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Inter-nesting habitat use by green turtles *Chelonia mydas* in the Great Barrier Reef

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ABSTRACT: Understanding green turtle habitat use during the nesting season is important for informing management decisions relating to green turtles and ecosystems that support them. Despite patterns such as migration being described, few studies investigate behaviour during the inter-nesting period. This research aims to describe and quantify the spatial distribution patterns of green turtles during 2 nesting seasons on Raine Island in the northern Great Barrier Reef. Satellite telemetry data were used to analyse the inter-nesting movements and patterns of green turtles in 2017 (n = 19) and 2018 (n = 20). The inter-nesting period ranged from 51 to 100 d (76.33 ± 15.98 d) across both seasons. The average inter-nesting area of individual turtles did not differ between nesting seasons (2017: 12.31 ± 13.22 km^2, 2018: 12.01 ± 21.92 km^2). In addition, it was established that 39 individuals are a sufficient sample size to describe the spatial distribution. Approximately half of the tracked individuals remained at the same reef for their entire inter-nesting season (n = 19), and half used habitat on nearby reefs (n = 20). Most turtles showed fidelity to Raine Island as a nesting site (n = 37), laying all their clutches on the island. However, 2 individuals travelled 479 and 337 km during the inter-nesting period. This study thus highlights where the habitats used by green turtles during the inter-nesting season are and how they are used. Therefore, management strategies and conservation decisions can be informed to maintain the viability of these essential habitats.

KEY WORDS: Inter-nesting · Movement · Spatial ecology · Distribution · Home range · Management

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1. INTRODUCTION

Effective management of threatened species is contingent upon our understanding of their behaviours, movements, and interactions within their environment. Studying these aspects of marine animals can be especially challenging because of their environment's complexity, enormity, and often remoteness. Tracking technology has led to ecological insights into the distribution, movement patterns, habitat use, and ecophysiology of numerous marine taxa (Hussey et al. 2015, Harcourt et al. 2019). The information gained from these studies can inform planning and conservation decisions (McGowan et al. 2017, Hays et al. 2019).

Satellite telemetry is a powerful tool when studying sea turtles, enabling researchers to determine the distribution of genetic stocks, key foraging habitats, and migratory pathways of different populations worldwide (Hamann et al. 2010, Rees et al. 2016). With advances in tag technology (e.g. size, battery life, and location accuracy), tracking turtles for a longer duration and at a finer scale is now possible. For example, recent research has tracked oceanic-stage juveniles (Mansfield et al. 2021), round-trip migrations (Pilcher et al. 2020), the spatial use of cryptic males (Cuevas et

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al. 2020), and diel patterns of movement (Shimada et al. 2016, Dujon et al. 2017, Chambault et al. 2020), all of which were previously challenging to undertake. Satellite tracking studies are also becoming an increasingly important tool in studying the reproductive cycle of sea turtles. Research has been historically limited to accessible nesting beaches; using satellite tracking, new insights have since been unveiled about mating behaviours (Bond & James 2017), male reproductive patterns (James et al. 2005, Hays et al. 2010, Arendt et al. 2012, Casale et al. 2013), and links between foraging sites to size and reproductive output have been identified (Patel et al. 2015).

The reproductive period for female sea turtles is an energetically demanding time, requiring the optimisation of stored energy to endure activities such as migration, breeding, and egg development (Miller 1997). Females employ various methods to minimise energy loss and maximise reproductive output during the nesting season. Managing energy can take the form of assisted resting (Walcott et al. 2012), neutral buoyancy resting (Hays et al. 2000), minimising movement by remaining near the nesting beach (Hays et al. 1999, Marcovaldi et al. 2010, Blanco et al. 2013, Chambault et al. 2016), or gaining energy by opportunistically foraging (Hays et al. 2002, Delcroix et al. 2009, Fuller et al. 2009, Cheng et al. 2013). However, even within conspecifics, behaviours from one population may not reflect those of others. For example, gravid green turtles *Chelonia mydas* at Raine Island and in northern Cyprus feed to a limited extent during the inter-nesting period, whereas those at Ascension Island fast, presumably a consequence of food availability (or lack thereof) in the nesting area (Tucker & Read 2001, Hays et al. 2002).

Green turtles of Queensland, Australia, are a protected species listed as vulnerable both by the state of Queensland (Nature Conservation Act 1992) and federally in Australia (The Environment Protection and Biodiversity Conservation Act 1999, Commonwealth of Australia 2017). The population of the northern Great Barrier Reef (GBR) is an independent genetic stock (Chaloupka et al. 2008, FitzSimmons & Limpus 2014), with the majority aggregating on Raine Island, the world's largest known green turtle rookery (Limpus et al. 2003). They have been well studied for decades, with concern for their population resulting in continued monitoring and beach re-profiling to enhance reproductive success (Dunstan & Robertson 2017). Green turtle migration, nesting, and hatching patterns have been described (Limpus et al. 1992, 2003, Jessop et al. 1999, Limpus 2008, Pike et al. 2015, Booth & Dunstan 2018, Booth et al. 2020), but there remain gaps in the understanding of their behaviour during the inter-nesting period. The inter-nesting period typically encompasses 2 or more months of intense embryological development. The breeding female ovulates and fertilises successive groups of ovarian follicles and prepares middle gastrulation embryos within clutches of shelled eggs for laying (Miller et al. 2003). Although occasional foraging (Tucker & Read 2001) and diving (Bell et al. 2009) patterns have been identified during the inter-nesting period, the movements and spatial use of gravid green turtles at Raine Island have yet to be described. With their vulnerable population status (Commonwealth of Australia 2017), it is important to understand this period better and how it may relate to reproductive success and the conservation of this critical population.

Using satellite tracking data, we examined the spatial distribution of inter-nesting habitat used by 39 nesting green turtles of the 2017 and 2018 seasons at Raine Island. Our objectives were to (1) identify inter-nesting home ranges and core areas and describe how they are used, (2) quantify the sample size of turtles needed to describe the collective inter-nesting habitat at Raine Island, (3) quantify the number of re-nesting periods necessary to understand the spatial distribution of an individual's inter-nesting habitat, (4) identify differences among individuals and between nesting seasons, and (5) identify relationships between in-water behaviour and reproductive output.

