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RESEARCH ARTICLE

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Variations in body condition of green turtles (*Chelonia mydas*) in two nearby foraging grounds indicate their sensitivity to foraging habitats

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Abstract

1. Coastal seagrass habitats are critical foraging grounds for endangered green turtles (*Chelonia mydas*). However, these habitats are vulnerable to anthropogenic effects, potentially leading to their degradation with consequent impacts on the health status of foraging green turtles.
2. Two foraging habitats of green turtles in Tun Mustapha Park, Sabah, Malaysia were surveyed: Kudat Mainland and Balambangan Island, by capturing green turtles and evaluating their physical body condition as well as assessing seagrass cover.
3. Despite having similar genetic compositions, the Kudat Mainland aggregation had significantly higher body size (curved carapace length: 61.7 ± 14.5 cm, body weight: 30.0 ± 22.2 kg), Fulton's body condition index (BCI: 1.49 ± 0.13), barnacle (*Chelonibia testudinaria*) occurrence (78.8%) and barnacle abundance (5.46 ± 9.90 barnacles/turtle) than the Balambangan Island aggregation (curved carapace length: 51.6 ± 8.1 cm, body weight: 17.3 ± 7.7 kg, BCI: 1.40 ± 0.09, barnacle occurrence: 31.0%, barnacle abundance: 0.50 ± 0.92 barnacles/turtle). The differences in BCI between the nearby aggregations could not be attributed to size and barnacle occurrence differences, suggesting the foraging habitat is the primary factor affecting the body condition of green turtles.
4. Seagrass cover at Kudat Mainland was only slightly higher than at Balambangan Island. These findings suggest that the body condition of green turtles is potentially sensitive to the quality of foraging habitats such as nutrients and water quality.
5. It is crucial to monitor the health of foraging habitats and their impact on the body condition of turtles. It is recommended that habitat-turtle dynamics are given conservation priority, in parallel to water quality monitoring – with action taken to reduce pollution if necessary. A holistic approach to turtle conservation is therefore required.

KEYWORDS

barnacle, body condition index, natal origin, sea turtle, seagrass, South-East Asia

1 | INTRODUCTION

Coastal ecosystems, such as coral reefs and seagrass beds, play a crucial role in generating biological productivity and biodiversity (Barbier et al., 2011). However, these habitats are vulnerable to anthropogenic effects (He & Silliman, 2019), and even nearby sites can exhibit differences in the structural complexity and community structure of organisms (Henseler et al., 2019). Given the concerns about the negative effects of anthropogenic stressors on wildlife health (Kophamel et al., 2022), such assessments in coastal ecosystems provide baseline information. The health assessments for endangered species are especially important for the management of conservation threats (Kophamel et al., 2022).

Green turtles (*Chelonia mydas*) are herbivorous marine reptiles that primarily feed on seagrass and macroalgae (Esteban et al., 2020). After being recruited to coastal areas as juveniles, green turtles use various coastal habitats as foraging grounds and exhibit varying diets (Hancock et al., 2018). Some green turtle populations have shown an increasing trend in abundance (Mazaris et al., 2018) – resulting in the overgrazing of seagrass beds (Christianen et al., 2021) – but the species is still globally endangered (Seminoff, 2004). In South-East Asia, illegal turtle harvesting remains a significant conservation issue (Joseph et al., 2019; Jeethvendra et al., 2023). The prevalence of fibropapillomatosis in foraging habitats that may be linked to anthropogenic activities has also become a major threat to green turtles (Adnyana, Ladds & Blair, 1997; Loganathan, Palaniappan & Subbiah, 2021). Further, despite continued debate about their effect on turtle health, the attachment of a relatively large number of barnacles is also reported (Lim, Syed Hussein & Palaniappan, 2020). Nevertheless, sea turtles exhibit different body conditions within nearby sites (Diez & van Dam, 2002; Lamont & Johnson, 2021), probably due to differences in the quality and availability of food and anthropogenic disturbances in coastal habitats. Therefore, establishing a health status baseline for green turtle foraging aggregations in South-East Asia is essential for understanding the characteristics of these habitats and their relationship to turtle health.

The objectives of this study were to characterize and compare the body condition of green turtle foraging aggregations in Tun Mustapha Park (TMP), Sabah, Malaysia. Body condition is an indicator of nutritional and health status (Stevensen & Woods, 2006), providing baseline information for wildlife health status. Body condition index (BCI), attachment of barnacles, injuries and tumours were evaluated. Body size composition, genetic composition and seagrass cover were also evaluated as factors possibly influencing body condition. The park was established as a multiple-use marine park in 2016, with observations of nesting and foraging sea turtles (Jumin et al., 2018; Lim et al., 2021; Jolis et al., 2023). However, no quantitative survey on foraging aggregations has yet been conducted. This study investigated multiple foraging aggregations within nearby coastal habitats, providing information for evaluating green turtle habitats and their associated health status. This study contributes to the description of the bio-physical features of foraging habitats and the health status of immature green turtles that have been globally prioritized (Wildermann et al., 2018).

2 | METHODS

2.1 | Fieldwork and sample collection

The TMP (7°1′3.09″ N, 117°2′37.21″ E) is the second-largest marine park in Malaysia (898,762.76 ha of marine area) and consists of the Kudat, Pitas and Kota Marudu districts (Sabah Parks, 2017). Kudat Mainland and Balambangan Island were surveyed as potential sites for green turtles in TMP (Figure 1), based on input from local communities, government agencies, environmental organizations, tourism operators, and published and unpublished literature. These sites are designated as Community-Use and Preservation Zones within the park (Sabah Parks, 2017). Sampling was conducted at three nearby sites on Kudat Mainland (Kelambu Island, Kimihang Beach and Lampu Island) and one site on Balambangan Island. Kudat Mainland is an inhabited area, but Balambangan Island is uninhabited, with a small river flowing from the north of the island.

Fieldwork was conducted over a period of 23 days in 2019 (April, June, August, September, October and November) and in 2020 (February, March and August; Table 1) to capture sea turtles using the netting technique, as described by Eaton et al. (2008). Turtles in the water were searched for using visual observation from a boat, and then surrounded with drift nets (600 m in length with a 6-inch mesh size). Each net deployment generally took less than 1 h. The sampling at Kudat Mainland was primarily conducted from August to November due to logistical constraints, while sampling at Balambangan Island was primarily conducted from February to April (Table 1). To capture the sea turtles trapped in the net, two free divers grasped the turtles' nuchal and posterior marginal scutes and slowly ascended to the surface. The captured turtles were carefully lifted onto the research boat and transported to a nearby beach.

The captured sea turtles were identified to species and measured for standard notch-to-tip curved carapace length (CCL), curved carapace width (CCW), straight carapace length (SCL) and body weight (BW). Measurements of CCL and CCW were taken using a 1.5-m plastic measuring tape with an accuracy of ±0.5 mm. SCL and BW were measured using a 1.0-m Mitutoyo stainless steel Vernier caliper with an accuracy of ±0.15 mm and an electronic scale with an accuracy of ±0.1 kg, respectively. Large barnacles on the carapace that could interfere with the CCL, SCL and CCW measurements were removed. Based on their CCL, captured turtles were categorized as juveniles (<65.0 cm CCL), sub-adults (65.0–85.0 cm CCL) and adults (>85.0 cm CCL) (Bell et al., 2019).

