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Insights into identifying habitat hot spots and migratory corridors of green turtles in the South China region

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Abstract

1. Sea turtles are globally endangered, and face daily anthropogenic threats, such as direct take, by-catch, and habitat degradation. Current research efforts on sea turtles in the South China region mainly focus on captivity and husbandry, haematology and blood chemistry, and nesting ecology. Published information on the marine habitat use of wild populations is limited.
2. This situation therefore creates a pressing need for scientific research on free-ranging sea turtles as a foundation for habitat management and species protection in South China. In this study, habitat use and oceanic movement of nesting, and by-catch or stranded green turtles, were determined by satellite tracking combined with home-range analysis.
3. Coupled with previous findings, the foraging grounds of several sea turtle species (green turtle *Chelonia mydas*, hawksbill turtle *Eretmochelys imbricata* and loggerhead *Caretta caretta*) were mainly distributed along the coasts of Hainan Island Province and Guangdong Province, mainland China, as well as Taiwan and the Philippines, and the outlying islands in the South China Sea and East China Sea.
4. Habitat hot spots and migratory corridors of green turtles, in particular nesting turtles in South China, were identified. Coastal waters near Wanning City of Hainan Island, the eastern Leizhou Peninsula, Iriomote-jima and Ishigaki-shima of the Ryukyu Islands of Japan, and Dao Bach Long Vi of Vietnam serve as foraging grounds for nesting green turtles from different origins in South China. Moreover, the Paracel (Xisha) and the Pratas (Dongsha) Islands in the South China Sea, Huidong Gangkou, and its vicinity in mainland China, and Liouciou Island and Penghu Island of Taiwan contain both nesting sites and foraging grounds for green turtles.
5. The sites that are associated with migratory corridors, in particular Hainan Island, eastern Leizhou Peninsula, and Liouciou Island, which currently lack conservation plans for sea turtles, should be given higher priority for habitat and species protection.

KEYWORDS

coastal, endangered species, fishing, green turtle, habitat mapping, habitat use, home range, migratory corridor, ocean, reptiles, satellite telemetry, South China region

1 | INTRODUCTION

Of the seven sea turtles species in the world, five species are found in the South China Sea: the green turtle (*Chelonia mydas*), the leatherback (*Dermochelys coriacea*), the olive ridley (*Lepidochelys olivacea*), the loggerhead (*Caretta caretta*), and the hawksbill (*Eretmochelys imbricata*) (Chan et al., 2007; Wang, 1993). These sea turtle species are migratory. Adults travel hundreds to thousands of kilometres between nesting beaches and foraging grounds. Among the five sea turtle species recorded in South China, the green turtle is the most common and is the only species that nests in the area (Chan et al., 2007; Ng et al., 2014; Wang, 1993; Wang & Li, 2008). The green turtle is a globally endangered species (International Union for Conservation of Nature, IUCN, 2015), and faces various anthropogenic threats, such as direct take and by-catch (Cheng & Chen, 1997; Wang & Li, 2008), trade pressure (Lam, Xu, Takahashi, & Burges, 2011; Pilcher, Chan, & Hiew, 2009), and habitat degradation (Wang & Li, 2008). Although green turtle nesting beaches on Wan-an Island of Taiwan, the Gangkou National Sea Turtle Nature Reserve of mainland China, and Sham Wan of Hong Kong are protected by local ordinances (IUCN & The UN Environment World Conservation Monitoring Centre, UNEP-WCMC, 2018), nesting populations of green turtles in South China have been dwindling for decades (Chan et al., 2007; Wang & Li, 2008).

Habitat degradation as a result of rapid coastal development and human activities, e.g. fishing pressure, remains one of the key drivers in the dwindling populations of sea turtles worldwide (Bohm et al., 2013; Casale et al., 2010; IUCN Marine Turtle Specialist Group, 2013; Mazaris, Matsinos, & Pantis, 2009; McClellan & Read, 2009). As an effective and adaptive measure to conserve these migratory species it is essential to identify and establish activity hot spots, such as habitat use in both the neritic and pelagic ocean, and migratory pathways (Arendt et al., 2012; Craig, Parker, Brainard, Rice, & Balazs, 2004; Scales et al., 2011), to develop protection measures, such as the delineation of management units, marine protected areas (MPAs) and threat mitigation (Casale et al., 2012; Howell et al., 2015; Howell, Kobayashi, Parker, Balazs, & Polovina, 2008; Polovina et al., 2006; Rees, Al-Kiyumi, Broderick, Papathanasopoulou, & Godley, 2012; Scott et al., 2012).

Using satellite telemetry to track the oceanic movements of sea turtles helps to identify their habitat hot spots at different life stages, notably migratory pathways (i.e. movement between nesting sites and foraging grounds), inter-nesting grounds (i.e. areas where nesting turtles rest underwater between consecutive nesting activities), and foraging sites. Home-range analysis (Casale et al., 2012; Gaos et al., 2012; Hart & Fujisaki, 2010; Seminoff, Resendiz, & Nichols, 2002) of sea turtle activity hot spots, such as inter-nesting grounds and foraging sites, describes the area traversed by a sea turtle during the inter-nesting period or while foraging, excluding migrations or erratic movements. The location, extent, and characteristics of the home range and habitat use of sea turtles provide a crucial foundation for wildlife conservation and management, e.g. for the delineation of MPAs to protect the habitats and food sources of species of concern (Craig et al., 2004; Gaos et al., 2012; Hart, Lamont, Fujisaki, Tucker, & Cathy, 2012; Seminoff et al., 2002), and the mitigation of threats such as unfavourable fisheries interactions (Hays, 2008; Kobayashi et al., 2011; Polovina et al., 2006).