2. MATERIALS AND METHODS

2.1. Study site

Raine Island is a small detached vegetated coral cay located in Australia's northern GBR (11.590° S, 144.035° E), measuring approximately 820 m long and 450 m wide (Fig. 1). A reef flat surrounds the island, with the water depth abruptly dropping off to in excess of 100 m within 750 m of the southern shore and 250 m of the western shore. The surrounding waters and reefs are within the Marine National Park (Green) Zone designation under the Great Barrier Reef Marine Park (GBRMP)/Great Barrier Reef Coastal Marine Park Zoning Plan, protecting the area from commercial fishing and other pressures. The island is not accessible to the public and is part of the Raine Island National Park (Scientific) Marine Park Preservation (Pink) Zone designation, including nearby Moulter Cay and McLennan Cay. The area's traditional owners are the Wuthathi and Meriam Nation (Ugar, Mer, Erub) peoples.

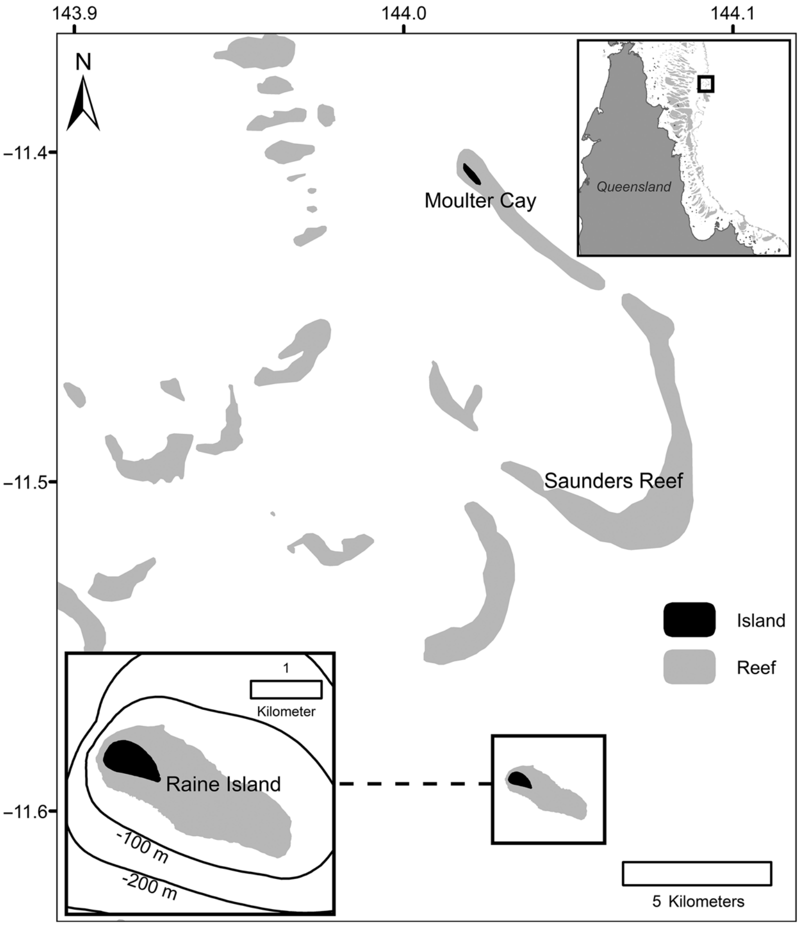

Fig. 1. Study area of the northern Great Barrier Reef stock of green turtles, including the nesting beaches Raine Island (inset) and Moulter Cay. Map produced in ArcGIS 10.7

2.2. Data acquisition

Adult female green turtles were captured during nesting attempts at Raine Island at the beginning of the nesting season in 2017 (n = 19) and 2018 (n = 20) and subsequently fitted with Wildlife Computers Argos-linked Fastloc GPS tags (Hamann et al. 2022). The Fastloc technology enables tags to send and receive signals within milliseconds (Hazel 2009), making it possible to track the female green turtles, who may only surface briefly. This technology allows for analysing the fine-scale movements and behaviours of sea turtles across spatial and temporal scales, because the accuracy of locations from Fastloc GPS tags is typically between 20 and 70 m (Hazel 2009, Shimada et al. 2012, Dujon et al. 2014). As per previous studies, the turtles were caught between 21:00, and 23:00 h and contained within open-topped wooden sided boxes on the beach. The only disturbance the turtles were exposed to was the research group moving a turtle between her clutch site and the tagging location and attaching the transmitters. Transmitters were attached to the carapace using an epoxy (Hamann et al. 2022), and the tags and the epoxy were coated in 2 coats of anti-foul paint (Micron 66). The turtles were released from the beach near their capture site at sunrise (~05:00 to 06:00 h) the following morning.

2.3. Analyses

Raw GPS data were obtained from the Wildlife Computers data portal and screened with the ddfilter and dupfilter functions in the SDLfilter package (Shimada et al. 2012, 2016) using R software version 4.0.3. This removes low-quality location fixes, duplicate locations, and biologically unrealistic locations based on travel speed and turning angle (the angle formed by 3 successive locations). All spatial analyses were then conducted using the filtered location data.

The re-nesting interval was calculated as the time between a successful nesting event and a subsequent attempt (Limpus et al. 2001), and the clutch period is the duration between successive clutches. We analysed the clutch period and the re-nesting interval to ensure that each female's movements between successful nesting events were scrutinised. Successful nesting events were determined by examining the haulout data from the tags and comparing them to the location data as per Hamann et al. (2022). In brief, we used a combination of location data, duration on the beach, and the elapsed days between successive nesting attempts to determine the success of each nesting event. ArcGIS 10.7 (Esri) was used to analyse the location points and remove the on-land locations associated with nesting events. The land layer was generated from real-time kinematic GPS and total station survey system surveys conducted at the start of each nesting season (see Dawson & Smithers 2010, Smithers & Dawson 2023). Each individual's movement patterns were examined with the moveVis package in R (Schwalb-Willmann et al. 2020). The total distance moved (TDM) per individual was calculated as the duration in days between tag attachment and her last clutch (inter-nesting period) or between consecutive clutches (clutch period).

