

Tracking the Confiscated Green Sea Turtles in the South China Sea: Where Did They Come From? Where Will They Go?

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Abstract The population of the green sea turtle (*Chelonia mydas*) is under decline, threatened by bycatch and illegal acquisition despite worldwide protection efforts. However, the confiscation of illegally acquired sea turtles could aid in tracking their origin and movement patterns, crucial for effective conservation strategies. Combining satellite tracking and genetic analysis offers an opportunity to investigate the relationship between the origins and migration directions of green sea turtles in the western Pacific. Here, we applied two methods to investigate the spatial ecology of 18 green turtles caught as bycatch in the South China Sea. Our results revealed the genetic origins and diverse movements of the turtles. Bayesian Mixed Stock Analysis (MSA) suggested that these turtles originated from the rookery of the Xisha Islands (49.6%), central Ryukyu (24.6%), NE Borneo (8%), and the Sulu Sea (5.2%), with other rookeries in meagre proportions (<2% each). Satellite tracking showed the ranges of their travel

were smaller than the whole contributed rookery range, but diverse. The haplotype diversity of these turtles is high, and Cmp19 stands out as both the most frequent and the most diverse haplotype in terms of swimming destinations. These results indicate that the South China Sea is likely an important transportation hub and mating spot for green turtles. Our findings provided evidence for the rehabilitation of these green turtles in the wild and illustrated the complexity of movement during the green turtle's life history, and the "mixed backgrounds" of the green turtles also highlight the need for joint conservation efforts of neighbouring countries in the South China Sea.

Keywords conservation, genetics, green sea turtle (*Chelonia mydas*), movement, rookery, satellite tracking

1. Introduction

The green sea turtle (*Chelonia mydas*) is a flagship species, playing a crucial role in maintaining the balance of the marine ecosystem (Bouchard and Bjorndal, 2000; Hamann *et al.*, 2010). Green turtle populations have experienced decline due to the overexploitation of nesting beaches and the unintended capture of adult individuals (Chan *et al.*, 2007). The exploitation and trade of sea turtle products have been widespread (Davenport, 1988; Shanker and Pilcher, 2003; Stiles, 2009), with illegal harvest occurring in the turtle's

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foraging grounds during regular fishing operations (Pilcher *et al.*, 2008). Developing a conservation strategy for widely distributed marine megafauna requires an explicit understanding of the spatial requirements embedded in their life history. Green sea turtles engage in migrations between foraging grounds and nesting sites repeatedly throughout their lives for feeding and reproductive purposes (Papi *et al.*, 1995). This migratory behavior raises connectivity concerns, which has been widely recognized as a key requirement for ensuring effective protection for migrating animals. The challenging aspect lies in researching their migrations and critical habitats throughout the life cycle on a fine scale. Satellite tracking has been employed to monitor the movements of green turtles post-nesting, juvenile and bycatch to find their foraging grounds (Al-Mansi *et al.*, 2021; Chambault *et al.*, 2018; Yeh *et al.*, 2014). While the released sea turtles returned to their original foraging grounds, these foraging grounds may often be mixed with multiple rookeries (Dethmers *et al.*, 2010; Nishizawa *et al.*, 2018). Satellite tracking thus does not reliably determine the origin of sea turtles. The MSA approach finds wide application in studies concerning sea turtle conservation and management, enabling the calculation of various rookeries' contributions. Based on haplotype frequency patterns derived from mtDNA D-loop segments (Bolker *et al.*, 2007), particularly has proven valuable in sea turtle research and guided conservation management (Formia *et al.*, 2007). Through MSA, it was revealed that the population foraging in Hawaii derived from a nesting population of French Frigate Shoals (Dutton *et al.*, 2008). Similarly, the turtles foraging off the coasts of Argentina mainly originated from Ascension Island's nesting population (Prosdociami *et al.*, 2012), and the green turtles foraging and aggregating off the main islands of Japan primarily originated from the rookeries in the Ogasawara Island Group (Nishizawa *et al.*, 2014). Such results have been helpful for the protection of nesting grounds, contributing to green turtle conservation.