Each turtle was thoroughly examined for pre-existing flipper tags. In cases where no tags were found, at least one metal Inconel tag (Style 681, National Band and Tag Company, Newport, Kentucky, USA) bearing the code MY(S) was applied proximal to and adjacent to the first large scale on the posterior edge of both front flippers. The examination also included checking for fibropapilloma tumours, epibiont load, missing or damaged limbs, and skin and carapace abnormalities. Any barnacles with a diameter of ≥5 mm found on the turtles' heads, carapace or plastron (Figure 2) were gently removed using a scraper following Lim, Syed Hussein & Palaniappan (2020).

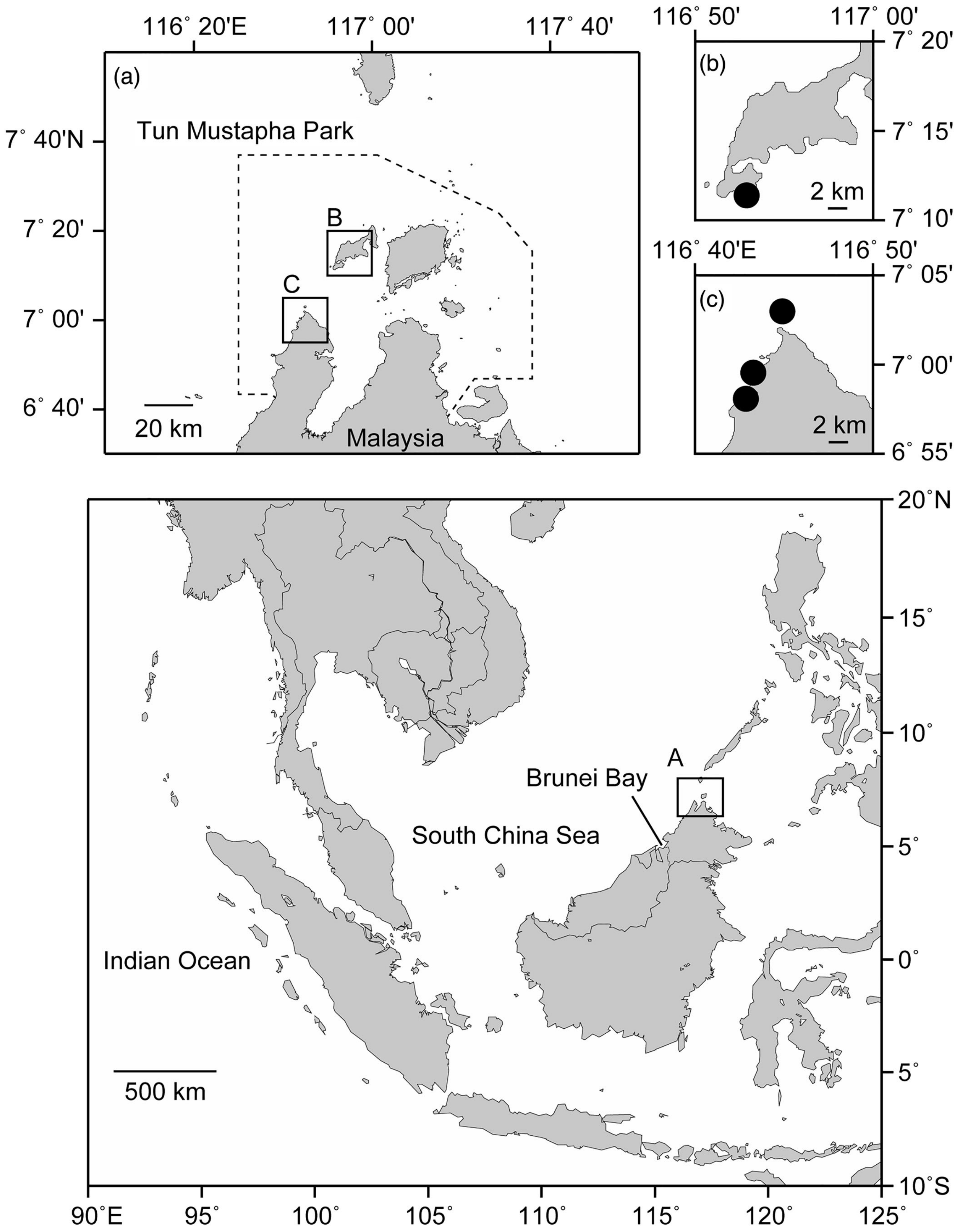

FIGURE 1 Geographic locations of (a) Tun Mustapha Park in Sabah, Malaysia, and sampling sites (circles) in (b) Balambangan Island and (c) Kudat Mainland, Lampu Island (north), Kelambu Island (middle) and Kimihang Beach (south).

TABLE 1 Summary of survey schedule in Balambangan Island and Kudat Mainland.

Year	Date	Sites
2019	5–6 April	Balambangan and Kudat Mainland
	15 June	Kudat Mainland
	15–16 August	Kudat Mainland
	28–30 September	Kudat Mainland
	18, 30–31 October	Kudat Mainland
	1–3 November	Kudat Mainland
2020	5–7 February	Balambangan
	11–13 March	Kudat Mainland
	14–16 August	Kudat Mainland

FIGURE 2 Barnacles attached to plastron of a green turtle.

Barnacles found elsewhere on the sea turtles (i.e., flippers and tails) were not included in this study. The barnacles were collected and stored in small plastic bottles and were later identified at the Borneo Marine Research Institute, Universiti Malaysia Sabah laboratory to the lowest taxonomic level, according to Monroe (1981). Head, carapace, plastron, tail and flippers of all turtles were photographed to document any injuries or abnormalities.

Blood samples were collected from the dorsal cervical sinus (Joseph et al., 2016) and preserved in lysis buffer at a 1:10 ratio of blood to buffer (Dutton, 1996; Joseph et al., 2016). All turtles were released immediately after measurements and sampling were completed to ensure ethical and responsible handling of the turtles. The sampling of sea turtles complied with the ethical guidelines and conduct under the Sabah Biodiversity Centre Access Licence JKM/MBS.1000-2/13 JLD.1 (27) and Sabah Parks Permit TTS/IP/100-6/2 Jld. 11 (119).

In February and March 2020, seagrass beds were surveyed in Kelambu Island, Kimihang Beach and Balambangan Island to estimate seagrass species diversity and coverage, following the Seagrass-Watch method (McKenzie, Campbell & Roder, 2003). Three fixed transects were established at each site, with a 25 m interval between transects. The transect line extended from the highest to the lowest zone of the seagrass meadow, running perpendicularly from the beach to the subtidal zone. A 1-m^2 quadrat was laid at 5-m intervals along each transect, for a total of 10 quadrats per transect. Seagrass cover within the quadrat was visually estimated using the percentage cover photo standards. Seagrass species were identified using taxonomic keys. Lampu Island, characterized by coral reefs and rocky shores, was not surveyed for seagrass.

