



Summer-restricted migration of green turtles *Chelonia mydas* to a temperate habitat of the northwest Pacific Ocean

Takuya Fukuoka^{1,*}, Tomoko Narazaki², Katsufumi Sato¹

¹Atmosphere and Ocean Research Institute, The University of Tokyo, Kashiwa, Chiba 277-8564, Japan

²Sea Mammal Research Unit, School of Biology, University of St Andrews, Fife KY16 8LB, UK

ABSTRACT: The foraging habitats of green turtles *Chelonia mydas* range from tropical to temperate areas. Previous studies have generally been biased toward tropical and sub-tropical areas; hence, available data do not accurately describe the species' foraging activity in temperate areas. To reveal seasonal patterns of habitat use in temperate areas, we conducted a by-catch survey, a mark-recapture study, and satellite tracking of green turtles along the Sanriku Coast, a temperate zone in the northwest Pacific Ocean. From July through November of 2005 to 2014, 78 green turtles were captured during a period of relatively high water temperatures (16 to 24°C). Straight carapace length (SCL) ranged from 36.8 to 85.6 cm (average: 49.4 ± 11.4 cm; n = 78), indicating that most of the turtles were juveniles. In the mark-recapture study, 14 of 72 tagged turtles were recaptured 5 to 426 d after release, 12 of which were recaptured south of the release point. Based on satellite tracking data, 3 turtles travelled more than 500 km to reach southern habitats, where water temperature was warmer (13 to 25°C) than along the Sanriku Coast (4 to 22°C). Our results revealed that the Sanriku Coast is a seasonally restricted habitat for juvenile green turtles, which migrate to southern habitats in winter, and that turtles in temperate areas migrated longer than those in tropical and sub-tropical areas. This is the first report of seasonal migration of juvenile green turtles to a temperate habitat in the northern Pacific Ocean.

KEY WORDS: By-catch · Mark-recapture · Satellite tracking · Temperate habitat · Juvenile turtles

INTRODUCTION

The green sea turtle *Chelonia mydas* is listed on the IUCN Red List as an Endangered species, and therefore conservation efforts are necessary (Seminoff 2004). Effective conservation planning requires a comprehensive understanding of a species' entire life cycle, a difficult task for green turtles since this species undergoes ontogenetic shifts in habitat use (Musick & Limpus 1997, Plotkin 2003). After several years in the pelagic zone, juvenile turtles return to coastal waters and occupy various habitats during development until they reach sexual maturity (Musick & Limpus 1997). Upon reaching maturity, turtles

begin breeding migrations between foraging habitats and nesting sites. These migrations are undertaken at multiple year intervals (Hirth 1997, Miller 1997).

Green turtles nest in tropical and sub-tropical areas, but their foraging habitats can extend into temperate zones (King 1982, Suganuma 1994). Most published reports on the life histories of sea turtles have focused on nesting females (e.g. Miller 1997, Godley et al. 2002, Troëng et al. 2005); consequently, the life-history stages and foraging habitats of juveniles and adults are less understood (but see Seminoff et al. 2002, Southwood et al. 2003, Makowski et al. 2006). Moreover, previous studies on foraging

*Corresponding author: t.fukuoka@aori.u-tokyo.ac.jp

habitats have been biased toward tropical and sub-tropical areas; hence, available data may not accurately describe the turtles' foraging activities in temperate areas. Therefore, investigation of foraging habitats in temperate areas is essential for a better understanding of the life history of green turtles.

The Sanriku Coast, located on the Pacific coast of northeastern Japan, is a temperate region more than 1500 km north of the major Japanese nesting sites for green turtles, such as the Ogasawara (Bonin) Islands and the Ryukyu Archipelago (see Fig. 1). Water temperature along the Sanriku Coast area fluctuates considerably, and drops below 4°C in March (Sato et al. 2007), in contrast to most tropical and sub-tropical areas where thermal conditions are more stable with little seasonal fluctuations. There is no nesting beach for sea turtles on the Sanriku Coast; however, there are anecdotal records of sea turtle by-catch in local set-nets. Therefore, this area could be a foraging habitat for green turtles, although it is unclear whether it is inhabited by turtles throughout the year. In addition, the tsunami generated by the 2011 Great East Japan Earthquake seriously damaged the environment of the Sanriku Coast (Ogasawara & Sakai 2012), and greatly disturbed the marine ecosystem (Mori et al. 2011). Green turtles are highly dependent on the coastal environment because their main food sources are seagrasses and seaweeds, which grow only in neritic areas (Bjorndal 1997). Thus, it is possible that the average body condition of turtles declined after the tsunami due to habitat degradation.

Previous studies using mark–recapture and satellite tracking have indicated that adult green turtles migrate more than 1000 km from nesting sites to foraging habitats (Plotkin 2003). During foraging periods, juveniles and adults in tropical and sub-tropical foraging areas establish narrow home ranges (i.e. 10s of km²; Renaud et al. 1995, Seminoff et al. 2002, Makowski et al. 2006, Kameda et al. 2013). Furthermore, juvenile green turtles in Australia displayed strong feeding site fidelity over many years (Limpus et al. 1994). Some studies have documented the presence of juvenile green turtles in temperate foraging areas during the summer (Epperly et al. 1995, González Carman et al. 2011), and González Carman et al. (2012) reported that juvenile green turtles in the southwest Atlantic Ocean migrated to lower latitude waters during the winter. On the other hand, winter dormancy of juvenile and adult green turtles has been observed in the Gulf of Mexico and the Gulf of California (Carr & Caldwell 1956, Felger et al. 1976). Thus, migration patterns of green turtles in temperate foraging areas are not well known. There are 2

possible alternatives for turtles along the Sanriku Coast: winter dormancy within the area, or migration to other foraging sites.

We conducted a by-catch survey to reveal in what season and at which life stage turtles were found along the Sanriku Coast, and a mark–recapture study with satellite tracking to evaluate post-release movements and behavioral responses associated with declining water temperatures. In addition, we compared the body condition of turtles before and after the tsunami of 2011 to evaluate the effect of the tsunami on this species. Our objective was to determine the seasonal migration pattern of green turtles in a temperate area.

MATERIALS AND METHODS

By-catch survey

From 2005 to 2014, several species of turtle, including loggerhead *Caretta caretta*, green *C. mydas*, black *C. mydas agassizii* and leatherback *Dermochelys coriacea*, were incidentally captured in coastal set-nets of commercial fisheries between Miyako and Ofunato on the Sanriku Coast (38° 55' to 39° 40' N, 141° 40' to 142° 05' E; Fig. 1). Some of the captured turtles were used for bio-logging (Narazaki et al.

