

Lost at sea: determining geographic origins of illegally traded green sea turtles (*Chelonia mydas*) rescued on Hainan Island, China

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Abstract

Context. Green sea turtles are threatened by exploitation for food and medicine markets, with Asian populations facing the heaviest pressures. Sea turtle confiscations that happen out at sea can give a general area that poachers are targeting, but it can be difficult to determine the impact on specific nesting rookeries. Previous studies circumvented this difficulty by using genetic markers to identify nesting rookery origins of confiscated green turtles.

Aims. To determine the impact on nesting rookeries from the illegal harvesting of green sea turtles by Hainan fishermen and describe the genetic diversity of the Paracel Islands' green sea turtle population.

Methods. In the present study, we sequenced 384 bp of mitochondrial DNA control region from 85 illegally traded green sea turtles rescued on Hainan Island, China, to investigate their population of origin. For reference-source data, we used previously published mtDNA haplotype data from rookeries from Australasian waters and mtDNA haplotype data from 16 newly collected samples from the Paracel Islands in the South China Sea, a previously unsampled area.

Key results. Ten and four mtDNA haplotypes, all being reported before, were detected from the Hainan confiscation and Paracel Islands rookery respectively. However, CmP19, an infrequent haplotype that has been found only in 10 green sea turtles previously, made up ~45% of our rescued samples and ~62% of the Paracel Islands sample, suggesting a potential association between CmP19 and the Paracel Island rookery. Haplotype diversity of the rescued green sea turtles was relatively high ($h = 0.7143 \pm 0.04$), whereas nucleotide diversity was relatively low ($\pi = 0.0031 \pm 0.00$), compared with other rookeries. Mixed-stock analysis suggested that the rookeries in the Paracel Islands (~57%) and the Sulu Sea (~29%) are experiencing the greatest impact from illegal harvesting by fishermen from Hainan and neighbouring countries.

Conclusions. The Paracel Islands population contains a unique genetic makeup compared with other studied rookeries, particularly the high frequency of the previously rare CmP19 haplotype. The current harvesting of green sea turtles by Hainan fishermen affects not only protected local populations (Paracel Islands), but also distant populations (Sulu Sea) in protected international waters.

Implications. Establishment of a large-scale Sea Turtle Nature Reserve in the South China Sea, including a special law enforcement team to monitor this National Marine Park, needs to be top priority to help curb illegal harvesting. The Paracel Islands represents a newly defined population, and conservation measures need to be taken immediately to preserve this distinct population.

Keywords: genetic, haplotype, mixed-stock, mtDNA, nesting rookery, South China Sea.

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Introduction

There are seven species of sea turtles found throughout the oceans of the world; however, despite this wide distribution, some species are globally endangered (*Chelonia mydas*) and some critically endangered (*Eretmochelys imbricata*, *Lepidochelys kempii*; IUCN 2020). To protect genetically and reproductively distinct populations, green sea turtles are currently grouped into 26 distinct stocks within Australasian waters in the Pacific Ocean (Fitzsimmons and Limpus 2014). Chaloupka *et al.* (2008) surveyed data from six green sea turtle rookeries (four Pacific and two Atlantic) and found that these rookery populations increased at various rates over a 20-year period (1982–2003). Sea turtle populations in Asia show both increases (Shanker and Pilcher 2003) and decreases (Chan *et al.* 2007), and these differences depend mainly on the local conservation efforts (Shanker and Pilcher 2003). Sea turtles that are illegally traded in one foraging ground can negatively affect faraway nesting rookeries because of their usage of multiple habitats in the course of their life cycle.

In Asia, green sea turtle populations are found in many different countries, with some showing decreasing population numbers (Ng *et al.* 2014) and others increasing in population numbers (Kondo *et al.* 2017). Green sea turtles receive various levels of protection from local governments, from quota-limited collection in Japan (Kondo *et al.* 2017) to complete bans on collection in the Philippines (Trono 1991). Population declines are mainly the result of by-catch and illegal harvesting of the green sea turtle for meat, shell products and use in traditional Chinese medicine (van Dijk and Sheperd 2004). From 2000 to 2008, Lam *et al.* (2011) noted 128 seizures among Hong Kong, Japan, Taiwan and China, resulting in 2062 whole animals, 789 scutes and 919.2 kg of shell being confiscated. The origin of these products had significant links to Indonesia, Malaysia and the Philippines. Whereas poaching of green sea turtles is known to exist in the Asia–Pacific region, it would be beneficial to determine which nesting rookeries and foraging grounds are experiencing the greatest declines, and to focus conservation efforts in these areas. The most direct way to determine the impact level would be to seize poachers as they are capturing green turtles; however, monitoring every nesting and foraging site for poachers would be labour and cost intensive. Satellite-telemetry studies from Peninsular Malaysia and Hainan, China, have shown that green sea turtles can migrate more than 2000 km to the waters off Sabah, Borneo, Malaysia (van de Merwe *et al.* 2009) and Palawan, Philippines (Yeh *et al.* 2014). Yeh *et al.* (2014) used satellite telemetry to track illegally traded green sea turtles post-release, and their results showed that some returned to the Philippines, suggesting this as a probable area of origin. Shimada *et al.* (2016), via telemetry, found that the majority of displaced and captive turtles did not lose their homing ability, or lose home fidelity, and returned to their home area. In addition to satellite-tracking, previous studies using mtDNA markers have shown that foraging grounds comprise turtles from multiple nesting rookeries that can be from both geographically proximate rookeries to rookeries >500 km away (Dethmers *et al.* 2010). This genetic approach could also be used for identifying areas of origins for illegally traded animals.

