Multiple satellite tracking datasets inform green turtle conservation at a regional scale

Luciana C. Ferreira | Michele Thums | Sabrina Fossette | Phillipa Wilson | Takahiro Shimada | Anton D. Tucker | Kellie Pendoley | Dave Waayers | Michael L. Guinea | Graham Loewenthal | Joanne King | Marissa Speirs | Dani Rob | Scott D. Whiting

Abstract

Aim: Satellite tracking studies of marine megafauna have grown over the last few decades. The number of these individual datasets are now at levels which if combined, can infer on population level movement and spatial use. Here we use this approach to quantify distribution and important areas for one of the largest populations of green turtles (Chelonia mydas) in the Indo-Pacific.

Location: Western Australia.

Method: We compiled satellite tracking data for 96 adult, female green turtles from 10 rookeries and two genetic stocks and split the data into nesting, migration and foraging using a state-space model to classify the movement behaviour underlying the track (resident or transient). We then used time (and number of turtles) in area analysis on each of these components to quantify the important areas of use, at both rookery and regional/stock scales. We also assessed the representativeness of the calculated distributions, based on the available sample sizes.

Results: 86% of post-nesting turtles had oceanic or coastal movement to neritic foraging grounds and 14% had local residency to their rookery. The foraging distribution consisted of the inshore waters of most of northwestern Australia. Our sample sizes used for inter-nesting distribution were adequate for 90% of rookeries, but still larger sample sizes were needed for post-nesting distributions.

Main conclusions: Despite some limitation with sample size, our analyses have provided a quantitative and robust approach to designate marine areas of importance for an endangered species. The spatial extent of the inter-nesting areas was encompassed by existing spatial protection for green turtles during the breeding season, but existing Biologically Important Areas are largely underestimating the foraging areas. Our study highlights the utility of our approach for providing quantitative outputs at scales needed for management (local and regional).
1 | INTRODUCTION

Populations of marine megafauna around the world are declining due to a range of threats (Bowler et al., 2020; Halpern et al., 2008; Maxwell et al., 2013). A key first step to impact assessment is to have accurate species distribution maps and knowledge of their important areas of use. For many marine migratory species, telemetry is one of the main ways to obtain this spatial data. However, in order to map population or stock level distribution, large numbers of individuals tracked from representative sub-populations are needed over relevant time scales, which individual tracking projects rarely achieve.

The green turtle (Chelonia mydas) is a highly migratory species of marine turtle with a circum-tropical distribution, listed by the International Union for Conservation of Nature (IUCN) as endangered (Seminoff, 2004) and listed as vulnerable in Australia by the Environment Protection and Biodiversity Conservation Act 1999. In the Indo-Pacific region, some of the largest rookeries of green turtles are found in Australia (Limpus, 2008; Prince, 1993) but there is the Indo-Pacific region, some of the largest rookeries of green turtles as habitat critical for the survival of green turtles (as an inter-nesting buffer). It has also defined so called Biologically Important Areas (BIA) (https://environment.gov.au/marine/marine-species/bias) which are often based on limited information and reliance on expert elicitation where peer-reviewed published literature are unavailable. Similar in concept to Ecological or Biologically Significant Areas (EBSAs), this approach of identifying the areas used for breeding, foraging, and migration is a useful tool for conservation managers to inform marine spatial planning and assist decision-making (Corrigan et al., 2014; Dunn et al., 2014). Although a qualitative approach is valid in the absence of quantitative data, in many cases it may be considered inadequate for basing decisions on. This is especially pertinent given that robust scientific data from satellite tag deployments is available and could be combined and analysed to support decision-making.

Here we assess all the satellite tracking data available for nesting female green turtles in Western Australia (see Tucker et al., 2020; Waayers et al., 2019) and use it to identify rookeries where transmitters have not been deployed. We use a combination of new satellite transmitter deployments (n = 20) and existing datasets we were able to access (n = 76) to quantify the inter-nesting and post-nesting movements and distribution of green turtles in Western Australia, comprising 10 rookeries and two of the three genetic stocks. We hypothesize that migratory routes and foraging areas will differ between the two stocks due to the disparate nesting locations. In addition, we assess the effect of grid cell size on the results and the representativeness of the distribution and important areas we calculate, based on the available sample sizes at both the rookery and stock scale.