Numerous previous and ongoing studies have led us to identify important places sea turtles thrive (Chambault *et al.*, 2018; Kot *et al.*, 2022; Nishizawa *et al.*, 2018). Conservation efforts have demonstrated the potential to increase green turtle populations in locations such as the Hawaii Archipelago, America and Ogasawara Islands, Japan (Kondo *et al.*, 2017; Mazaris *et al.*, 2017). However, those isolated cases do not change the overall decline in the Pacific population (Mazaris *et al.*, 2017). In the South China Sea, green sea turtles have been abundant (Wang, 1993), but declined significantly in recent decades (Wei, 2016). With the promulgation of the *China Sea Turtle Conservation Action Plan* at the end of 2018 (Ministry of Agriculture and Rural Affairs of the People's Republic of China, 2018), the capture and bycatch of sea turtles, as well as

trade, have been curbed and controlled in this area. Research in this region is insufficient for effective management, given the complex nature of green turtles as long-distance migrants. Previous genetic analyses and satellite tracking data revealed the migration of nesting sea turtles in this area is complex and that the sources are diverse (Cheng, 2007; Song *et al.*, 2022; Song *et al.*, 2002; Yang *et al.*, 2015). For instance, Cheng (2000) discovered that after nesting in the Penghu Islands, some of the green turtles headed toward Japan, while others went to Vietnam; Song *et al.* (2002) discovered a migratory route from the South China Sea to Japan Sea; Yeh *et al.* (2014) tracked an illegally traded green turtle reached Patongong Island, Palawan, Philippines after released in Hainan Island. Faced with confiscated green turtles, all we usually know is the approximate location where they were captured. Gaillard (2020) deduced the illegally traded green turtles in Hainan Island seemed to be "lost in the sea" through genetic studies, and suggested tracking turtles in this area to elucidate migratory connections. Recent studies suggested that the Xisha Islands rookery is an independent management unit (Gaillard *et al.*, 2020; Li *et al.*, 2023; Lin *et al.*, 2023). The question remains: What proportion will the Xisha rookery contribute to the green turtles obtained in the South China Sea? Should they mostly swim to the areas around Xisha Islands after being released? Or multiple rookeries were contributing to the green turtles obtained in the South China Sea, and they will swim diverse routes after being released?

In this study, we tracked and tested the mtDNA fragments of 18 green turtles unintentionally caught and confiscated in the South China Sea from 2020 to 2021. We aimed to address the questions regarding their origin, destination, and potential correlation between their genetic origin and travel destination, enhancing contribution to the conservation and restoration efforts for green turtles in the South China Sea by a comprehensive approach.

2. Materials and Methods

2.1. Sample information 18 green turtles were involved in this study. They were all caught as bycatch and confiscated in the waters surrounding Hainan Island. Health checks were conducted, and the curved carapace length (CCL) was measured before they were set free. Information of the individuals and their tracking are included in Table 1.

2.2. DNA sample collection and testing Skin samples were collected from the hind limb of each tracked turtle after disinfection with 75% alcohol. Samples were stored in 95% alcohol at room temperature. DNA extraction was carried out using the Tiangen Micro DNA Kit (TIANamp Genomic DNA Kit, Beijing, China). The mtDNA D-loop was amplified by two

Table 1 Details of the tracked green turtles.

ID	Sex	CCL (cm)	Release date	Release latitude	Release longitude	Last signal date	Tracking time (d)
198453	PF	78.0	20210728	18.38501	109.98498	20220213	200
220699	PF	63.0	20210728	18.38501	109.98498	20211108	106
220695	PF	62.0	20210728	18.38501	109.98498	20210907	41
220696	PF	67.3	20210728	18.38501	109.98498	20210928	62
220693	PF	62.0	20210728	18.38501	109.98498	20210815	18
220704	PF	80.0	20210728	18.38501	109.98498	20210911	45
198445	PF	84.0	20210405	18.35271	109.74682	20211105	215
198451	F	95.9	20210405	18.35271	109.74682	20211002	181
198446	M	79.0	20210118	18.56587	110.14822	20210805	200
198448	UN	54.1	20210118	18.56587	110.14822	20210604	168
198450	PF	76.7	20210118	18.56587	110.14822	20210512	115
198436	PF	77.0	20200808	18.58201	110.19297	20200910	33
198438	PF	74.6	20200808	18.58201	110.19297	20210806	364
198439	PF	80.0	20200808	18.58201	110.19297	20201121	106
198440	PF	69.5	20200808	18.58201	110.19297	20201108	93
198441	F	89.5	20200808	18.58201	110.19297	20200907	31
198442	PF	73.0	20200808	18.58201	110.19297	20200908	30
198443	PF	79.0	20200808	18.58201	110.19297	20200823	16

Note: PF: Presumptive Female; F: Female; M: Male; UN: Unknown.