The 95% (home range) and 50% (core area) utilisation distributions (UDs) of each individual were created with the adehabitatHR package in R (Calenge 2006). These were calculated using the biased random bridge (BRB) approach, which is a movement-based kernel density estimator that incorporates both diffusive and advective (i.e. drift) components as opposed to purely diffusive ones (Benhamou & Cornélis 2010, Benhamou 2011). A collective home range and core area were then created by overlapping and summing all individual home ranges and core areas.

Statistical analyses were performed using R software version 4.0.3. All data were checked for distribution normality (Shapiro-Wilk test) and homogeneity of variance (Levene test), and the statistical significance value was $p = 0.05$. A non-parametric Mann-Whitney *U*-test was used to determine differences in TDM, core area size, and home range size between the 2017 and 2018 individuals. Values are reported as mean ± SD. A Pearson correlation was used to test the relationships between TDM, the number of clutches laid, and the number of nesting attempts.

Our tracking data sample size (n = 39) was assessed using the boot_overlap and asymptote functions in the SDLfilter package in R (Shimada et al. 2021a). This overlap probability approach calculates the probability of an individual being within the merged habitat of all other individuals. This analysis was used to (1) determine the sufficiency of the sample size of our tracking data to describe the collective home range and (2) determine the number of clutch periods required to represent the home range of an individual inter-nesting female adequately.

Since dive data were unavailable, the corresponding maximum depth for each location point was used to determine what type of areas turtles used during their inter-nesting period and the proximity to shallow areas (i.e. shallow or deep). Depth values were evaluated by superimposing a 30 m resolution bathymetric layer of the GBR (Beaman 2010) in ArcGIS.

3. RESULTS

3.1. Nesting characteristics

Each turtle was tracked from the date of tag application until she laid her last clutch and departed on a migration back to her foraging area. The 2017–2018 tracking period occurred from late October to early February, and the 2018–2019 tracking period occurred from mid-October to late January, with the inter-nesting periods of individuals ranging from 51 to 100 d (mean ± SD = 76.33 ± 15.98 d, Table 1). The tracked turtles (n = 39) laid 4 to 10 clutches (Table 1), with a higher average number of attempts per clutch in the 2017–2018 season than in the 2018–2019 season (2.2 attempts vs. 1.8 attempts). No significant correlation was found between the cumulative number of attempts and the total number of clutches laid throughout the season (Pearsons's $t = 0.44284$, df = 37, $r = 0.07261017$, $p > 0.050$). The clutch period (total duration between clutches) ranged between 8 and 25 d, with an average duration of 12.4 d, and the re-nesting interval (duration between clutch and next attempt) ranged between 8 and 22 d, with an average of 11.3 d. Re-nesting intervals were 0.5–1 d longer at the start of the season (i.e. between clutch 1 and the first attempt at clutch 2) compared to the end of the season (the last re-nesting interval).

3.2. Inter-nesting area

The collective home range area (95% UD) for all 39 individuals of the 2017 and 2018 nesting seasons was 205.43 km^2, with a core area (50% UD) of 25.53 km^2 (Fig. 2). The home range area per individual ranged from 0.77 to 101.21 km^2, and the core area ranged from 0.09 to 10.40 km^2, with individuals tracked in 2017 having a slightly greater average home range area than the individuals tracked in 2018 (12.31 ± 13.33 vs. 12.01 ± 21.92 km^2) but a slightly smaller core area (1.27 ± 1.29 vs. 1.31 ± 2.22 km^2). Neither difference was statistically significant (home range area: Mann-Whitney *U*-test, $p = 0.687$; core area: Mann-Whitney *U*-test, $p = 0.646$).

3.3. Overlap probability

Collectively, the overlap probability reached an asymptote at 10 individuals, implying that our sample size of females tracked during this study (n = 39) was sufficient to understand the spatial distribution of inter-nesting habitats at Raine Island (Fig. 3). The cumulative proportion of overlap for the inter-nesting area was 0.98. At an individual turtle scale, the overlap probability reached an asymptote ranging between 2 and 4 clutch periods, with an average of 2 clutch periods adequately representing the home range of each inter-nesting female (Fig. 4a) (2 individuals failed to reach an asymptote, and 1 was unable to

Table 1. Clutch frequency and inter-nesting duration for 39 (2017: n = 19, 2018: n = 20) green turtles *Chelonia mydas* tracked during the 2017 and 2018 nesting seasons at Raine Island. TDM: total distance moved

Year/ Turtle ID	Clutches laid	Date tagged	Date of last clutch	Inter-nesting period (d)	TDM (km)
2017					
45730	5	1 Nov 2017	22 Dec 2017	51	547.37
45731	6	4 Nov 2017	6 Jan 2018	63	261.85
45732	9	1 Nov 2017	7 Feb 2018	98	866.23
45755	4	2 Nov 2017	23 Dec 2017	51	427.85
45767	10	31 Oct 2017	6 Feb 2018	98	261.09
45769	6	31 Oct 2017	31 Dec 2017	61	542.05
45770	9	2 Nov 2017	5 Feb 2018	95	588.99
45771	8	31 Oct 2017	8 Feb 2018	100	1638.10
45774	8	3 Nov 2017	2 Feb 2018	91	758.34
45778	5	31 Oct 2017	30 Dec 2017	60	394.65
45782	5	4 Nov 2017	29 Dec 2017	55	461.11
45784	8	4 Nov 2017	19 Jan 2018	76	459.39
45786	9	4 Nov 2017	8 Feb 2018	96	1195.28
45787	6	3 Nov 2017	25 Jan 2018	83	923.11
45788	6	3 Nov 2017	9 Jan 2018	67	491.94
45789	5	31 Oct 2017	25 Dec 2017	55	650.51
45791	7	2 Nov 2017	27 Jan 2018	86	434.98
45793	8	3 Nov 2017	8 Feb 2018	97	401.83
45797	7	31 Oct 2017	20 Jan 2018	81	527.37
2018					
45764	8	19 Oct 2018	11 Jan 2019	84	206.17
65520	7	20 Oct 2018	30 Dec 2018	71	393.11
65521	6	18 Oct 2018	16 Dec 2018	59	437.72
65522	9	20 Oct 2018	20 Jan 2019	92	517.51
65526	5	23 Oct 2018	14 Dec 2018	52	179.85
65527	9	22 Oct 2018	26 Jan 2019	96	632.67
65535	7	20 Oct 2018	17 Dec 2018	58	548.18
65536	9	19 Oct 2018	17 Jan 2019	90	571.32
65542	7	22 Oct 2018	07 Jan 2019	77	473.85
65543	7	21 Oct 2018	28 Dec 2018	68	492.26
65544	8	21 Oct 2018	13 Jan 2019	84	404.00
65546	8	22 Oct 2018	12 Jan 2019	82	362.79
65547	8	19 Oct 2018	20 Jan 2019	93	637.42
65556	6	21 Oct 2018	19 Dec 2018	59	292.60
65557	6	19 Oct 2018	22 Dec 2018	64	229.92
65558	7	23 Oct 2018	01 Jan 2019	70	362.08
65559	9	19 Oct 2018	17 Jan 2019	90	656.98
65561	6	22 Oct 2018	23 Dec 2018	62	546.79
65562	6	19 Oct 2018	29 Dec 2018	71	298.77
65563	9	21 Oct 2018	20 Jan 2019	91	357.75