2 | METHODS

2.1 | Data collection and compilation

Satellite tracking data from 76 adult female green turtles comprising island (nearshore and offshore) and mainland rookeries (n = 10) covering all Western Australian stocks except Ashmore Reef (Spring & Pike, 1998) were identified from Waayers et al. (2019) and compiled (Figure 1). One of the datasets is from a peer-reviewed paper (Waayers et al., 2011) and the remainder are from unpublished...
The turtles were tagged between 2001 and 2018 during the breeding season (October to April) with satellite-linked transmitters that provided ARGOS locations only ($n = 37$), or both Argos and FastlocGPS locations ($n = 39$) (Table 1) during both the inter-nesting and post-nesting periods. Based on the locations of previous satellite transmitter deployments, combined with information on the main rookeries in Western Australia (Limpus, 2008; Pendoley et al., 2016), we identified nesting areas where new deployments should be undertaken in order to have representation across the main rookeries of the Western Australia green turtle stocks. These were Rosemary Island (6 tags), Legendre Island (4 tags) and Middle Island (10 tags) (Figure 1). Logistical considerations also played into the site selection, in that very distant sites such as Browse Island and Ashmore Reef were not selected. The twenty transmitters (half were Wildlife Computers [WC] models SPOT 375B and the remainder WC SPLASH10-BF-334D) were deployed on nesting green turtles during November 2017 (Table 1). Transmitter attachment followed the protocols detailed in Fossette et al. (2017) and is outlined in the Supplementary Material.
**Table 1** Details of the tracking datasets for each genetic stock/sub-stock, including tagging site and location, the data type obtained from the transmitter, date of deployment (sometimes more than one), the number of turtles tagged at each site (N) and the mean ± SD curved carapace length (CCL). Also shown are median and range track duration, total distance travelled and mean ± SD rate of movement during migration.

| Tagging site         | Lat/Lon        | Data type                        | Deployment date                | N   | CCL (cm) | Track duration (days) | Distance² (km) | Rate of movement (km/day) |
|----------------------|----------------|----------------------------------|--------------------------------|-----|----------|-----------------------|----------------|--------------------------|
| NWS stock-Pilbara    |                |                                  |                                |     |          |                       |                |                          |
| Rosemary Is          | −20.48, 116.58 | Argos only (3), Argos&GPS (3)    | Nov 2017                       | 6   | 98 ± 7   | 117.70–289            | 289,447²      | 39 ± 1                   |
| Legendre Is          | −20.41, 116.93 | Argos only (2), Argos&GPS (2)    | Nov 2017                       | 4   | 98 ± 3   | 135, 91–163           | 209, 172–767  | 51 ± 14                  |
| Middle Is            | −20.93, 115.32 | Argos only (5), Argos&GPS (5)    | Nov 2017                       | 10  | 95 ± 3   | 111, 67–184           | 531, 116–2,390| 53 ± 20                  |
| Barrow Is            | −20.75, 115.37 | Argos only                       | Jan 2001 & 2003, Dec 2013     | 11  | 98 ± 6   | 75, 33–346            | 341, 89–2,683 | 34 ± 13                  |
| Muiron Is            | −21.80, 114.07 | Argos & GPS                      | Nov-Dec 2018                   | 6   | 101 ± 3  | 271, 141–274          | 170, 60–189   | 34 ± 7                   |
| Ningaloo             | −21.67, 114.35 | Argos & GPS                      | Nov-Dec 2018                   | 7   | 97 ± 5   | 223, 144–264          | 248, 67–1,177 | 44 ± 16                  |
| Montebello Is        | −20.4, 115.6   | Argos only                       | Nov 2016                       | 5   | 96 ± 4   | 171, 99–266           | 354, 140–1,099| 45 ± 12                  |
| Summary              |                |                                  |                                | 49  | 97 ± 5   | 160, 33–346           | 306, 60–2,683 | 44 ± 22                  |
| NWS stock-Kimberley  |                |                                  |                                |     |          |                       |                |                          |
| Lacepede Is          | −16.85, 122.12 | Argos & GPS                      | Dec 2009 & 2010                | 11  | 98 ± 5.4 | 187, 90–537           | 1,194, 320–3,157| 85 ± 30                  |
| Maret Is             | −14.45, 124.99 | Argos only                       | Dec 2006, Dec 2007, Mar-Apr 2008 | 21  | 96 ± 5.5 | 110, 19–322           | 569, 103–2,418| 37 ± 8                   |
| Summary              |                |                                  |                                | 32  | 94 ± 6.2 | 155, 19–537           | 733, 103–3,157| 48 ± 26                  |
| Scott-Browse stock   |                |                                  |                                |     |          |                       |                |                          |
| Scott Reef           | −14.06, 121.78 | Argos only (4), Argos & GPS (11) | Oct 2002, Jan 2004, Jan-Feb 2010 | 15  | 98 ± 7.3 | 69, 46–152            | 1,025, 479–2,308| 42 ± 7                   |

²Did not include turtles with post-nesting local residence in the vicinity of the nesting grounds (e.g. turtles that did not migrate and used the same or similar area post-nesting as they did during inter-nesting).