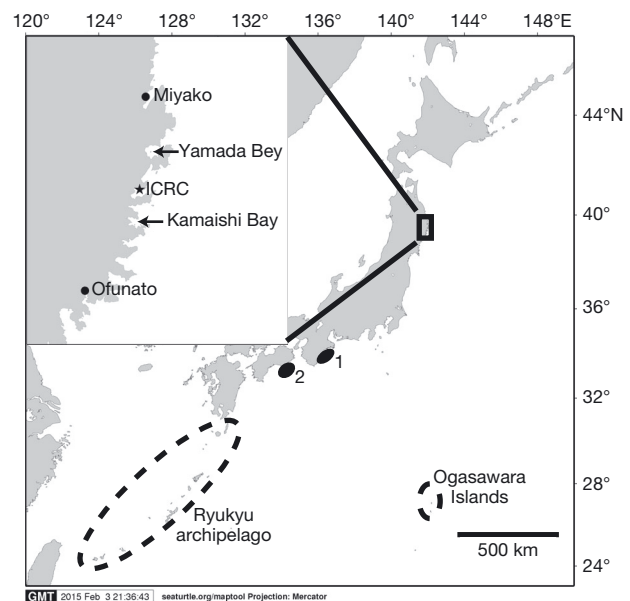


Fig. 1. Study site on the Japanese archipelago. Areas enclosed by dashed lines illustrate major nesting sites of green turtles *Chelonia mydas* (Suganuma 1994). Black ovals: previous study areas (1, Okamoto et al. 2011; 2, Ishihara et al. 2006). Inset: magnification of study site (enclosed area with open rectangle); ★: International Coastal Research Center (ICRC)

2009, 2013), an epibiosis study (Hayashi et al. 2011), functional morphology studies (Marshall et al. 2012, 2014) or DNA analyses (Nishizawa et al. 2014a,b). The present study only reports information on green and black turtles (the latter are considered to be a sub-species of green turtle). Black turtles were identified phenotypically (Hayashi et al. 2011) and genetically (Nishizawa et al. 2014b). The number of set-nets involved varied over the study periods (see Table 1). No survey was conducted in 2011, because set-net fisheries could not operate due to the tsunami caused by the Great East Japan Earthquake. The set-net location and sea surface temperature were recorded when turtles were captured. In cases where temperature was not documented, the mean daily temperature of the bay at the nearest observation point was used for analysis (Iwate Fisheries Information Report System; www.suigi.pref.iwate.jp). All turtles were transferred to concrete tanks ($3.6 \times 1.5 \times 1.0$ m) at the International Coastal Research Center (ICRC; Fig. 1), Atmosphere and Ocean Research Institute at the University of Tokyo. Turtles were housed in separate tanks for 1 to 58 d, and fed the soft tissue of Japanese common squid *Todarodes pacificus* or holey sea lettuce *Ulva pertusa*. Straight carapace length (SCL), the projected length between the front and the rear tips of the carapace, was measured using calipers with an accuracy of 0.1 cm; body mass (BM) was measured using a hanging scale with an accuracy of 0.5 kg. Some turtles were excluded from BM analysis due to lack of BM information. At Ogasawara Islands (the nesting beach origin for most of the green turtles on the Sanriku Coast; Nishizawa et al. 2014b), the minimum SCL of nesting females was 87 cm (Hatase et al. 2006). Therefore, for the purposes of the present study, turtles with SCLs <87 cm were considered putative juveniles.

Mark–recapture study

Plastic and Inconel alloy tags used in this study were issued from the Sea Turtle Association of Japan (www.umigame.org). Tags were attached to both sides of the fore and hind limbs. From 2005 to 2009, only plastic tags were used; beginning in 2010, both plastic and Inconel alloy tags were used. Turtles were released in the Otsuchi Bay of Iwate Prefecture in Japan ($39^{\circ}20'N$, $141^{\circ}56'E$). An ID number and the phone number of the Sea Turtle Association of Japan were printed on each plastic or Inconel alloy tag so that when the tagged turtles were recaptured, pertinent information was obtained via the Sea Tur-

tle Association of Japan. In this study, only turtles that were recaptured outside the study sites were used for analyses.

Satellite tracking

To track the migration path of turtles, satellite relay data loggers (SRDL), manufactured by the Sea Mammal Research Unit (SMRU) at the University of St Andrews, UK (www.smru.st-andrews.ac.uk) were attached to the carapaces of 7 turtles between 2012 and 2013. Following Hatase et al. (2006), the SRDLs were attached with epoxy resin (Loctite E-60NC; Henkel) and fiberglass cloth. Location data were downloaded and managed via the Argos system (www.argos-system.org), which consists of 6 different location code classes (3, 2, 1, 0, A, and B). Class 3 is presumed to provide the highest accuracy with an approximate error in longitude and latitude of ≤ 150 m; Class 2 accuracy is estimated at between 150 and 350 m, Class 1 is between 350 and 1000 m, and Class 0 is >1000 m. Classes A and B are unclassified accuracy (ARGOS 1996). The most accurate positions (Classes 3, 2, 1, and A; Hays et al. 2001), excluding locations that required a high travelling speed (7.2 km h^{-1}), were used to reconstruct routes and calculate travel distances. The SRDLs contained an internal clock, a pressure sensor, and a temperature sensor, and recorded diving depth every 4 s. The start of a dive was defined as the time that the saltwater switch on the SRDL perceived that the transmitter was submerged, or the depth was >3 m for 30 s. The end of a dive was defined as the time the saltwater switch recorded the transmitter breaking the surface, or the depth was <3 m. The SRDL transmitted the time and depth of the 5 most significant points of inflection during the dive, along with the dive duration and time of the end of the dive. Due to the limited bandwidth of the Argos system, not all dive data were obtained. Water temperature data at 2 m depth were also collected by the SRDLs. Water temperature was transmitted with a resolution of 0.01°C and an accuracy of 0.1°C . The seasonal change in water temperature measured by SRDLs was compared with the temperature at 3 m depth in Kamaishi Bay, an adjacent bay to the south of the release point. In 2012, we used data from a depth of 5 m in Yamada Bay, an adjacent bay to the north of the release point, because temperature data from Kamaishi Bay were not available due to damage from the tsunami in the previous year. Temperature data at Kamaishi and Yamada Bays were obtained from

the web site of the Iwate Fisheries Information Report System. A comparison of water temperature between Kamaishi and Yamada Bays from 2005 to 2010 revealed that the average difference was $<1^{\circ}\text{C}$.