primers, LCM15382 (5' GCT TAA CCC TAA AGC ATT GG 3') and H950g (5' GTC TCG GAT TTA GGG GTT TG 3') (Abreu-Grobois *et al.*, 2006). The PCR amplification mixture (40 mL) contained 8 mL of 5×HF buffer, 2 mL of 10 mmol/L dNTPs; 1 mL of each forward and reverse primer (10 μmol/L); 0.4 mL of Phusion DNA polymerase (2 U/μL); and 1.5 mL of DNA. The total volume was adjusted to 40 mL with ultrapure water. The PCR was run at the following conditions: pre-denaturation at 94 °C for 80 s followed by 42 cycles of denaturation at 94 °C for 42 s, annealing at 56 °C for 30 s, extension at 72 °C for 50 s; final extension at 72 °C for 5 min and storage at 4 °C. The PCR products were purified and sequenced by Shanghai Sangon Biological Engineering Technology and Services Co. Ltd.

2.3. Genetic analysis Through NCBI BLAST searching to confirm the D-loop gene sequences obtained were belonging to green sea turtles. D-loop segments were commonly trimmed to a length of 384 bp for comparison with the available data in the Indo-Pacific region using the standardized CmP nomenclature (Jensen *et al.*, 2019). To identify existing haplotypes or confirm new haplotypes, trimmed sequences were used BLAST to compare to GenBank. The haplotype frequencies of the mitochondrial D-loop in these mixed stocks were estimated using the software DnaSP (Librado and Rozas, 2009). Both haplotype diversity (h) and nucleotide diversity (π) indices were calculated by DnaSP.

2.4. Mixed-stock analysis The Bayesian MSA approach (Pella and Masuda, 2001) was used to run MSAs based on haploid genetic marker data. The data were obtained from source populations and one or more mixed populations (Pella and Masuda, 2005). Stock contributions were determined using both uniform priors and an informative priors analysis referring to the methodology of Dethmers *et al.* (2010). We used the same haplotype frequencies as those reported for Pacific nesting rookeries in Nishizawa *et al.* (2018), Jensen *et al.* (2016), Gaillard *et al.* (2020), Song *et al.* (2022), Li *et al.* (2023), and Hamabata *et al.* (2014). 30 Markov Chain Monte Carlo (MCMC) chains were run and each one began with 95% of all of the samples. Each chain contained 10 000 iterations and the first 5 000 discarded as burn-in. Meanwhile, the convergence of MCMC sampling was assessed using the Gelman-Rubin shrink factor, with a value below 1.2 indicating convergence (Raftery and Lewis, 1992).

2.5. Satellite tracking After carefully cleaning the turtles' shells, we attached the trackers (SPOT-6, Wildlife Computers Inc.) with epoxy resin and fiberglass cloth (Balazs *et al.*, 1996). The duty cycle of the SPOT-6 tracker was set as 18 h on/6 h off. The turtles' locations were obtained through the Argos satellite system and were categorized into six location classes (LC): LC3, 150 m; LC2, 150–350 m; LC1, 350–1 000 m; LC0, 1 000 m; LCA and LCB, no accuracy given; and LCZ, invalid values (rejected locations) (Hays *et al.*, 2001). The tracked turtles were released in southern Hainan Island in August

2020, January 2021, April 2021, and July 2021 (the release date and location are in Table 1). When positional locations of the tracked turtles clustered in one area for over a month, it was assumed they reached their destinations (Christiansen *et al.*, 2017; Parker *et al.*, 2009).

To reduce the data bias and ensure the robustness of the analysis results, we screened the inaccurate and invalid location points (e.g., travel speed (>5 km/h), points located on land; Chan *et al.*, 2003; Gaos *et al.*, 2012; Yasuda and Arai, 2005), and retain the location points classified as LC1–LC3. After removing invalid and drifting points, the remaining satellite tracking data were performed fitting in ArcGIS 10.8 (ESRI, Inc., Redlands, California, USA) to draw the map of the turtles' active routes for subsequent analysis.

3. Results

3.1. Genetic analysis A 900 bp length of mtDNA D-loop was obtained from 18 tracked green turtles and was trimmed to 384 bp for subsequent analysis. A total of 8 haplotypes was identified, and eighteen turtles belonged to four haplotypes: CmP19, CmP20, CmP39, CmP49, CmP50, CmP54, CmP57, and CmP126 (Table S1; Jensen *et al.*, 2019), their average h was 0.843 ± 0.076 and π was 0.01607 ± 0.00395 . Notably, the h value was higher than that in populations from other sea areas, and π was generally surpassed the global average diversity ($\pi = 0.0093$) and other regions (Table 2).