Previous studies used genetic markers for a variety of wildlife forensic applications (Wu *et al.* 2005; Dawnay *et al.* 2008;

Dalton and Kotze 2011), and this type of forensic application could be useful in determining the general areas of illegally harvested turtles and to identify which nesting rookeries are sustaining the greatest impact. Joseph *et al.* (2014) used mtDNA markers, a mixed-stock analysis (MSA), and previous genetic data from nesting rookeries (Dethmers *et al.* 2006; Cheng *et al.* 2008; Nishizawa *et al.* 2011), to determine the possible nesting origins of confiscated green sea turtles from the 2007 Mantanani incident (a large seizure of more than 200 sea turtles by Malaysian authorities). Their analysis showed stock contributions mainly from the Sulu, Celebes and Arafura Seas, which are in the heart of the Coral Triangle. Yang *et al.* (2015) collected green sea turtle samples from various sources on Hainan Island and found haplotypes that are common to the Coral Triangle. In addition, they also found the CmC2 haplotype to comprise >70% of their samples. The high concentration of the CmC2 haplotype is unexpected, because no other rookery nor feeding grounds harbour such high frequencies of this haplotype. It appears the nesting rookery has not yet been identified for this haplotype. Joseph *et al.* (2014) encouraged the genotyping of unstudied nesting rookeries to potentially identify genetically distinct populations.

From 2012 to 2018, we collected samples from illegally traded green sea turtles from local fishermen or the Hainan Department of Fisheries on Hainan Island, and from hatchling turtles in the Paracel Islands, which is commonly called Xisha Islands in China. Local fishermen collect different age classes from waters nearby Hainan Island, and farther out to sea, and bring back both live and deceased individuals (F. Yeh, pers. comm). These turtles are collected via by-catch, targeted collecting and egg harvesting (Paracel Islands), and are used to supply the demand for food, tourism products and green sea turtle farms in China. Local fishery officers and Buddhist monks rescue some animals and, if needed, these animals are treated for injuries or illnesses, and, ultimately, released into offshore waters. Currently, the Paracel Islands are home to the most important and largest active nesting beaches in the northern portion of the South China Sea and understanding potential impacts to this rookery is of important conservation value. Our purpose was: (1) to use MSA to determine sources of origin for these illegally traded specimens; (2) to determine which nesting rookeries are sustaining the greatest impact from poaching; and (3) to determine the genetic composition of a previously unstudied and highly vulnerable nesting population in the South China Sea (Paracel Islands).

Materials and methods

Sampling and genetic sequencing

From 2012 to 2018, 85 samples in total were taken from green sea turtles that were rescued by the local Hainan Department of Fisheries officers (tissue or blood), from fishermen on Hainan Island (tissue or blood) or from farms by local Buddhists (tissue or blood), and 16 hatchling samples (tissue) were taken from different nests in the Paracel Islands (Fig. 1). Carapace length was measured to the nearest 0.1 cm and age classes were determined following the methods described by Balazs (1980). Sex was confirmed for males whose tails were elongated relative to females. Skin-tissue samples were taken from the rear flipper

