Satellite tracking reveals critical habitats and migratory pathways for green and hawksbill turtles nesting in Montserrat, Eastern Caribbean

**Jack Wiggins[1],*, Brendan J. Godley[1], John Jeffers[2], Kristian Metcalfe[1],
Alwyn R. Ponteen[2], Peter B. Richardson[3], Amdeep Sanghera[3], Nicola Weber[1],
Sam B. Weber[1]**

[1]Centre for Ecology and Conservation, Faculty of Environment, Science and Economy, University of Exeter, Penryn,
Cornwall TR10 9FE, UK
[2]Fisheries and Ocean Governance Unit, Department of Agriculture, Ministry of Agriculture, Lands, Housing and Environment,
Government of Montserrat, Brades, Montserrat
[3]Marine Conservation Society, Ross on Wye, Hereford HR9 5NB, UK

ABSTRACT: The United Kingdom Overseas Territory of Montserrat supports modest but regionally important nesting populations of green and hawksbill turtles. However, knowledge of the spatial ecology and regional connectivity of these populations is limited. Here, we provide the first detailed description of the spatial distribution, migratory connectivity, and habitat use of 9 adult female green turtles *Chelonia mydas* and 1 adult female hawksbill turtle *Eretmochelys imbricata* tagged with satellite transmitters at 4 nesting beaches in Montserrat. Two critical aggregation areas for inter-nesting green turtles were identified along the western coast of Montserrat which could act as focal points for spatial protection. Nine individuals, including the hawksbill turtle, performed transboundary post-nesting migrations, covering distances from 45 to 1013 km, and crossing 10 different national jurisdictions. Green turtles migrated to foraging grounds in Antigua and Barbuda (n = 4), United States Virgin Islands (n = 2), Puerto Rico (n = 1), and Dominican Republic (n = 1), whereas the hawksbill turtle migrated to a foraging ground in Guadeloupe. One green turtle remained resident in Montserrat. Within foraging grounds, green turtles primarily occupied sand, seagrass, and hardbottom algal habitats located in shallow (<25 m) coastal waters. On average, turtles spent 22 and 24 % of their time within Marine Protected Areas during migration and foraging periods, respectively. Our results provide novel insights into the ecology of individuals nesting at a previously understudied rookery that can be used to inform local and regional management.

KEY WORDS: Sea turtle · Satellite tracking · Migration · Foraging · Inter-nesting · Habitat use · Montserrat · Caribbean · *Chelonia mydas* · *Eretmochelys imbricata*

1. INTRODUCTION

Many marine megavertebrates (i.e. marine mammals, seabirds, elasmobranchs, and marine reptiles) are threatened throughout their distribution and are of serious conservation concern due to the multitude of anthropogenic stressors they face, including fisheries, habitat degradation, and climate change (Dias et al. 2019, Albouy et al. 2020, Patrício et al. 2021, Senko et al. 2022, Sherman et al. 2023). Historically, these species have been challenging to study due to their complex life histories and highly

mobile and elusive natures. However, advancements in biologging technology, such as improved battery life, reduced tag size, and better location accuracy, have enabled conservation practitioners to obtain fundamental information on the ecology and behaviours of marine megavertebrate species (McIntyre 2014, Yoda 2019, Renshaw et al. 2023), including marine turtles (Hays & Hawkes 2018), as well as provide crucial insights into their interactions with anthropogenic stressors (Bartumeus et al. 2010, Queiroz et al. 2016, 2019, Aschettino et al. 2020). This information can be used as a foundation to construct tailored conservation frameworks and policies required to achieve conservation objectives (Gredzens et al. 2014, Metcalfe et al. 2020).

Since the publication of the first marine turtle satellite tracking study over 4 decades ago (Stoneburner 1982), all 7 extant species have been tracked with satellite telemetry devices which has yielded invaluable insights into their intricate ecology and behaviours (see review by Hays & Hawkes 2018). Tracking studies have elucidated many details of the complex life histories of marine turtles, including ontogenetic shifts in habitat use (Doherty et al. 2020, Mansfield et al. 2021, Barbour et al. 2023) and adult reproductive migrations between foraging and breeding areas (Stokes et al. 2015, Peel et al. 2024). Such studies have also frequently been used to identify important inter-nesting and foraging areas (Snape et al. 2018, Hamilton et al. 2021, Webster et al. 2022, Lamont et al. 2023) that can be prioritised for spatial management (e.g. marine protected area [MPA] designation), provide insights into their exposure to various anthropogenic threats across life stages (e.g. fisheries and marine traffic, da Silva et al. 2011, Ashford et al. 2022, Iverson et al. 2020), and assess the level of protection afforded by current and proposed spatial management plans (Scott et al. 2012, Hart et al. 2013, Patrício et al. 2022, Lamont et al. 2023). Additionally, tracking studies have enhanced the ability of researchers to approximate key demographic parameters needed for accurate estimates of population sizes and trends, such as clutch frequencies, breeding intervals, and nest site fidelity (Weber et al. 2013, Santos et al. 2021, Shimada et al. 2021). As the availability of high-accuracy tracking devices (e.g. Fastloc-GPS; Hays et al. 2021) and remotely sensed habitat data has increased, more in-depth studies into the spatial ecology of marine turtles are now possible. This enables researchers to move beyond the earlier 'where do turtles go' paradigm, which primarily focused on identifying migratory routes and general movement patterns (Blumenthal et al. 2006, Hawkes et al. 2012, Becking et al.

2016). In practice, however, few studies have combined these datasets to study fine-scale habitat utilisation (Tanabe et al. 2023). Such studies can provide conservation practitioners with the information necessary to tailor management plans to precisely protect key habitats for populations (Tanabe et al. 2023).

Marine turtle nesting and foraging is extensive throughout the Wider Caribbean Region (WCR) (Eckert & Eckert 2019), and tracking studies have shown that populations within the WCR display wide regional connectivity, often transiting multiple geo-political zones between nesting sites and foraging grounds (Hart et al. 2019, Evans et al. 2024, Maurer et al. 2022, 2024). However, despite the comprehensive application of satellite telemetry in marine turtle research, notable data gaps remain (Hamann et al. 2010, Mazaris et al. 2014). One such example is the Lesser Antillean Island of Montserrat, where nests of 4 species of marine turtle have been recorded: the green turtle *Chelonia mydas*, hawksbill turtle *Eretmochelys imbricata*, loggerhead turtle *Caretta caretta*, and leatherback turtle *Dermochelys coriacea*. Nesting populations of green and hawksbill turtles in Montserrat have historically been described as modest yet regionally important at the Eastern Caribbean scale, whereas nesting by leatherback and loggerhead turtles has only occasionally been documented (Maylan 1983, Martin et al. 2005). While sporadic monitoring of marine turtle nesting in Montserrat has occurred since the 1990s, there is currently no information on the in-water distribution, migratory connections, or location of critical habitats for the island's marine turtle populations.

Montserrat has a traditional marine turtle fishery (Richardson et al. 2006) which is currently regulated by the Montserrat Turtles Act (1951, revised 2002). This legislation primarily protects breeding adults by enforcing a closed season between 1 June and 30 September that coincides with the peak marine turtle nesting season (Martin et al. 2005). During the open season (1 October–31 May), any marine turtle over 20 lbs (ca. 9.1 kg) as well as marine turtle eggs can be harvested, bought, and sold on the island, although rates of harvest are believed to be very low (Richardson et al. 2006). Incidental captures of marine turtles and other marine megavertebrates (e.g. sharks) in gillnets, Antillean fish pots or traps, and beach seines have been reported to occur in Montserrat, but the spatiotemporal distribution and rates of bycatch remain unquantified.

Montserrat does not yet have any MPAs or marine management zones designated for the protection and

preservation of species or habitats. However, the Government of Montserrat is currently considering refinements to the Turtles Act (1951, revised 2002), along with reviewing a new Fisheries, Aquaculture, and Ocean Resources Management Regulation and Plan, and National Ocean Policy. A marine spatial plan (MSP) was also recently proposed for Montserrat that suggests a series of nearshore management zones for conservation and human use (Flower et al. 2020). However, this did not include information on the in-water distribution of marine turtles (or any other marine megavertebrates) due to the lack of available data. To help address these knowledge gaps, this study presents the first detailed description of the spatial ecology of green and hawksbill turtles nesting in Montserrat based on analysis of satellite tracking data. We map inter-nesting distributions, regional migratory connectivity, and foraging areas, use recently developed regional habitat maps to assess habitat use, and evaluate the level of spatial protection afforded by existing and recently proposed management zones.