3.2. Mixed-stock analysis Based on the haplotypes reported in rookeries by Nishizawa *et al.* (2018), Jensen *et al.* (2016), Gaillard *et al.* (2021), Song *et al.* (2022), Li *et al.* (2023) and Hamabata *et al.* (2014), we estimated mixed stock contributions with 95% confidence intervals, which revealed that the major stock contributions were from Xisha Islands (49.6%, 95% CI [29.5–78.4]) and Central Ryukyu (24.6%, 95% CI [8.6–47.4]), minor stock contributions were from NE Borneo (8%, 95% CI [0–17.7]), and the Sulu Sea (5.4%, 95% CI [0–11.9]), while very few stock contributions were detected from CNMI/Guam (1.91%, 95% CI [0–12.6]), Aru (1.89%,

95% CI [0–13.7]), Ashmore Reef (1.84%, 95% CI [0–15.1]), Vanuatu (1.82%, 95% CI [0–16.8]), N New Guinea (1.72%, 95% CI [0–13.6]), Micronesia (1.16%, 95% CI [0–13.6]), Palau (1.14%, 95% CI [0–14.3]), Marshall Islands (1.14%, 95% CI [0–12.6]) (Figure 1).

3.3. Satellite tracking The tracking durations ranged from 16–364 d (mean: 112.44 ± 90.54 d) (Table 1). The total travel distance ranged from 1 691–9 072 km (mean: $4 043 \pm 2 015$ km) (Figure 1). Out of the tracked 18 green sea turtles, 11 (identified as 198453, 220699, 220704, 198445, 198451, 198446, 198448, 198450, 198438, 198439, and 198442) clustered in one area for over a month, suggesting that they have reached their destinations (Christiansen *et al.*, 2017; Parker *et al.*, 2009) and stayed until the signal stopped, while the remaining 7 turtles (IDs: 220693, 198441, 198443, 220695, 220696, 198436, and 198440) ceased transmitting signals stopped along their migrations (Figure 2). The 11 turtles reached a total of 8 destinations, including the regions of northern Calamian Islands and Mindoro Strait, Philippines; Dongsha Islands, China; the northern waters of Santiago Island, Philippines; the western edge of Lingayen Gulf; the northern waters of Taiwan Island, China; northwest Borneo; Gulf of Thailand; and Fukue Island, Japan, and the waters of Southern Hainan Island, China (Figures 2–3).

4. Discussion

4.1. Genetic diversity and genetic stock composition For endangered species, genetic diversity is critical for the persistence and stability of a population. Despite the limited sample size—only 18 captured green turtles, the h ($h = 0.8430 \pm 0.076$) and π ($\pi = 0.016 \pm 0.00395$) values were higher compared with those in other regions (Table 2). Previous studies also examined high genetic diversity in small sample sizes of green turtles in the South China Sea and deduced they have not experienced population expansion (Ng *et al.*, 2014; Song *et al.*, 2022). Formia *et al.* (2006) concluded that the reason for the higher genetic

Table 2 Genetic diversity of the green turtles from the South China Sea compared with the data from other regions.

Zone	Sample size	(π)	(SD)	(h)	(SD)	Reference
South China Sea	18	0.016070	0.003950	0.8430	0.0760	This study
Caribbean	28	0.005372	0.00344	0.6481	0.089	Ruiz-Urquiola <i>et al.</i> (2010)
Southeast Atlantic	26	0.003100	0.002300	0.5692	0.1100	Formia <i>et al.</i> (2006)
W Indian Ocean	33	0.0084	0.0049	0.1174	0.0732	Bourjea <i>et al.</i> (2015)
Southwest Pacific	31	0.0229	0.0122	0.4577	0.096	Read <i>et al.</i> (2015)
Eastern Pacific	77	0.004336	0.002855	0.6483	0.0486	Dutton <i>et al.</i> (2013)
Northwest Pacific	103	0.017470	0.009198	0.7057	0.0440	Nishizawa <i>et al.</i> (2013)
Southeast Asia	68	0.006410	0.005978	0.7881	0.0346	Jensen <i>et al.</i> (2016)