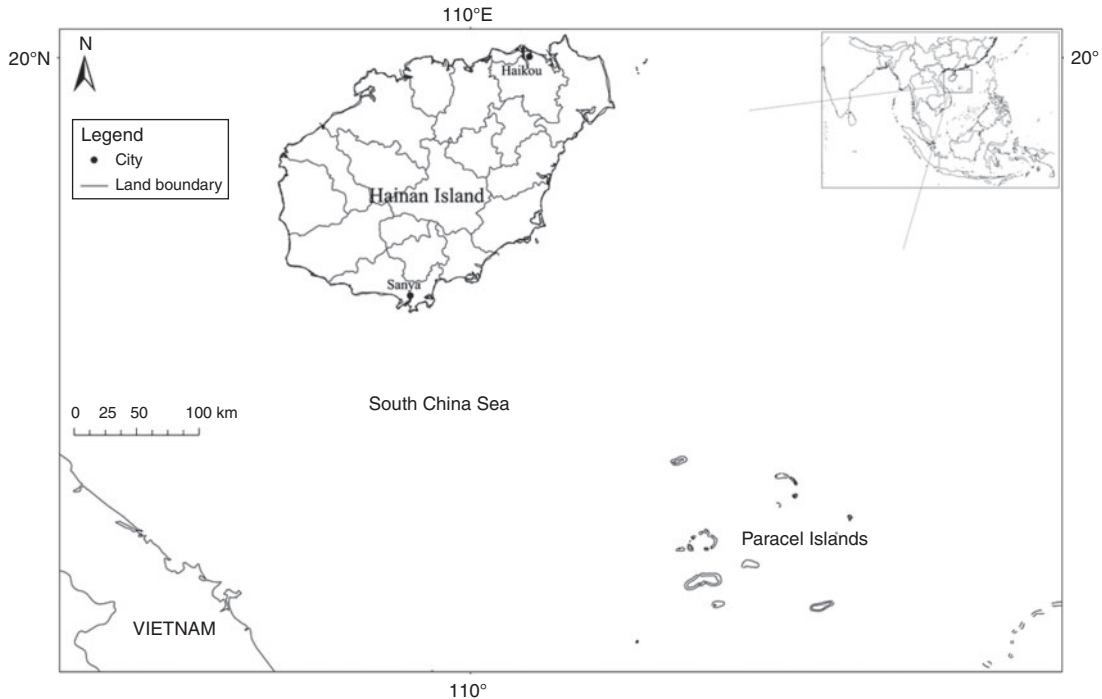


Fig. 1. Map of sample location in Hainan and the Paracel Islands.

with a 4.5-mm-diameter hole punch plier, placed into 70% ethanol, and stored at room temperature until DNA extraction. For some individuals, genetic samples were derived from blood samples taken from the dorsal cervical sinus with a 22-gauge needle (0.7-mm diameter, 30-mm length). DNA was extracted using a Qiagen DNeasy Blood & Tissue Extraction Kit (Qiagen, Valencia, CA, USA), following manufacturer's instructions. Primers and thermocycler conditions were the same as used in Dethmers *et al.* (2006). Samples were gel-checked using a 1% agarose gel to confirm amplification. Amplicons were purified and sequenced in both directions using BigDye on an ABI 3730XL sequencing system (Applied Biosystems, Foster, CA, USA).

Statistical analysis

All sequences were aligned and checked for quality using Sequencher 5.1 (Gene Codes Corporation, Ann Arbor, MI, USA). A Blast search was performed for identification of matches with existing mtDNA haplotypes or confirmation of novel haplotypes (the GenBank database; <http://blast.ncbi.nlm.nih.gov/Blast.cgi>, accessed 25 August 2020). Sequences were aligned to known green sea turtle haplotypes found in nesting grounds in Asia and Southeast Asia (Cheng *et al.* 2008; Dutton *et al.* 2014; Nishizawa *et al.* 2013; Hamabata *et al.* 2014; Read *et al.* 2015; Jensen *et al.* 2016a). Haplotypes were of various sizes and all were trimmed to match the 384-bp sequence of our data and this sequence length was used in all analyses. We used Arlequin ver. 3.5.2.1 (Excoffier and Lischer 2015) to determine nucleotide and haplotype diversity for our samples, using the model of Tamura and Nei (1993), and compared them to nesting grounds mentioned above, the confiscated samples from the

Table 1. Frequency of haplotypes from harvested Hainan green sea turtles and hatchlings from different nests in the Paracel Islands

MtDNA haplotype	<i>n</i>	Frequency (%)
Hainan	85	
CmP49.1 (C3)	10	11.8
CmP87.1 (C4)	2	2.4
CmP40.1 (C5)	2	2.4
CmP88.1 (C7)	1	1.2
CmP91.1 (C14)	6	8.2
CmP57.1 (D2)	20	23.5
CmP20.1 (A3)	1	1.2
CmP75.1	3	3.5
CmP104.1	1	1.2
CmP19	39	45.9
Paracel Islands	16	
CmP83.1 (C3)	4	25.0
CmP18	1	6.3
CmP19	10	62.5
CmP54	1	6.3

Mantanani Islands of Sabah, Malaysia (Joseph *et al.* 2014), and the foraging grounds at Brunei Bay (Joseph *et al.* 2016; Table 1). We compared genetic differentiation on the basis of pairwise F_{ST} , using exact tests (100 000 Markov-chain Monte Carlo (MCMC) chains) in Arlequin ver. 3.5.2.1 with a P -value set to 0.05 for significance.