2. MATERIALS AND METHODS

2.1. Study site

The volcanic island of Montserrat (16.75, −62.20) is a United Kingdom Overseas Territory situated in the northeastern Caribbean, located approximately 45 km southwest of Antigua (Fig. 1). The island has a coastline of approximately 49 km, with the majority of green and hawksbill turtle nesting reported to take place along the leeward western coast between June and November, peaking in September (Martin et al. 2005). Montserrat's sandy beaches are dominated by black volcanic sand, with the exception of Rendezvous Bay, which primarily consists of white calcareous sand and is located on the northwest of the island (Martin et al. 2005). The coastal waters of Montserrat contain a variety of habitats including seagrass beds, algal reefs, and coral reefs (Gore et al. 2019, Flower et al. 2020) that support both juvenile and adult green and hawksbill turtle foraging aggregations (Martin et al. 2005). However, the in-water abundance and distribution of these populations remain unquantified. Between 1995 and 2010, the island's inshore and coastal habitats — including marine turtle nesting beaches — in the southern part of the island were severely impacted by multiple eruptions of the Soufrière Hills Volcano (Gore et al. 2019, Flower et al. 2020). Therefore, it has been suggested that marine

turtle nesting in the south of the island is very limited, yet this also remains unquantified. Due to continued seismic activity, a strictly controlled exclusion zone currently extends across approximately two-thirds of the island (Fig. 1A).

2.2. Tag deployment and data processing

Between 15 and 22 August 2021, 9 nesting green turtles and 1 nesting hawksbill turtle were equipped with Wildlife Computers SPLASH10-F Fastloc-GPS enabled satellite transmitters at 4 different nesting beach locations (Fig. 1A). Four transmitters were deployed at Rendezvous Bay (16.80869, −62.20493), 3 (including a single tag on a hawksbill turtle) at Woodlands Bay (16.76274, −62.22368), 2 at Isles Bay (16.73907, −62.23255), and one at Bunkum Bay (16.77136, −62.22066) (Fig. 1A, see Table 1). To prolong battery life, tags were programmed on a duty cycle to transmit only between the hours of 20:00−03:00 and 08:00−16:00 h GMT, which coincided with Argos satellite coverage across the Eastern Caribbean region. A daily limit of 250 Argos transmissions and 100 Fastloc-GPS attempts was also set (maximum successful GPS positions: $2\ h^{-1}$ or $24\ d^{-1}$), with an Argos repetition rate of 18 s at sea and 88 s during 'haul out' periods. In this case, a haul out — indicative of a potential nesting attempt — was defined as a period of 10 consecutive minutes in which the tag was dry for >30 s in 1 min. As an additional means of confirming nesting activity, tags also transmitted daily summary histograms of hours during which tags were dry for >60% of the time. Prior to deployment, tags were coated with 2 coats of copper-based antifouling paint (Micron 66, International Paints) to prolong tag life and minimise hydrodynamic drag associated with biofouling of the device.

Transmitters were deployed post-oviposition once nest covering was complete; while females were held in a wooden pen (2 × 2 m) to minimise movement and reduce the risk of injury. Prior to transmitter attachment, the curved carapace length (CCL) and curved carapace width (CCW) of each turtle were measured to the nearest 0.5 cm using a flexible tape measure. CCL was measured from notch-to-tip and CCW as the width across the widest point of the carapace, as described by Weber et al. (2017). The attachment site was then cleared of epibionts, lightly sanded with a 40 grit sanding block, and cleaned with acetone. As per established protocols (Esteban et al. 2017, Hays & Hawkes 2018, Hays et al. 2021), transmitters were attached to the second vertebral carapace scute using fibreglass cloth and a 2-part marine epoxy, and the
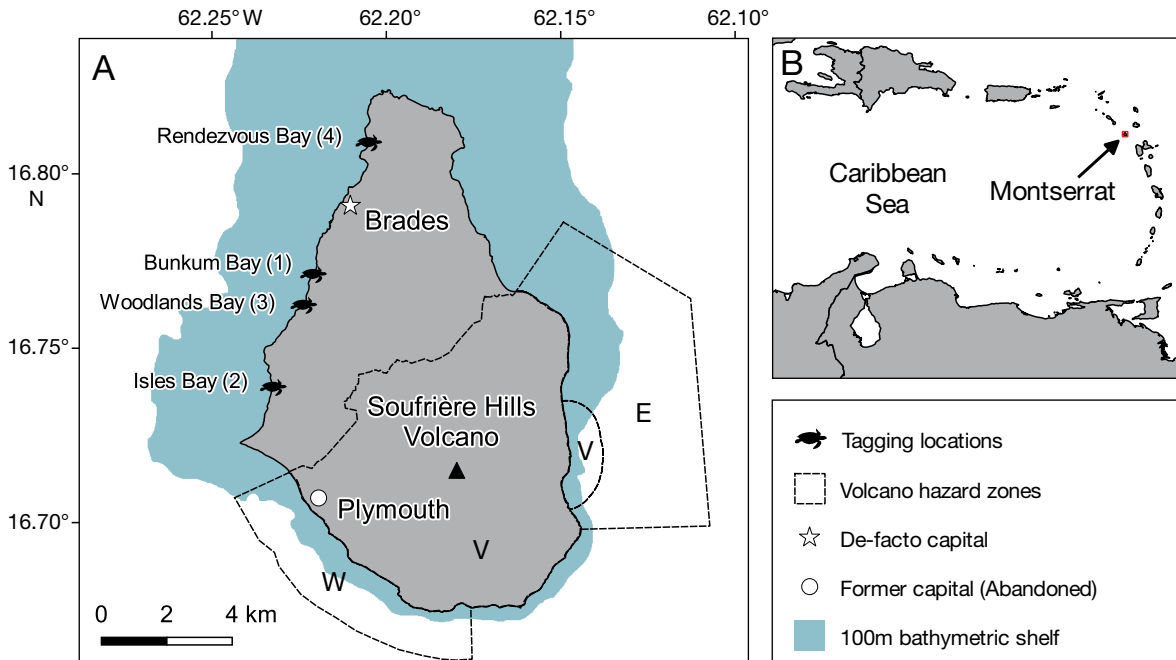
Fig. 1. (A) Locations where satellite transmitters were deployed on nesting green (n = 9) and hawksbill (n = 1) turtles. (B) Location of Montserrat within the Wider Caribbean Region. Numbers in parentheses: number of satellite transmitters deployed at each nesting beach. At hazard level 1 (as of 1 April 2024), volcano hazard zone V allows controlled access (no public access), and maritime zones E and W allow daytime transit only. Turtle illustration (Ray Chatterji) sourced from www.phylopic.org (© 2023 T. Michael Keesey)

entire footprint was covered in anti-fouling paint. Turtles were released immediately upon completion of the tagging procedure.

Telemetry data were downloaded using the Wildlife Computers Data Portal (https://www.wildlifecomputers. com) and filtered using the R package 'argosfilter' (Freitas 2022) to remove anomalous locations. A speed threshold of 5.4 km h^{-1} was used to remove biologically implausible Argos locations, based on the maximum travel speed recorded between consecutive, high-accuracy Fastloc-GPS positions in this study. This is similar to the threshold of $\geqslant$5 km h^{-1} that has previously been applied to tracking data for hard-shelled turtles (Witt et al. 2010b, Doherty et al. 2020, Haywood et al. 2020). All locations within 5 km of the previous position are automatically retained by the filter to account for Argos location errors. Argos positions with location class Z and Fastloc-GPS locations with a residual error value of >35 were also removed to improve the accuracy of the data (Dujon et al. 2014, Thomson et al. 2017, Hays et al. 2021).

2.3. State–space modelling

To identify inter-nesting areas, migration routes and foraging grounds, a 2-stage analysis process

was applied (for details see McClintock 2017). First, continuous-time correlated random walk (CTCRW) models were fitted to each individual track via the R package 'crawl' (Johnson & London 2018) and used to generate temporally regular positional estimates at 1 h intervals. The CTCRW model implemented in crawl consists of a movement model, which represents a position at any given time as the sum of autocorrelated velocities across previous steps plus a starting location, and an error model, which describes uncertainty in the observed locations (Johnson et al. 2008). Here, Argos location errors were assumed to follow a bivariate normal distribution based on the anisotropic error ellipse reported by the Argos System (McClintock et al. 2015), while Fastloc-GPS location errors were assigned based on the number of satellite fixes using empirical estimates in Dujon et al. (2014). GPS errors were assumed to be isotropic with a radius equal to the 63.2% quantile of observed errors from Dujon et al. (2014), which is equivalent to the $\sqrt{2}$-sigma ellipses provided by Argos (McClintock et al. 2015). A Laplace prior was specified for the autocorrelation parameter in the movement model as it resulted in the best convergence and model diagnostics across individuals. Fitted CTCRW models were then used to simulate 100 realisations of the position process for each track, resulting in 100 pos-

terior estimates of an individual's location at each hourly interval.

Next, discrete-time hidden Markov models (HMMs) were fitted to the CTCRW model outputs to differentiate between 2 behavioural states: 'resident' (area-restricted-search-type movements) and 'migration' (directional-travel-type movements) based on step length and turning angle in the interpolated tracks. HMMs were implemented in the R package 'momentuHMM' (McClintock & Michelot 2018) using the 'multiple imputation' method, which accommodates temporal irregularity and location error (McClintock 2017). The method involves fitting HMMs to multiple, temporally regular tracks simulated from the posterior of the CTCRW models and pooling the resulting parameter estimates to determine the most probable state sequence for each track. For computational efficiency, 10 posterior tracks were sampled per individual for HMM fitting, and the state assignments for each location were then joined to the 100 posterior tracks sampled in the previous step. A k-means clustering algorithm ($k = 2$) was used to select appropriate starting values for the state-dependent probability distribution parameters (Clark et al. 2019), assuming a gamma distribution for step length and a von Mises distribution with a mean of zero for turning angle. Tracks were pooled by species for the HMM analysis to identify consistent movement behaviours across individuals (see 'Data availability').