be analysed due to too few clutch periods [laid 4 clutches; Fig. 4b]).

3.4. Inter-nesting movements

More individuals of the 2017 season spent time away from Raine Island (i.e. on other reefs) (n = 12) as opposed to solely remaining near the island (n = 7) for the entire inter-nesting period. The converse is valid for the 2018 season, with more individuals spending the whole inter-nesting period at Raine Island (n = 12) and fewer at other reefs (n = 8). The 2017 individuals had a measurable but not statistically different average TDM than the 2018 individuals (622.74 ± 337.87 vs. 430.09 ± 145.44 km; Table 1; Mann-Whitney *U*-test, p = 0.061), with a significant positive correlation between total TDM and cumulative number of attempts (Pearson's *t* = 2.100, df = 37, r = 0.326, p = 0.043). No significant correlation was found between the total number of clutches (per individual) and total TDM for the inter-nesting period (Pearson's *t* = 1.953, df = 37, r = 0.306 p = 0.058). The TDM per clutch period

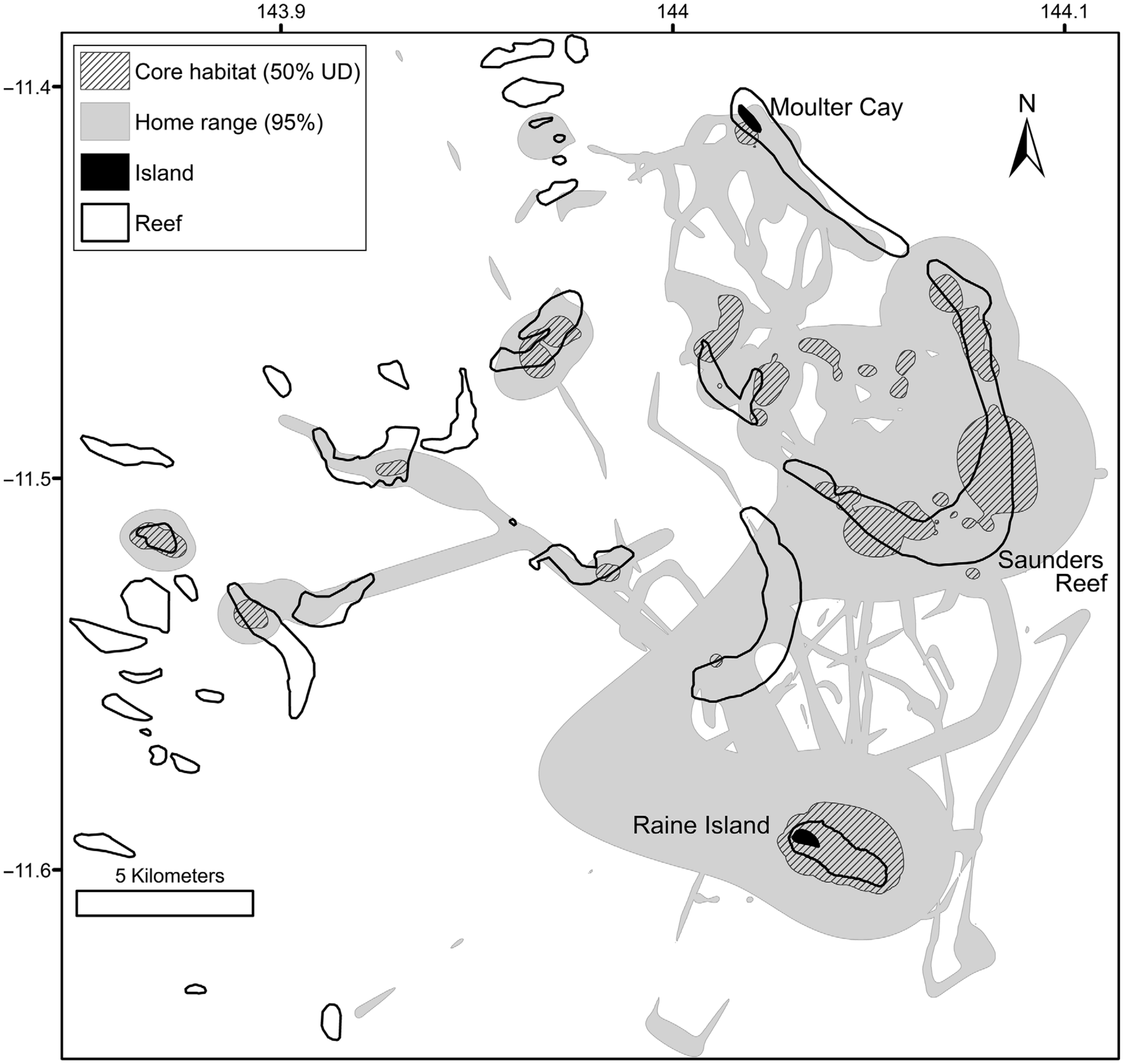

Fig. 2. Collective home range and core use areas of nesting green turtles at Raine Island (n = 39). UD: utilisation distribution

ranged from 10.14 to 340.36 km (82.60 ± 45.50 km) and had a significant positive correlation with the number of attempts per clutch (Pearson's $t = 5.091$, df = 235, r = 0.315182, $p = 7.31 \times 10^{-7}$).