Mixed-stock analysis

To determine the proportion of stock contributions to the Hainan green sea turtle samples, we used previously published

haplotype frequencies from Australasian nesting grounds (Appendix S1) and a Bayesian MSA implemented in the program Bayes (Pella and Masuda 2001). Two MSA approaches were used following Dethmers *et al.* (2010), with one analysis using uniform priors (UP) and one using informative priors (IP) weighted on the basis of source-population size. For both approaches, we estimated possible contributions for nesting rookeries. We ran 30 chains, one for each of the contributing stocks and 100 000 MCMC for every chain. For each chain in the UP analysis, a different stock was started at 95% contribution with a burn-in set to 50 000 to determine posterior probabilities. For each chain, the IP analysis of the percentage contribution of each stock was based on its estimated population size. The Gelman and Rubin shrink factor was used to check for convergence for each chain (Pella and Masuda 2001). If convergence was not met after 100 000 MCMCs, stock estimates with a shrink factor of >1.2 were not considered valid.

Results

Genetic diversity

Estimates of demographic data such as age, sex and body measurements were obtained for 24 individuals to represent all turtles sampled in the study. Body sizes ranged from 23.10 to 104.0 cm (mean = 61.1 cm, $\sigma = 25.0$ cm). These samples contained 14 juveniles, four subadults (1 male) and six adults (1 male, 4 females). MtDNA sequences of 384 bp were obtained from 84 samples, from which we identified 10 haplotypes from illegally traded green sea turtles sampled from Hainan and four haplotypes from the Paracel Islands (Table 1). The haplotype and nucleotide diversity indices for the Hainan samples were $h = 0.721 \pm 0.04$ and $\pi = 0.005 \pm 0.00$, and for the Paracel Islands, $h = 0.575 \pm 0.12$ and $\pi = 0.009 \pm 0.01$ (Table 2). Exact tests showed that Hainan samples were different from those from all rookeries and feeding grounds ($P = 0.00\text{--}0.046$). However, in the pairwise F_{ST} analysis, Hainan samples were significantly different from those of all other sites ($P = 0.00\text{--}0.01$) except the Paracel Islands ($P = 0.06$). Exact tests showed that the Paracel Islands were distinct from all other rookeries ($P = 0.00\text{--}0.00$), whereas F_{ST} values showed that the islands were not distinct from Peninsular Malaysia (0.072 ± 0.033) and Cocos (Keeling) Islands (0.180 ± 0.033).

Mixed-stock analysis

The MSA estimated that the Hainan samples comprised primarily two genetic stocks, with possible contributions from other stocks. (Table 3). Because of different factors, the MSA can result in large confidence intervals (CIs) that include zero, indicating that the suggested stock contributions are a more general estimate than an absolute one (Joseph *et al.* 2014; Jensen *et al.* 2016b). Our results showed large CIs for all but two rookeries. Rookeries with stock estimates of $<5\%$ showed large CIs and these intervals included zero. However, the Paracel Islands and Sulu Sea rookeries (Philippine and Malaysia Turtle Islands) contributed $>85\%$ of stock contribution to our samples, and these two sites showed smaller CIs that did not include zero, indicating a greater confidence in these estimates. The uniform and informative prior MSA yielded similar results for all rookeries. Mixed-stock analysis from the UP analysis showed major

stock contributions from the Paracel Islands (57.0%) and Sulu Sea (29.2%). Minor contributions were observed from Aru (4.6%), and West Java (2.1%). MSA results based on IP analysis showed major stock contributions from the Paracel Islands (56.9%) and Sulu Sea (29.3%). Minor contributions came from Aru (4.8%) and West Java (1.8%). All stock contributions had a shrink factor of less than 1.2. Results from both analyses showed that nesting sites from the Paracel Islands and the Sulu Sea comprise the majority of stock contributions in our samples (Table 3).

Discussion

Haplotype diversity in the illegally traded animals was relatively high (0.721 ± 0.04) when compared with rookeries in the western Pacific (mean 0.440 ± 0.250), with only western New Caledonia (0.820 ± 0.02) and eastern Borneo (0.764 ± 0.04) having higher haplotype diversity (Table 2). However, nucleotide diversity was relatively low in the illegally traded animals (0.005 ± 0.00) when compared with the average for all other rookeries (0.011 ± 0.010). The Hainan samples are distinct from all rookeries except for the Paracel Islands in the F_{ST} analysis. Our Paracel Islands sample size ($n = 16$) was relatively small compared with that in other rookeries in our analyses, but the results suggested a higher than average haplotype diversity (0.575 ± 0.12) and near-average nucleotide diversity (0.009 ± 0.01). Exact tests indicated that the Paracel Islands are distinct from all rookeries; however, according to our F_{ST} analysis, they are not distinct from peninsular Malaysia and Cocos (Keeling) Islands. Peninsular Malaysia shares both the CmP88.1 and CmP49.1 haplotypes, whereas, Cocos (Keeling) Islands shares only the CmP49.1 haplotype. Without any confirmed migrations via telemetry or tags, it is not possible to confirm whether gene flow is occurring between the Paracel Islands and these two rookeries; however, these data suggest it could be a possibility. Further work needs to be undertaken in tracking of turtles in these areas, so as to elucidate potential migratory connections.