Data analysis

To compare the body condition of turtles before and after the tsunami in 2011, a body condition index (BCI) was calculated using the following equation: $\text{BCI} = \text{BM} / \text{SCL}^a$, where BM is the body mass (in kg), SCL is the straight carapace length (in cm) and a is the coefficient of a described case (e.g. Bjornndal et al. 2000, Seminoff et al. 2003). Previous studies (Bjornndal et al. 2000, Seminoff et al. 2003) used $a = 3$, meaning analogous growth. However, green turtles might not show analogous growth; therefore in this study, a was calculated from the equation of SCL and BM. A Wilcoxon rank-sum test was then used to compare the turtles' BCIs before and after the tsunami.

We estimated the behavioral aerobic dive limit (behavioral ADL), which is the 97.5 percentile of the values for the ratio of dive duration (min), following the method of Bradshaw et al. (2007). Spearman's rank correlation was then used to examine the effect of water temperature on behavioral ADL for each turtle that carried a SRDL. Although the temperature information was not available for each dive, the SRDLs transmitted temperature information every 2 d on average. Thus, we used monthly averages of water temperatures for this analysis. The significance level of all statistical tests was set at $\alpha < 0.05$.

RESULTS

By-catch survey

From 2005 to 2014 (excluding 2011 because of the tsunami), a total of 78 green turtles (including 3 black turtles) were captured in set-nets; 74 were alive (Table 1). All of the living turtles were used for the mark–recapture study except for 2 black turtles, which were transferred to Suma Aqualife Park, Kobe, Japan for further detailed morphological study. By-catch incidents after 2011 indicated that turtles continued to migrate to the Sanriku Coast after the tsunami. The turtles were captured between mid-July and late November (Fig. 2). Water temperatures when turtles were captured ranged from 16 to 24°C with an average of $20.7 \pm 1.7^{\circ}\text{C}$ (Fig. 3). SCL values ranged from 36.8 to 85.6 cm with an average

Table 1. Summary of by-catch surveys each year (May to January) along the Sanriku Coast. SCL: straight carapace length

Year	No. of set-nets investigated	No. of turtles captured	No. of dead turtles	Range of SCL (cm)
2005	1	1	0	44.8
2006	15	8	0	41.8–73.3
2007	15	12	0	41.4–85.6
2008	22	11	0	40.7–60.4
2009	22	7	0	43.3–53.8
2010	22	9	0	43.8–76.9
2012	7	15	3	38.9–76.8
2013	10	11	1	36.8–73.3
2014	13	4	0	41.8–57.6

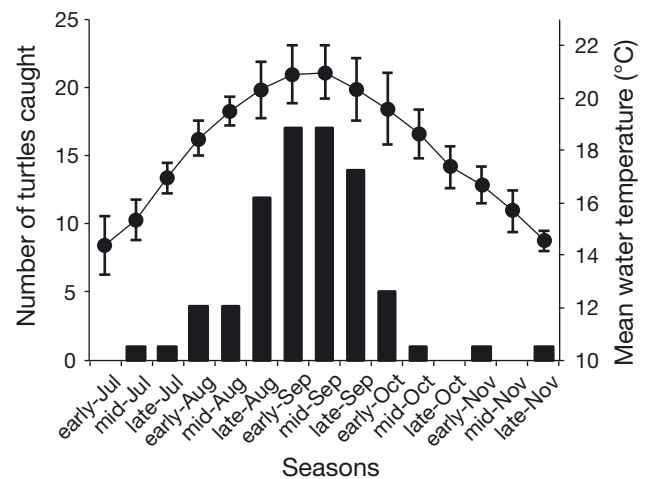


Fig. 2. Number of green turtles *Chelonia mydas* (black bars) captured in set-nets from 2005 to 2014. Black circles: mean (\pm SD) water temperatures measured at fixed observation points in Kamaishi and Yamada bays. Early-, mid- and late-designations for months correspond to successive 10 d periods

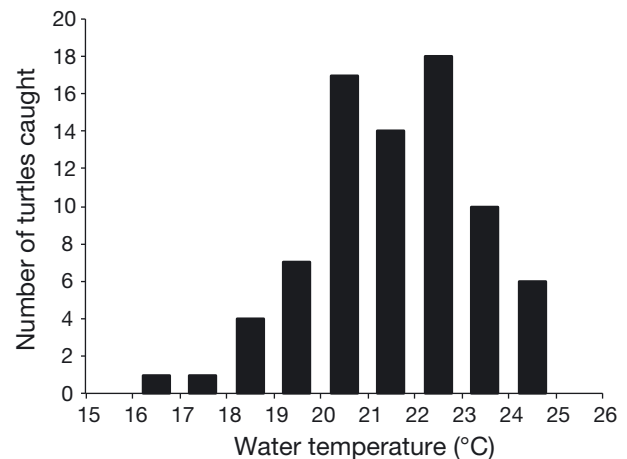


Fig. 3. Water temperature distribution at time of capture of green turtles *Chelonia mydas*

of 49.4 ± 11.4 cm ($n = 78$; Fig. 4a) and BM values ranged from 7 to 85 kg with an average of 20.4 ± 17.7 kg ($n = 75$; Fig. 4b). SCL and BM were significantly correlated ($R^2 = 0.98$, $F = 3945.6$, $p < 0.05$) and the regression curve was $BM = 1.64 \times 10^{-4} \times SCL^{2.97}$ ($n = 75$; Fig. 4c).

There was no significant difference in body condition index ($BCI = BM / SCL^{2.97}$) before ($1.64 \times 10^{-4} \pm 1.39 \times 10^{-5}$, $n = 45$) and after ($1.65 \times 10^{-4} \pm 1.24 \times 10^{-5}$, $n = 30$) the tsunami ($W = 662.5$, $p = 0.90$).