HMMs fit to 2-dimensional tracking data cannot distinguish between different forms of resident-type or migratory-type behaviour. Therefore, additional criteria were applied to further classify the HMM states into 5 distinct movement phases based on prior knowledge of marine turtle breeding cycles (inter-nesting, inter-nesting migration, post-nesting migration, migratory stopovers, and foraging). We defined any migratory-type behaviour displayed before the final nesting event (i.e. haul out) as 'inter-nesting migration' and migratory-type behaviour following the final nesting event as 'post-nesting migration'. Resident-type behaviour that occurred prior to a post-nesting migration (or for 7 d following the final nesting event if a post-nesting migration did not take place) was defined as 'inter-nesting', while resident behaviour displayed after the final bout of post-nesting migration (or >7 d after the final haul out) was defined as 'foraging'. Short bouts of resident behaviour that occurred in the middle of post-nesting migrations were classed as migratory 'stopovers'. These classifications do not imply that feeding does not occur at nesting grounds or during stopovers but serve to separate the major phases of movement.

Fastloc-GPS technology has greatly improved the accuracy of location data compared to Argos locations and has been shown to yield more accurate estimates of fine-scale movements of marine turtles (Thomson et al. 2017). Therefore, CTCRW models were also run using only Fastloc-GPS locations. The outputs from these models were used to assess fine-scale space and habitat use, in comparison to models that incorporated both Fastloc-GPS and Argos locations, which are provided in the Supplement at www.int-res.com/articles/suppl/n055p295_supp.pdf.

2.4. Spatial analyses

2.4.1. Locations on land

Like most state—space models for marine vertebrate tracking data, the CTCRW models we used do not account for the presence of land when simulating movement paths, meaning terrestrial position estimates need to be handled post hoc. Most previous studies have either removed locations on land or moved them to the closest coastal location (Hawkes et al. 2012, Shimada et al. 2016, Dawson et al. 2017, Tanabe et al. 2023), although neither approach is ideal, as the former discards information and both may introduce unquantified spatial biases. Here, rather than treating terrestrial locations as single points to be moved or removed, we use their correct interpretation as probability ellipses to redistribute portions of the probability density that overlap land. For each hourly location in the CTCRW simulated tracks, any posterior samples that fell on land were removed and resampled from a bivariate normal distribution approximating the posterior of the CTCRW model. This procedure was repeated until no terrestrial locations remained, resulting in 100 posterior draws from the portion of the error ellipse that overlaps the sea. In rare cases where the entire error ellipse overlapped land, these locations were excluded from further analysis.

2.4.2. Home ranges and core use areas

To identify home ranges and core use areas during inter-nesting intervals and within foraging grounds (i.e. periods of 'resident-type' behaviour), 2-dimensional kernel density estimation (KDE) was performed using the R function 'kde2d' in the R package 'MASS' (Venables & Ripley 2002). Kernel density estimations were calculated using all posterior estimates generated from each CTCRW model. The output res-

olution of the KDE was 0.1 km^2 and was used to generate volume contours representing the 10–90% utilisation distributions (UDs) at 10% increments and the 95% UD. The smoothing parameter for each UD was determined using the reference bandwidth calculated using the 'bandwidth.nrd' function in the R package 'MASS' (Venables & Ripley 2002). Individual green turtle inter-nesting KDEs were also overlayed and averaged to generate population-level inter-nesting UDs. This analytical approach was performed to minimise biases in sampling durations by ensuring all green turtles contributed equally to the generation of the population-level inter-nesting UDs, irrespective of inter-nesting tracking duration. Inter-nesting and foraging home ranges and core use areas were defined as 95% UD and 50% UD, respectively (i.e. the smallest area in which turtles have a 95 and 50% probability of being located).

2.4.3. Inter-nesting intervals and nest site fidelity

Inter-nesting intervals of marine turtles differ across species and populations, spanning from one to several weeks (Robinson et al. 2022). Therefore, we defined inter-nesting intervals as the duration between 2 consecutive haul out events that occurred more than 5 d apart. Haul out events that occurred within 5 or fewer consecutive days were grouped as 'nesting attempts' for the same clutch. The final haul out event observed for each group of nesting attempts was then classified as a successful nesting event and used to calculate individual clutch frequencies and nest site fidelity.

2.4.4. MPA and Exclusive Economic Zone use

The spatial distribution of tagged turtles during inter-nesting intervals was also compared to the most recent MSP proposed for Montserrat by Flower et al. (2020) (Fig. 2). The proposed zoning plan shapefile was used to calculate the percentage of inter-nesting posterior estimates from the CTCRW models that fall within each of the proposed zone types ('zone use'). The R package 'terra' (Hijmans 2023) was used to assign inter-nesting posterior estimates from the CTCRW

models a zone type. Zone use estimates for each simulated inter-nesting track (100 posterior tracks per individual) were then combined to estimate mean zone use and 95% credible intervals (CI) for each individual using the R package 'tidybayes' (Kay 2023). Mean zone use estimates of the tracked green turtles were also combined to calculate population-level inter-nesting zone use estimates and 95% credible intervals. The same methods were also applied to estimate the spatial distribution of the tracked turtles within foraging grounds in relation to MPA boundaries. Migratory transits through Exclusive Economic Zones (EEZs) and MPAs were calculated in QGIS v.3.34.3 using spatial polygons of EEZs and MPAs downloaded from the Marine Regions (Flanders Marine Institute 2024) and Protected Planet (UNEP-WCME and IUCN 2023) databases, respectively.

2.4.5. Habitat use within foraging grounds

To estimate habitat utilisation within foraging grounds, a recently developed high-resolution (4 m) benthic habitat map of the Caribbean was used to assign a habitat class to each 'foraging' posterior estimate from the CTCRW models using the R package 'terra' (Hijmans 2023). Habitat use estimates for each posterior foraging track (100 posterior tracks per individual) were then combined to estimate mean habitat use and 95% credible intervals for each individual and
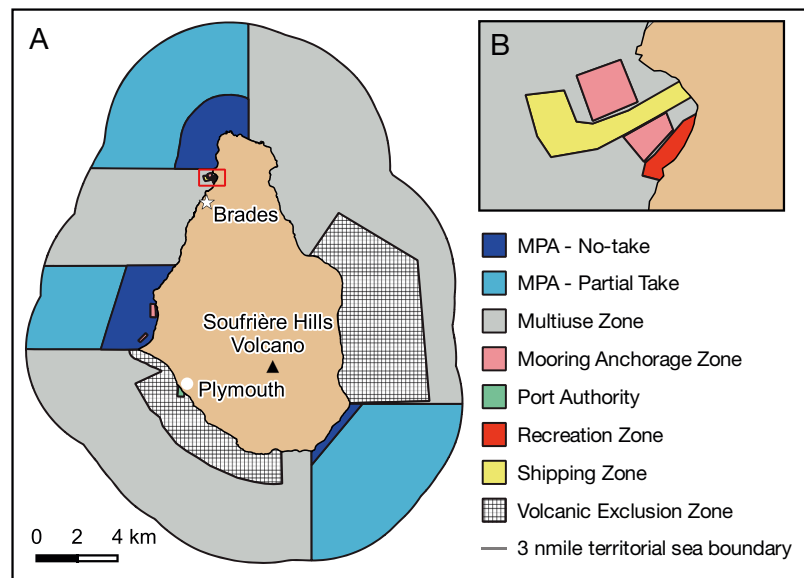

Fig. 2. (A) Marine spatial plan for Montserrat proposed by Flower et al. (2020). Red polygon: Little Bay. (B) Close-up of shipping, mooring, and recreation zones proposed for Little Bay

at the population level for the tagged green turtles using the R package 'tidybayes' (Kay 2023). Benthic habitat rasters were generated by Schill et al. (2021) from supervised classification of satellite imagery and distinguished 13 shallow marine habitat classes (up to 30 m water depth), with an overall accuracy of 80%. Water column depth occupancy during inter-nesting intervals and within foraging grounds was also calculated using gridded bathymetric rasters downloaded from the General Bathymetric Chart of the Oceans (GEBCO; https://download.gebco.net/).