Ten previously described mtDNA control-region haplotypes were identified from the Hainan samples, and four haplotypes from the Paracel Islands samples (Cheng *et al.* 2008; Nishizawa *et al.* 2013; Jensen *et al.* 2016a) from this study (Table 1). Of these haplotypes, the most common ones from our samples were CmP49.1, CmP57.1, CmP91.1 and CmP19. Haplotype CmP49.1 (Jensen *et al.* 2016a) is widespread in many nesting and foraging grounds in Asian waters. The CmP57.1 (Jensen *et al.* 2016a) haplotype, which comprises over 30% of the MSA stock contributions, is also found commonly in the Sulu and Celebes Sea. Haplotype CmP91.1 (Jensen *et al.* 2016a) is most commonly found in the Aru and Vanuatu Islands and less frequently in the Celebes Sea; however, it is likely that the Celebes Sea is the source for these haplotypes in the Hainan samples because of its proximity. In previous studies, outside of turtles collected from Hainan, Haplotype CmP19 was previously found in only 10 individuals, namely in one from a nesting rookery on Wan'an Island, Taiwan (Cheng *et al.* 2008), two from a foraging ground near Yaeyama Island, Japan (Nishizawa *et al.* 2013), one from a rookery in the Gulf of Carpentaria, one from a feeding aggregate at Howick Group in northern Australia

Table 2. Genetic diversity of green sea turtle samples from Hainan compared with nesting sites in western Pacific

Region	Nesting or feeding grounds	Haplotypes	Haplotype diversity (<i>h</i>) ± s.d.	Nucleotide diversity (π) ± s.d.	Sample size
Hainan		10	0.721 ± 0.04	0.005 ± 0.00	85
South-west Pacific Ocean	Northern Great Barrier Reef ^A	12	0.632 ± 0.06	0.012 ± 0.00	81
	Coral Sea ^A	9	0.480 ± 0.05	0.023 ± 0.01	97
	Southern Great Barrier Reef ^A	3	0.164 ± 0.05	0.009 ± 0.01	102
	Western New Caledonia ^A	11	0.817 ± 0.02	0.031 ± 0.02	64
	Vanuatu ^A	3	0.497 ± 0.09	0.021 ± 0.01	31
	Marshall Islands ^A	6	0.460 ± 0.05	0.026 ± 0.01	128
	American Samoa ^A	3	0.559 ± 0.08	0.026 ± 0.01	17
	French Polynesia ^A	2	0.222 ± 0.17	0.000 ± 0.00	9
North-west Pacific Ocean	Northern New Guinea ^A	3	0.216 ± 0.12	0.012 ± 0.01	18
	Micronesia ^A	8	0.621 ± 0.02	0.035 ± 0.02	538
	Palau ^A	2	0.056 ± 0.05	0.002 ± 0.00	36
	Commonwealth of Northern Mariana Islands/ Guam ^A	2	0.042 ± 0.04	0.000 ± 0.00	47
South China Sea	Peninsular Malaysia ^A	8	0.645 ± 0.09	0.008 ± 0.00	29
	Western Borneo ^A	3	0.450 ± 0.11	0.009 ± 0.01	22
	Paracel Islands	4	0.575 ± 0.12	0.009 ± 0.01	16
Sulu Sea	Sulu Sea ^A	3	0.323 ± 0.07	0.001 ± 0.00	62
Celebes Sea	Eastern ^A Borneo	5	0.763 ± 0.04	0.007 ± 0.00	29
	North-eastern Borneo ^A	7	0.633 ± 0.04	0.004 ± 0.00	92
Arafura Sea	Aru ^A	2	0.071 ± 0.07	0.004 ± 0.00	28
	Gulf of Carpentaria ^A	7	0.659 ± 0.05	0.011 ± 0.01	50
	Cobourg Peninsula ^A	5	0.573 ± 0.08	0.002 ± 0.00	37
Timor Sea	Ashmore Reef ^A	5	0.632 ± 0.04	0.005 ± 0.00	44
	Scott/Browse Reef ^A	4	0.510 ± 0.06	0.001 ± 0.00	65
East Indian Ocean	West Java ^A	3	0.515 ± 0.08	0.001 ± 0.00	22
	North-west Shelf ^A	7	0.418 ± 0.07	0.001 ± 0.00	77
	Cocos 'Keeling' Island ^A	2	0.199 ± 0.11	0.007 ± 0.01	19
Japan	Ogasawara ^B	13	0.706 ± 0.04	0.016 ± 0.01	103
Taiwan	Wanan ^C	3	0.483 ± 0.06	0.028 ± 0.01	40
	Lanyu ^C	1	0.000 ± 0.00	0.0000 ± 0.00	14
Non-nesting	–	6	0.847 ± 0.04	0.018 ± 0.01	20
	–	10	0.812 ± 0.04	0.012 ± 0.01	42