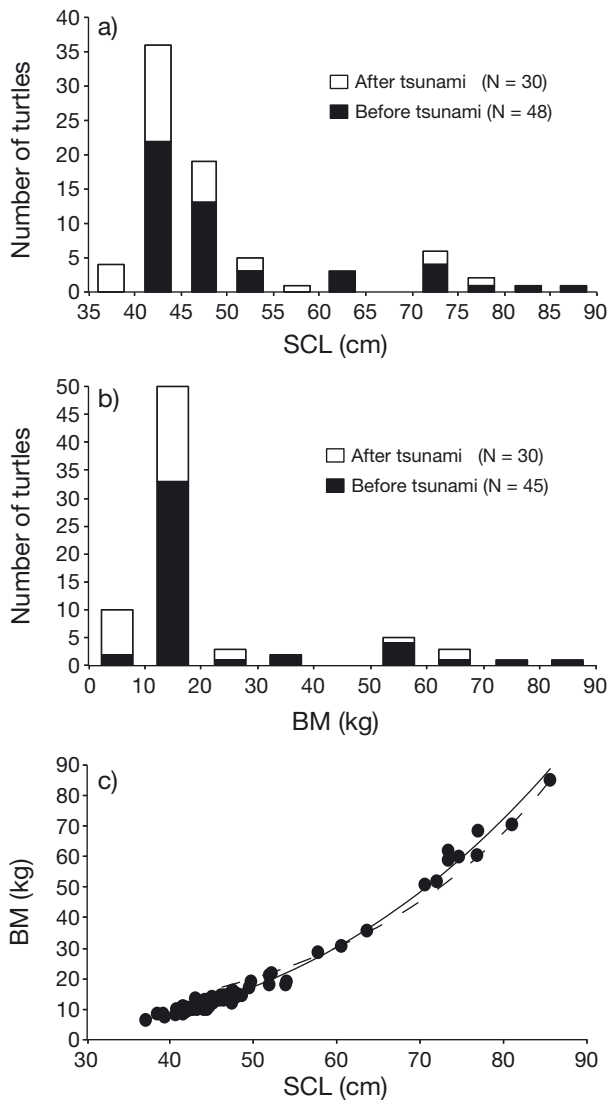


Fig. 4. Size of green turtles *Chelonia mydas* captured at the study site: (a) straight carapace length (SCL) and (b) body mass (BM). (c) Relationship between SCL and BM. Solid line: regression curve from this study ($BM = 1.64 \times 10^{-4} \times SCL^{2.97}$, $n = 75$); dashed line: regression curve from previous study in the eastern Pacific Ocean (Seminoff et al. 2003: $BM = 2.8621 e^{0.0396 \times SCL}$)

Mark-recapture study

During the study period, 72 green turtles (including 1 black turtle) were tagged and released in Otsuchi Bay between August and November. A total of 14 turtles were recaptured outside the study site 5 to 426 d after release. Two turtles were recaptured approximately 100 km north of the study site 7 and 11 d after release, respectively. The other 12 turtles were recaptured south of the study area (Fig. 5).

Satellite tracking

Seven green turtles were instrumented and released around Otsuchi Bay in September 2012 and 2013. However, 4 of the 7 turtles were tracked for less than 2 wk due to instrument failure or turtle mortality; these short duration tracking data were excluded from the analysis. Consequently, we obtained tracking data from 3 turtles (turtles A, B, and C; released 2, 3 and 2 d after first by-caught, respectively) for 338, 374 and 41 d, respectively (Table 2). Turtles A, B

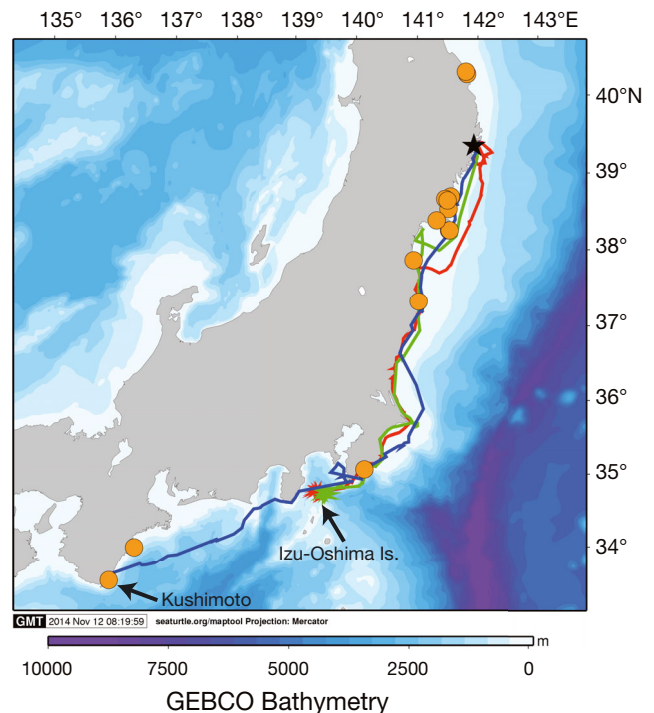


Fig. 5. Migration paths of the green turtles *Chelonia mydas* equipped with satellite relay data loggers (SRDLs) and recapture points of tagged turtles in the mark-recapture study. Star: release point; orange circles: recapture points; solid lines: migration paths of turtle A (red), B (green), and C (blue)

Table 2. Data obtained from turtles equipped with satellite relay data loggers (SRDL). SCL: straight carapace length; BM: body mass. Date is given as yyyy/mm/dd

ID	SCL (cm)	BM (kg)	Release date	Tracking period (d)	Total accumulated distance (km)	No. of dives	Max. dive duration (min)	Water temperatures experienced by turtles (range, °C)
A	76.8	59	2012/09/29	338	852	3218	270	13.7–23.7
B	49.5	19.5	2013/09/21	374	754	1786	330	14.3–25.1
C	73.3	62	2013/09/30	41	1180	566	150	20.0–24.1

and C made 3218, 1786, and 566 dives, respectively, and travelled a total of 852, 754, and 1180 km, respectively during the migration period. The average travel speed was 43 km d⁻¹ for turtle A, 24 km d⁻¹ for turtle B, and 31 km d⁻¹ for turtle C. Because of the relatively short time frame for which we obtained data from turtle C, we only used the tracking data, since conclusions regarding seasonal changes in diving or temperature patterns cannot be ascertained from this short tracking period.

Following release, the turtles remained in the study area for up to 10 d before migrating southward within the coastal area (Fig. 5). Turtles A and B reached Izu-Oshima Island (approximately 500 km south of the release site) 20 and 31 d, respectively, after departing the study site; they stayed there for approximately 10 and 11 mo, respectively. Turtle C also migrated southward and reached Kushimoto in the Wakayama Prefecture (approximately 300 km further west of Izu-Oshima Island) 38 d after departing the study area (Fig. 5). Unfortunately, turtle C died within 1 wk of its arrival at Kushimoto (Sea Turtle Association of Japan pers. comm.).

The water temperature experienced by the satellite-tracked turtles during the entire tracking period ranged from 13.7 to 25.1°C (Table 2), and was higher than water temperatures along the Sanriku Coast during the same time period (4.5 to 22.3°C; Fig. 6).