2.4.6. Diurnal and nocturnal space use

The spatial distribution and size of diurnal and nocturnal foraging UDs for each individual were also assessed to identify whether turtles displayed diel variation in space use within foraging grounds. Firstly, foraging posterior estimates from the CTCRW models were assigned as either day or night based on local sunrise and sunset times calculated using the R package 'suncalc' (Thieurmel & Elmarhraoui 2022). The degree of overlap between diurnal and nocturnal UDs was then assessed using Bhattacharyya's affinity (BA) index using the 'kerneloverlaphr' function from the R package 'adehabitatHR' (Calenge 2023). The BA index ranges between 0 (no overlap) and 1 (complete overlap) and has been widely used and often considered the most appropriate index for measuring the similarity between UDs generated from animal tracking data (Fieberg & Kochanny 2005, Oppel et al. 2018, Hardin et al. 2024). To assess whether the observed diurnal—nocturnal overlap was significantly different than expected by chance when data is partitioned, the R package 'permute' (Simpson 2022) was used to perform restricted permutations (n = 100) via randomized cyclic shifts of the day and night labels within each posterior simulated foraging track and the BA index recomputed at each iteration. The p-values were then calculated based on the proportion of permuted kernel overlaps that were smaller than the observed overlap (i.e. if less than 5% of permuted overlaps are less than the observed overlap then we assume that the diurnal and nocturnal UDs are significantly different at $p < 0.05$). Differences in the area (km^2) of diurnal and nocturnal foraging home ranges and core use areas were analysed using Wilcoxon signed-rank tests. Comparisons between diurnal and nocturnal space use overlap during inter-nesting periods were not calculated, as behaviour inferences can be confounded due to nocturnal nesting and mating.

3. RESULTS

3.1. Study animals and tracking durations

The 9 satellite-tagged green turtles *Chelonia mydas* had a mean (±SD) CCL of 109.7 ± 5.8 cm (range: 96—116 cm) and CCW of 98.4 ± 5.2 cm (range: 89—106 cm), whereas the tagged hawksbill turtle *Eretmochelys imbricata* measured 84 cm CCL and 77 cm CCW. Turtles were tracked for a total of 2531 tracking days; green turtles were tracked for between 218 and 262 d (mean ± SD: 252 ± 15 d) and the hawksbill turtle was tracked for 260 d (Table 1). A total of 26 280 GPS positions and 43 221 Argos positions were received. Of the Argos positions received, 19% were classified as location classes (LC) 1—3, while 81% were classified as LC 0, A, and B. The estimated error radius for the different Argos LC are as follows: >1500 m for LC 0, between 500 and 1500 m for LC 1, between 250 and 500 m for LC 2, and <250 m for LC 3. Argos is unable to assign estimated errors for LC A and B (Argos 2017).

3.2. Inter-nesting behaviour and space use

Post transmitter deployment, 9 of the tagged turtles, including the hawksbill turtle, remained within Montserrat's coastal waters throughout the duration of the nesting season. However, one green turtle (Turtle J), after laying 3 clutches in Montserrat, commenced a 197 km (maximum straight-line displacement: 152 km) inter-nesting migration 27 d after transmitter attachment in a southerly direction towards Dominica. This turtle then spent 2 d in the coastal waters of northwest Dominica, displaying inter-nesting (resident) type behaviours before migrating back to Montserrat, where she laid 4 more clutches (Fig. S1). This individual travelled a distance of 424 km during this period.

Inter-nesting movements were tracked for a total of 618 d, spanning 50 inter-nesting intervals between 15 August and 12 November. Individual inter-nesting intervals ranged from 8 to 22 d (mean ± SD: 11 ± 2 d, n = 48) for the green turtles and from 14 to 16 d (15 ± 1 d, n = 2) for the hawksbill turtle. Throughout the nesting season, green turtles laid a minimum of 4—8 clutches (mean ± SD: 6 ± 1 clutches) across 1—4 beaches (mean ± SD: 2 ± 1 beaches), whereas the hawksbill turtle laid a minimum of 3 clutches on Woodlands Bay (Table 1, Fig. S2). It is important to note that individuals may have nested prior to transmitter attachment; therefore, actual clutch frequencies may have been higher than observed. Additionally, estimated green turtle clutch frequency should be regarded as conservative, as occa-

Table 1. Summary data for the 9 nesting green turtles *Chelonia mydas* (CM) and the single nesting hawksbill turtle *Eretmochelys imbricata* (EI) tagged with satellite transmitters in Montserrat, Eastern Caribbean, during August 2021. Inter-nesting and foraging home ranges and core use areas are classified as 95 and 50% utilisation distributions (UDs), respectively. Note that Turtle B did not perform a post-nesting migration and remained resident within Montserrat's coastal waters following completion of nesting until tag transmissions ceased. Coordinates are for the location of foraging area centroids. PTT: platform terminal transmitter; CCL: curved carapace length; CCW: curved carapace width; USVI: United States Virgin Islands

Turtle ID	Species	PTT	CCL (cm)	CCW (cm)	Tagging date (dd/mm/yyyy)	Tagging location	Tracking duration (d)	50 and 95% inter-nesting UDs	Migration period (d)	Migratory path length (km)	Migratory displacement (km)	No. of EEZs and MPAs transited	Location of foraging grounds (coordinates)	50 and 95% foraging UD (km²)
A	CM	214195	111	106	15/08/2021	Rendezvous Bay	239	0.9 and 8.6	15	1013.1	897.8	7 and 4	Dominican Republic (18.19211, −70.53676)	1.8 and 10.9
B	CM	214196	96	89	16/08/2021	Bunkum Bay	261	0.5 and 4.3	0	0	0	0	Montserrat (16.77392, −62.22327)	0.2 and 0.9
C	CM	214197	108.5	97	20/08/2021	Woodlands Bay	257	0.6 and 6.2	4	331.9	299.6	6 and 2	USVI (17.67799, −64.88197)	0.4 and 1.7
D	EI	214198	84	77	17/08/2021	Woodlands Bay	260	0.1 and 0.5	4	152	135.1	3 and 1	Guadeloupe (16.21719, −61.07905)	0.2 and 2.1
E	CM	214199	108	99	22/08/2021	Rendezvous Bay	255	0.2 and 1.5	7	506.2	465.7	7 and 4	Puerto Rico (17.94310, −66.44417)	2.0 and 12.3
F	CM	214200	116	104.5	22/08/2021	Rendezvous Bay	218	1.3 and 17.8	1	44.8	41	2 and 0	Antigua (17.07294, −61.90777)	3.0 and 19.3
G	CM	214201	109	101	16/08/2021	Isles Bay	261	0.5 and 4.8	7	322.6	290.5	6 and 5	USVI (17.68767, −64.80932)	0.1 and 1.0
H	CM	214202	114.5	95	15/08/2021	Rendezvous Bay	262	1.4 and 14.5	1	124.8	103.6	2 and 3	Barbuda (17.68870, −61.88604)	0.6 and 3.4
I	CM	214203	112	95	18/08/2021	Woodlands Bay	259	0.5 and 3.1	1	119.2	95.5	2 and 1	Barbuda (17.58089, −61.81607)	0.1 and 0.5
J	CM	214204	112	99	18/08/2021	Isles Bay	259	0.3 and 2.0	2	67.8	46.7	2 and 0	Antigua (17.01723, −61.89650)	0.6 and 4.2

sional long inter-nesting intervals (e.g. 22 d interval of Turtle E) may indicate missed nesting events due to tag error or gaps in satellite coverage.

Of the 57 recorded green turtle nesting events (including those during which tags were deployed), 29.8% (n = 17) occurred outside of the existing closed season for legal turtle harvesting. In contrast, all recorded hawksbill nesting events occurred during the closed season. For green turtles that nested on multiple beaches, the straight-line distance between the 2 beaches that were the furthest distance apart ranged between 1.3 and 15 km (mean: 4.7 km). During inter-nesting intervals, 75.7% (CI: 75.2–76.2%) of green turtle locations and 99.7% (CI: 98.9–100%) of the hawksbill locations were in waters ≤25 m deep (Table S1).

Individual inter-nesting home ranges (95% UD) and core use areas (50% UD) of the green turtles ranged from 1.5–17.8 km^2 (mean ± SD: 7.0 ± 5.7 km^2) and 0.2–1.4 km^2 (0.7 ± 0.4 km^2), respectively (Table 1, Fig. S2), whereas the tagged hawksbill turtle had a considerably smaller inter-nesting home range of 0.5 km^2 and core use area of 0.1 km^2 (Fig. 3B, Table 1). The mean overlap of the 9 green turtles' inter-nesting UDs revealed a population-level inter-nesting home range of 16.7 km^2 and 4 population-level core-use

areas along the western coast of Montserrat which covered an area of 1.7 km^2 (Fig. 3A).