2.2 | Laboratory analysis

Genomic DNA was extracted from blood samples using the Vivantis GF-1 Tissue Blood Combi DNA Extraction kit (Vivantis Technologies, Malaysia) with minor modifications for sea turtle blood samples. The 800-bp variable control region of mitochondrial DNA (mtDNA) was amplified using primers LCM15382 and H950g (Abreu-Grobois et al., 2006). Polymerase chain reaction (PCR) amplification was performed using the Applied Biosystem Thermal Cycler PCR. Amplification reactions were conducted in a 50-μL total reaction volume containing 25–50 ng sea turtle genomic DNA, 1 U/50 μL Taq polymerase (Vivantis Technologies, Malaysia), 10 mM TBE buffer, 2.5 mM magnesium chloride $MgCl_2$, 0.125 mM deoxynucleotide triphosphates (dNTPs) and 0.2 μM of each primer. The cycling parameters consisted of an initial denaturation at 94°C for 3 min, followed by 30 cycles of 30-s denaturation at 94°C, annealing at 55°C for 30 s and extension at 72°C for 60 s, followed by a final elongation step at 72°C for 3 min. Amplified samples were verified by 1% agarose gel electrophoresis for the targeted band size (Bruford et al., 1992). Genetic analyses were conducted at the Genetics Laboratory of the Borneo Marine Research Institute, Universiti Malaysia Sabah. The PCR products were outsourced to NextGene (Kuala Lumpur, Malaysia) for purification and sequencing for both strands.

Sequences were read and checked using Chromas ver 2.6.6 (Chromas, Technelysium Pty Ltd.), and multiple sequence alignments were performed using the Molecular Evolutionary Genetics Analysis (MEGA) Software ver 11 (Tamura, Stecher & Kumar, 2021). Haplotypes were identified by searching a collated database of known green turtle haplotypes such as the Southwest Fisheries Science Center, NOAA Fisheries Service (https://swfsc.noaa.gov) for the mtDNA sequences published for the Pacific and Indian Ocean green turtles. The GenBank database (National Center for Biotechnology Information, USA: NCBI website http://www.ncbi.nlm.nih.gov) was also consulted for control region sequence comparisons.

2.3 | Data analysis

Statistical analyses were performed using R ver 4.1.3 (R Core Team, 2022). Differences in CCL, CCW and BW between Balambangan Island and Kudat Mainland were tested by Wilcoxon rank sum tests using the rstatix package (Kassambara, 2021) since the normality of data was not supported. The difference in the occurrence of barnacles (ratio of sea turtles with barnacles) between Balambangan Island and Kudat Mainland was tested by the chi-square test. The abundance of barnacles (number of barnacles attached to individual turtles) was tested by a likelihood ratio test after negative binomial generalized linear modelling that incorporated the site (Balambangan Island or Kudat Mainland) and CCL as explanatory variables using MASS package (Venables & Ripley, 2002).

The body condition index (BCI) based on Fulton's K (BCI = [BW (kg) / SCL (cm)^3] × 10,000; Ricker, 1975; Bjorndal, Bolten & Chaloupka, 2000) was calculated to evaluate the relative 'fatness' of each captured turtle. The difference in BCI values between Balambangan Island and Kudat Mainland were tested using linear modelling. The occurrence of barnacles *Chelonibia testudinaria* was found to differ between the two sites (see Section 3); therefore, the presence or absence of *C. testudinaria* and its interaction with sites and CCL were included as explanatory variables in the modelling.

The frequencies of haplotypes in the Kudat Mainland and Balambangan aggregations were compared using exact tests (50,000 iterations in a Markov chain with a 10,000-iteration dememorization) implemented in Arlequin ver. 3.5 (Excoffier & Lischer, 2010). The haplotype frequencies were also compared to those reported from the South China Sea, Brunei Bay aggregation (Joseph et al., 2016; Nishizawa et al., 2018), Mantanani aggregation (Jensen, Pilcher & FitzSimmons, 2016) and Pulau Tiga carcasses (Joseph et al., 2019). Since the haplotype frequency did not differ significantly between Kudat and Balambangan aggregations (see Section 3), the data were combined. The natal origin was estimated using Bayesian mixed stock analysis with the BAYES software (Pella & Masuda, 2001). The analysis settings followed those of Nishizawa et al. (2018) (see Appendix S1 for details).

3 | RESULTS

3.1 | Foraging aggregations and body size composition

Foraging grounds of sea turtles were successfully identified in two locations within the TMP: Balambangan Island and Kudat Mainland. A total of 42 and 53 individual turtles were captured in Balambangan Island and Kudat Mainland, respectively. Among the captured turtles, all were green turtles except for one hawksbill turtle (*Eretmochelys imbricata*) at Kudat Mainland, which was not considered in further analyses.

Among the three sampling areas for seagrass assessment, Kimihang Beach showed the highest overall percentage coverage (14.1%), comprising two species: *Halodule pinifolia* (9.3%) and *Halophila ovalis* (4.8%). The second highest coverage was observed at Balambangan Island (8.8%), comprising one species: *H. pinifolia*. The lowest coverage was observed at Kelambu Island (4.6%), also comprising of only *H. pinifolia*. The water depth range at Balambangan Island and Kelambu Island was 2–3 m, whereas at Kimihang Beach it was 1–3 m.

Green turtles larger than 66.5 cm CCL and 64.0 cm CCW were observed only in the Kudat Mainland aggregation (Table 2). As a result, the green turtles in the Kudat Mainland aggregation were significantly larger than those in the Balambangan aggregation (Wilcoxon rank sum test; CCL: W = 581, p = 0.0001; CCW: W = 601, p = 0.0002), and significantly heavier (Wilcoxon rank sum test, W = 577.5, p = 0.0002). In Balambangan, two (4.76%) green turtles were categorized as subadults, and 40 (95.24%) were assigned as juveniles. In Kudat Mainland, four (7.69%), 12 (23.08%) and 36 green turtles (69.23%) were assigned as adults, subadults and juveniles, respectively (Figure 3).

TABLE 2 Summary of green turtle foraging aggregations in Balambangan Island and Kudat Mainland.

