. The *dashed line* indicates the longest dive duration ever recorded for this species (i.e. 614 min, no temperature information) reported in an adult in Mediterranean (Broderick et al. 2007)

Fig. 9 Examples of dive profiles for 18-h periods: **a** summer dives recorded on 15–16 October 2010 by L1005 while experiencing water temperature of 25.8 °C (i.e. daily median temperature at 2 m depth); **b** winter dives recorded on 12 December 2011 by L1005 while experiencing water temperature of 22.8 °C

and siphonophores (e.g. Dodd 1988; Narazaki et al. 2013). While some coastal scyphozoan jellyfish disappear during winter, many siphonophores and urochordates can be found in the open ocean throughout the year (Doyle et al. 2013). Although these species generally distribute in the deep-water column beyond the regular reach of turtles, overwintering turtles may still be able to feed on these mesopelagic prey because many siphonophores and urochordates conduct diel vertical migration into the upper 100 m during night (Angel and Pugh 2000). In fact, some mesopelagic species (e.g. *Phyrosoma atlanticum*) were found in the stomach of loggerhead turtles captured in central North Pacific (Parker et al. 2005). It is also possible that some deep dives (>200 m) were associated with deep-water foraging. However, such deep dives (>200 m) were recorded sporadically in oceanic habitats (Fig. 4) and are more likely to be exploratory dives as seen in deep-diving leatherback turtles (Houghton et al. 2008).

Both the wide spatial distribution associated with the Kuroshio Extension Current and active dives presented in this study are suggestive of active pelagic foraging during winter, which highly contrasts to the 'hibernation' strategy

mostly reported for post-nesting females (Broderick et al. 2007; Hawkes et al. 2007; Hatase et al. 2007). Our results showed that juveniles in the western North Pacific predominantly stayed in water >15 °C although water temperature significantly decreased during winter (Fig. 6). Some juveniles in the north-west Atlantic seemed to adopt similar active overwintering strategies where they migrate large geographic distances in association with the warm Gulf Stream (Mansfield et al. 2009). It might be more beneficial for juveniles to continue foraging in relatively warm water during winter because the higher food intake rates and temperature result in faster growth rates (Balazs and Chaloupka 2004). Foraging ecology of loggerhead turtles appears to be more plastic than previously believed, and facultative oceanic-to-neritic shifts have been reported for large juveniles (McClellan and Read 2007; Casale et al. 2008; Mansfield et al. 2009) and adult females (e.g. Hatase et al. 2002b; Hawkes et al. 2006). In this study, two turtles migrated southward along the coast by the end of summer although their overwintering habitats were unknown due to short tracking durations. In addition, according to a mark-and-recapture survey conducted concurrent with our study, a few turtles were recaptured at Kochi and Mie prefecture in the south-western part of Japan during the winter (Narazaki 2009; Narazaki et al. unpublished data). It is possible that juveniles in western North Pacific have dichotomous seasonal migration strategies (oceanic vs neritic) as

demonstrated in North Atlantic population (McClellan and Read 2007; Mansfield et al. 2009). Additional tracking of turtles linking with long-term diet study (e.g. stable isotope analysis) will help elucidate polymorphism in foraging and overwintering strategies in this population.

North Pacific loggerhead turtles are a genetically distinct population (Hatase et al. 2002c) that experienced drastic population declines over the past three decades (Kamezaki et al. 2003). By combining bycatch surveys and satellite tracking, we demonstrated that the Sanriku coastal area (summer) and Kuroshio Extension region (winter) are important foraging habitats for large juvenile loggerhead turtles in the western North Pacific. The use of temperate foraging habitats and seasonal migrations to oceanic habitats by large juveniles have been reported for the North Atlantic population (McClellan and Read 2007; Mansfield et al. 2009), but never for the North Pacific population. Fortunately, bycatch mortality rate in the Sanriku coastal area was only 2 % during this study. There was low risk of drowning primarily because the set nets adopted in the study site consist of large nets stretched vertically from the sea surface to the bottom without covering the top of the nets. However, the use of large geographic areas of western North Pacific by large juveniles implies that they are at considerable risk of fishery-induced mortality because pelagic longline fishery effort is generally high throughout the year in the western and central North Pacific (Lewison et al. 2004; Roe et al. 2014). A stage-based population model based on demographic data for loggerhead turtles suggested that conservation efforts should be focused on large juveniles for effective population recovery (Crouse et al. 1987; Crowder et al. 1994). Our study provided a new insight about year-round behaviour of North Pacific large juveniles, suggesting that special mitigation measures should be considered in their oceanic habitats in the western North Pacific. It is clear that subsequent studies integrating turtles' movements and regional fishing effort data will help identifying the priority areas for conservation management.

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