3.3. Post-nesting migrations

Tracked turtles displayed 2 types of post-nesting movement strategies. Nine turtles, including the hawksbill turtle, displayed migration strategies (Fig. 4) — undergoing oceanic and/or coastal movements to neritic foraging grounds — whereas Turtle B displayed a resident strategy, remaining resident in Montserrat and displaying post-nesting movements within the same area as the individual's inter-nesting home range. Migratory path lengths (i.e. total distance between first migration location and foraging core use area centroid) for the 8 green turtles that exhibited migration strategies ranged from 44.8–1013.1 km (mean ± SD: 316.3 ± 323.6 km) and their migratory displacements (i.e. straight-line distance between first migration location and foraging core use area centroid) ranged from 41.0–897.8 km (280.0 ± 291.1 km). The tagged hawksbill turtle had a migratory path length of 152.0 km and a migratory displacement of 135.1 km. Green turtles migrated at average speeds ranging between 2.4 and
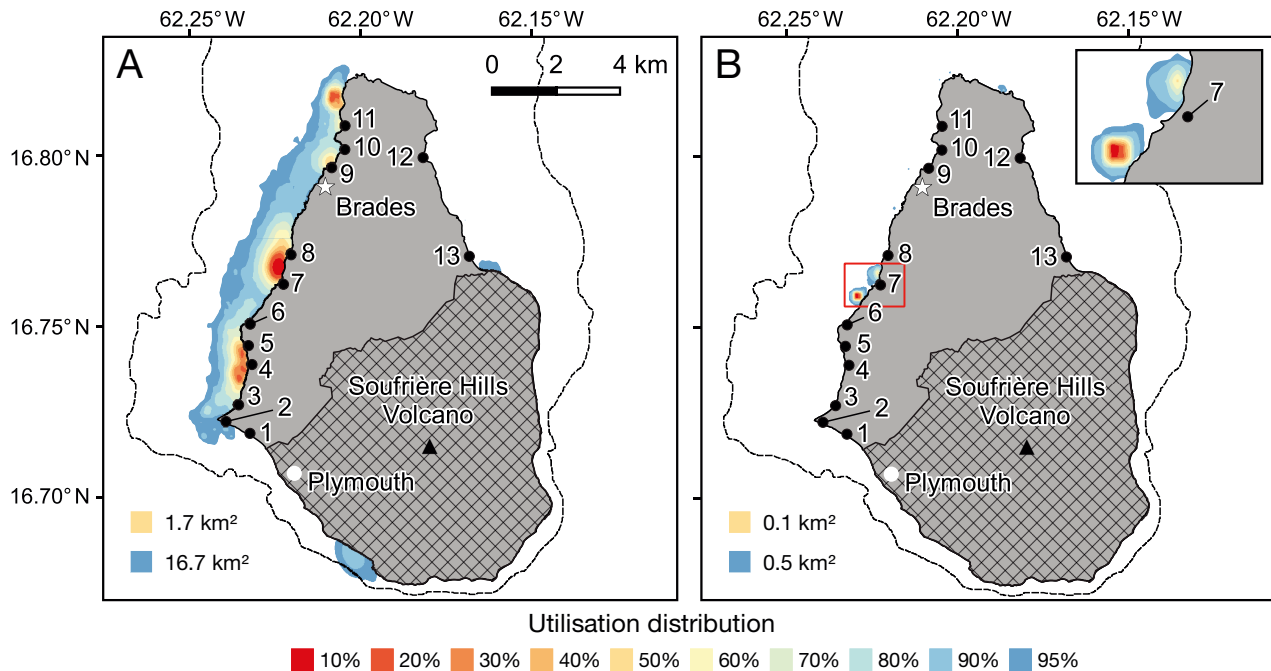

Fig. 3. (A) Population-level inter-nesting utilisation distribution for the 9 tracked green turtles and (B) inter-nesting utilisation distribution of the tracked hawksbill turtle. Black hatched area: terrestrial portion of the volcanic exclusion zone; white star: location of Brades, the de-facto capital of Montserrat; white circle: location of Plymouth, the former capital of Montserrat (now abandoned). The km^2 values in each panel refer to the respective 50% utilisation distribution (light orange) and 95% utilisation distribution (dark blue). Black dashed line: the 100 m bathymetric shelf; black dots: location of marine turtle nesting beaches currently monitored by the Government of Montserrat Fisheries and Ocean Governance Unit. Beach names indicated by numbers: 1: Barton Bay; 2: Bransby Point; 3: Fox's Bay; 4: Isles Bay; 5: Old Road Bay; 6: Lime Kiln Bay; 7: Woodland Bay; 8: Bunkum Bay; 9: Carr's Bay; 10: Little Bay; 11: Rendezvous Bay; 12: Margarita Bay; 13: Bottomless Ghaut Beach

3.5 km h^{-1} (mean ± SD: 3.0 ± 0.3 km h^{-1}) for between 1 and 15 d (mean ± SD: 5 ± 5 d), whereas the hawksbill travelled at a slower average speed of 1.6 km h^{-1} across 4 d. Four green turtles migrated north-eastward to foraging grounds in Antigua (n = 2) and Barbuda (n = 2) (Fig. 4B), while the remaining 4 migrated in a north-westward direction to foraging grounds in the United States Virgin Islands (n = 2), Puerto Rico (n = 1), and Dominican Republic (n = 1) (Fig. 4A). In contrast, the hawksbill turtle migrated south-eastward to a foraging ground located within the coastal waters of Guadeloupe between La Désirade and the Petite Terre Islands (Fig. 4C). Four turtles (Turtles C, E, F, and I) displayed continuous directed movements towards their final foraging grounds, whereas Turtles A, D, G, H, and J made short stopovers (i.e. short bouts of resident-type behaviours <24 h) during their migrations prior to reaching their final foraging grounds (Fig. S3). Eight of the turtles that displayed post-nesting migration strategies, including the hawksbill turtle, commenced their post-nesting migrations within 7 d following their final nesting event. However, after initially displaying resident-like behaviours around Montserrat, Turtle C subsequently began a delayed post-nesting migration towards a foraging ground in St. Croix, US Virgin Islands, 183 d after her final nesting event, where she remained until transmissions ceased. During post-nesting migrations, turtles transited between 2 and 7 (mean ± SD: 4 ± 2) EEZs (Table 1, Fig. S3).

3.4. Foraging areas and habitat use

Turtles were tracked to 10 unique foraging grounds across 6 different countries and territories throughout the WCR (Table 1, Fig. 5). Green turtle movements within foraging grounds were tracked for a total of 1474 d, with individual movements at final foraging grounds tracked for between 20 and 220 d (mean ± SD: 163 ± 60 d). The foraging movements of the hawksbill turtle were tracked for 220 d. Green turtle foraging home ranges (95% UD) and core use areas (50% UD) ranged from 0.5–19.3 km^2 (mean ± SD: 6.0 ± 6.6 km^2) and 0.1–3.0 km^2 (1.0 ± 1.0 km^2), respectively, whereas the foraging home range and core use area of the hawksbill turtle were 2.1 and 0.2 km^2, respectively (Fig. 5). Within foraging grounds, green turtles predominately utilised shallow coastal waters, with an average of 95.6% of locations being observed within water column depths of ≤25 m (Table S2). In contrast, just 58.4% of the hawksbill's locations were observed within water column depths of ≤25.0 m, with the remaining 41.6% falling within depths ranging between 26 and 50 m (Table S2).
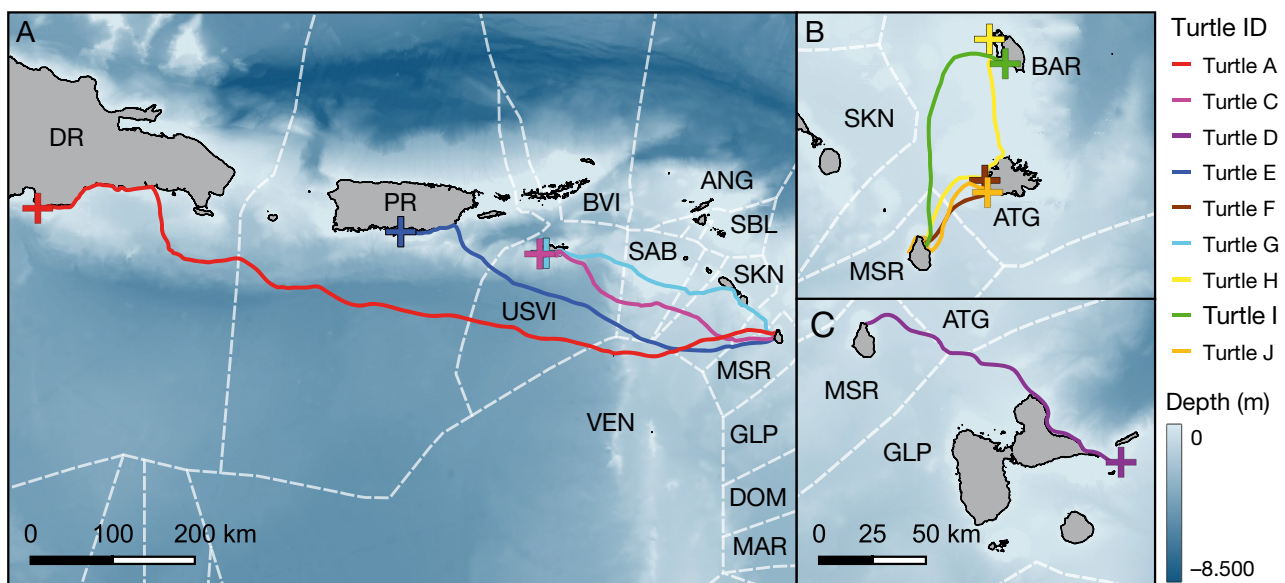