In China, tracking studies have primarily focused on the post-nesting movements of green turtles (Figure 1). Chan, Chan, Lo, and Balazs (2003) and Ng et al. (2014) determined the post-nesting migratory pathways of nesting green turtles from Hong Kong to their foraging grounds in eastern Hainan Island, China, and Dao Bach Long Vi, Vietnam. Nesting green turtles from Gangkou National Sea Turtle Reserve in China travelled to their foraging pastures on the east coast of Leizhou Peninsula and Okinawa Island in southern Japan (Song et al., 2002). After nesting, green turtles from Wan-an Island, Taiwan, migrated to their foraging aggregations in coastal waters off northern Taiwan, the Guangdong coastline, Hainan Island, the northern Philippines, and the Ryukyu Archipelago of Japan (Cheng, 2000); other nesting green turtles were found to migrate within Taiwanese waters (Chan et al., 2007). Cheng (2007) also determined the post-nesting movement of green turtles from Taipin Island of the Nansha Archipelago in the South China Sea to coastal waters of the Philippines and Malaysia.

Although these studies have provided important information about the movement and distribution of green turtles in South China, there are severe knowledge gaps in the habitat use of green turtles at different life stages (e.g. juvenile and subadult) and the extent of the home range of key at-sea habitats in this region. Nesting green turtles are vital to sustain populations, although juvenile and non-breeding green turtles are also important considering that they comprise the majority of turtle populations. Baseline information on their habitat use and movement is hence essential for conservation, in terms of the spatial management of habitat protection and threat mitigation. This study therefore aims to determine the movement patterns, migratory corridors, and habitat hot spots of by-catch or stranded and nesting green turtles, and to estimate the home-range extent of foraging/inter-nesting habitats used by green turtles in the South China region that covers Hong Kong, Guangdong, and Taiwan. Research priorities for conserving and managing migratory green turtles will also be identified.

2 | METHODS

Habitat use and hot spots of green turtles were identified by satellite telemetry, aided by home-range analysis. In this study, green turtles were sourced from: (i) by-catch (e.g. with direct reports from the