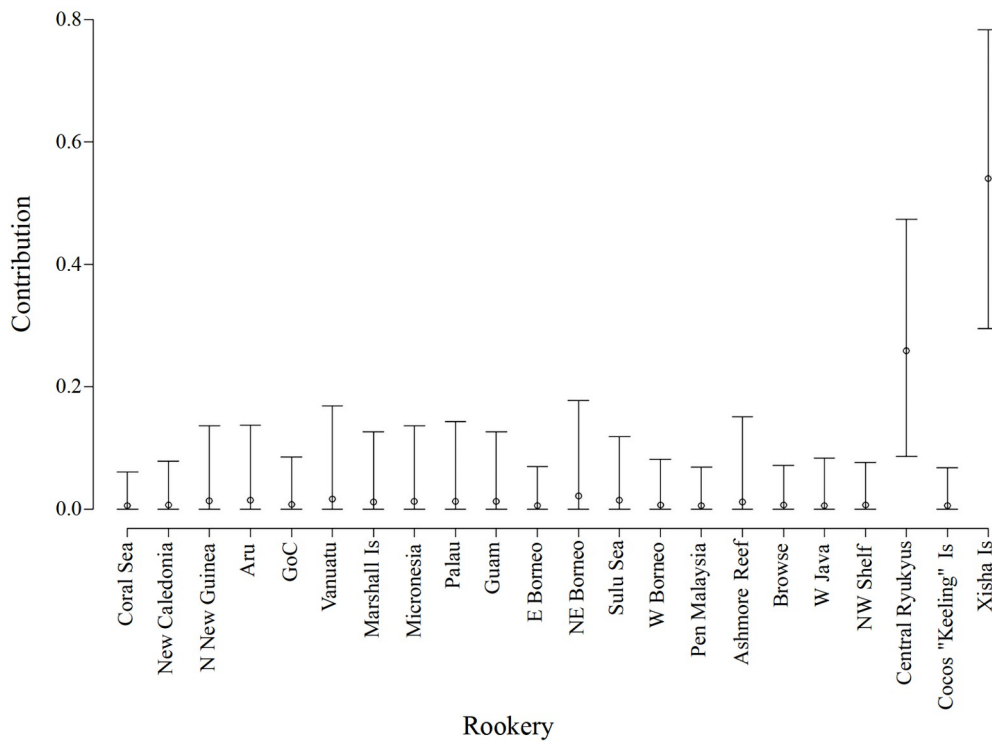


Figure 1 MSA results for tracked green turtles. Note: Estimated stock contribution of Pacific nesting stocks to the green sea turtles in this study. The bars above and below point estimates represent the two-tailed 95% confidence interval around stock estimates.

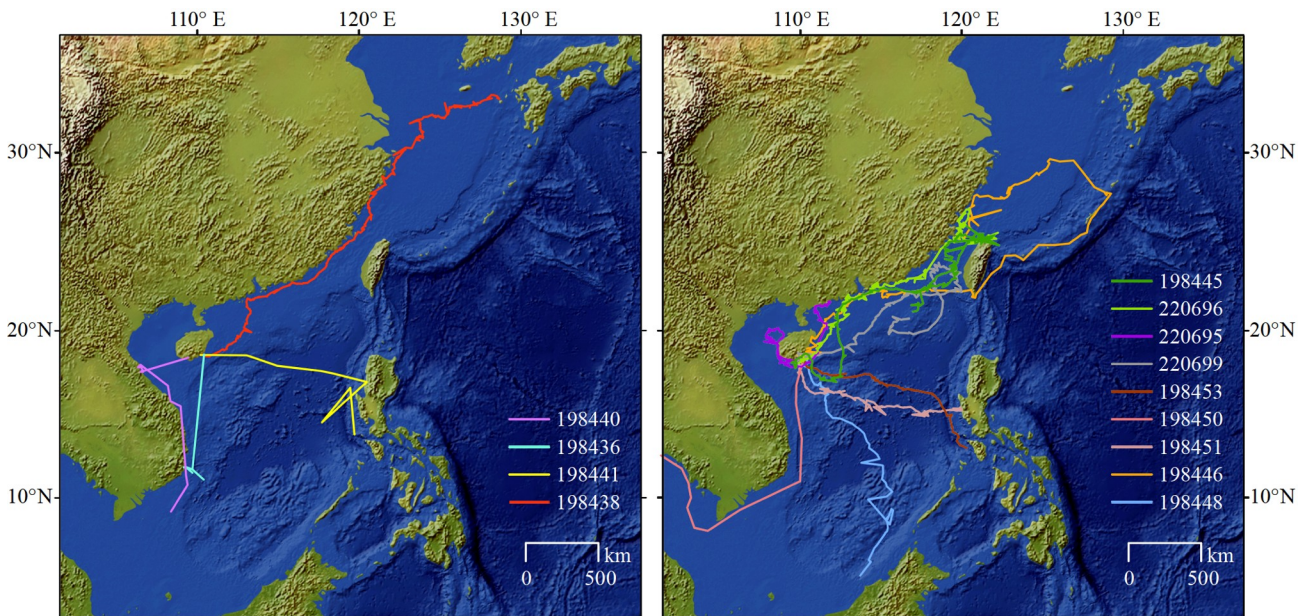


Figure 2 Migration routes of the green turtles. The left shows the turtles released in 2020; the right shows the turtles released in 2021.

diversity in small populations may be due to the recent integration of green turtle populations from different

rookeries or the presence of lineages with larger ancestral populations in the area.