Fig. 4. Migration pathways and foraging area centroids of 9 green turtles and 1 hawksbill turtle tagged after nesting in Montserrat, Eastern Caribbean. (A) Long-distance migrations performed by 4 green turtles to foraging grounds in Dominican Republic, Puerto Rico, and St. Croix, US Virgin Islands. (B) Short- and mid-range migrations of 4 green turtles to foraging grounds in the neighbouring islands of Antigua and Barbuda. (C) Mid-range migration of the tracked hawksbill to a foraging ground in Guadeloupe. Turtle IDs match those in Table 1. No post-nesting migration was observed for Turtle B. White lines: Exclusive Economic Zone boundaries. DR: Dominican Republic; PR: Puerto Rico; BVI: British Virgin Islands; USVI: United States Virgin Islands; ANG: Anguilla; SAB: Saba; SBL: Saint-Barthélemy; SKN: Saint Kitts and Nevis; ATG: Antigua; BAR: Barbuda; MSR: Montserrat; GLP: Guadeloupe; DOM: Dominica; MAR: Martinique; VEN: Venezuela
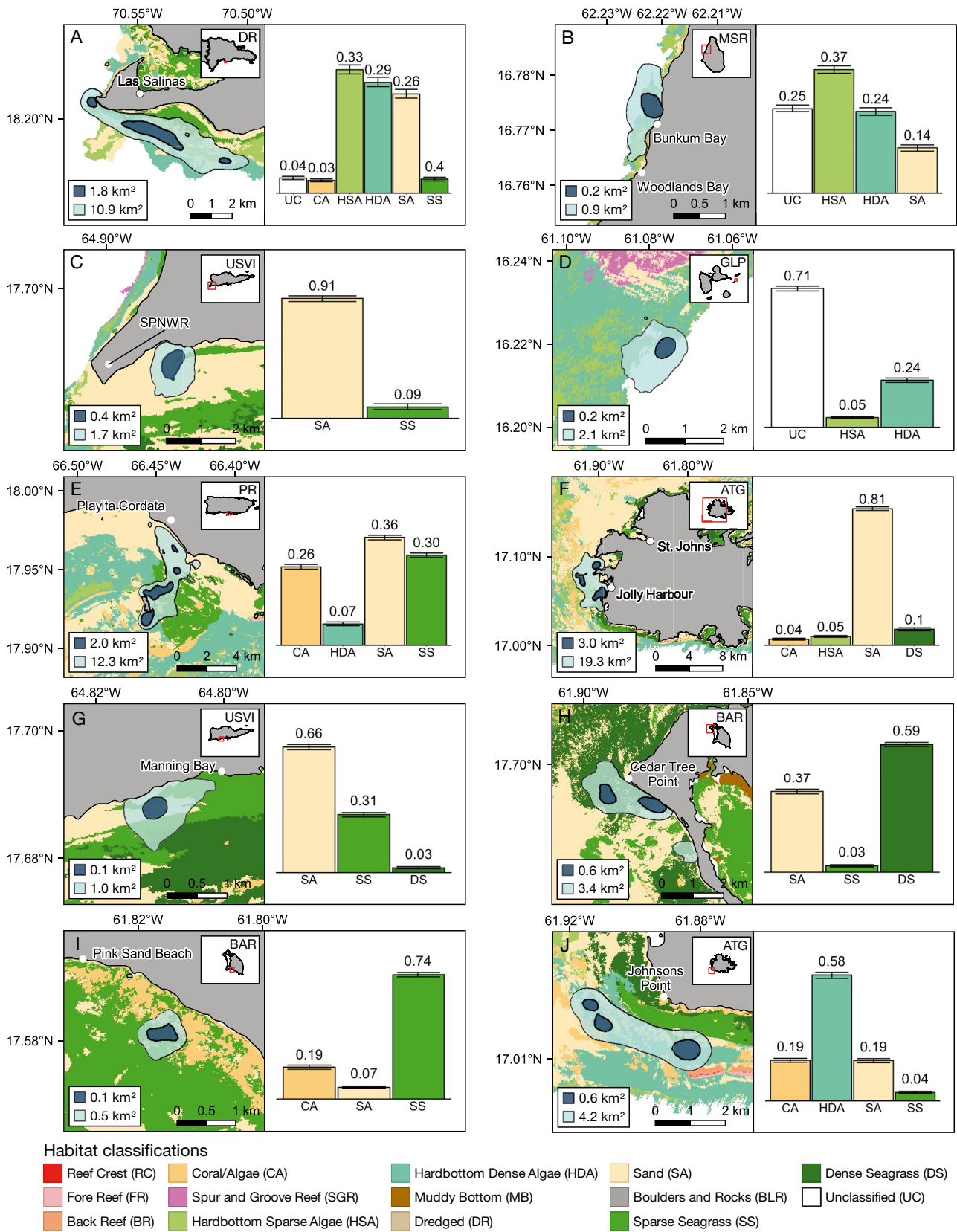
Fig. 5. Foraging areas of (A–C,E–J) 9 nesting green turtles and (D) 1 hawksbill turtle tagged in Montserrat, overlaid on a regional remotely sensed benthic habitat map (for details see Schill et al. 2021). Light blue shaded areas: foraging home ranges (95% UD); dark blue shaded areas: foraging core use areas (50% UD). Bar plots: estimated proportion of time spent in each benthic habitat type; error bars: associated 95% credible intervals. Habitats with use estimates of <0.01 are not displayed. Inset maps display location of foraging areas (red box) in relation to the corresponding country, territory, or island. Figure labels match turtle IDs in Table 1. Abbreviations for countries, territories and islands as in Fig. 4. Note different scales

Within foraging grounds, the diurnal home range and core use area of green turtles averaged 5.2 ± 5.7 km^2 (range: 0.5–17.6 km^2) and 0.8 ± 0.9 km^2 (range: 0.1–2.7 km^2; Fig. S4), respectively, whereas their nocturnal home range and core use area averaged 3.9 ± 4.3 km^2 (range: 0.4–10.4 km^2) and 0.5 ± 0.6 km^2 (range: 0.1–1.8 km^2; Fig. S4), respectively. The diurnal foraging home range and core use area of the hawksbill turtle were 2.6 and 0.6 km^2, whereas its nocturnal foraging home range and core use area were 0.8 and 0.1 km^2, respectively (Fig. S4). Even though diurnal home ranges and core use areas were slightly larger than nocturnal home ranges and core use areas, no significant difference between the size of diurnal and nocturnal home ranges or between the size of diurnal and nocturnal core use areas was observed (home ranges: Wilcoxon signed-rank, $V = 44.5$, $p = 0.09$; core use areas: $V = 31$, $p = 0.08$). However, the observed overlap of diurnal and nocturnal foraging UDs was significantly lower than expected by random chance (mean BA index: 0.60; permutation test, all $p < 0.03$; Table S3), indicating significant diel variation in space use within foraging grounds.

Overlaying tracking data with regional benthic habitat maps revealed that, on average, green turtles were predominately observed within sand (mean: 41.9%; CI: 41.6–42.3%), sparse seagrass (mean: 17.1%; CI: 16.8–17.4%), hardbottom dense algae (mean: 13.2%; CI: 13.0–13.5%), hardbottom sparse algae (mean: 8.3%; CI: 8.1–8.5%), and dense seagrass (mean: 8.1%; CI: 7.9–8.2%) habitat types (Fig. 5, Table S4), whereas the hawksbill turtle predominantly utilized hardbottom dense algae (mean: 24.1%; CI: 22.9–25.2%) and hardbottom sparse algae (mean: 5.0%; CI: 4.4–5.6%) habitat types (Fig. 5, Table S4). However, due to the limited extent of the benthic habitat maps (i.e. up to 30 m water depth), 70.9% (CI: 69.6–72.1%) of the hawksbills foraging locations were unable to be assigned a habitat type as they were situated outside the boundary of classified habitats. In contrast, only 3.4% (CI: 3.3–3.5%) of green turtle foraging locations were unable to be assigned a habitat type (Fig. 5, Table S4).

3.5. Local and regional protection

Overlaying tracking data with the proposed MSP for Montserrat (for details, see Flower et al. 2020) revealed that during inter-nesting periods, green turtles were predominately located within the boundaries of multiuse zones (mean: 50.7%; CI: 50.5–50.9%) and proposed no-take MPAs (mean: 39.5%; CI: 39.2–

39.9%), and the hawksbill turtle was observed predominately utilising areas within the boundaries of proposed no-take MPAs (mean: 72.2%; CI: 71.6–72.8%) and multiuse zones (mean: 25.5%; CI: 24.9–26.2%) (Table S5).