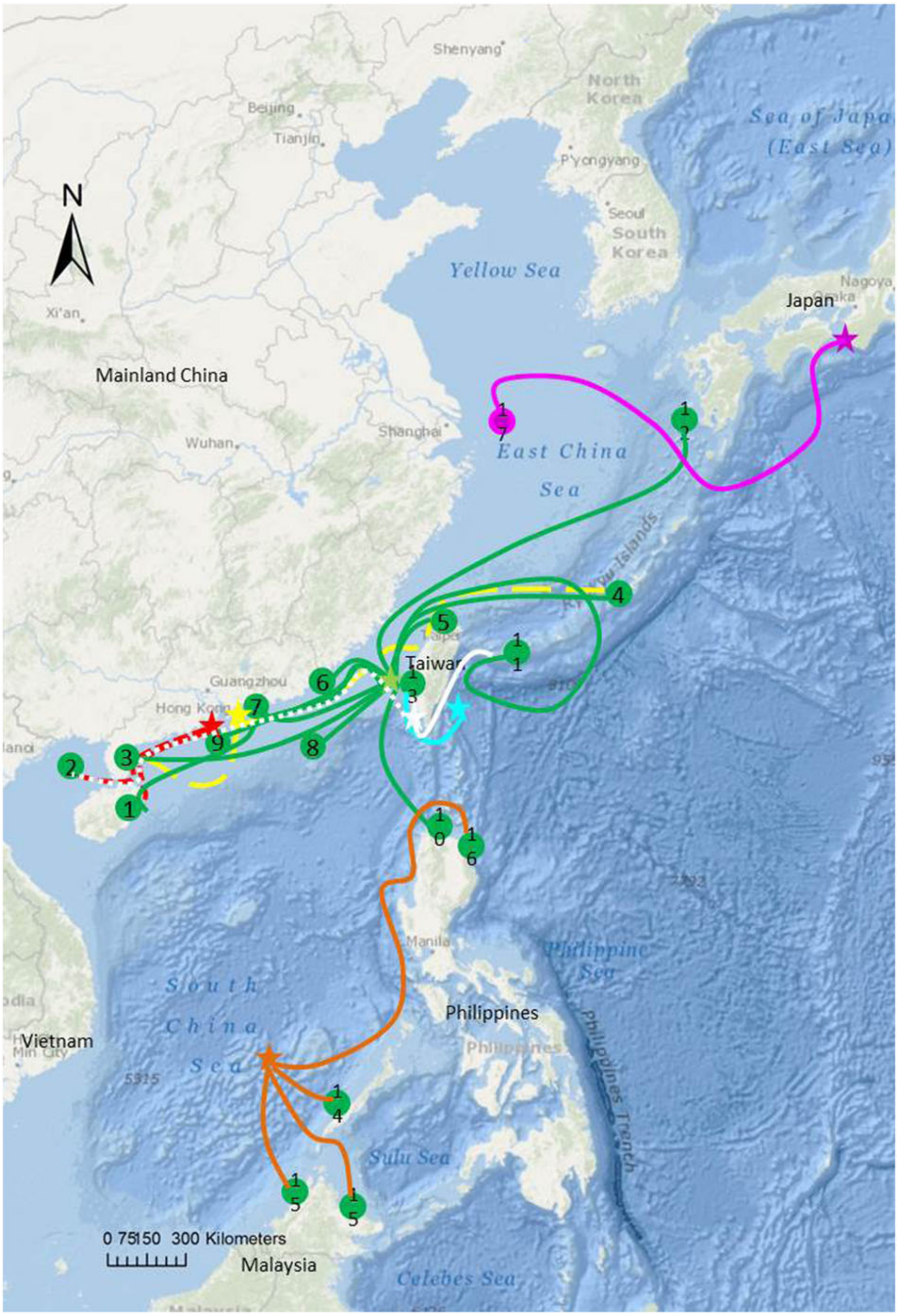

FIGURE 1 Nesting sites, foraging grounds, and migratory pathways of green turtles and loggerhead turtles as determined by satellite telemetry in the South China Sea. The red star and line denote a green turtle nesting site in Hong Kong and post-nesting movement; yellow, Gangkou; light green, Wan-an; blue, Lanyu; white, Liouciou Island; orange, Taipin, Nansha Island; fuschia, loggerhead in Minabe, Japan. The numbers in closed circles represent foraging grounds: 1, Wanning, Hainan; 2, Dao Bach Long Vi in Vietnam; 3, the east coast of Leizhou Peninsula; 4, Okinawa Island in southern Japan; 5, coastal waters off northern Taiwan; 6, Qinpeng-Dao of Nanao Island at Shantou; 7, Huidong; 8, the Pratas (Dongsha) Islands; 9, Dangan Liedao of Wanshan Archipelago; 10, northern Philippines; 11, Iriomote-jima and Ishigaki-shima of the Ryukyu Archipelago; 12, Koshiki, Okinawa Island, in southern Japan; 13, coral reefs in the southern Penghu Archipelago, north of Chimei Island; 14, coastal waters off Palawan Island, the Philippines; 15, the north coast of eastern Malaysia; 16, the east coast of Luzon Island, the Philippines; 17, the East China Sea. References refer to Table S3

fishermen involved; n = 6) or stranding incidents (n = 17) after rehabilitation in the South China region; and (ii) nesting in Hong Kong (n = 1) and Taiwan (n = 2) from 2006 to 2014. The home-range extent of another nesting green turtle from Hong Kong was determined from tracking data published in Ng et al. (2014). The tagging and satellite telemetry of these turtles generally followed the methods described in Balazs, Miya, and Beavers (1996) and Balazs (1999). After a health assessment to ensure that each turtle was clinically healthy and physically fit for release, the turtle was tagged with Inconel tags on its fore- and/or hindlimbs for identification prior to release (Balazs, 1999). The straight carapace length (SCL)/curved carapace length (CCL) of the turtle was measured. Life stage was defined using carapace-length intervals recorded for the best available and geographically closest green turtle population in Hawaii, as described by Balazs (1980). The following size classes were used: a juvenile is defined as a post-hatchling individual with an SCL of up to 65 cm; a subadult is an individual with an SCL of 65–81 cm; and an adult is an individual with an SCL of >81 cm that is reproductively mature. According to the conversion between SCL and CCL, where CCL = −0.414 + 1.039 SCL (Bjorndal & Bolten, 1989), the life stages of green turtles based on CCL are defined as: juvenile, post-hatchling with CCL ≤67 cm; subadult, CCL = 67–84 cm; and adult, CCL > 84 cm. A satellite Argos-linked transmitter was also attached to the carapace of each turtle with fiberglass resin following the protocol described by Balazs et al. (1996). The weight of the transmitter package was less than 5% of the body weight of the turtles in order to minimize any potential impact to their health (Watson & Granger, 1998). Of the 26 transmitters deployed, nine had GPS function.

Tracks of the oceanic movement of each turtle were plotted using MAPTOOL (SEATURTLE.ORG, Inc., http://www.seaturtle.org/maptool/), primarily with positional Argos data derived from the more accurate GPS and location class 1–3 (LC1–LC3) signals; large spatial gaps were filled using data points of LCA and LCB, where appropriate, following visual filtering for obviously inaccurate points (Chan et al., 2003; Parker, Balazs, King, Katabira, & Gilmartin, 2009; Witt et al., 2010; Yasuda & Arai, 2005), on the basis of excluding biologically unreasonable results of location points, including unrealistic travel speed (>5 km/h), points located on land, and a turn of greater than 90° in less than a 24-hour period (Gaos et al., 2012; Parker et al., 2009). A maximum of one fix per day was selected with the highest accuracy LC, and if more than one fix had this LC, the one closest to midday was selected (Casale, Affronte, et al., 2012; Casale, Broderick, et al., 2012; Parker et al., 2009). Positional fixes during directional movement were connected with lines for ease of illustration. A bathymetry layer was included for movements in the open ocean. The end of a track was determined either by the last Argos position or when positional locations aggregated at a specific area, 'inshore' if the turtle settled within estuaries or 'near shore' if the turtle settled in areas along the open coast, generally for approximately 1 month, implying that the tracked turtle had arrived and settled down at its inter-nesting ground (Gaos et al., 2012) or foraging ground (Parker et al., 2009). The speed of the tracked green turtle during inter-nesting, in transit, or foraging was obtained by dividing the distance travelled during each specific activity by the corresponding duration of tracking. Two-sample Student's *t*-tests were used to determine any significant differences ($P < 0.05$) in speed during transit and foraging. Correlations between speed during transit and foraging and carapace length as a proxy for age (Balazs, 1980; Hirth, 1997) were examined by parametric Pearson correlation analysis. Satellite tracks in the present study were compiled with relevant findings of previous studies to generate an overview of oceanic movements of sea turtles in the region. Any threats to habitat hot spots and migratory corridors identified in this study were also reviewed and identified as far as possible.