3.5. Movement patterns

Two broad inter-nesting movement patterns were observed: females who stayed exclusively around the Raine Island reef throughout the entire inter-nesting period (i.e. all clutch periods were spent at Raine Island, 'residents', n = 19) and females who used nearby reefs in addition to Raine Island's reef ('travellers', n = 20). Excluding time between unsuccessful clutch attempts, the travellers can be further grouped by females who spent all their time at other reefs and only returned to a nesting location to make a nesting attempt (n = 5) or females who spent time at the reef associated with their nesting site (Raine Island or Moulter Reef for no. 65542, who nests at both islands) and other reefs (n = 15) during their re-nesting interval (i.e. the time between a successfully laid clutch and the subsequent attempt). For both, the time between unsuccessful clutch attempts was typically spent near the nest site (i.e. Raine Island or Moulter Cay). However, 7 individuals spent time at other reefs before returning for another attempt.

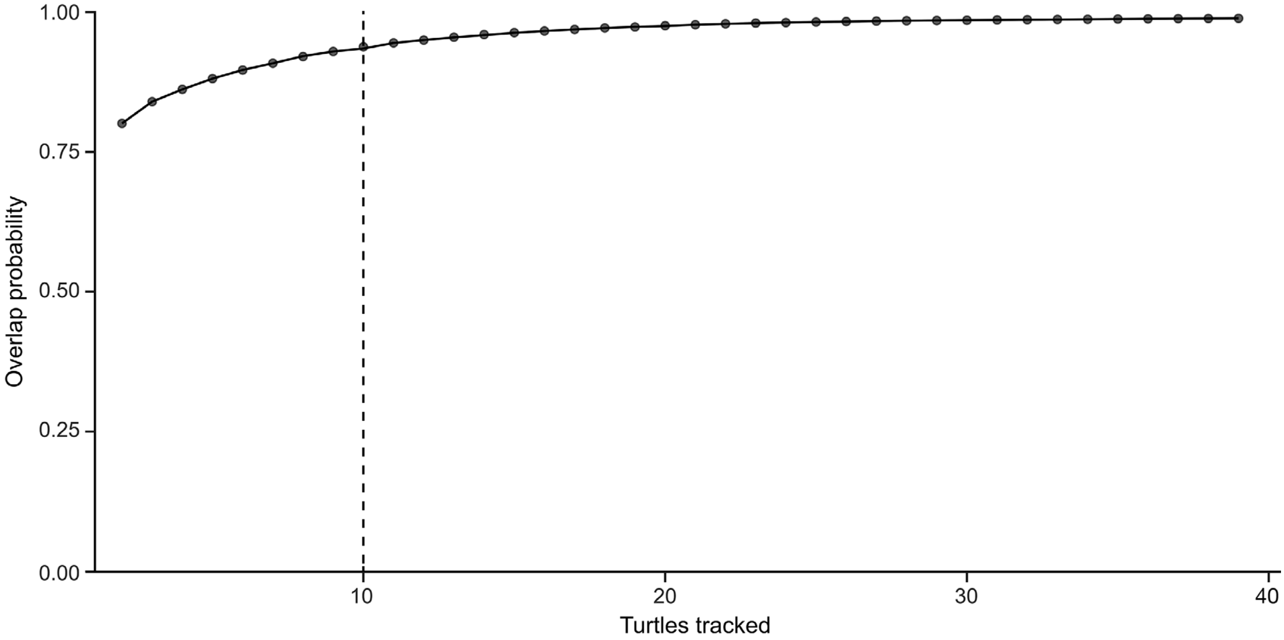

Fig. 3. Effect of sample size (number of turtles tracked) on estimating the spatial distribution of green turtles during the inter-nesting period. Each point on the curve is the mean value calculated from 1000 permutations. An asymptote was reached once the mean overlap probability reached 0.95 (dashed line); thus, the sample size was deemed sufficient to characterise spatial distribution

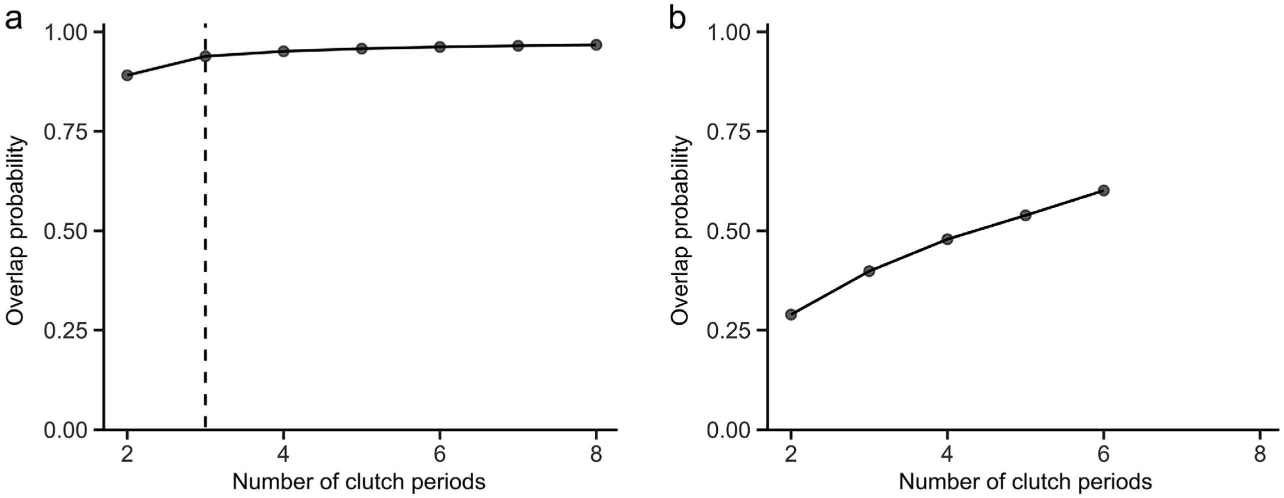

Fig. 4. Effect of sample size (number of clutch periods) on estimating the spatial distribution of an individual green turtle during the inter-nesting period. Each point on the curve is the mean value calculated from 1000 permutations. (a) An asymptote was reached once the mean overlap probability earned 0.95 (dashed line); thus, the sample size was deemed sufficient to characterise spatial distribution. (b) Note the absence of an asymptote, indicating insufficient samples