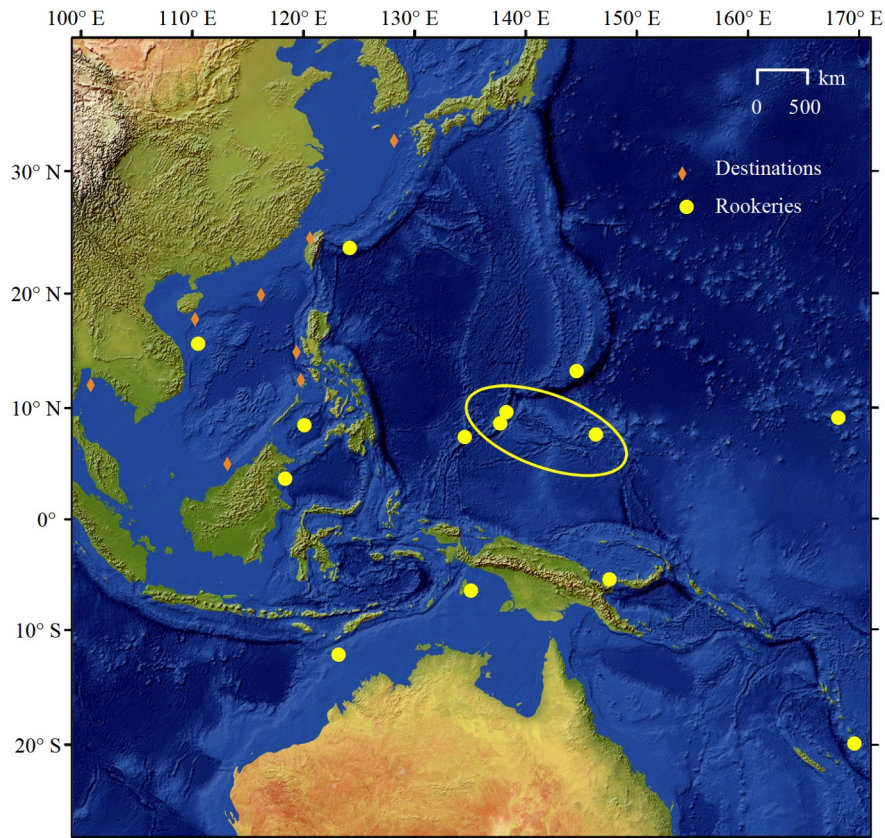


Figure 3 Map of rookery sites and the destinations of the tracked green turtles. The yellow circles represent the rookery's source. The yellow elliptical line encloses the rookery scattered on the small islands. The orange diamonds represent the end locations of their destination.

MSA results showed our studied turtles have multi genetic origins. This diverse range of rookeries extends from the South Pacific Ocean with a minor contribution from Vanuatu, to the Indian Ocean, as seen in the case of Ashmore Reef, situated approximately halfway between the northwestern coast of Australia and the coast of Indonesia, known for its rich marine biodiversity. The broad rookeries contribution may also hint at the presence of lineages with larger ancestral populations in this area. But the Xisha Islands (49.6%) contributed the most, followed by the Central Ryukyus (24.6%) (Figure 1), from where the turtles captured in the South China Sea predominantly originated. In contrast to the findings of Gaillard *et al.* (2020), their MSA indicated the rookeries in the Xisha Islands (57%) and the Sulu Sea (29%) are severely suffering from illegally acquired turtles from Hainan Island and surrounding regions. Recently researchers also found that the Xisha Islands is the most important nesting ground in the South China Sea (Song *et al.*, 2022).

Although the haplotype diversity is high, we found that Cmp19 plays the predominant role. Initially considered rare, Cmp19 was once only found in Taiwan, Wan'an, Guangdong, Gangkou Reserve in China and the Gulf of Carpentaria in

Australia (Cheng *et al.*, 2008; Ng *et al.*, 2017). Subsequent studies reshaped our understanding. Cmp19 represents a substantial proportion in the studies on the Xisha Islands by Gaillard *et al.* (2020) (53.8%, 7 out of 13 nests from Xisha Islands), Song *et al.* (2022) (62.5%, 10 out of 16 nests), and Li *et al.* (76.4%, 55 out of 72 samples). Among the rescued samples in Hainan, Cmp19 comprises 8 out of 18 individuals in our study, accounting for 44.4%, and a similar proportion of 45.9% (39 out of 85) reported by Gaillard *et al.* (2020).