Home-range analysis in terms of minimum convex polygon (MCP) and 50, 90, and 95% utilization distribution (UD) of the kernel density estimate (KDE), used to pinpoint any core-use area and/or overall home range, was performed using the Home Range Tools (HRT) extension of ARCVIEW 9 (ESRI, Redlands, CA, USA). No home ranges were calculated for turtles with fewer than 20 location points during the inter-nesting or foraging phases (Casale, Broderick, et al., 2012; Gaos et al., 2012; Hart & Fujisaki, 2010; Rodgers, Carr, Smith, & Kie, 2005; Seminoff et al., 2002). MCP typically overestimates home ranges when the area is biased by extreme outliers in locality data (Hooge, Eichenlaub, & Solomon, 1999), whereas KDEs can be overestimated in the cases of few or dispersed locations (Casale, Broderick, et al., 2012). In view of the possible over-estimation of home-range size by both MCP and KDE, the estimated home-range extents in this study are provided for comparison with other studies in order to discuss conservation implications, rather than for exact home-range estimation.

3 | RESULTS

The physical features of each green turtle released, with tracking results and home-range extent (if available), are presented in Table S1. Home-range extent at each respective foraging/inter-nesting ground in this study and other studies is presented in Table S2. Movements for all by-catch or stranded turtles and nesting green turtles by satellite tracking are exhibited in Figures S1 and S2, respectively.

3.1 | By-catch or stranded green turtles in Hong Kong, Guangdong, and Taiwan

A total of 23 by-catch ($n = 6$) or stranded ($n = 17$) green turtles were released after rehabilitation and tracked by satellite transmitters for their movements in this study. Among these turtles, 13 were released from Hong Kong, three were released from Gangkou Reserve, Guangdong, one was released from Yangjiang, Guangdong, five were released from the National Museum of Marine Biology and Aquarium (NMMBA) of Taiwan, and one was released from Penghu Islands, Taiwan.

The results of the satellite tracking (Figures S1; Table S1A) revealed that green turtles arrived at their foraging grounds in the coastal waters of various places in the South China Sea: eastern Hong Kong waters (where Yan Chau Tong Marine Park and Tung Ping Chau Marine Park are located), the coastal areas of Fujian Province, Hainan Island, the Pratas (Dongsha) Islands, Taiwan coastal waters, and as far as Luzon and Palawan in the Philippines (Table S2). The total integrated distance travelled by these turtles ranged from 13 to 3232 km, and the duration of tracking varied from 18 to 382 days. The speed of travel in transit (0.06–2.00 km/h), i.e. during movement/migration before reaching the foraging ground, was significantly higher than the speeds recorded after the turtles reached their foraging ground (0.01–1.37 km/h; $n = 18$; two-sample Student's *t*-test, $P = 0.024$). No significant correlations between the size of green turtles (i.e. SCL/CCL) and the speed of travel in transit ($n = 22$, $r = 0.177$, $P = 0.399$) or during foraging ($n = 18$, $r = -0.101$, $P = 0.689$) were observed in this study.

There were no correlations between turtle size or tracking duration and the area of foraging home ranges (Blanco, Morreale, Bailey, et al., 2012; Gaos et al., 2012; Hawkes et al., 2012). The results of the home-range extent analysis of all green turtles were compiled in this study (Table S2). Home-range extent at the neritic foraging grounds ranged from 1 to 1017 km^2 (median 203 km^2) in terms of MCP, from 0.2 to 974 km^2 (median 64 km^2) for KDE 50%, from 1 to

3978 km^2 (median 285 km^2) for KDE 90%, and from 2 to 5148 km^2 (median 355 km^2) for KDE 95%.

3.2 | Nesting green turtles in Hong Kong and Liouciou Island, Taiwan

Nesting green turtles in Hong Kong started their migration from the nesting site to the foraging grounds (Wanning City of Hainan Island, China, and Dao Bach Long Vi, Vietnam) from September to October (Ng et al., 2014). The extent of the inter-nesting area of a nesting green turtle in Hong Kong during its three nesting activities in 2003, 2008, and 2012 ranged from 27 to 376 km^2 (median 52 km^2) in terms of MCP, from 5 to 118 km^2 (median 11 km^2) for KDE 50%, from 45 to 560 km^2 (median 68 km^2) for KDE 90%, and from 59 to 719 km^2 (median 86 km^2) for KDE 95%. The inter-nesting areas were generally located in coastal waters around Lamma Island (where the turtle nested), with the core area in southern Lamma (Figures S2; Table S1B).

According to the satellite tracking results (Figures S2; Table S1B), two nesting green turtles migrated from the nesting site in Liouciou Island, Taiwan, from September to October in 2013, and arrived at their respective foraging grounds at Iriomote-jima in the Ryukyu Islands, Japan, and Dao Bach Long Vi Island, Vietnam (respective home range also reported in Table S1B). The total integrated distance travelled by these nesting turtles was 862 and 1506 km, respectively. The duration of the tracking was 64 and 177 days.

4 | DISCUSSION

4.1 | Habitat hot spots and migratory corridors of sea turtles in the South China Sea

Broderick, Coyne, Fuller, Glen, and Godley (2007) demonstrated that green turtles exhibited high levels of fidelity to migratory routes and foraging areas, both between and within years and after successive breeding migrations. Foraging grounds of sea turtles identified by satellite telemetry, news reports (mainly in Chinese), and interviews with local people on sea turtle strandings or sightings in the South China Sea from the present study and from previous studies are summarized in Table S3 and are presented graphically in Figures 1 and 2.