When comparing travellers and residents within each nesting season, travellers had a significantly higher TDM than residents (2017–2018 season: Mann-Whitney $U = 10$, p = 0.005; 2018–2019 season: Mann-Whitney $U = 8$, p = 0.001) (Table 2). In the 2017–2018 season, there was no significant difference between travellers and residents in the number of clutches laid (Mann-Whitney $U = 44$, p = 0.897) or the number of cumulative attempts (Mann-Whitney $U = 44.5$, p = 0.865). Similarly, the travellers of the 2018–2019 season did not significantly differ in the number of clutches laid (Mann-Whitney $U = 29$, p = 0.142) or the number of cumulative attempts (Mann-Whitney $U = 29.5$, p = 0.162).

Table 2. Comparison of travellers and residents of Raine Island in the 2017 and 2018 nesting seasons. All values are reported as mean ± SD. TDM: total distance moved

Year/movement pattern	n	TDM (km)	No. of clutches	No. of cumulative attempts
2017				
Travellers	12	750 ± 364	6.8 ± 1.9	15.4 ± 4.3
Residents	7	404 ± 106	7.0 ± 1.6	15.7 ± 4.3
2018				
Travellers	8	552 ± 90	7.9 ± 1.1	14.5 ± 3.5
Residents	12	349 ± 116	7.0 ± 1.3	11.8 ± 4.4

3.6. Fidelity to the nest site and loop trips

Most turtles (n = 37) exhibited fidelity to the nest site at Raine Island, with only 2 individuals laying clutches at Raine Island and nearby at Moulter Cay (e.g. Table 3, no. 45782 in 2017 and no. 65542 in 2018). During the nesting season, most females remained within 20 km of their nesting site(s), spending time at reefs at Raine, Moulter, Saunders, and other nearby unnamed reefs. Two individuals tracked during the 2017 nesting season travelled away from the Raine Island region after laying a clutch of eggs before returning to lay a subsequent clutch on Raine Island. One female travelled 220 km to the Torres Strait (no. 45771), and one travelled 120 km toward the mainland in Shelburne Bay, Queensland (no. 45787) (Fig. 5). Those clutch periods were excluded from home range and core area analyses, as those 2 data points were presumed to be outliers that were not representative of the average spatial use by the individual or sampled animals.

Female no. 45771 departed Raine Island on December 11, the day after she laid her fourth clutch of eggs at Raine Island (Fig. 5). She swam to the northeast into the eastern Torres Strait. She did not appear to stop in any location for longer than a day. On December 13, she reached Torres Strait and began her return trip to Raine Island. She was outside of the boundary of the GBRMP for 2 d. She returned to the Raine Island reef on December 17 and came ashore the following night to lay her fifth (of 8) clutch of eggs. Her total trip was 479 km long and took 7 d (68 km d^{-1}). She remained at the Raine Island reef and laid an additional 3 clutches. Once she laid her final clutch for the season, rather than migrating into the Torres Strait, she migrated to a foraging site in Bathurst Bay in the northern GBR. Female no. 45787 departed Raine Island on January 8, the day after laying her fifth clutch of eggs. She arrived at a coastal location on January 11 and remained there until January 19. She then swam back to Raine Island, arriving and laying her sixth and last clutch of eggs on January 25. The loop trip was 337 km long — 146 km from Raine Island to the coastal site (48 km d^{-1}) and a return trip of 191 km (28 km d^{-1}). On January 26, she migrated back to the same coastal area and remained there for the tracking duration.

Table 3. Nesting patterns of 2 female green turtles, with evidence of switching rookeries between clutches and within attempts for a single clutch. Turtle no. 45782 was tagged in 2017, and turtle no. 65542 was tagged in 2018

Turtle ID/ date	Location	Nesting activity
45782		
3 Nov	Raine Island	Clutch 1 laid, tag applied
16 Nov	Moulter Cay	Clutch 2 laid (2 attempts on same night)
2 Dec	Raine Island	Clutch 3 laid (7 attempts over 6 nights)
12 Dec	Moulter Cay	Clutch 4 laid (single attempt)
23 Dec	Moulter Cay	Attempt, duration 212 min
24 Dec	Moulter Cay	Attempt, duration 108 min
25 Dec	Moulter Cay	Attempt, duration 564 min
26 Dec	Moulter Cay	Attempt, duration 565 min
27 Dec	Raine Island	Attempt, duration 84 min
28 Dec	Raine Island	Attempt, duration 328 min
29 Dec	Raine Island	Clutch 5 laid
30 Dec	Raine Island	Departed for foraging area
65542		
22 Oct	Raine Island	Clutch 1 laid, tag applied
5 Nov	Moulter Cay	Clutch 2 laid
17 Nov	Moulter Cay	Attempt, duration 478 min
18 Nov	Moulter Cay	Attempt, duration 514 min
19 Nov	Moulter Cay	Clutch 3 laid
30 Nov	Raine Island	Attempt, duration 299 min
1 Dec	Raine Island	Attempt, duration 28 min
2 Dec	Raine Island	Clutch 4 laid
14 Dec	Moulter Cay	Clutch 5 laid
24 Dec	Moulter Cay	Attempt, duration 408 min
25 Dec	Moulter Cay	Attempt, duration 45 min
26 Dec	Moulter Cay	Clutch 6 laid
7 Jan	Moulter Cay	Clutch 7 laid