Turtles A and B experienced a seasonal change in water temperature of approximately 10°C (Table 2), and showed a strong seasonal pattern in dive duration. The duration of the behavioral ADL was negatively correlated with water temperatures (turtle A: $r_s = -0.81$, $n = 11$, $p < 0.05$; Fig. 7a; turtle B: $r_s = -0.98$, $n = 13$, $p < 0.05$; Fig. 7b). The longest dive duration was 330 min (5.5 h), recorded 4 times for turtle B in January and February when water temperature was 14 or 15°C. Not only did these turtles make prolonged dives, but they also conducted short dives even when the water temperature was low (Fig. 7a,b). The monthly median dive duration for turtle A was always <30 min (Fig. 7a).

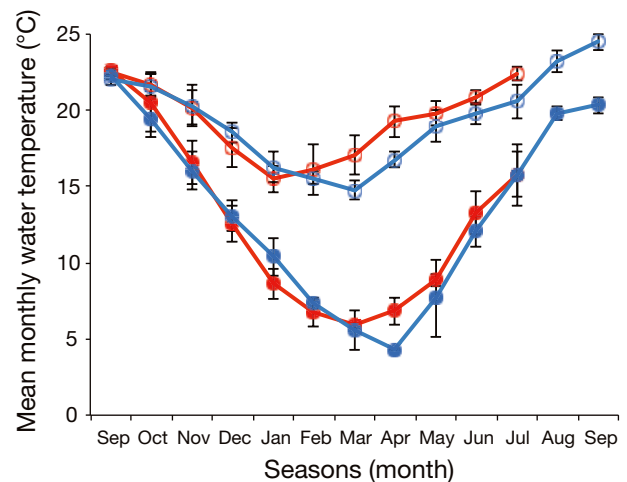


Fig. 6. Monthly mean (\pm SD) water temperatures along the Sanriku Coast (filled circles) and mean monthly water temperatures experienced by green turtles *Chelonia mydas* (open circles) during the tracking period. Red and blue lines: 2012 and 2013, respectively

DISCUSSION

Characteristics of the green turtles migrating to the Sanriku Coast

Fisheries by-catch, especially in trawls, gillnets, and longlines, is one of the largest threats to sea turtles, with mortality rates of 8 to 40% (Lewison et al. 2013). By-catch from set-nets could also be life threatening because some set-nets are deployed in mid-water; sea turtles caught in these nets are unable to surface, and eventually drown (Shiode et al. 2006). However, the set-nets used in our study site were usually located at the surface, and the top of the nets was left open. In this study, only 4 turtles were found dead in set-nets (mortality rate = 5.1%). Thus, the Sanriku Coast is a favorable area to study habitat use and migratory movements of by-caught green turtles during foraging periods, because most of the turtles are encountered alive.

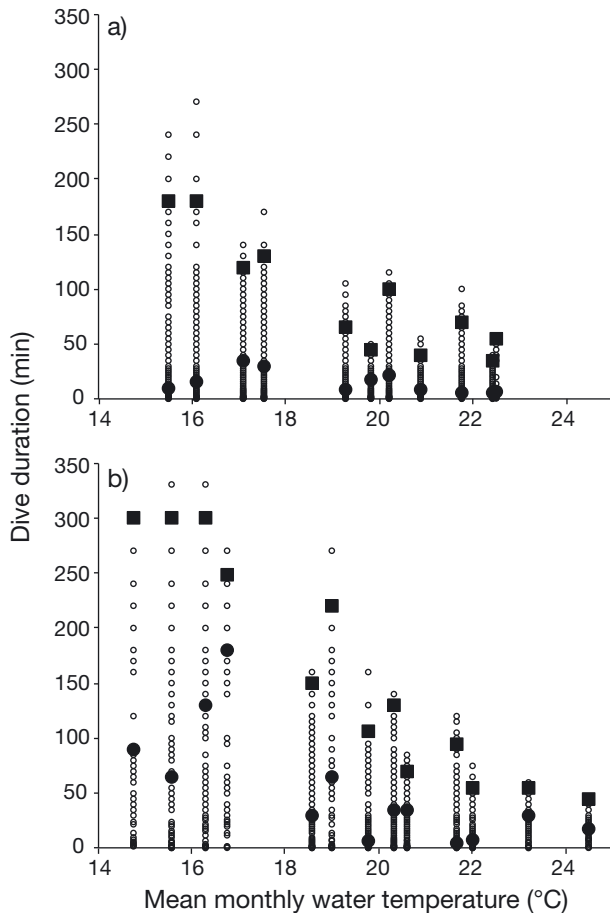


Fig. 7. Relationship between green turtle *Chelonia mydas* dive duration and monthly mean water temperature recorded by satellite relay data loggers (SRDLs) for (a) turtle A and (b) turtle B. Open circles: duration of each dive; filled squares: duration of behavioral aerobic dive limit (ADL); filled circles: median dive duration for each monthly mean water temperature

Three turtles captured in this study were identified as black turtles. The black turtle is considered a subspecies of the green turtle, and its nesting grounds are found exclusively in the eastern Pacific (Pritchard 1999). Black turtles are rare in Japan (Abe & Minami 2008), but our study provides further evidence of long-distance dispersal in this species.

Set-net fisheries operate from May to January, and the fishing effort is constant during this period. Thus, the occurrence of green turtles in this area is strictly limited to summer and autumn. This seasonal by-catch pattern was similar to the pattern observed in temperate areas of the Atlantic Ocean (Epperly et al. 1995, González Carman et al. 2011). Moreover, the majority of turtles were captured when water temperature was higher than 20°C, indicating that the Sanriku Coast is a seasonal habitat for green turtles.

The Sanriku Coast is known as one of the most highly productive areas in Japan, because the Tsugaru Warm Current flowing southward, the cold nutrient-rich Oyashio water, and the warm Kuroshio water occupy this area alternatively and interact with each other (Sugimoto & Tameishi 1992). There is an abundant supply of marine algae and seagrass (Ministry of the Environment 2011), which comprise the main diet of green turtles (Bjorndal 1997); hence, the Sanriku Coast may be an important foraging area for this species. Further research (including the evaluation of food density and food consumption rate) is necessary because this additional information may help to more fully explain the migration patterns in this area.