Satellite telemetry in the present study supports the findings of previous studies on the important foraging grounds of green turtles, in particular post-nesting individuals: e.g. coastal waters along Guangdong Province and Fujian Province (Chan et al., 2007; Frazier et al., 1988); the northern, eastern, and southern coasts of Hainan Island (Chan et al., 2003; Cheng, 2000; Song et al., 2002); the Pratas (Dongsha) Islands (Cheng, 2000); the Paracel (Xisha) Islands (Wang & Li, 2008); Taiwan coastal waters (Cheng, 2000; Cheng & Chen, 1997); and north and south of the Philippines (Cheng, 2000, 2007; Xia & Gu, 2012). Ng, Chen, and Balazs (2014) also identified the waters off Keelung, northern Taiwan, associated with drifting mats of *Sargassum*, as habitat used by pelagic-phase green turtles. Moreover, the genetic analysis by Ng et al. (2017) indicated coastal Guangdong, the Taiwan Strait, and the East China Sea as habitat used by pelagic-phase green turtles hatched from nesting beaches in Taiwan and mainland China.

Moreover, the tracking results, together with site verification at locations where the tracking ended, allow for the identification of foraging grounds of green turtles on a finer scale, not documented previously. The tracking outcomes in this study confirm that coastal waters along Guangdong Province, specifically Gangkou/Huidong (ID 104688, Table S1), Shanwei (ID 60991, 60992), Wanshan Archipelago (ID 104684, 52099), Shantou (Nanao Island), Xuwen, Nao Zhou, Hainan Island, as well as southern Penghu (ID 129723, 88057), Taitung (East Taiwan) (ID 53748, 71914), and Liouciou Island in Taiwan, contain suitable foraging habitats for green turtles. The movement range of green turtles with satellite tag ID 76441 and 60995, together with reports of green turtle sightings by fishermen in this study, indicates the possible year-round occupancy of green turtles in Mirs Bay and Daya Bay and nearby waters.

Post-nesting green turtles travelled from August to October, and possibly before nesting from April to June, via various major pathways and straits to reach their respective foraging grounds (Figures S1; Table S3): coastal waters off Guangdong and Fujian Province, Qiongzhou Strait between Leizhou Peninsula and Hainan Island, Taiwan Strait between mainland China and Taiwan, Taiwan coastal waters, Luzon Strait between Taiwan and the Philippines, coastal waters off Palawan and the northern Philippines, Lumbucan Channel connecting the South China Sea with the Sulu Sea, and the East China Sea. Gu (2014) and Ye, Chen, Gu, and Li (2015) have also suggested the Taiwan Strait and the nearshore sea between Hainan and Leizhou Peninsula as important migratory routes of green turtles released from Gangkou National Nature Reserve.

Based on the results of the present study and previous studies, a number of sites harbour foraging grounds for a mixed stock of nesting green turtles from different places (Figure 2). Nesting green turtles from Hong Kong and Gangkou Reserve of mainland China shared the same foraging areas near Wanning City on Hainan Island. The east coast of Leizhou Peninsula also provided foraging grounds for nesting green turtles from Gangkou Reserve and the Wan-an Island of Taiwan. The Ryukyu Islands of Japan served as foraging grounds for nesting green turtles from Wan-an Island and Liouciou Island, Taiwan. Dao Bach Long Vi Island in Vietnam also harboured foraging areas for nesting green turtles from Hong Kong and Liouciou Island. In addition, several locations contain nesting sites and foraging grounds for juvenile and adult green turtles (Figures 1 and 2): namely Gangkou and its vicinity, Liouciou Island, Penghu Island, the Paracel (Xisha) Islands (also for hawksbill and loggerhead turtles), and the Pratas (Dongsha) Islands (also for hawksbill turtles). These sites associated with the migratory corridors should be given higher priority for habitat and species protection in the face of limited resources and when imminent threats to sea turtle population (s) are identified.

4.2 | Home range and conservation implications

The home-range extent of green turtles at each foraging ground identified in this study generally fell within the range determined by other studies in the Pacific, Atlantic, and the Mediterranean Sea (Table S2). Overall, differences in the usage of foraging areas could be arise from