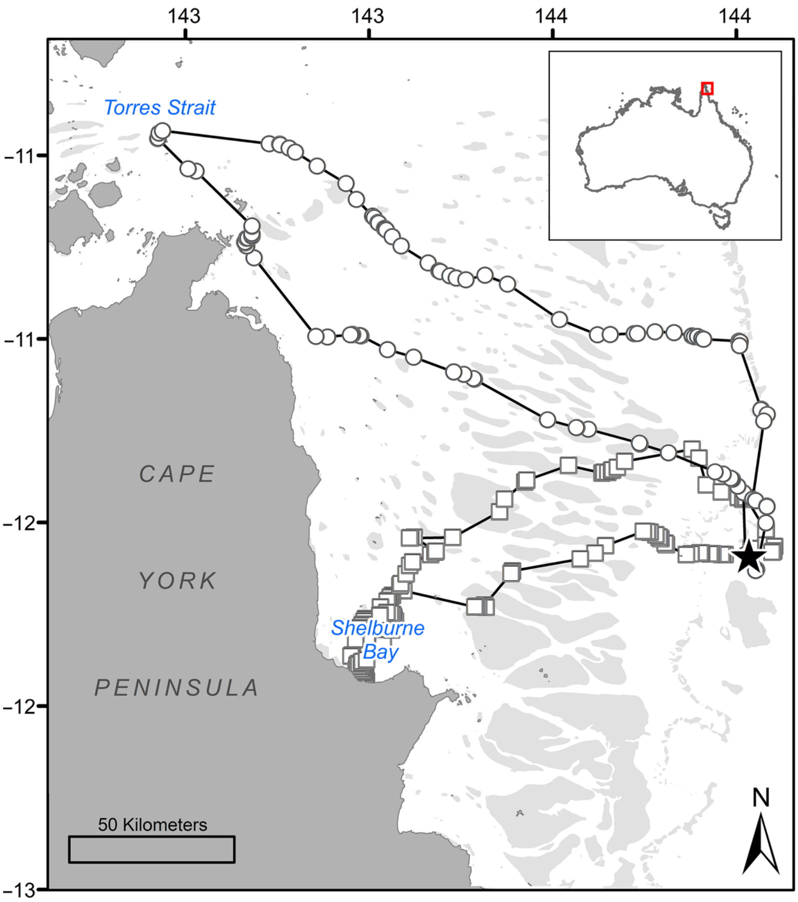

Fig. 5. Loop trips of 2 female green turtles during an inter-nesting interval before returning to Raine Island. Circles show the loop trip of individual no. 45771, and squares show the loop trip of individual no. 45787. Both individuals began their trips at the star (Raine Island)

3.7. Depth

The majority of locations (points) for all nesting turtles (87.8%) were within waters less than 50 m deep, with nearly half the locations (42.9%) within waters with a maximum depth of 10 m. Those points were found mainly within reef flats and coastal waters. The remaining points were located above sea level (<10 m) (2.9%) within reef flats, within waters of a maximum depth between 50 and 100 m (4.7%) around and past reef edges and the open sea, and within waters over 100 m deep (4.7%), away from reefs.

4. DISCUSSION

The nesting green turtles of Raine Island exhibit a high degree of fidelity to their nest area, with only 2 individuals splitting their clutches between Raine Island and Moulter Cay. All but 2 females (95%) remained close to their nesting beach (<20 km) throughout the inter-nesting period, consistent with other stocks of green turtles (Liew & Chan 1992, Hays et al. 1999, Blanco et al. 2013, Esteban et al. 2015, Hart et al. 2017, Tucker et al. 2020, Shimada et al. 2021b). In general, females displayed 2 main movement patterns during clutch periods, either remaining solely at Raine Island's reef or spending time at nearby reefs in addition to Raine Island (or Moulter Cay's reef if a clutch was laid there). The collective (i.e. overlapped) home range area for all 39 females of the 2017–2018 and 2018–2019 seasons was 205 km^2, encompassed within the 20 km radius defined as the critical inter-nesting habitat for this northern GBR stock (Commonwealth of Australia 2017).

Most females in this study (n = 37) laid all their clutches at Raine Island, though there were 2 individuals (1 in each season) who laid clutches at Moulter Cay as well, which has been previously observed in this population (Limpus et al. 2003). Although most females display a high degree of intra- and inter-season fidelity to their nesting area (Limpus et al. 1992, Limpus 2008), varying degrees of fine-scale (inter-clutch) infidelity to the nest site occur for green turtles who nest in regions with islands or beaches near one another (Blumenthal et al. 2006, Hart et al. 2013, 2017, Weber et al. 2013, Esteban et al. 2015, Shimada et al. 2021b, this study). This mixing of nesting sites within and among seasons could convey short-term advantages by mixing clutches into cooler or warmer locations and long-term adaptive advantages for coping with changes to island or beach conditions and geomorphological changes.

Identifying the factors contributing to reproductive output is important in monitoring this key rookery's long-term trends. Reproductive output may be related to the breeding history of an individual and the length of the nesting season (Hamann et al. 2003, 2022) as well as a complex set of interactions between environmental conditions, foraging area quality, and morphology, meaning populations within the same species will vary in their reproductive output (Limpus et al. 2001, Broderick et al. 2003, Shimada et al. 2021b). However, there have been limited studies on the impacts of inter-nesting activities and clutch frequency (i.e. the number of clutches laid per individual in a season). As sea turtles are primarily aphagic during the nesting season (Bjorndal 1985, Hays et al. 1999), minimising energy expenditure and optimising energy reserves is likely crucial. It therefore seems logical that conserving energy via restricting movements or selecting particular micro-habitats would be the preferred strategy to contribute to the higher reproductive output (e.g. Hays et al. 1999, Chambault et al. 2016, Raposo et al. 2023). However, this was not uniformly the case for tracked individuals in this study. Differences in clutch frequency between travellers and residents tracked for both seasons were minor and not statistically significant.

Further, total TDM was not correlated with the number of clutches laid. These results suggest that clutch frequency is unrelated to movement patterns during the inter-nesting period. There was a weak positive correlation between TDM and the number of attempts, which may be attributed to unsuccessful attempts and associated return trips to the nesting beach for successful oviposition. Alternatively, this correlation may be influenced by small sample sizes, as there was high variation between individuals. Despite this correlation, the cumulative number of attempts did not seem to affect the clutch frequency either: the 2017 travellers had nearly the same number of average cumulative attempts and clutches as the 2017 residents, and the 2018 travellers had a greater number of cumulative attempts but also a greater average number of clutches than residents (albeit differences were not statistically significant).