4.2. Satellite tracking and relations with genetic background

Our tracking results have uncovered bigger plasticity in green turtles on their behavior and ecology, enriching our understanding beyond what was known in previous studies, as well as revealing the intricacies of green turtle migration in the South China Sea, especially immature turtles, emphasizing the involvement of diverse sources that may contribute to multiple rookeries. Green sea turtles from multiple sources spend their juvenile years, the so-called "lost years", in the South and East China Seas, which has become a "transportation hub" in their life histories. They may also have genetic exchanges in adulthood causing high haplotype diversity.

Combining satellite tracking and MSA, we found that green sea turtles did not return to their nesting grounds in the Xisha Islands (i.e., the closest point being the southern waters of Hainan Island). However, their movements were not as extensive as their entire rookery distributions. Considering the high proportion of the contribution rookeries in Gaillard *et al.* (2020) and our study, as Figure 3 marked, destination B is near Central Ryukyu, destination D (the waters of Southern Hainan Island, China) is near Xisha Islands, and destination F (the northern waters of Santiago Island, Philippines, the western of Lingayen Gulf) is near Sulu. The distance from Xisha to Hainan is approximately 250 km. MSA suggested that when the rookeries separated over 1 000 km, they differed significantly, but rookeries within 500 km didn't show genetic differentiation across the Pacific Islands (Dutton *et al.*, 2014). Cmp39 and Cmp126 were popular in Japan (Hamabata *et al.*, 2014; Nishizawa *et al.*, 2011), but in our study, turtle 198439 (Cmp39) stayed near Hainan for 106 d and 198440 (Cmp126) swam to Vietnam, while 198440's signal was lost in waters off Ho Chi Minh respectively. Satellite tracking revealed the haplotypes of Cmp39 and Cmp126 maybe with broader distributions or long migration routes.

Combination of biotic and environmental factors drive the movements of sea turtles. Immature sea turtles' movements have been considered mysterious (Wildermann *et al.*, 2018). It is noteworthy that the majority of the turtles we tracked were immature, and did not exhibit a clear inclination to return to their nesting grounds. Our tagged green sea turtles are mostly immature with CCL ranging from 54.1 cm to 95.9 cm, only with two adults for their CCL over 85 cm (Mark *et al.*, 2006). Pelagic phase green turtles swim following the ocean currents and feed on plankton, and when they reach 44 cm about in CCL, they go to a neritic foraging habitat, even turtles born in the same spawning ground may drift to different areas in the sea by ocean currents (Arthur *et al.*, 2008; Limpus *et al.*, 2005). When they grow to adults, they usually display fidelity to foraging grounds, and even fidelity within and between seasons (Broderick *et al.*, 2007). Subadult green turtles may be recruited to different foraging grounds compared to fixed foraging grounds for adults, potentially increasing the probability of genetic exchange between green turtle populations from different waters, which is confirmed by our satellite tracking results. As the popular haplotype in our study and previous studies (Song *et al.* 2022; Gaillard *et al.* 2021), Cmp19, in our satellite tracking results, showed a broad movement range. Among these eight turtles, three remained in the southern waters of Hainan Island (IDs: 198442, 220693, 220704); two migrated to Philippines (198441), and reached the northern western waters of Lubang Islands, 198453 reached the regions of northern Calamian Islands and

Mindoro Strait, green turtles have been recorded nesting in Calamian Islands and they forage the surrounding areas (Poonian *et al.*, 2016). One turtle went to Guangdong, China (ID: 220695), reaching the bay between the mainland and Hailing Island. Another one went to Taiwan, China (ID: 220696), which followed the coastlines of the mainland, and eventually reached the confluence of lower Fujian and Zhejiang, crossed the Taiwan Strait, and eventually reached the waters of northern Taiwan. Additionally, one turtle swam to northwest Borneo (ID: 198448), arriving at the northwest waters of Sabah, East Malaysia (North Borneo).