	Balambangan Island	Kudat Mainland
CCL (cm)	51.6 (36.0–66.5, n = 42)	61.7 (37.9–105.5, n = 52)
CCW (cm)	46.7 (31.3–64.0, n = 42)	55.4 (33.5–91.5, n = 52)
BW (kg)	17.3 (5.7–35.8, n = 41)	30.0 (6.5–127.0, n = 51)
Occurrence of *Chelonibia testudinaria*	31.0% (n = 13 out of 42)	78.8% (n = 41 out of 52) 81.1% (n = 30 out of 37)
Abundance of *C. testudinaria*	0.50 ± 0.92 barnacles (n = 42)	5.46 ± 9.90 barnacles (n = 52) 4.43 ± 8.44 barnacles (n = 37)
Occurrence of *Stomatolepas transversa*	88.1% (n = 37 out of 42)	71.2% (n = 37 out of 52) 70.3% (n = 26 out of 37)
Abundance of *S. transversa*	3.74 ± 2.92 barnacles (n = 42)	3.83 ± 3.71 barnacles (n = 52) 3.38 ± 3.13 barnacles (n = 37)
BCI	1.40 ± 0.09 (n = 41)	1.49 ± 0.13 (n = 51) 1.48 ± 0.13 (n = 37)

Note: CCL, CCW and BW are shown as mean (range), while the other variables, except the occurrence of barnacles, are shown as mean ± standard deviation (SD). The second lines of Kudat Mainland aggregation indicate mean ± SD of green turtles ≤66.5 cm CCL. Abbreviations: BCI, body condition index; BW, body weight; CCL, curved carapace length; CCW, curved carapace width.

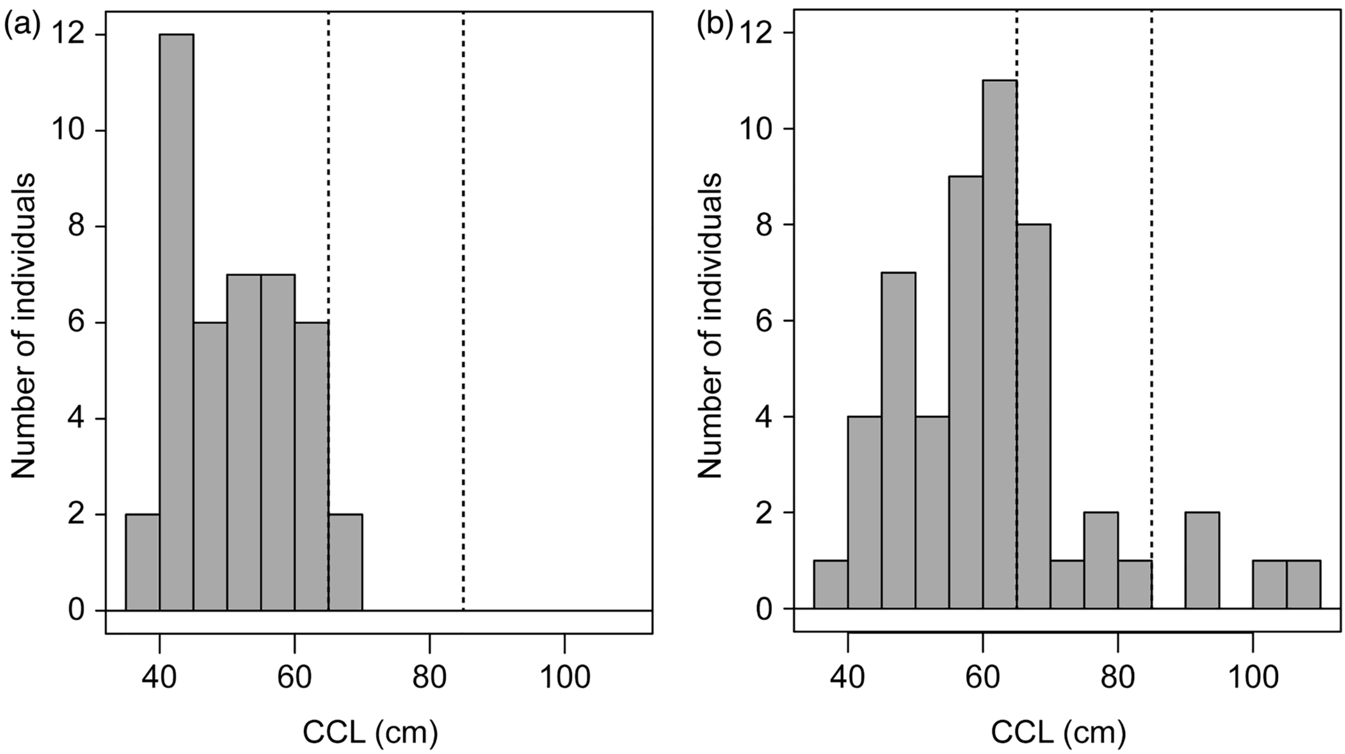

FIGURE 3 Histogram of standard curved carapace length (CCL) of (a) Balambangan Island and (b) Kudat Mainland aggregations of green turtles. Dotted lines indicate 65 and 85 cm that were used for categorizing juveniles, subadults and adults.

3.2 | Body condition

Two of the captured green turtles were observed to have healed minor injuries, one on a right front flipper and the other on the carapace. None of the turtles showed evidence of serious injuries or tumours. Three species of barnacles attached to green turtles were identified: *C. testudinaria*, *Stomatolepas transversa* and *Platylepas haexastylos*. The latter was not considered in any further analyses because it was observed only on two green turtles.

The occurrence of *C. testudinaria* was significantly different between Balambangan and Kudat Mainland (chi-square test, $\chi^2 = 19.886$, df $= 1$, $p < 0.001$; Table 2), whereas that of *S. transversa* was not significantly different ($\chi^2 = 3.034$, df $= 1$, $p = 0.08$; Table 2). The abundance of *C. testudinaria* was also significantly higher in Kudat Mainland than in Balambangan (likelihood ratio test, $\chi^2 = 29.044$, df $= 1$, $p < 0.001$; Table 2), but the abundance of *S. transversa* was not significantly different ($\chi^2 = 0.051$, df $= 1$, $p = 0.821$; Table 2). The effect of CCL on abundance was not significant either in *C. testudinaria* ($\chi^2 = 3.437$, df $= 1$, $p = 0.064$) or *S. transversa* ($\chi^2 = 0.078$, df $= 1$, $p = 0.780$).

The Fulton's BCI values of Balambangan Island and Kudat Mainland were 1.40 ± 0.09 and 1.49 ± 0.13, respectively. Kudat Mainland had a significantly higher BCI than Balambangan (df $= 1$, F $= 10.46$, $p = 0.002$; Table 2), while the effects of CCL or *C. testudinaria* were not significant (Table 3, Figure 4). These differences may be attributable to the size difference in sea turtles, that is, larger turtles at Kudat Mainland. However, the results were not different when turtles ≤66.5 cm CCL from Kudat Mainland were included (Table 2).

3.3 | Genetic composition

The mtDNA haplotypes were determined for 38 and 49 green turtles from Balambangan and Kudat Mainland, respectively (Table 4). A total of 12 haplotypes were identified, of which six were observed in both aggregations. No significant difference in haplotype frequency was observed between Balambangan and Kudat Mainland foraging aggregations (exact test, $p > 0.05$). Moreover, the haplotype frequency of these aggregations was not significantly different from those observed in Brunei Bay aggregation (Joseph et al., 2016; Nishizawa et al., 2018), Mantanani aggregation (Jensen, Pilcher & FitzSimmons, 2016) or Pulau Tiga carcasses (Joseph et al., 2019). Based on mixed stock analysis, the estimated natal origin of these aggregations was mainly from Sarawak and Sabah Turtle Islands Park (see Appendix S1 for details).