The SCL of turtles captured in this study ranged from 30 to 80 cm, indicating that most of the migrating turtles along the Sanriku Coast were likely juveniles. Furthermore, the majority of SCLs were between 40 and 50 cm (Fig. 4a). The average SCL of turtles along the Sanriku Coast (49.4 ± 11.4 cm, $n = 78$) was smaller than in other study sites on the south coast of Japan (Ishihara et al. 2006: 67.4 ± 19.9 cm, $n = 94$; Okamoto et al. 2011: 67.0 ± 22.9 cm, $n = 26$; Fig. 1). In addition, juvenile green turtles were reported to have SCLs >40 cm following recruitment to neritic developmental habitats in the northwestern Pacific Ocean (Ishihara 2012). This suggests that some turtles may have just recruited from oceanic habitat to the neritic Sanriku Coast.

A previous equation describing the mean relationship between SCL and BM was calculated for black turtles in Baja California, Mexico ($BM = 2.8621 e^{0.0396 \times SCL}$; Seminoff et al. 2003, Fig. 4c). In green turtles, equations have been calculated using the CCL (curved carapace length) of adult-sized turtles on a nesting beach ($BM = 4.585 \times CCL - 349.22$; Hays et al. 2000) or juvenile to adult turtles with a small sample size ($BM = 0.06 \times CCL^2 - 7.35 \times CCL + 219$, Godley et al. 2003). Therefore, our data is valuable for estimating the BM of juvenile green turtles from SCLs.

Effects of the tsunami on green turtles migrating to the Sanriku Coast

Although the Sanriku Coast was seriously damaged by the tsunami in 2011, the BCI of the turtles was not significantly different before and after the incident. There are 2 possible explanations for this. One involves the habitat utilization pattern of turtles in this area. The turtles that migrated to the Sanriku Coast also use other, more southern areas as foraging

sites. Therefore, it is possible that their BCI did not change significantly because they were able to feed in other areas. The other possible explanation is related to their diet. Along the Sanriku Coast, large amounts of seagrass (e.g. *Zostera marina*) disappeared (Sasa et al. 2012); however, the distribution of some marine algae (e.g. *Sargassum* and *Laminaria* spp.) expanded after the tsunami (Sakamoto et al. 2012). It has been documented that green turtles mainly feed on marine algae along the southern coast of Japan (Kameda & Ishihara 2009). Therefore, if marine algae are the main food source for the turtles along the Sanriku Coast, it is possible that adverse effects of the tsunami were minimal because food was still available.

Post-release migration pattern from the Sanriku Coast

Previous studies in tropical and sub-tropical foraging areas have indicated that juvenile green turtles display strong site fidelity (i.e. 10s of km²; Makowski et al. 2006, Kameda et al. 2013) over many years (Limpus et al. 1994). However, according to the mark-recapture and satellite tracking in this study, most recaptured turtles and all tracked turtles migrated southward more than 500 km. A similar migration pattern was obtained from a juvenile aggregation in a temperate area of the southwest Atlantic Ocean (González Carman et al. 2012). These results suggest that green turtles in temperate foraging areas undertake longer distance migrations (i.e. 100s of km) compared to those in tropical and sub-tropical foraging areas.

The results of our study indicate that the captured turtles were not residents of the Sanriku Coast all year, and that they migrated mainly southward after their release (Fig. 5). Although 2 turtles were recaptured north of the release site along the Sanriku Coast, we assumed that these turtles had not yet initiated their seasonal migration since they were captured only 7 and 11 d after release. Low water temperatures during the winter months could explain the southward migration. In 2012 and 2013, sea surface temperatures at Kamaishi and Yamada Bays fell to around 5°C in March and April. In contrast, satellite-tracked turtles never experienced water temperatures below 13°C. Sea turtles are known to become lethargic and float due to physiological failure at temperatures below 10°C (Milton & Lutz 2003), and cold-stunning has been widely reported when water temperatures fall below 8°C (Witherington & Ehrhart

1989). Green turtles in the Gulf of California become dormant in water temperatures of approximately 15°C (Felger et al. 1976). Therefore, it is expected that the turtles can tolerate water temperature around 13°C; however, they likely cannot tolerate the low water temperatures (i.e. <10°C) that occur during the winter around the Sanriku Coast. Their southward migration may be a behavioral response to avoid the lethally cold water.

We considered 2 possible explanations for this migration pattern. One is seasonal migration. Substantial amounts of marine algae and seagrass grow along the Sanriku Coast (Ministry of the Environment 2011), presumably providing favorable habitat for green turtles. Our results indicate that the turtles appeared along the Sanriku Coast in the summer and autumn, whereas they migrated to southern foraging sites in winter. Therefore, it is possible that the turtles routinely conduct seasonal migrations between the Sanriku Coast and overwintering sites. Another possible explanation for this pattern is an ontogenetic north-to-south migration. The 2 tracked turtles did not migrate north again the following summer. In the Atlantic, juvenile green turtles change their foraging habitat before maturity (Bjørndal et al. 2005). Our results indicate that most of the turtles leave the Sanriku Coast area when they reach ~50 cm SCL, and the size distribution of turtles along the Sanriku Coast is smaller than that of turtles in the southern foraging areas in Japan (Ishihara et al. 2006, Okamoto et al. 2011). Therefore, the life-history strategy of green turtles in the northwest Pacific Ocean might be to leave the Sanriku Coast for southern foraging sites located closer to their nesting sites.

Water temperature affected dive duration of the turtles during the tracking periods: the duration of the behavioral ADL was negatively correlated with water temperature. Maximum dive duration was 5.5 h (recorded from turtle B). To the best of our knowledge, this is the longest dive duration recorded for this species. Prolonged dive duration during the winter was reported in several satellite tracking studies (e.g. Godley et al. 2002, Broderick et al. 2007), and these repeated long dives suggested seasonally reduced activity (Ultsch 2006). However, the turtles in this study (especially turtle A) also made short-duration dives in the winter. Hays et al. (2004) illustrated that flipper beat frequency increases with decreasing dive duration, and that the short dives indicate active swimming. Hence, we suggest that the turtles do not become completely inactive in the southern foraging sites as was previously thought, and that they might feed here, even during the winter.

CONCLUSIONS

This study revealed that the Sanriku Coast provides a seasonal habitat for juvenile green turtles, and that turtles still migrated to this area after the tsunami in 2011. Turtles migrated to southern foraging sites located more than 500 km away from the release site along the Sanriku Coast, indicating that turtles in temperate foraging area travel farther than those in tropical and sub-tropical areas. Our results also illustrated that the study of temperate habitats will help us to better understand the entire life history of green turtles.