Overall, the cumulative number of attempts was not correlated with the number of clutches. Instead, differences in clutch frequency of travellers and residents may be attributed to other factors. The density of turtles in the 2 seasons studied here differed greatly, with the density of turtles in the 2017–2018 season 10-fold that of the 2018–2019 season (Hamann et al. 2022). This higher-density nesting can negatively affect nesting success through interactions with conspecifics such as competition for space or disturbance while digging (Limpus et al. 2003, Tiwari et al. 2006). However, it does not appear to impact the ability of females to persist through additional attempts and throughout the nesting season (Jessop 2001, Hamann et al. 2003). This resilience is facilitated by the ability of turtles to downregulate their adrenocortical response when faced with the challenges and density-related disturbances of mass nesting behaviour (Jessop et al. 1999). Previous studies report the influence of the impact of ENSO and primary productivity (Ramírez et al. 2021) or the size of females (Broderick et al. 2003) on clutch frequency, and further studies are warranted to determine the effects of these factors on this population.

A unique feature of our study was tracking turtles across what is likely to be their entire inter-nesting period (i.e. all or nearly all movements throughout the nesting season) instead of a short period of the inter-nesting period. This enabled us to examine each clutch period and estimate the number of intervals needed to characterise the inter-nesting habitat for an individual (as per Shimada et al. 2012, 2016). The 2017 season had more travellers, and tracked turtles had a more extensive home range, potentially resulting from a higher density of nesting females in the inter-nesting habitats for that season (approximately 10-fold; Hamann et al. 2022). Just as the high density of turtles on the beach can negatively affect nesting success (Limpus et al. 2003), it is possible that the density of turtles in a nesting season can affect the availability of preferred in-water inter-nesting habitats. This may have driven more turtles to seek reef habitats elsewhere to rest (again, more travellers in 2017–2018). Alternatively, they might have fidelity to an inter-nesting site across seasons, but this remains to be tested (Walcott et al. 2012). A key knowledge gap that could be addressed by coupling satellite telemetry with tri-axial data loggers and hydrodynamic modelling would be examining the habitat choices of turtles as they rest between clutches.

Sea turtles are capital breeders who primarily rely on stored lipids as their energy source during the nesting season (Hamann et al. 2003). Thus, they typically remain near their nesting beach to conserve energy (Hays et al. 1999, Blanco et al. 2013). The use of satellite telemetry has revealed that some individuals, however, will undertake an extensive trip during the inter-nesting period before returning to their nesting beach (green turtles *Chelonia mydas*: Troëng et al. 2005, Blumenthal et al. 2006, Hart et al. 2013, Chambault et al. 2016; loggerhead turtles *Caretta caretta*: Rees et al. 2010, Schofield et al. 2010). In our study, 2 females in the 2017–2018 season, nos. 45770 and 45787, travelled beyond the nearby reefs, undertaking an oceanic loop to Torres Strait and Shelburne Bay, respectively, during a clutch period before returning to Raine Island to nest. This behaviour may be associated with foraging, as it is believed that some populations will forage if resources are available (Hays et al. 2002, Delcroix et al. 2009, Fuller et al. 2009, Cheng et al. 2013), and possibly turtles at Raine Island (Tucker & Read 2001). However, marine turtles need an approximately empty digestive tract if they are to have sufficient space within their fixed-volume body cavity to facilitate the creation and movement of an entire clutch of eggs. For 1 of the 2 turtles, Shelburne Bay was subsequently revealed to be the foraging area of tracked female no. 45787; hence, she would have known it was a seagrass-foraging habitat. However, the other turtle (no. 45771) moved into the eastern Torres Strait. Although it was not her resident foraging area (she eventually migrated a similar distance but south to the Queensland coastline), it is an area with year-round seagrass and known as a habitat for green sea turtles and dugong. These 2 females may be exhibiting behavioural plasticity, wherein some females choose to gain energy by foraging. In contrast, most conserve energy by resting or remaining close to their nesting habitats (data from Hays et al. 2002 and this study). Whether these females foraged is not confirmed; however, no. 45771 was only within eastern Torres Strait for 2 d. Although this behaviour could be explored in future studies with the use of stable isotopes, 3-dimensional data loggers, animal-borne digital cameras (Fuller et al. 2009), video footage recorded from an ROV (Patel et al. 2016), or jaw/beak movement sensors (Fossette et al. 2008, Hochscheid et al. 2013), low sample sizes would likely hinder a structured survey.

Raine Island and Moulter Cay are situated outside the edge of the continental shelf and thus adjacent to deep water (>100 m depth). Yet, our tracked females were mainly found in shallower waters, with nearly half the locations within waters less than 10 m deep. In addition, hotspots of habitat use were generally concentrated along reef edges, as opposed to deeper water or reef flats (see Dawson & Smithers 2014), and there was little similarity in the locations of reef crest habitats used in 2017 and 2018. This use of shallower reef edge/crest waters is consistent with studies of other populations of nesting green turtles (Liew & Chan 1992, Sato et al. 1998, Hays et al. 2000, Blanco et al. 2013, Hart et al. 2013, 2017, Chambault et al. 2016, Mettler et al. 2020) and has been observed in this population as well (Bell et al. 2009). The choice of shallow waters may be influenced by factors such as the preferred depth for obtaining neutral buoyancy (Hays et al. 2000), the presence of resting ledges on the reef crest (Hays et al. 2002, Bell et al. 2009), or avoidance of predators such as tiger sharks *Galeocerdo cuvier* (Hammerschlag et al. 2016).

5. CONCLUSION

Understanding how turtles use their inter-nesting habitats is key to protecting these areas from anthropogenic impacts and setting targets for management intervention, especially in areas with no spatial protection or areas where turtles move in and out of protected habitats. Our results support prior research that indicates turtles have high, but variable, intra-season site fidelity for nesting sites, and micro-habitat selection does not appear to influence reproductive output. Based on our results, tracking females for a sub-set of their clutches would likely generate similar home range estimates to those in studies tracking turtles for the whole nesting season. This justifies the use of archival-based data logger tags, which are less expensive and tend to be deployed for smaller time frames.

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