^AJensen *et al.* (2016a).^BNishizawa *et al.* (2011).^CCheng *et al.* (2008).^DJoseph *et al.* (2014) (Mantanani confiscation).^EJoseph *et al.* (2016) (a feeding ground at Brunei Bay).

(Jensen *et al.* 2016a) and five from the Layang/Mantanani feeding grounds (Jensen *et al.* 2016b). While it may not be common in other rookeries and foraging grounds, it appears to be a common haplotype collected by Hainan fishermen. Not only did CmP19 comprise 45.90% of our samples, but the CmC2 haplotype found in Yang *et al.* (2015) is a 100% sequence match to the longer CmP19 haplotype and comprises 71% of their 89 samples. We found that 62.5% of the hatchlings from the Paracel Islands contained the CmP19 haplotype, implying the Paracel Islands are the likely source rookery for this haplotype. From the MSAs, it appears that the collection of green sea turtles by Hainan fishermen might have strong impact on the rookeries of the Paracel Islands and the Sulu Sea. While Yang *et al.* (2015) did not use MSA to determine stock contributions of their Hainan samples, the other haplotypes from their study are most commonly found in Peninsular Malaysia and western Borneo

(CmP82.1) and the Sulu Sea and Celebes Sea (CmP57.1), suggesting that the samples from Yang *et al.* (2015) were likely to have originated from the same regions as our samples.

Previously, Chinese vessels have been seized in the Sulu and Celebes Sea for illegally harvesting green and hawksbill turtles (Pilcher *et al.* 2008; S. Schoppe, and R. A. S. Antonia, unpubl. report, 2009, 'Marine turtle trade in the Philippines') and Hainan fishermen, who admitted of turtle poaching in the Coral Triangle (Lam *et al.* 2011), have been arrested. In addition, Joseph *et al.* (2014) used MSA to determine the possible origins of a subset of the green turtle carcasses from the 2007 Mantanani poaching incident. Their results showed that the majority of stock contributions were from the Sulu Sea (24.3% UP; 12.7% IP), Gulf of Carpentaria (23.1% UP; 16.3% IP) and Aru Island (24.9% UP; 10.7% IP) in the Arafura Sea, and Berau Islands (9.7% UP; 52.3% IP) in the Celebes Sea.

Table 3. Estimated mixed-stock contributions from regions and rookeries on the basis of uniform-prior and informative-prior mixed-stock analysis