In the paper of Ng *et al.* (2017), they tracked a pelagic-phase turtle (CCL: 35 cm) whose haplotype is Cmp19 and released it in Hong Kong, China. It moved north after release, passed through the Taiwan Strait, and lost signal in the offshore waters of Zhejiang, China. In our study, the CCL of Cmp19 individuals was from 54.1 cm to 80 cm, except for 198441. We also considered another reason for multi-routes: some of our samples were close to mature. Immature turtles are sedentary till close to sexual maturity, then migrate in Siegwalt *et al.* (2020). We suspected that 198441 was heading to nesting grounds, given its CCL of 89.5 cm, exceeding the typical threshold of 85 cm. Unfortunately, tracking data was limited to only 31 d, making it uncertain whether it would have settled in a nesting area during this period. Moreover, the biggest individual 198451 (CCL: 91 cm), belonged to Cmp49, a haplotype widespread in the Indo-Pacific (Hamabata *et al.*, 2014), swam to Iba and Botolan of the Philippines, then along the western coast, reaching the north waters of Santiago Island. Iba and Botolan have records of sea turtle nesting (SWOT, <https://www.seaturtlestatus.org/>); Santiago Island, an extension of the western edge of Lingayen Gulf. One of Cmp50, 198445 was also considered near mature, as its CCL was 84 cm. It passed by the Penghu Islands and reached close to the Dongsha Islands. Both the Penghu Islands and the Dongsha Islands serve as nesting places for green turtles in the South China Sea (Chan *et al.*, 2007). 220699, another Cmp50 in our samples, reaching the waters of the north Taiwan Island, but then to the southwest, finally arriving at the Dongsha Islands. While 220699's CCL was only 63 cm (still a juvenile). 198445 may be a subadult or a small size adult and may migrate for nesting purposes, however, there is a lack of current monitoring on the Dongsha Islands.

Sea turtles from various rookeries migrate or forage in the South China Sea, creating opportunities for populations with different origins to interact. In our results, their activity patterns did not perfectly align with their genetic patterns. In other words, the destinations of the turtles were not necessarily predicted by their origins (Gaillard *et al.*, 2021). This might be the reason for the high genetic diversity of the

captured turtles. The South China Sea thus provides a crucial connection of different rookeries and is conducive to their long-term survival.

4.3. Conservation implication Local variation in the green turtle history took place both regionally, among various genetic stocks, and in regional management units (RMUs). Our results support the Xisha Islands as the most comprehensive RMU nesting ground for green turtles in the South China Sea (Song *et al.*, 2022; Wei, 2016). In previous records, green turtles accounted for 87% of all turtle species in the South China Sea (Wang, 1993). In the South China Sea, turtles actively navigate the waters, potentially encountering sea turtles from adjacent rookeries. It is essential to protect the foraging grounds, nesting grounds, and migration channels used by green turtles (FitzSimmons and Limpus, 2014). Several factors, such as the size of natal rookeries, the proximity of foraging to nesting areas, and ontogenetic changes in habitat preferences impact the composition of sea turtle populations at foraging aggregations (Jensen *et al.*, 2013). These factors contribute to the movement patterns and population structure of sea turtles. Safeguarding these routes as part of the MPA network could help ensure the safety of green turtle populations during their extensive movements.

According to our tracking results, coastal areas of China also play a crucial role in green turtle protection. In our study, upon release from Hainan, 220696 and 198438 followed the coastal continental shelf, particularly navigating estuarine regions such as the Pearl River and the Yangtze River. The runoff from these rivers carries an amount of dissolved nutrients and toxic waste into the sea, fostering the growth of phytoplankton in the coastal regions (Ning *et al.*, 2004; Sun, 2017). Although 198446 and 198445 did not consistently follow the coastal route, both turtles passed by the estuary of the Pearl River. After a specific period of passive pelagic migration, juveniles actively migrate to development habitats of demersal neritic. These coastal waters serve as temporary foraging places, allowing turtles to replenish energy on their way to their permanent foraging grounds (Cheng, 2000). However, green turtles are particularly vulnerable to substantial near shore fisheries of the China coast. The conservation of these coastal areas, especially those with estuaries rich in nutrients, is thus critical for the protection and well-being of green turtles throughout their life stages, emphasizing the need for sustainable practices and protective measures in these regions.

5. Conclusion

Our study unveiled the intricacies of green turtle migration in the South China Sea, especially immature individuals. The

results highlighted the involvement of diverse sources and contribution to multiple rookeries with the Xisha Islands being most important. These findings further underscored the importance of the South China Sea as a crucial area for green turtle conservation. To safeguard their extensive movements in their life history, establishing a marine protected network involving neighboring countries is essential, ensuring the safety and well-being of these remarkable marine species. Next, we look forward to monitoring the spawning grounds of the Xisha Islands to see if any of our released female turtles can land to nest.

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