4 | DISCUSSION

The present study covered two foraging aggregations in TMP, Balambangan Island and Kudat Mainland. Size composition was significantly different between the Balambangan Island and Kudat Mainland aggregations. The difference in size composition between

TABLE 3 Summary of linear modelling for body condition index.

Variable	Sum of square	df	F	*p*-Value
Site	0.143	1	10.46	0.002**
Presence of *C. testudinaria*	0.005	1	0.33	0.565
CCL	0.037	1	2.72	0.103
Site: presence of *C. testudinaria*	0.003	1	0.22	0.640
Residuals	1.188	87		

Abbreviation: CCL, curved carapace length.
**$p < 0.01$.

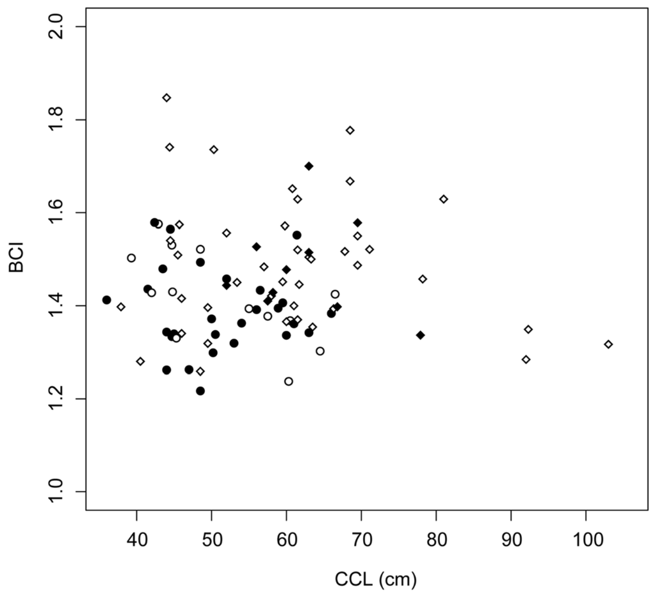

FIGURE 4 The relationship between body condition index (BCI) and curved carapace length (CCL) of green turtles at Balambangan Island (circles) and Kudat Mainland (diamonds). Filled and hollow symbols indicate the absence and presence of barnacles *Chelonibia testudinaria*, respectively.

nearby aggregations was not surprising (Hayashi & Nishizawa, 2015; Lamont & Johnson, 2021). As Balambangan Island hosts only small green turtles ≤66.5 cm CCL, this indicates that green turtles may change their foraging grounds when they reach ~65.0 cm CCL. The ontogenetic shift of foraging grounds by green turtles generally occurs due to resource partitioning by size and/or size-specific predation risk (Meylan, Meylan & Gray, 2011). In South-East Asia, this is supported by different size compositions, but similar genetic composition between Mantanani (<65.0 cm CCL; Pilcher, 2010; Jensen, Pilcher & FitzSimmons, 2016) and Brunei Bay (Joseph et al., 2016). Green turtles larger than 66.5 cm CCL were observed at Kudat Mainland, although smaller green turtles were dominant compared to Brunei Bay. It should be noted that the catching technique in this study was suitable for catching smaller turtles although it cannot be ruled out that larger green turtles were missed by the surveys of the Kudat Mainland foraging aggregations.

The BCI values of both the Kudat Mainland and Balambangan Island aggregations were generally comparable with the global mean of healthy green turtles (1.31 in small juveniles, 1.41 in large juveniles and adults; Nishizawa & Joseph, 2022). No serious damage or fibropapilloma tumours also indicate good body condition of green turtles at both Kudat Mainland and Balambangan Island. By contrast, the higher BCI of the Kudat Mainland turtles compared to Balambangan with a similar genetic composition suggests that seagrass availability or quality is better in Kudat. The BCI is a rough proxy for nutritional status and can change between nearby aggregations (Diez & van Dam, 2002; Thomson et al., 2009; Lamont & Johnson, 2021). The difference in BCI might result from different size compositions and attachment of *C. testudinaria* between these two aggregations. However, the effects on BCI were not supported in linear modelling. Thus, the difference in BCI between aggregations indicates a difference in foraging habitats.

Seagrass cover at Kimihang on Kudat Mainland was slightly higher than at Balambangan Island. However, there is a fluctuation in seagrass cover due to seasonal monsoons (Saleh, Yap & Gallagher, 2020). In addition, *H. ovalis* was observed in Kimihang, but not at Balambangan Island. *H. ovalis* tends to have relatively lower content of indigestible cell walls than *Halodule* spp. (Waldron, Baydoun & Brett, 1989; Hirayama et al., 2005); thus, foraging of *H. ovalis* may result in higher BCI of green turtles at Kudat Mainland. However, it is difficult to attribute the difference in BCI to only the difference in seagrass species because *H. pinifola* was also dominant at Kudat Mainland. Instead, one possible factor is the difference in nutritional contents of seagrass that may change geographically depending on nutrient supply and availability (McGlathery, 1995; Fourqurean & Zieman, 2002). Alternatively, water quality itself may influence the body condition, as observed in fishes (e.g., Maceda-Veiga, Green & De Sostoa, 2014).

Higher occurrence and abundance of *C. testudinaria* in Kudat Mainland than Balambangan Island aggregations can also be explained if nutrient supply and availability were higher in the coastal waters of the Kudat Mainland. Barnacle occurrence and abundance are known to differ between sea turtle species (Lim, Syed Hussein & Palaniappan, 2020; Boyd et al., 2021) and aggregations (Boyd et al., 2021; Kim et al., 2022). Low water temperature is one of the factors for the low occurrence and abundance of barnacles (Kim et al., 2022), but persistent differences in water temperature among nearby aggregations are unlikely. In contrast to previous research, the higher abundance of barnacles on larger turtles was not supported,

TABLE 4 Haplotype composition of green turtle aggregations.

Haplotype	GenBank accession no.	Balambangan Island	Kudat Mainland	Brunei Bay	Mantanani	Pulau Tiga (carcass)
CmP49.1	AB819808	9	16	8	19	8
CmP49.3	KJ502572		3	2	3	1
CmP49.5	KM923921	1			2	
CmP20.1	AB819808	2	4	3	4	
CmP57.1	KJ502588	5	8	14	11	12
Cmp57.2	KJ502567	2	3	2	4	4
CmP91.1	KF311750	6	4	2	7	6
CmP91.2	MF109839					1
CmP87.1	KJ502589	11	9	8	13	4
CmP87.2	MF109838					1
CmP19.1	KM986629		1		4	
CmP67.1	KF311758		1			
CmP82.1	KJ502584	1		1	1	1
CmP104.1	KJ502569	1		3	3	
CmP40.1	KF311750			2	2	1
CmP75.1	KJ502574			1		
CmP32.1	KF311749			1		
CmP154.1	KM923922			1	3	
CmP187.1	KM923923				1	
CmP215.1	KM923924				1	
CmP230.1	KX057745			1		
Total		38	49	49	78	39
Reference		This study	This study	a, b	c	d