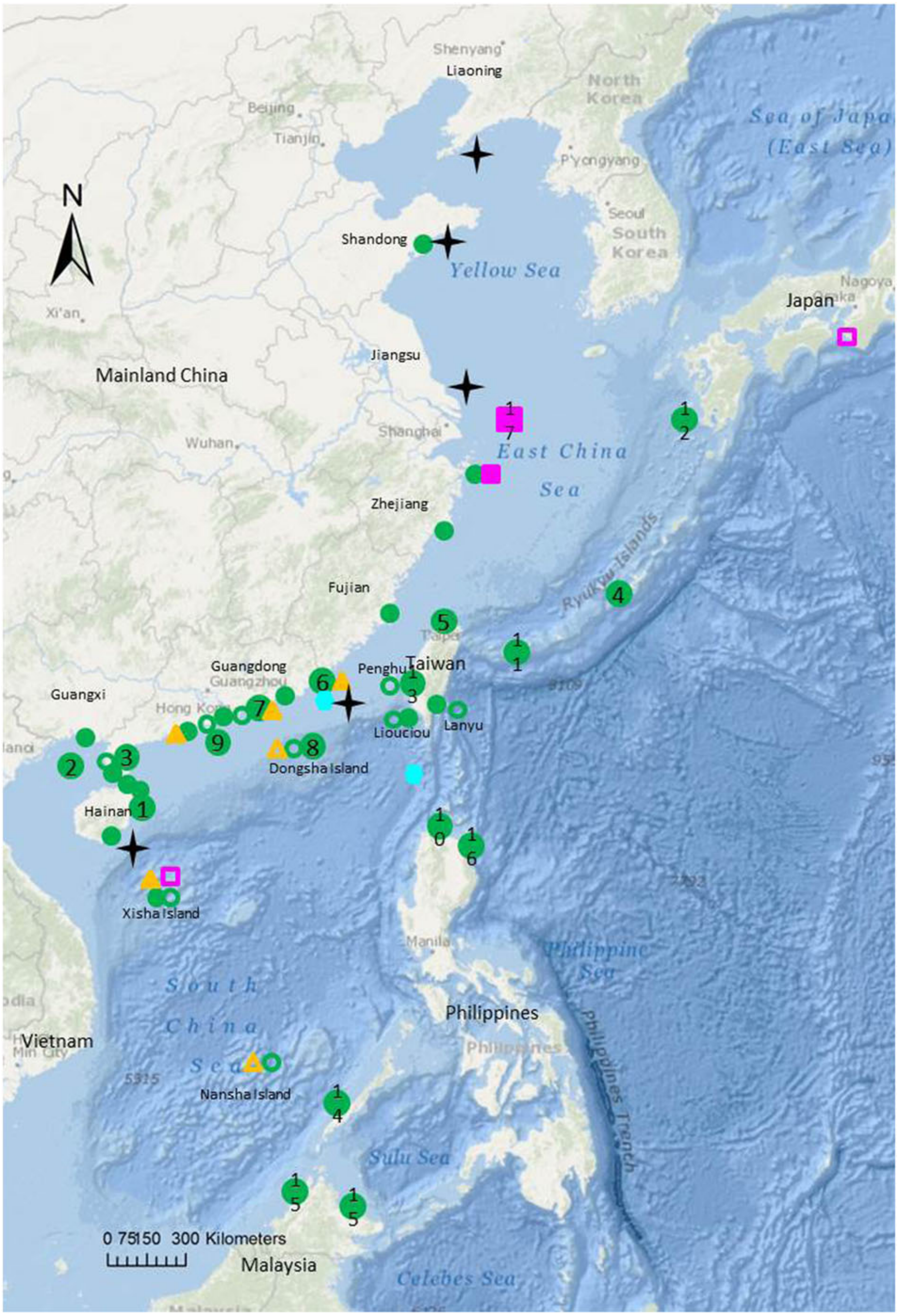

FIGURE 2 The distribution of major nesting and foraging grounds of sea turtles in the South China Sea. Green closed circles denote green turtle foraging grounds; open circles denote nesting grounds. Orange closed triangles denote hawksbill turtle foraging grounds; open triangles denote nesting grounds. Blue closed pentagons denote olive ridley foraging grounds at Shantou and between Taiwan and the Philippines. Fuschia closed squares denote loggerhead turtle foraging grounds; open squares denote nesting grounds. Black stars denote leatherback turtle foraging grounds. Numbers in closed circles represent foraging grounds as described for Figure 1. References refer to Table S3

different foraging strategies (Godley et al., 2003), the food availability at different sites or within the same area (Berube, Dunbar, Rutzler, & Hayes, 2012; Cuevas, Abreu-Grobois, Guzman-Hernandez, Liceaga-Correa, & VanDam, 2008; Makowski, Seminoff, & Salmon, 2006; Seminoff et al., 2002), and seasonality, particularly in temperate zones (Hawkes et al., 2011; Shaver, Hart, Fujisaki, Rubio, & Sartain, 2013). Site fidelity to specific segments of foraging grounds among juvenile green turtles has been documented in several foraging areas, such as Hawaii, South Texas, Florida, and Mexico (e.g. Brill et al., 1995; Makowski et al., 2006; Renaud, Carpenter, & Williams, 1995; Seminoff et al., 2002; Senko, Lopez-Castro, Koch, & Nichols, 2010), and among nesting green turtles (Broderick et al., 2007; Rees, Hafez, Lloyd, Papathansopoulou, & Godley, 2013) and nesting hawksbill turtles (Berube et al., 2012; Parker et al., 2009). The home ranges of these juvenile and nesting green turtles are particularly small. Such a specific distribution of foraging habitats could be attributed to clustered and localized food sources and quality of food (Berube et al., 2012; Brill et al., 1995; Cuevas et al., 2008; Hazel, Hamann, & Lawler, 2013; Makowski et al., 2006; Mendonca, 1983; Renaud et al., 1995; Seminoff et al., 2002; Whiting & Miller, 1998). In general, the home range extent of foraging green turtles near islands (e.g. the Pratas (Dongsha) Islands, Penghu Island, Wanshan Archipelago, Dao Bach Long Vi, and the Ryukyu Islands) was relatively smaller than that observed in coastal waters in this study (Table S2). This difference in home-range extent among habitat types (i.e. 100–1000 km^2 of KDE 95% at islands versus up to several thousand km^2 of KDE 95% in coastal waters) may be linked to variation in the availability and spatial distribution of food and shelter.

The identification of specific sites of key habitat areas (e.g. foraging grounds) is conducive to delineating areas for strategic protection by MPAs (Hart & Fujisaki, 2010). Overlapping home ranges may be an indication of high-quality habitat in an area (Berube et al., 2012; Casale, Broderick, et al., 2012; Hart et al., 2012; Seminoff et al., 2002). The results in this study implied that Luzon in the northern Philippines, eastern Taiwan waters, the Pratas (Dongsha) Islands, Penghu Island, Wanshan Archipelago, eastern Hong Kong waters, and Dao Bach Long Vi, where an overlapping use of habitats by green turtles was observed (Table S2), are likely to constitute high-quality habitat, and hence these areas should be accorded high priority for further study on habitat characterization to better understand the ecological niches of green turtles for appropriate habitat management.