Acknowledgements. Field surveys were conducted under the conditions of the Ethics Committee of the University of Tokyo. Field sampling was financially supported by the Tohoku Ecosystem-Associated Marine Sciences (TEAMS), the Bio-Logging Science, the University of Tokyo (UTBLS), and the Japanese Society for the Promotion of Science (24241001). We are grateful to all volunteers from the Fisheries Cooperative Association of Funakoshi Bay, Hirota Bay, Kamaishi Bay, Kamaishi-Tobu, Miyako, Ofunato, Okirai, Omoe, Otsuchi, Ryori, Sanriku-Yamada, Sasaki, Toni, Yamaichi, and Yoshihama, who assisted us with collecting the turtles. Special thanks to K. Okamoto and the Sea Turtle Association of Japan for the information on recaptured turtles. We also thank K. Morita, M. Kurosawa, J. Takada, M. Hirano, Y. Fujiwara, S. Takuma, H. Murasaki, K. Onitsuka, I. Nakamura, N. Miyata, S. Nobata, T. Iwata, M. Yamane, and H. Nishizawa for their assistance in the field. We thank 2 anonymous reviewers and Cassondra Williams for their valuable comments on this manuscript. We acknowledge the use of the Map-tool (www.seaturtle.org) program for mapping the study site and turtle recapture sites.

LITERATURE CITED

- Abe O, Minami H (2008) Mitigation measures to reduce incidental catch of sea turtles: status of sea turtle populations and holistic management. *Bull Jpn Soc Sci Fish* 74: 230–233 (in Japanese)
- ARGOS (1996) User's manual. CLS/Service ARGOS, Toulouse
- Bjorndal KA (1997) Nutritional ecology of sea turtles. In: Lutz PL, Musick JA (eds) *The biology of sea turtles*. CRC Press, Boca Raton, FL, p 237–283
- Bjorndal KA, Bolten AB, Chaloupka MY (2000) Green turtle somatic growth model: evidence for density dependence. *Ecol Appl* 10:269–282
- Bjorndal KA, Bolten AB, Chaloupka MY (2005) Evaluating trends in abundance of immature green turtles *Chelonia mydas* in the greater Caribbean. *Ecol Appl* 15:304–314
- Bradshaw CJA, McMahon CR, Hays GC (2007) Behavioral inference of diving metabolic rate in free-ranging leatherback turtles. *Physiol Biochem Zool* 80:209–219
- Broderick AC, Coyne MS, Fuller WJ, Glen F, Godley BJ (2007) Fidelity and over-wintering of sea turtles. *Proc R Soc B* 274:1533–1538
- Carr A, Caldwell DK (1956) *The ecology and migrations of sea turtles, 1. Results of field work in Florida, 1955*. *Mus Novit* 1793:1–23
- Epperly SP, Braun J, Veishlow A (1995) Sea turtles in North Carolina waters. *Conserv Biol* 9:384–394
- Felger RS, Clifton K, Regal PJ (1976) Winter dormancy in sea turtles: independent discovery and exploitation in the Gulf of California by two local cultures. *Science* 191: 283–285
- Godley BJ, Reardon S, Broderick AC, Coyne MS, Glen F, Hays GC (2002) Long-term satellite telemetry of the movements and habitat utilisation by green turtles in the Mediterranean. *Ecography* 25:352–362
- Godley BJ, Lima EHS, Åkesson S, Broderick AC and others (2003) Movement patterns of green sea turtles in Brazilian coastal waters described by satellite tracking and flipper tagging. *Mar Ecol Prog Ser* 253:279–288
- González Carman V, Alvarez K, Prosdocimi L, Inchaurrega MC and others (2011) Argentinian coastal waters: a temperate habitat for three species of threatened sea turtles. *Mar Biol Res* 7:500–508
- González Carman V, Falabella V, Maxwell S, Albareda D, Campagna C, Mianzan H (2012) Revisiting the ontogenetic shift paradigm: the case of juvenile green turtles in the SW Atlantic. *J Exp Mar Biol Ecol* 429:64–72
- Hatase H, Sato K, Yamaguchi M, Takahashi K, Tsukamoto K (2006) Individual variation in feeding habitat use by adult green sea turtles (*Chelonia mydas*): Are they obligately neritic herbivores? *Oecologia* 149:52–64
- Hayashi R, Takuma S, Narazaki T, Sato K (2011) *Chelonia mydas agassizii* (Black [Pacific] sea turtle). *Epibiont barnacles*. *Herpetol Rev* 42:264–265
- Hays GC, Adams CR, Broderick AC, Godley BJ, Lucas DJ, Metcalfe JD, Prior AA (2000) The diving behaviour of green turtles at Ascension Island. *Anim Behav* 59: 577–586
- Hays GC, Åkesson S, Godley BJ, Luschi P, Santidrian P (2001) The implications of location accuracy for the interpretation of satellite tracking data. *Anim Behav* 61: 1035–1040
- Hays GC, Metcalfe JD, Walne AW, Wilson RP (2004) First records of flipper beat frequency during sea turtle diving. *J Exp Mar Biol Ecol* 303:243–260
- Hirth HF (1997) Synopsis of the biological data on the green turtle *Chelonia mydas* (Linnaeus 1758). Biological report 97(1), US Department of the Interior, Fish & Wildlife Service, Washington, DC
- Ishihara T (2012) Life history. In: Kamezaki N (ed) *Natural history of sea turtles in Japan*. University of Tokyo Press, Tokyo, p 57–83 (in Japanese)
- Ishihara T, Kamezaki N, Yamazaki C, Yamashita S (2006) Sea turtles appearing around Muroto city, Kochi Prefecture. *Umigame Newsl Jpn* 70:14 (in Japanese)
- Kameda K, Ishihara T (2009) Gut contents analysis of green turtles (*Chelonia mydas*) in Japan. *Umigame Newsl Jpn* 81:17–23 (in Japanese with English summary)
- Kameda K, Wakatsuki M, Kamezaki N (2013) Population structure and growth rate of the green turtle *Chelonia mydas*, on feeding grounds at Kuroshima Island, of Yaeyama group, Ryukyu archipelago. *Biol Mag Okinawa* 51:93–100 (in Japanese with English summary)
- King WF (1982) Historical review of the decline of the green turtle and the hawksbill. In: Bjorndal KA (ed) *Biology and conservation of sea turtles*. Smithsonian Institution Press, Washington, DC, p 183–188
- Lewis R, Wallace B, Alfaro-Shigueto J, Mangel JC, Maxwell SM, Hazen EL (2013) Fisheries bycatch of mar-