Note: a, Joseph et al. (2016); b, Nishizawa et al. (2018); c, Jensen, Pilcher & FitzSimmons (2016); d, Joseph et al. (2019).

but this has been observed elsewhere (Hayashi & Tsuji, 2008; Lim, Syed Hussein & Palaniappan, 2020). Higher food availability may result in a higher growth rate of barnacles (Burrows et al., 2010; Inatsuchi, Yamato & Yusa, 2010), so a higher abundance of *C. testudinaria* in Kudat Mainland may reflect higher water column nutrient loading. Another possible reason is that green turtles in Kudat Mainland may rest for longer periods – barnacle colonization is known to occur when resting turtles contact pelagic or benthic substrata (Frick & Pfaller, 2013). The difference between green turtle aggregations at Kudat Mainland and Balambangan should be carefully interpreted as they were captured in different months. Body condition and barnacle attachments of green turtles may change seasonally; thus, seasonal change in body condition and barnacle attachment should be further studied.

Differences in natal origin or genetics, rather than differences in habitats and nutrients, may explain the differences in BCI. However, the genetic composition results did not significantly differ between Balambangan and Kudat Mainland foraging aggregations, and were similar to nearby aggregations in Brunei Bay (Joseph et al., 2016; Nishizawa et al., 2018) and Mantanani (Jensen, Pilcher & FitzSimmons, 2016). Therefore, the difference in body condition due to differences in habitats and nutrients was supported. The genetic composition was similar to carcasses found in Pulau Tiga, TMP (Joseph et al., 2019), indicating that foraging aggregations in TMP may be (illegally) harvested. This should be investigated further as larger turtles dominated the carcasses compared to the live aggregations of this study, reflecting different catching techniques and/or over-harvesting; the foraging aggregations in TMP have a conservation priority.

These findings emphasize the importance of long-term monitoring of foraging habitats (Kophamel et al., 2022) and ongoing conservation efforts to protect green turtle foraging habitats. In particular, the potential sensitivity of green turtle body condition to the quality of foraging habitats is shown. Nutrients in the water column and sediments or water quality are candidate causes of the difference in green turtle body condition. Further, identification of the causative relationships between seagrass provision and green turtle condition should become a local conservation priority, since this can have profound effects on the turtle population characteristics. Understanding seasonal and inter-annual variability would significantly improve understanding of this relationship, and therefore how to most effectively support the turtle populations. It is therefore recommended that sediment and water quality should be regularly monitored, and action taken to reduce pollution levels taken if/when necessary. Given local geomorphological and anthropogenic factors, it is reasonable that Kudat Mainland waters contain more nutrients, but this should be empirically verified. Importantly, since it is known that excessive eutrophication causes negative effects on seagrass (Burkholder, Tomasko & Touchette, 2007), higher background nutrient loading places this area at risk of disrupting seagrass health. This study shows that such a change would have knock-on effects on turtle health. Ongoing development in the coastal area in the Kudat Mainland area (e.g., the silica sand mining project at Sikuati, adjacent to Kimihang Beach), will probably disrupt the foraging habitats of green turtles. Even if the habitats are not physically destroyed, these results suggest that any deterioration in water quality will negatively affect the health of the local sea turtle population (Jones et al., 2022). Sustainable management of the foraging habitats and sea turtle aggregations in TMP is therefore necessary to protect them from human activities, complemented by direct monitoring of the turtle–habitat dynamics.

AUTHOR CONTRIBUTIONS

Conceptualization: Hideaki Nishizawa, Juanita Joseph and Gavin Jolis. *Investigation*: Gavin Jolis, Juanita Joseph and Sofia Johari. *Resources*: Irwan Isnain, Hussien Muin, Sofia Johari and Ejria Saleh. *Research approval*: Irwan Isnain and Hussien Muin. *Funding acquisition*: Juanita Joseph and Ejria Saleh. *Analysis*: Hideaki Nishizawa and Gavin Jolis. *Writing original draft*: Hideaki Nishizawa, Juanita Joseph and Gavin Jolis. *Writing—review and editing*: Hideaki Nishizawa, Juanita Joseph and Ejria Saleh.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Raw data are available from the corresponding author upon reasonable request.

ETHICS APPROVAL CONSENT TO PARTICIPATE

Sabah Biodiversity Centre (SaBC) Access Licence JKM/MBS.1000-2/13 JLD.1 (27) and Sabah Parks Permit TTS/IP/100-6/2 Jld. 11 (119).

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REFERENCES

Abreu-Grobois, F.A., Horrocks, J., Formia, A., Leroux, R., Velez-Zuazo, X., Dutton, P. et al. (2006). New d-loop primers which work for a variety of marine turtle species may increase the resolution capacity of mixed stock analyses. In: *Book of abstract at the 26th annual symposium on sea turtle biology and conservation. Crete, Greece: International Sea Turtle Society, p. 179*.

Adnyana, W., Ladds, P.W. & Blair, D. (1997). Observations of fibropapillomatosis in green turtles (*Chelonia mydas*) in Indonesia. *Australian Veterinary Journal*, 75(10), 736–742. https://doi.org/10.1111/j.1751-0813.1997.tb12258.x

Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C. & Silliman, B.R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs*, 81(2), 169–193. https://doi.org/10.1890/10-1510.1

Bell, I.P., Meager, J., van de Merwe, J.P. & Hof, C.A.M. (2019). Green turtle (*Chelonia mydas*) population demographics at three chemically distinct foraging areas in the northern Great Barrier Reef. *Science of the Total Environment*, 652, 1040–1050. https://doi.org/10.1016/j.scitotenv.2018.10.150

Bjorndal, K.A., Bolten, A.B. & Chaloupka, M.Y. (2000). Green turtle somatic growth model: evidence for density dependence. *Ecological Applications*, 10(1), 269–282. https://doi.org/10.1890/1051-0761(2000)010[0269:GTSGME]2.0.CO;2

Boyd, L.L., Zardus, J.D., Knauer, C.M. & Wood, L.D. (2021). Evidence for host selectivity and specialization by epizoic *Chelonibia* barnacles between hawksbill and green sea turtles. *Frontiers in Ecology and Evolution*, 9, 807237. https://doi.org/10.3389/fevo.2021.807237

Bruford, M.W., Hanotte, O., Brookfield, J.F.Y. & Burke, T. (1992). Single locus and multilocus DNA fingerprinting. In: Hoelzel, A.R. (Ed.) *Molecular genetic analysis of populations—a practical approach*. Oxford: IRL Press, pp. 227–229.