Region	Rookery	Uniform prior				Informative prior			
		Mean	2.50%	Median	97.50%	Mean	2.50%	Median	97.50%
South-west Pacific Ocean	Northern Great Barrier Reef	0.04	0.00	0.00	0.49	0.04	0.00	0.00	0.49
	Coral Sea	0.04	0.00	0.00	0.46	0.04	0.00	0.00	0.44
	Southern Great Barrier Reef	0.04	0.00	0.00	0.50	0.04	0.00	0.00	0.47
	Western New Caledonia	0.04	0.00	0.00	0.46	0.04	0.00	0.00	0.49
	Vanuatu	1.02	0.00	0.00	9.81	0.93	0.00	0.00	9.53
	Marshall	0.08	0.00	0.00	1.00	0.08	0.00	0.00	1.01
	American Samoa	0.04	0.00	0.00	0.45	0.04	0.00	0.00	0.47
	French Polynesia	0.04	0.00	0.00	0.51	0.04	0.00	0.00	0.51
North-west Pacific Ocean	Western New Guinea	0.74	0.00	0.00	5.04	0.77	0.00	0.00	5.09
	Micronesia	0.08	0.00	0.00	0.97	0.08	0.00	0.00	0.96
	Palau	0.10	0.00	0.00	1.33	0.10	0.00	0.00	1.29
	Commonwealth of Northern Mariana Islands/Guam	0.10	0.00	0.00	1.27	0.10	0.00	0.00	1.28
South China Sea	Peninsular Malaysia	1.25	0.00	0.00	10.14	1.25	0.00	0.00	10.20
	Western Borneo	1.67	0.00	0.87	7.16	1.58	0.00	0.66	7.06
	Paracel Islands	57.02	43.64	56.87	71.05	56.91	43.56	56.78	70.81
Sulu Sea	Sulu Sea	29.16	15.55	29.34	41.82	29.30	15.91	29.43	42.00
Celebes Sea	Eastern Borneo	1.66	0.00	0.00	17.10	1.64	0.00	0.00	16.81
	North-eastern Borneo	0.63	0.00	0.00	7.90	0.59	0.00	0.00	7.53
Arafura Sea	Aru	4.60	0.00	4.57	13.46	4.81	0.00	4.89	13.53
	Gulf of Carpentaria	0.06	0.00	0.00	0.73	0.06	0.00	0.00	0.72
	Cobourg Peninsula	0.06	0.00	0.00	0.64	0.06	0.00	0.00	0.63
Timor Sea	Ashmore Reef	0.57	0.00	0.00	5.50	0.56	0.00	0.00	5.41
	Scott/Browse	0.10	0.00	0.00	1.15	0.10	0.00	0.00	1.16
East Indian Ocean	West Java	2.07	0.00	0.00	19.67	1.84	0.00	0.00	19.76
	North-west Shelf	0.12	0.00	0.00	1.38	0.14	0.00	0.00	1.58
	Cocos 'Keeling' Islands	0.13	0.00	0.00	1.55	0.13	0.00	0.00	1.58
Japan	Ogasawara	0.04	0.00	0.00	0.47	0.04	0.00	0.00	0.49
Taiwan	Wanan	0.04	0.00	0.00	0.49	0.04	0.00	0.00	0.50
	Lanyu	0.16	0.00	0.00	1.96	0.16	0.00	0.00	1.89

Joseph *et al.* (2014) urged for more studies to be conducted on green turtle nesting/foraging sites in these understudied areas, so as to fill in knowledge gaps, and we strongly agree with this sentiment. Prior to the present study, the origin of the CmP19 haplotype was unknown, and we were able to identify the source rookery only after sampling a previously unstudied site, the Paracel Islands. By identifying this unique population, we were not only able to determine the rookery being affected by Hainan fishermen, but also begin to construct appropriate conservation plans to protect this unique rookery.

Conservation implications

Green sea turtles that travel across international jurisdictions are vulnerable to poaching in areas that are distant from their foraging or nesting grounds (Joseph *et al.* 2014). Therefore, multinational cooperation is needed to properly protect green sea turtles. Currently, in the Asia Pacific region, there is only one such agreement in place between the governments of the Philippines and Malaysia, called the Turtle Islands Heritage Protection Area (TIHPA). This agreement covers areas of the Sulu archipelago between the Philippines and Sabah, Malaysia, and is part of the Coral Triangle, which is not only home to the most biodiverse marine region on the planet (Carpenter *et al.* 2011), but also is home to the highest concentrations of green and hawksbill sea turtles (Lam *et al.* 2011).

From our results, we determined that roughly 30% of the green turtles collected by Hainan fishermen are likely to be coming from the TIHPA area (Fig. 2). However, what we cannot determine is whether the fishermen are directly collecting from this area, or whether they are collecting from a highly diverse foraging ground near the Paracel Islands. We sampled only hatchlings for our study, but larger green turtles have been spotted feeding near the islands (H. B. Huang, pers. comm.). Genetic sampling of foraging turtles is needed to determine whether animals from the TIHPA area are foraging around the Paracel Islands. However, fishermen from Hainan were found collecting directly from the Mantanani foraging grounds, and Jensen *et al.* (2016b) determined that most juveniles from this foraging ground originate from north-western Borneo, north-eastern Borneo (Sulu Sea) and Peninsular Malaysia. Their green sea turtle samples contained 5.6% (5/90) of the most common haplotype in the Paracel Islands, namely CmP19, and a *post hoc* MSA analysis attributed roughly 8.5% stock contribution to the Paracel Islands, suggesting that there is potential migration between these two areas. Regardless of whether Hainan fishermen are directly poaching from the TIHPA area or collecting turtles from a foraging ground, it shows that these rookeries are threatened by illegal collection. Collection of green sea turtles by Hainan fishermen could potentially be affecting rookeries from a greater distance than our data show. Kolinski *et al.* (2014)