When overlapping the population-level inter-nesting home range for green turtles with the proposed MSP for Montserrat, 47.9% (8.0 km^2) fell within the boundaries of proposed multiuse zones, 40.3% (6.7 km^2) within proposed no-take MPAs, 9.1% (1.5 km^2) within proposed maritime volcanic exclusion zones, and 2.7% (0.4 km^2) within other proposed zone types combined (i.e. mooring anchorage, shipping, and recreation zones; Fig. 6). Similarly, 47.1% (0.8 km^2) of the green turtles' population-level inter-nesting core use area was situated within the boundaries of proposed multiuse zones, 41.2% (0.7 km^2) fell within proposed no-take MPAs, and 11.8% (0.2 km^2) within proposed mooring anchorage zones (Fig. 6).

During migrations, turtles transited between 0 and 6 (mean $\pm$ SD: 3 ± 2) MPAs (Table S6), crossing a total of 19 unique MPAs throughout the WCR. However, on average, only 21.7% (CI: 21.2–22.5%) of migratory time was spent within MPA boundaries (range: 0.0–75.5%; Table S6). Current MPA coverage of green turtle foraging grounds was on average 15.3% (CI: 15.3–15.4%, range: 0–75.7%; Table S6). Four of the 9 green turtles foraged partially within MPAs in Puerto Rico and Antigua and Barbuda, while the remainder had no protection within foraging grounds. However, of the 4 turtles that foraged partially within MPAs, only 2 individuals spent more than 50% of their time within MPAs, whereas the other 2 individuals spent less than 1% of their time foraging within MPA boundaries (Table S6). In contrast, 100% (CI: 100–100%) of the hawksbill's foraging locations were located within current MPA boundaries (Table S6).

4. DISCUSSION

This study presents the first detailed investigation of the spatial ecology of green *Chelonia mydas* and hawksbill *Eretmochelys imbricata* turtles nesting in the Caribbean island of Montserrat and highlights several challenges and opportunities for local and regional protection across key adult reproductive phases.

4.1. Local governance on Montserrat

During inter-nesting periods, green and hawksbill turtles were observed to predominantly utilise inshore
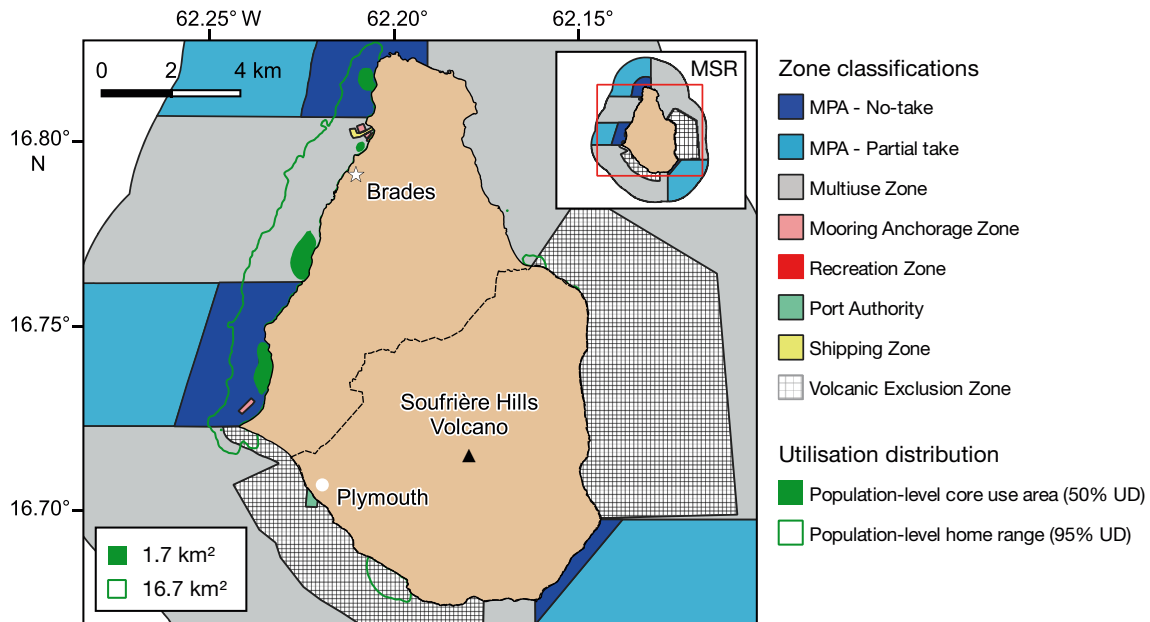
Fig. 6. Population-level inter-nesting home range (95% utilisation distribution, UD) and core use area (50% UD) for green turtles (n = 9) tagged with satellite transmitters after nesting in Montserrat in relation to the marine spatial plan (MSP) proposed for Montserrat by Flower et al. (2020). White star: location of Brades, the de-facto capital of Montserrat; white circle: location of Plymouth, the former capital of Montserrat (now abandoned). The inset map shows the location of the population-level inter-nesting home range and core use areas for green turtles in relation to Montserrat (MSR) and the proposed MSP

waters close to nesting beaches, consistent with behaviours described at other nesting sites (Walcott et al. 2012, Hart et al. 2013, Chambault et al. 2016, Hart et al. 2017, Snape et al. 2018). Two critical aggregation areas for green turtles during inter-nesting periods were identified along the western coast of Montserrat — situated between Old Road Bay and Fox's Bay and within the waters surrounding Woodlands Bay and Bunkum Bay — that were used by multiple individuals, including those nesting at non-adjacent beaches. Although our sampling efforts focused on the western coast of Montserrat, where the majority of sea turtle nesting has previously been reported (Martin et al. 2005), island-wide nesting distributions remain unquantified. As a result, it is possible that our sampling efforts may not have fully captured the island's nesting distributions. Broader tracking studies could provide a more comprehensive understanding of inter-nesting distributions around Montserrat. Nonetheless, our results offer valuable insights into key inter-nesting areas around Montserrat that could serve as focal points to guide local spatial management.

An MSP for Montserrat was recently proposed (Flower et al. 2020), and the Government of Montserrat is also currently considering several refinements to the Turtles Act (1951, revised 2002), informed by the results of this study, that would enhance the protection of Montserrat's marine turtle populations. These recommendations are outlined in a recently developed 5 yr marine turtle species action plan for Montserrat and include the extension of the closed season to enhance protection of nesting females and eggs and the designation of marine turtle management zones to protect critical habitats. For example, while one of the critical inter-nesting areas identified for green turtles in Montserrat is within the boundaries of the western no-take MPA proposed by Flower et al. (2020), the other lies just north of this proposed MPA within a multiuse zone. Given that marine turtles are not believed to be heavily impacted by trap fishing, which is one of the primary methods used by fishers in Montserrat (Flower et al. 2020), enhanced protection could be achieved through targeted restrictions on specific gear types with high bycatch risk (e.g. fixed gillnets) within multiuse areas. Alternatively, protection of this critical inter-nesting area could also be achieved by a northward expansion of the proposed western no-take MPA towards Bunkum Bay, although this would require consultation with key stakeholders to avoid any foregone opportunity costs.

While most turtles migrated following the completion of nesting, one green turtle remained resident within the coastal waters of Montserrat. Differences in post-nesting migration strategies within and between green turtle populations have been well documented (Troëng et al. 2005, Stokes et al. 2015, Becking et al. 2016, Hart et al. 2017), and plasticity

within individual migratory behaviours has also been reported (Blumenthal et al. 2006). The presence of year-round residents at nesting grounds has been documented in other green turtle rookeries across the WCR (St Eustatius: Esteban et al. 2015; Buck Island, US Virgin Islands: Hart et al. 2017; Southwest Florida, USA: Sloan et al. 2022) and elsewhere (Cocos (Keeling) Islands: Whiting et al. 2008; Sri Lanka: Richardson et al. 2013; Western Australia: Ferreira et al. 2021). Such local residency of nesting females to rookeries has implications for management that often primarily focusses on breeding periods.

In the context of Montserrat, a legal marine turtle fishery persists on the island, and any marine turtle over 20 lbs (9.1 kg) in weight as well as marine turtle eggs are allowed to be taken, bought, and sold during the open season, which spans from 1 October to 31 May (Turtles Act 1951, revised 2002). Our findings, in conjunction with findings from previous studies (Martin et al. 2005, Evans et al. 2024, Maurer et al. 2024) and unpublished observations, have revealed that Montserrat's inshore waters are utilised by juveniles, inter-nesting individuals, year-round resident females, and nesting females from neighbouring islands. This evidence, although limited, suggests Montserrat's inshore waters may be of a wider regional significance for marine turtles than previously recognised and may advocate for the consideration of an extension to the existing closed season (1 June–31 September) and restrictions on harvesting adult turtles (e.g. through maximum size limits), which appears to have some level of public support (authors' pers. obs.). Additionally, the implementation of an MSP, such as the one proposed by Flower et al. (2020), if appropriately managed, would not only enhance the protection of Montserrat's nesting turtle populations and their critical habitats but would also benefit migrants from other nesting populations throughout the region.