Burkholder, J.M., Tomasko, D.A. & Touchette, B.W. (2007). Seagrasses and eutrophication. *Journal of Experimental Marine Biology and Ecology*, 350(1-2), 46–72. https://doi.org/10.1016/j.jembe.2007.06.024

Burrows, M.T., Jenkins, S.R., Robb, L. & Harvey, R. (2010). Spatial variation in size and density of adult and post-settlement *Semibalanus balanoides*: effects of oceanographic and local conditions. *Marine Ecology Progress Series*, 398, 207–219. https://doi.org/10.3354/meps08340

Christianen, M.J.A., van Katwijk, M.M., van Tussenbroek, B.I., Pagès, J.F., Ballorain, K., Kelkar, N. et al. (2021). A dynamic view of seagrass meadows in the wake of successful green turtle conservation. *Nature Ecology and Evolution*, 5(5), 553–555. https://doi.org/10.1038/s41559-021-01433-z

Diez, C.E. & van Dam, R.P. (2002). Habitat effect on hawksbill turtle growth rates on feeding grounds at Mona and Monito Islands, Puerto Rico. *Marine Ecology Progress Series*, 234, 301–309. https://doi.org/10.3354/meps234301

Dutton, P.H. (1996). Methods for collection and preservation of samples for sea turtle genetic studies. In: Bowen, B.W., & Witzell, W.N. (Eds.) *Proceedings of the international symposium on sea turtle genetics*. Florida: US Department of Commerce, NOAA Technical Memorandum, NMFS-SEFSC-396, pp. 17–24.

Eaton, C., McMichael, E., Witherington, B., Foley, A., Hardy, R. & Meylan, A. (2008). *In-water sea turtle monitoring and research in Florida: review and recommendations*. Florida: US Department of Commerce, NOAA Technical Memorandum NMFS-OPR-38. Available at: https://doi.org/10.20798/wildlifeconsjp.9.2_69 [Accessed 14th September 2022].

Esteban, N., Mortimer, J.A., Stokes, H.J., Laloë, J.-O., Unsworth, R.K.F. & Hays, G.C. (2020). A global review of green turtle diet: sea surface temperature as a potential driver of omnivory levels. *Marine Biology*, 167, 183. https://doi.org/10.1007/s00227-020-03786-8

Excoffier, L. & Lischer, H.E.L. (2010). Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources*, 10(3), 564–567. https://doi.org/10.1111/j.1755-0998.2010.02847.x

Fourqurean, J.W. & Zieman, J.C. (2002). Nutrient content of the seagrass *Thalassia testudinum* reveals regional patterns of relative availability of nitrogen and phosphorus in the Florida Keys USA. *Biogeochemistry*, 61, 229–245. https://doi.org/10.1023/A:1020293503405

Frick, M. & Pfaller, J.B. (2013). Sea turtle epibiosis. In: Wyneken, J., Lohmann, K.J., & Musick, J.A. (Eds.) *The biology of sea turtles volume III*. Florida: CRC Press, pp. 399–426.

Hancock, J.M., Vieira, S., Jimenez, V., Rio, J.C. & Rebelo, R. (2018). Stable isotopes reveal dietary differences and site fidelity in juvenile green turtles foraging around São Tomé Island, West Central Africa. *Marine Ecology Progress Series*, 600, 165–177. https://doi.org/10.3354/meps12633

Hayashi, R. & Nishizawa, H. (2015). Body size distribution demonstrates flexible habitat shift of green turtle (*Chelonia mydas*). *Global Ecology and Conservation*, 3, 115–120. https://doi.org/10.1016/j.gecco.2014.11.008

Hayashi, R. & Tsuji, K. (2008). Spatial distribution of turtle barnacles on the green sea turtle, *Chelonia mydas*. *Ecological Research*, 23, 121–125. https://doi.org/10.1007/s11284-007-0349-0

He, Q. & Silliman, B.R. (2019). Climate change, human impacts, and coastal ecosystems in the Anthropocene. *Current Biology*, 29(19), R1021–R1035. https://doi.org/10.1016/j.cub.2019.08.042

Henseler, C., Nordström, M.C., Törnroos, A., Snickars, M., Pecuchet, L., Lindegren, M. et al. (2019). Coastal habitats and their importance for the diversity of benthic communities: a species- and trait-based approach. *Estuarine, Coastal and Shelf Science*, 226, 106272. https://doi.org/10.1016/j.ecss.2019.106272

Hirayama, T., Ogura, G., Sudo, K., Higa, T., Kawashima, Y., Mukai, H. et al. (2005). Chemical composition of seagrasses at Okinawa Island and Amami-Oshima Island. *Wildlife Conservation Japan*, 9(2), 69–75. (in Japanese with English abstract) https://doi.org/10.20798/wildlifeconsjp.9.2_69

Inatsuchi, A., Yamato, S. & Yusa, Y. (2010). Effects of temperature and food availability on growth and reproduction in the neustonic pedunculate barnacle *Lepas anserifera*. *Marine Biology*, 157, 899–905. https://doi.org/10.1007/s00227-009-1373-0

Jeethvendra, K., Nishizawa, H., Alin, J., Muin, H. & Joseph, J. (2023). Illegal tortoiseshell harvest of hawksbill turtles (*Eretmochelys imbricata*) in Southeast Asia: evidence from Baturua Reef, Semporna, Sabah, Malaysia. *Journal of Sustainable Science and Management*, 18(7), 54–67. https://doi.org/10.46754/jssm.2023.07.004

Jensen, M.P., Pilcher, N. & FitzSimmons, N.N. (2016). Genetic markers provide insight on origins of immature green turtles (*Chelonia mydas*) with biased sex ratios at two foraging grounds in Sabah, Malaysia. *Endangered Species Research*, 31, 191–201. https://doi.org/10.3354/esr00763

Jolis, G., Joseph, J., Nishizawa, H., Isnain, I. & Muin, H. (2023). Marine turtle nesting and hatching in Tun Mustapha Park, Malaysia, revealed by community-based monitoring. *Herpetological Conservation and Biology*, 18(2), 275–289.

Jones, K., Limpus, C.J., Brodie, J., Jones, R., Read, M., Shum, E. et al. (2022). Spatial distribution of fibropapillomatosis in green turtles along the Queensland coast and an investigation into the influence of water quality on prevalence. *Conservation Science and Practice*, 4(8), e12755. https://doi.org/10.1111/csp2.12755

Joseph, J., Nishizawa, H., Alin, J.M., Othman, R., Jolis, G., Isnain, I. et al. (2019). Mass sea turtle slaughter at Pulau Tiga, Malaysia: genetic studies indicate poaching locations and its potential effects. *Global Ecology and Conservation*, 17, e00586. https://doi.org/10.1016/j.gecco.2019.e00586

Joseph, J., Nishizawa, H., Arshaad, W.M., Syed Kadir, S.A.S., Jaaman, S.A., Bali, J. et al. (2016). Genetic stock compositions and natal origin of green turtle (*Chelonia mydas*) foraging at Brunei Bay. *Global Ecology and Conservation*, 6, 16–24. https://doi.org/10.1016/j.gecco.2016.01.003

Jumin, R., Binson, A., McGowan, J., Magupin, S., Beger, M., Brown, C.J. et al. (2018). From Marxan to management: ocean zoning with stakeholders for Tun Mustapha Park in Sabah, Malaysia. *Oryx*, 52(4), 775–786. https://doi.org/10.1017/S0030605316001514

Kassambara, A. (2021). *rstatix: pipe-friendly framework for basic statistical tests*. R package version 0.7.0. Available at: https://CRAN.R-project.org/package=rstatix [Accessed 27th April 2022].