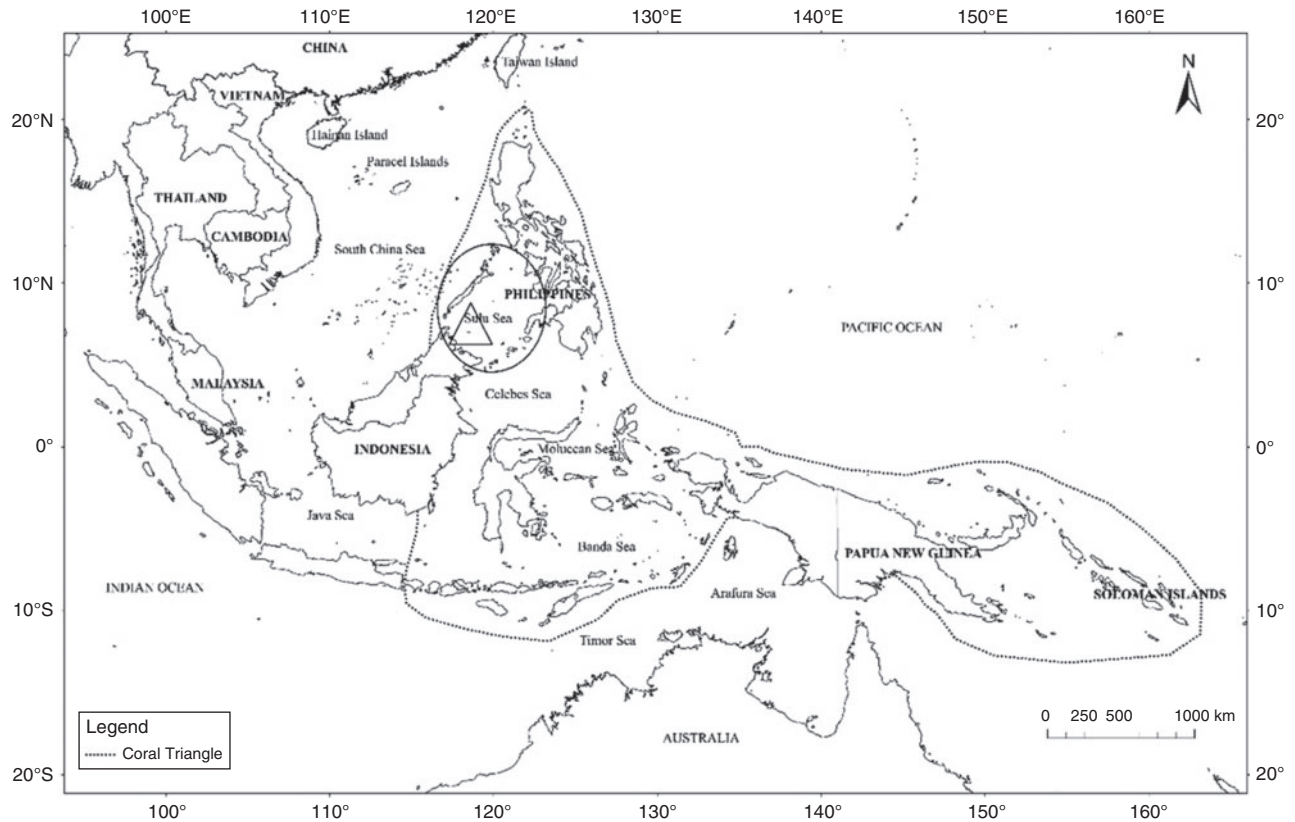


Fig. 2. Map of the Coral Triangle region, with the Sulu Sea (circle) and the Turtle Island Heritage Protection Area (triangle) being highlighted.

tracked one green sea turtle that travelled between Hainan and the Parcel Islands during its migration from Gielop Island in Yap State of Micronesia to Peninsular Malaysia, and other green sea turtles in their study migrated to the Sulu Sea.

The high levels of green sea turtle poaching from the Coral Triangle have already caused local population declines (WWF 2011) and could cause local extirpations without conservation intervention. In addition to the Coral Triangle, fishermen from Hainan are likely to be harvesting green sea turtles from the Parcel Islands as the CmP19 haplotype made up 45.9% of our samples and ~71% of samples in Yang *et al.* (2015). Lam *et al.* (2011) found that catches from Hainan made up 34% (659 specimens) of all sea turtle confiscations in China over a 10-year period and Hainan fishermen were seized multiple times in international waters with hundreds of sea turtles. This rate of harvesting seems unsustainable and urgent action is needed to develop conservation action plans to protect this unique population in the Parcel Islands. As the largest and most important nesting habitat of green sea turtles in the northern portion of the South China Sea, the Parcel Islands harbour a unique haplotype that is rare outside of the islands, suggesting that the population is somewhat isolated from other rookeries and foraging grounds. To protect this unique population, management agencies should establish a nature reserve for this sea turtle population to prevent coastal development at nesting beaches, and deploy a special law-enforcement team to provide protection, especially during nesting seasons.

Conflicts of interest

The authors declare no conflicts of interests.

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