4.3 | Plasticity in the movement and feeding behaviors of green turtles

Blanco, Morreale, Bailey, et al. (2012) reported that the largest foraging ground of a nesting green turtle included a combination of both nearshore and offshore waters providing different food items (seagrass in nearshore areas versus plankton-like jellyfish offshore) in Central America. Similarly, a relatively large home range of foraging loggerhead turtles (8702–60 797 km^2), spanning neritic and oceanic zones, was observed in the Mediterranean by Casale, Broderick, et al. (2012). This observation is comparable with the home-range extent of individuals that adopt plasticity in their feeding habits by alternating between neritic and pelagic environments, e.g. the green turtle that foraged in the Taiwan Strait in this study (ID 104685 in Table S1). Moreover, a few green turtles (ID 60991, 104684, and 104685) in the present study demonstrated cyclic movement with ocean currents: these currents create hot spots of high productivity (e.g. chlorophyll *a*) in the open ocean (Kobayashi et al., 2008; 2011). These green turtles are likely to demonstrate plasticity in their feeding habits, alternating between neritic and pelagic environments. The same pelagic foraging behaviour was also observed in a nesting green turtle from Gangkou Reserve, Guangdong, China (Song et al., 2002), and an adult green turtle that resided in the middle of the Taiwan Strait for nearly 4 months (Wang & Li, 2008). The same strategy was reported in adult female green turtles in the South China Sea by Hatase, Sato, Tamaguchi, Takahashi, and Tsukamoto (2006) and in loggerheads following mesoscale eddies in the East China Sea off the coast of Taiwan by Kobayashi et al. (2008, 2011). Further studies on the association of sea turtle movement with oceanographic features in the China region and the South China Sea should be pursued to characterize their pelagic habitats, and ultimately to assess their interactions with human activities in these habitats.

4.4 | Overview of threats to sea turtle hot spots and migratory corridors

Successful tracking of the majority of sea turtles in this study provided evidence for the post-release survivorship of the rehabilitated sea turtles in the wild; however, according to the satellite tracking results, site visits of this and previous studies, and news reports, some tagged green turtles have been incidentally captured in China in the previous and the current studies. Ye et al. (2015) also highlighted the by-catch of green turtles released from Gangkou Reserve during a tracking study. The female green turtle released from Yangjiang (ID 52100 in Table S1) in this study was incidentally caught by fishermen in Xinliao, Xuwen County, China, and then released immediately by fishermen and the local authority. Another female green turtle released from Hong Kong (ID 104687) was also incidentally caught in the East Harbour of Fujian and subsequently released. C. K. Y. Ng et al. (2014) also reported that a female green turtle found to nest in Hong Kong was reported to be entangled in a fishing net on its migratory pathway back to its foraging ground in Dao Bach Long Vi, Vietnam, and was found dead when fishermen recovered the net in early October 2012.

The incidental capture and direct take of sea turtles for trading purposes has been commonly reported: in Hainan Island, and in the Dongsha, Nansha, and Xisha archipelagos in the South China Sea; in Southeast Asia, in particular Vietnam, the Philippines, Malaysia, and Indonesia (Chan et al., 2007; Cheng, 1996; Hamann, Cuong, Hong, Thuoc, & Thuhien, 2006; Lam et al., 2011; Wang & Li, 2008); and in the coastal waters along Guangdong and Fujian provinces, such as Xuwen and Shantou, as observed in the present study. These localities overlap with the habitat hot spots and migratory corridors of nesting green turtles identified in the present study. The incidental take of sea turtles in the South China Sea was further illustrated by the satellite tracking of a green turtle rescued from a market in Hainan, China, reported by Yeh, Balazs, Parker, Ng, and Shi (2014). According to the tracking data, the turtle was apparently caught in the waters near Palawan in the Philippines, one of the hot spots for sea turtle poaching to satisfy the growing demand in the sea turtle trade in mainland China (Lam et al., 2011). The release of animals including sea turtles is a long-standing tradition in Chinese culture (Balazs, Ng, Gu, & Zhang, 2013; Kuo et al., 2017). In this study, two green turtles released for religious reasons and found in Hong Kong were tracked, and finally settled at Shanwei (ID 60991) and in the East China Sea offshore of Zhejiang (ID 134341). These findings imply that the turtles possibly originated from and were caught in these areas. The cross-boundary take of sea turtles is not uncommon. Lam et al. (2011) reported 128 seizures involving East Asian countries between 2000 and 2008, with a trade volume of over 9180 marine turtle products, including whole specimens (2062 turtles), crafted projects (6161 pieces), and raw shell (789 scutes of 919 kg). Moreover, the largest seizure reported by Lam et al. (2011) involved 387 dead turtles aboard a Chinese fishing vessel in the Derawan Archipelago in East Kalimantan, Indonesia; the poachers were presumed to have targeted locations widely distributed across the Sulu and Celebes Sea, corresponding to a major migratory corridor used by nesting green turtles from Taipin Island in the Nansha Archipelago. Curbing the opportunistic and direct take of sea turtles for the booming trade demand rests on the effective multi-national management of these migratory species.