Kim, H.K., Chan, B.K.K., Yi, C., Kim, I.-H. & Choi, Y.N. (2022). Barnacle epibiosis on sea turtles in Korea: a west Pacific region with low occurrence and intensity of *Chelonibia testudinaria* (Cirripedia: Chelonibiidae). *Frontiers in Ecology and Evolution*, 10, 785692. https://doi.org/10.3389/fevo.2022.785692

Kophamel, S., Illing, B., Ariel, E., Difalco, M., Skerratt, L.F., Hamann, M. et al. (2022). Importance of health assessments for conservation in noncaptive wildlife. *Conservation Biology*, 36, e13724. https://doi.org/10.1111/cobi.13724

Lamont, M.M. & Johnson, D. (2021). Variation in species composition, size and fitness of two multi-species sea turtle assemblages using different neritic habitats. *Frontiers in Marine Science*, 7, 608740. https://doi.org/10.3389/fmars.2020.608740

Lim, K.K., Syed Hussein, M.A. & Palaniappan, P. (2020). Abundance, placement and sexual identity of the epizoic barnacle *Chelonibia testudinaria* relative to the size and species of host turtles in Mabul Island, Malaysia. *Journal of the Marine Biological Association of the United Kingdom*, 100, 1299–1309. https://doi.org/10.1017/S0025315420001198

Lim, V.-C., Justine, E.V., Yusof, K., Wan Mohamad Ariffin, W.N.S., Goh, H.C. & Fadzil, K.S. (2021). Eliciting local knowledge of ecosystem services using participatory mapping and photovoice: a case study of Tun Mustapha Park, Malaysia. *PLoS ONE*, 16(7), e0253740. https://doi.org/10.1371/journal.pone.0253740

Loganathan, A.L., Palaniappan, P. & Subbiah, V.K. (2021). First evidence of Chelonid Herpesvirus 5 (ChHV5) infection in green turtles (*Chelonia mydas*) from Sabah, Borneo. *Pathogens*, 10(11), 1404. https://doi.org/10.3390/pathogens10111404

Maceda-Veiga, A., Green, A.J. & De Sostoa, A. (2014). Scaled body-mass index shows how habitat quality influences the condition of four fish taxa in north-eastern Spain and provides a novel indicator of ecosystem health. *Freshwater Biology*, 59(6), 1145–1160. https://doi.org/10.1111/fwb.12336

Mazaris, A.D., Schofield, G., Gkazinou, C., Almpanidou, V. & Hays, G.C. (2018). Global sea turtle conservation successes. *Science Advances*, 3, e1600730. https://doi.org/10.1126/sciadv.1600730

McGlathery, K.J. (1995). Nutrient and grazing influences on a subtropical seagrass community. *Marine Ecology Progress Series*, 122, 239–252. https://doi.org/10.3354/meps122239

McKenzie, L.J., Campbell, S.J. & Roder, C.A. (2003). *Seagrass-watch: manual for mapping and monitoring seagrass resources*, Cairns: QFS, NFC.

Meylan, P.A., Meylan, A.B. & Gray, J.A. (2011). The ecology and migrations of sea turtles 8. Tests of the developmental habitat hypothesis. *Bulletin of the American Museum and Natural History*, 357, 1–70. https://doi.org/10.1206/357.1

Monroe, R. (1981). Studies in the Coronulidae (Cirripedia): shell morphology, growth and function, and their bearing on subfamily classification. *Memoirs of the Queensland Museum*, 20(2), 237–251.

Nishizawa, H. & Joseph, J. (2022). Differences in the morphological body condition index of sea turtles between species and size classes. *Journal of the Marine Biological Association of the United Kingdom*, 102(7), 479–485. https://doi.org/10.1017/S0025315422000765

Nishizawa, H., Joseph, J., Chong, Y.K., Syed Kadir, S.A., Isnain, I., Ganyai, T.A. et al. (2018). Comparison of the rookery connectivity and migratory connectivity: insight into movement and colonization of the green turtle (*Chelonia mydas*) in Pacific–Southeast Asia. *Marine Biology*, 165, 77. https://doi.org/10.1007/s00227-018-3328-9

Pella, J. & Masuda, M. (2001). Bayesian methods for analysis of stock mixtures from genetic characters. *Fishery Bulletin*, 99(1), 151–167.

Pilcher, N. (2010). Population structure and growth of immature green turtles at Mantanani, Sabah, Malaysia. *Journal of Herpetology*, 44(1), 168–171. https://doi.org/10.1670/08-115.1

R Core Team. (2022). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: https://www.R-project.org/ [Accessed 27th April 2022].

Ricker, W.E. (1975). Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada*, 191, 1–382.

Sabah Parks. (2017). *Tun Mustapha Park integrated management plan*. Sabah Parks.

Saleh, E., Yap, T.K. & Gallagher, J.B. (2020). Seagrass coverage and associated fauna at Gaya Island, Sabah, Malaysia: a pilot seagrass transplantation. *Borneo Journal of Marine Science and Aquaculture*, 4(1), 14–19. https://doi.org/10.51200/bjomsa.v4i1.1786

Seminoff, J.A. (2004). Chelonia mydas. The IUCN red list of threatened species 2004. Available at: https://doi.org/10.2305/IUCN.UK.2004.RLTS.T4615A11037468.en [Accessed 27th April 2022].

Stevensen, R.D. & Woods, W.A. (2006). Condition indices for conservation: new uses for evolving tools. *Integrative and Comparative Biology*, 46(6), 1169–1190. https://doi.org/10.1093/icb/icl052

Tamura, K., Stecher, G. & Kumar, S. (2021). MEGA11: Molecular Evolutionary Genetics Analysis version 11. *Molecular Biology and Evolution*, 38(7), 3022–3027. https://doi.org/10.1093/molbev/msab120

Thomson, J.A., Burkholder, D., Heithaus, M.R. & Dill, L.M. (2009). Validation of a rapid visual-assessment technique for categorizing the body condition of green turtles (*Chelonia mydas*) in the field. *Copeia*, 2009, 251–255. https://doi.org/10.1643/CE-07-227

Venables, W.N. & Ripley, B.D. (2002). *Modern applied statistics with S*, 4th edition, New York: Springer.

Waldron, K.W., Baydoun, E.A.-H. & Brett, C.T. (1989). Comparison of cell wall composition of tissues from the seagrasses *Halophila* and *Halodule*. *Aquatic Botany*, 35(2), 209–218. https://doi.org/10.1016/0304-3770(89)90106-X

Wildermann, N.E., Gredzens, C., Avens, L., Barrios-Garrido, H.A., Bell, I., Blumenthal, J. et al. (2018). Informing research priorities for immature sea turtles through expert elicitation. *Endangered Species Research*, 37, 55–76. https://doi.org/10.3354/esr00916

SUPPORTING INFORMATION

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

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