4.2. Regional connectivity and management

Interestingly, while most turtles showed high fidelity to Montserrat's inshore waters during inter-nesting periods, 1 green turtle (Turtle J) performed a 197 km inter-nesting migration to north-west Dominica after nesting 3 times in Montserrat before returning to Montserrat to nest on 4 more occasions. Similar movements away from and then returning to the vicinity of nesting sites during the breeding season have previously been observed in green turtles nesting in St. Eustatius, Dutch Caribbean (Esteban et al. 2015),

Bioko Island, Equatorial Guinea (Mettler et al. 2020), and Raine Island, Australia (Perez et a. 2024) as well as in loggerhead turtles nesting in Greece (Schofield et al. 2010) and may serve to replenish energy reserves or maximise reproductive success through prospecting for the best available nesting sites (Perez et al. 2024, Schofield et al. 2010). Even though this individual did not apparently nest in Dominica, such observations indicate that some green turtles nesting in Montserrat utilise neighbouring islands during the nesting season, emphasising the need for regional cooperation in conservation efforts.

High regional connectivity was also revealed by post-nesting migrations. After leaving Montserrat, tagged turtles dispersed widely along the Antillean chain, traversing 10 national jurisdictions and settling in 9 distinct foraging areas within 5 Caribbean countries, potentially exposing them to a wide range of threats and management regimes. Migration tracks suggest the presence of 2 principle migratory routes for green turtles nesting in Montserrat: one heading northeast towards foraging grounds in Antigua and Barbuda (44% of individuals), and the other heading northwest towards foraging grounds located in the United States Virgin Islands, Puerto Rico, and Dominican Republic (44% of individuals). Previous tracking studies have shown that these corridors are also utilised by adult female turtles migrating from other nesting populations throughout the WCR (Hart et al. 2017, 2019, Evans et al. 2024, Maurer et al. 2022, 2024) highlighting their wider importance for marine turtle populations in the region.

Marine turtles are currently afforded legal protection in all countries that the tagged turtles migrated to (including under the US Endangered Species Act in the US Virgin Islands (United States Fish and Wildlife Service 1973) and Puerto Rico and the Environmental Protection and Management Act 2019 of Antigua and Barbuda). However, both legal and illegal exploitation is reported to occur throughout the region (Revuelta et al. 2012, Humber et al. 2014, Pheasey et al. 2021, Senko et al. 2022), and turtles are exposed to a range of anthropogenic threats from marine traffic and commercial and artisanal fisheries. For example, the Bay of Ponce in Puerto Rico, the location of the foraging ground of Turtle E, is reported to be a heavy transit area for recreational boats and shipping and is a known area for illegal take of marine turtles (C. Diez pers. comm.).

While Caribbean nations have made advances in MPA coverage, spatial protection afforded to Montserrat's marine turtles was limited, with only 21.7 and

24.0% of time spent during migration and foraging periods, respectively, occurring within protected areas on average. Similar levels of protected area occupancy during foraging periods have previously been reported in other nesting populations within the WCR (Revuelta et al. 2015). Of the 5 green turtles that partially foraged within MPAs, 2 individuals spent more than 50% of their time within MPAs, whereas the other 3 individuals spent less than 1% of their time foraging within MPA boundaries (Table S11). Some of the foraging areas identified in this study are also used by turtles from other nesting sites (Dominican Republic: Hawkes et al. 2012; Montserrat: Maurer et al. 2024; St. Croix, United States Virgin Islands: Hart et al. 2017, 2019), suggesting these areas may be of wider significance and potential focal points for protection.

Our findings corroborate those from previous studies that marine turtle populations throughout the Caribbean display high levels of regional connectivity (Hart et al. 2015, 2019, Nivière et al. 2018, Evans et al. 2021, Uribe-Martínez et al. 2021) This not only highlights the need for international cooperation to ensure the preservation of marine turtle populations across the region but also emphasises the complexity of conserving highly migratory species, which often comprises multiple countries and stakeholders with varying conservation frameworks and policies as well as diverse socio-economic, environmental, and cultural values (Stringell et al. 2015, Barrios-Garrido et al. 2019).

4.3. Habitat selection and space use

Overlaying foraging movement data on remotely sensed benthic habitat maps revealed that green turtles primarily migrated to shallow, coastal areas dominated by sand, seagrass and hardbottom algal habitats, which is consistent with known habitat preferences. Interestingly, green turtles only migrated northwards to foraging grounds, even though islands to the south have similar extensive habitats (see http://caribbeanmarinemaps.tnc.org/) that are known to support foraging green turtle populations (Luke et al. 2004, Whitman et al. 2019). Similar directed migrations have been reported elsewhere; for example, in green turtles nesting on Ascension Island (Mortimer & Carr 1987, Luschi et al. 1998, Hays et al. 1999), Sri Lanka (Richardson et al. 2013), French Guiana, and Suriname (Baudouin et al. 2015), despite suitable foraging areas being available in other directions. It has previously been suggested that post-

nesting females from Eastern Caribbean rookeries may tend to utilise the prevailing west-northwesterly current to assist migration back to foraging grounds (Van Dam et al. 2008, Horrocks et al. 2011). While this might explain the directed northward migrations of the post-nesting green turtles tagged in Montserrat, the southward migration of the tagged hawksbill turtle aligns with findings from other studies in the region, indicating that post-nesting migrations against prevailing currents also occur and that individuals from the same nesting population often disperse in multiple directions (Van Dam et al. 2008, Hart et al. 2017, 2019, Hawkes et al. 2012, Evans et al. 2024, Maurer et al. 2024). In addition to ocean currents, other environmental factors such as physical oceanographic features, magnetic cues, and wind and water-borne chemical signatures have been suggested to influence the direction of marine turtle migrations (Luschi et al. 2003, Cheng & Wang 2009, Endres et al. 2016). Given the relatively small number of individuals tracked across a single nesting season, further tagging studies may reveal additional migratory pathways used by marine turtles nesting in Montserrat and provide deeper insights into the drivers of foraging site selection in these populations.

Following completion of post-nesting migrations, tagged turtles showed restricted movements and high fidelity to specific foraging grounds, spending 95% of their time in areas ranging between 1.2 and 25.1 km^2, which is comparable to estimates from other populations (Christiansen et al. 2017, Hamilton et al. 2021). The majority of turtles appeared to be most active during the day, moving further offshore and utilising larger foraging areas than at night, which is consistent with evidence that they are predominantly diurnal foragers (Blumenthal et al. 2009, Witt et al. 2010a, MacDonald et al. 2013, Okuyama et al. 2013, Christiansen et al. 2017). The remotely sensed benthic habitat maps used in this study were characterised as 80% accurate (Schill et al. 2021). Combined with the inherent error associated with satellite locations and gaps in satellite coverage, this makes it difficult to confidently assess fine-scale habitat utilisation patterns (e.g. on sub-diel cycles). However, this study shows how the availability of remote sensing data is enabling new avenues of research that could help identify suitable habitat areas and assess carrying capacity at both local and regional scales. Additionally, such data combined with higher spatial and temporal resolution technologies (e.g. Motes; Hays et al. 2021) could enable investigations into fine-scale patterns of habitat use.

5. CONCLUSIONS

This study provides further evidence of the challenges associated with managing migratory species such as marine turtles, particularly in geo-politically complex regions like the Caribbean, characterised by many small intersecting EEZs. Complex movement behaviours such as inter-nesting migrations, year-round residency at nesting sites, and post-nesting migrations expose individuals to various management regimes and threats throughout different life phases, highlighting the need for international cooperation throughout the region. Pan-Caribbean initiatives like CaMPAM (Caribbean Marine Protected Area Management Network and Forum), CAMAC (Caribbean Marine Megafauna and Anthropogenic Activities), and WIDECAST (Wider Caribbean Sea Turtle Conservation Network) seek to address such concerns through improving knowledge, strengthening regional collaboration, and facilitating information exchange among conservation practitioners, managers, and stakeholders. However, achieving regional cooperation and conservation objectives is complex and often challenging. Therefore, it has been proposed that the implementation of management conservation frameworks at the national level, as opposed to relying solely on multilateral agreements, is critical for achieving regional conservation objectives (Richardson et al. 2013, Stringell et al. 2015).

Our results highlight several national steps that could be implemented in Montserrat to safeguard adult green turtles. These measures include extension of the closed season, size restrictions on legal harvests, and spatial protection of key aggregation areas. As a result of stakeholder engagements in Montserrat using a similar Community Voice Method approach as employed in the Turks and Caicos Islands (Cumming et al. 2022), these measures have been incorporated into a recently developed 5 yr marine turtle action plan for Montserrat. However, the success of any conservation framework relies upon the support of stakeholders. Therefore, attaining an understanding of the social acceptability of any potential management plans, regulations, and policies prior to their implementation is imperative and should be considered a priority (Rees et al. 2016, Cumming et al. 2022). Additionally, further studies focusing on the spatial ecology of marine turtles, in particular nesting hawksbill turtles, adult male turtles, and other life stages (e.g. juveniles and sub-adults) in Montserrat, as well as regional meta-analyses of tracking data, are needed if effective conservation measures for these populations are to be suggested and implemented.

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