4.5 | Attributes of satellite tracking

The speed of travel varies with the behaviour of individual green turtles, such as during inter-nesting, migration, and foraging (Hays, Luschi, Papi, del Seppia, & Marsh, 1999; Hochscheid, 2014; Rice & Balazs, 2008). Blanco, Morreale, Bailey, et al. (2012) reported that there was no correlation between turtle size and speed of travel. The same result was also obtained in the present study. The speed of travel of green turtles in transit was significantly higher than that after the turtles reached their foraging grounds in the present study, although this is based on a relatively small sample size (n = 18). The same pattern was also observed by Casale, Freggi, Cina, and Rocco (2013), Gaos et al. (2012), and Papi, Luschi, Crosio, and Hughes (1997), where periods of submergence were shorter and more frequent during migration than during the time spent at foraging grounds. Broderick et al. (2007) reported that short shallow dives in summer were indicative of active foraging. These differences in speed of travel, together with apparent residence at a specific area, help to characterize the behaviour of green turtles during a tracking study.

4.6 | Recommendations

The habitat hot spots and migratory corridors of green turtles, in particular nesting turtles, in the South China region that were identified by satellite tracking and site verification in this study, and in previous studies, are under varying levels of protection (Figures 1 and 2). Of these key sites, the coastal waters of Dao Bach Long Vi in Vietnam, Iriomote-jima and Ishigaki-shima of the Ryukyu Islands in Japan, Gangkou and its bay area, the south-western part of Leizhou Peninsula in mainland China, Dazhoudao Island in the south-eastern and Sanya in the southern waters of Hainan Island, Wan-an of Penghu Island in Taiwan, Paracel (Xisha) Island, and the Pratas (Dongsha) Islands have been designated as protected areas by the corresponding local governments (International Union for Conservation of Nature (IUCN) & UN Environment World Conservation Monitoring Centre (UNEP-WCMC), 2018). The operation of gill nets is not allowed in coastal waters of Liouciou Island to avoid the entanglement and drowning of foraging green turtles there, but the waters surrounding island is not formally an MPA. Although these existing protected areas should be maintained or enhanced, more resources should be directed to protect other key sites that are currently lacking conservation management, in particular a large part of Hainan Island, the eastern Leizhou Peninsula, and Liouciou Island, as they are part of a network of critical habitats used by migratory green turtles.

To advance our knowledge of the distribution of nesting and foraging grounds, and to enrich our understanding of the migratory corridors/connectivity of sea turtle populations in the South China region, including their extent and seasonality, more tracking and/or genetic studies should be conducted on nesting sea turtles. In particular, major nesting grounds in the South China Sea, which are under-studied, such as for green turtles and hawksbills in the Pratas (Dongsha) Islands (Cheng, 1995) and the Paracel (Xisha) Islands (Anonymous, 1975; Wang & Li, 2008), as well as other potential nesting sites, should be studied. Tracking a large number of adults from one foraging area, such as Liouciou Island in Taiwan, may help to identify multiple breeding sites (Luschi & Casale, 2014). Stable isotope analysis can also be used to infer the connectivity of foraging grounds with nesting grounds (Ceriani et al., 2014). Resources and effort should be devoted to the monitoring of nesting sea turtles at existing and potential nesting grounds, such as by fishermen and citizen scientists in coastal communities.

Further quantitative studies on the availability and spatial distribution of marine resources (Hart, Lamont, Sartain, Fujisaki, & Stephens, 2013; Hart, Zawada, Fujisaki, & Barbara, 2013), and dietary studies (Berube et al., 2012; Ng, Ang, Russell, Balazs, & Murphy, 2016), should be performed to characterize the habitat requirements of sea turtles (e.g. food-item availability, seasonality, landscape, etc.) at the major foraging grounds in the South China region identified in this study. Habitat characterization is complementary to the application of home range when designating MPAs in a strategic and cost-effective fashion. More information on the home ranges of foraging sea turtles should also be acquired to identify a common and repeatable pattern of habitat use and residency at each specific foraging ground.

In addition to habitat protection and further research studies, the threat of direct take or by-catch of sea turtles should be quantitatively assessed and mitigated in the activity hot spots and migratory corridors identified in the South China Sea. The only published study on the spatial and temporal distribution of incidental capture of sea turtles by coastal set-nets in Taiwan was conducted more than 20 years ago (Cheng & Chen, 1997). Observer programmes should be established in close liaison with fishermen to identify areas of high by-catch risk and to quantify the interactions between fisheries and sea turtles at a preliminary stage. Further quantitative studies on interactions of by-catch species with oceanographic features and fisheries could be pursued in these by-catch hot spots, if identified. An adaptive management tool similar to TurtleWatch to reduce the by-catch of loggerhead (Howell et al., 2008) and leatherback turtles (Howell et al., 2015) by the Hawaiian fishery in the Pacific could then be developed and implemented for China. Moreover, to combat the poaching and trading pressure on sea turtles, legal enforcement and public awareness campaigns targeting the local public, tourists, vendors, and fishermen involved in the illegal sale and/or capture of sea turtles should be implemented. Sea Turtles 911 (http://www.seaturtles911.org),aseaturtleconservation organization based in Hainan, has been delivering educational talks to tourists and the local public to discourage the illegal purchase of sea turtle products in collaboration with hotels in Hainan, one of the hot spots of the sea turtle trade. More importantly, trans-regional and multi-national commitments to deter the sea turtle trade should be strengthened across international boundaries, such as in the form of forums, workshops, and memoranda. One recent workshop co-hosted by government representatives from Indonesia, Malaysia, the Philippines, and Vietnam focused on improving intergovernmental efforts to curb the illegal trade of sea turtles being harvested in the Coral Triangle (Traffic, 2014). China's participation in multi-national task forces would be an important step in combating the sea turtle trade in the South China Sea and beyond.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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