- ine turtles: lessons learned from decades of research and conservation. In: Wyneken J, Lohmann KJ, Musick JA (eds) The biology of sea turtles, Vol 3. CRC Press, Boca Raton, FL, p 329–352
- Limpus CJ, Couper PJ, Reed MA (1994) The green turtle *Chelonia mydas* in Queensland: population structure in a warm temperate feeding area. Mem Queensl Mus 35: 139–154
- Makowski C, Seminoff JA, Salmon M (2006) Home range and habitat use of juvenile Atlantic green turtles (*Chelonia mydas* L.) on shallow reef habitats in Palm Beach, Florida, USA. Mar Biol 148:1167–1179
- Marshall CD, Guzman A, Narazaki T, Sato K, Kane EA, Sterba Boatwright BD (2012) The ontogenetic scaling of bite force and head size in loggerhead sea turtles (*Caretta caretta*): implications for durophagy in neritic, benthic habitats. J Exp Biol 215:4166–4174
- Marshall CD, Wang J, Rocha Olivares A, Godinez Reyes C and others (2014) Scaling of bite performance with head and carapace morphometrics in green turtles (*Chelonia mydas*). J Exp Mar Biol Ecol 451:91–97
- Miller JD (1997) Reproduction in sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles. CRC Press, Boca Raton, FL, p 51–81
- Milton SL, Lutz PL (2003) Physiological and genetic responses to environmental stress. In: Lutz PL, Musick JA, Wyneken J (eds) The biology of sea turtles, Vol. 2. CRC Press, Boca Raton, FL, p 163–197
- Ministry of the Environment (2011) Marine biodiversity conservation strategy. Nature Conservation Bureau, Ministry of the Environment, Tokyo
- Mori N, Takahashi T, Yasuda T, Yanagisawa H (2011) Survey of 2011 Tohoku earthquake tsunami inundation and run up. Geophys Res Lett 38:L00G14, doi:10.1029/2011-GL049210
- Musick JA, Limpus CJ (1997) Habitat utilization and migration in juvenile sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles. CRC Press, Boca Raton, FL, p 137–163
- Narazaki T, Sato K, Abernathy KJ, Marshall G, Miyazaki N (2009) Sea turtles compensate deflection of heading at the sea surface during directional travel. J Exp Biol 212: 4019–4026
- Narazaki T, Sato K, Abernathy KJ, Marshall G, Miyazaki N (2013) Loggerhead turtles (*Caretta caretta*) use vision to forage on gelatinous prey in mid-water. PLoS ONE 8: e66043
- Nishizawa H, Narazaki T, Fukuoka T, Sato K, Hamabata T, Kinoshita M, Arai N (2014a) Genetic composition of loggerhead turtle feeding aggregations: migration patterns in the North Pacific. Endang Species Res 24:85–93
- Nishizawa H, Narazaki T, Fukuoka T, Sato K, Hamabata T, Kinoshita M, Arai N (2014b) Juvenile green turtles on the northern edge of their range: mtDNA evidence of long-distance westward dispersals in the northern Pacific Ocean. Endang Species Res 24:171–179
- Ogasawara T, Sakai S (2012) Characteristics on damages of 2011 Tohoku tsunami in Iwate coast. Jpn J Multiphase Flow 26:28–35 (in Japanese with English Abstract)
- Okamoto K, Ishihara T, Taniguchi M, Yamashita N, Kamezaki N (2011) Occurrence of the sea turtles at the coastal water of Kumamonada. Umigame Newsl Jpn 88:13–17 (in Japanese)
- Plotkin P (2003) Adult migrations and habitat use. In: Lutz PL, Musick JA, Wyneken J (eds) The biology of sea turtles, Vol 2. CRC Press, Boca Raton, FL, p 225–242
- Pritchard PCH (1999) Status of the black turtle. Conserv Biol 13:1000–1003
- Renaud ML, Carpenter JA, Williams JA, Manzella-Tirpak SA (1995) Activities of juvenile green turtles, *Chelonia mydas*, at a jettied pass in south Texas. Fish Bull 93: 586–593
- Sakamoto SX, Sasa S, Sawayama S, Tsujimoto R, Terauchi G, Yagi H, Komatsu T (2012) Impact of huge tsunami in March 2011 on seaweed bed distributions in Shizugawa Bay, Sanriku Coast, revealed by remote sensing. Proc SPIE 85251B:1–7
- Sasa S, Sakamoto SX, Sawayama S, Tsujimoto R, Terauchi G, Yagi H, Komatsu T (2012) Did huge tsunami on 11 March 2011 impact seagrass bed distributions in Shizugawa Bay, Sanriku Coast, Japan? Proc SPIE 85250X:1–6
- Sato K, Otsuki M, Morita K, Kurosawa M, Takada J (2007) Result of hydrographic and meteorologic observation in 2006. Annual report of International Coastal Research Center, University of Tokyo 32:37–47 (in Japanese)
- Seminoff JA (2004) *Chelonia mydas*. The IUCN Red List of Threatened Species, version 2014.3. www.iucnredlist.org (accessed on 16 Nov 2014)
- Seminoff JA, Resendiz A, Nichols WJ (2002) Home range of green turtles *Chelonia mydas* at a coastal foraging area in the Gulf of California, Mexico. Mar Ecol Prog Ser 242: 253–265
- Seminoff JA, Jones TT, Resendiz A, Nichols WJ, Chaloupka MJ (2003) Monitoring of green turtles (*Chelonia mydas*) at a foraging habitat in the Gulf of California, Mexico: multiple indices describe population status. J Mar Biol Assoc UK 83:1355–1362
- Shiode D, Kawahara N, Tokai T (2006) Result of survey about incidental catches of sea turtles by large set nets. Teichi 109:54–62 (in Japanese)
- Southwood AL, Reina RD, Jones VS, Jones DR (2003) Seasonal diving patterns and body temperatures of juvenile green sea turtles at Heron Island, Australia. Can J Zool 81:1014–1024
- Suganuma H (1994) Green sea turtle. In: Fisheries Agency (ed) Basic report of rare wild aquatic species of Japan, Vol. 1. Japan Fisheries Resource Conservation Association, Tokyo, p 469–478
- Sugimoto T, Tameishi H (1992) Warm-core rings, streamers and their role on the fishing ground formation around Japan. Deep-Sea Res 39:S183–S201
- Troëng S, Evans DR, Harrison E, Lagueux CJ (2005) Migration of green turtles *Chelonia mydas* from Tortuguero, Costa Rica. Mar Biol 148:435–447
- Ultsch GR (2006) The ecology of overwintering among turtles: where turtles overwinter and its consequences. Biol Rev Camb Philos Soc 81:339–367
- Witherington BE, Ehrhart LM (1989) Hypothermic stunning and mortality of marine turtles in the Indian River lagoon system, Florida. Copeia 1989:696–703