³Migratory movements were recorded for only two turtles at Rosemary Is, with remaining turtles (4) displaying local residency, thus the values displayed are the median for each turtle.
2.2 | Turtle movement model and metrics

A Bayesian switching state-space model (SSM) (Jonsen et al., 2003, 2005) was applied to the raw ARGOS location data to account for location error and estimate behavioural states for each individual track using the R (R Core Team, 2019) package bsam (Jonsen et al., 2017). The SSMs were fitted using a switching first-difference hierarchical correlated random walk model (hDCRWS) with a total of 100,000 Markov Chain Monte Carlo (MCMC) iterations after an initial burn in of 10,000 samples with every 10th iteration kept after burn in. For tracks that did not converge, the model was re-run with an additional 10,000 iterations until it converged. We used a 6-hr time step for the model to generate 4 location estimates per day. Tracks with large gaps (>7 days) were split and analysed with a hierarchical model that analysed each portion of data separately. One of two behavioural modes (b) was assigned to each location estimate; either transient (locations with a SSM behaviour value \( b < 1.5 \)) or resident (locations with a SSM behaviour value \( b > 1.5 \)) (Jonsen et al., 2005).

Resident movement behaviour occurs during the nesting season and on the foraging grounds and to separate these two we used the methods outlined in Thums et al. (2017) and Thums et al. (2018): (1) all locations classified as resident by the SSM from the start of the deployment until the first switch to transient movement behaviour were defined as inter-nesting and (2) all other locations classified by the SSM as resident were classified as foraging (including any that occurred during periods of transient). Transient movement behaviour in between the end of the inter-nesting behaviour (defined at point 1 above) and the first occurrence of foraging behaviour (as defined at point 2 above) was defined as migration. All other transient behaviour not classified as migration was defined as simply transit (transit between foraging areas, where more than one foraging area occurred -which was rare). Some individuals \( n = 19 \) did not migrate and used the same/similar area post-nesting as they did during inter-nesting for the duration of the deployment and therefore all the resulting SSM behaviour values were \( b > 1.5 \) (resident). In order to split the tracking data into inter-nesting and foraging for these individuals, we used the median date of the end of inter-nesting behaviour for all other turtles in the same nesting area as a cut-off. For transmitters that also provided FastLocGPS data (Table 1), FastLocGPS locations were filtered, with extreme locations (using a speed filter of 5 km/hr; Luschi et al., 1998) and/or those locations obtained from <5 satellites removed and the remaining locations subsequently added to the SSM tracks. By spatially overlaying the locations provided by the FastLocGPS with the SSM location estimates and our classification of behavioural state described above, we were then able to assign behaviours to the FastLocGPS locations (inter-nesting, migration, foraging or transit). To describe migratory movements, we calculated total distance travelled during this period as the cumulative horizontal distance between successive locations and mean rate of movement (km/day) for each turtle. We present all values as mean ± SD unless indicated otherwise. Each individual’s movement behaviour was classified into one of four general migration strategies according to Godley et al. (2008): A1—oceanic and/or coastal movement to neritic foraging grounds, A2—coastal shuttling between summer foraging and wintering sites, A3—local residence and B—pelagic living. Turtles with A1 movement were further classified as oceanic (i.e. movement beyond continental shelf at 200 m) and coastal (i.e. movement within the shelf in depths ≤200 m).

2.3 | Time-weighting

Time-weighting was applied to the SSM tracks based on a modified version of the method described by Block et al. (2011). This was done to account for bias due to differences in deployment duration and the associated decrease in the number of individuals tracked with time due to premature detachment, or tag failure not uncommon with satellite tracking datasets (Hays et al., 2007). For each individual’s track, we weighted the time spent between two successive locations by the inverse of the number of individuals that had locations on the same relative day \( (1 = \text{first day of track}, n = \text{last day of tracking days}) \) of their track:

\[
w_t = \frac{1}{n_t}
\]

Where \( w_t \) is the weight for the \( t^{\text{th}} \) relative day of an individual’s track and \( n_t \) is the number of individuals with a location estimate on the \( t^{\text{th}} \) relative day. This time-weighting was done for all relative days of the track until a threshold corresponding to the 85th percentile of track lengths as recommended by Block et al. (2011).

2.4 | Quantification of spatial distribution and important areas

The analyses of inter-nesting distributions were done at the scale of rookeries and for the analysis of post-nesting distribution, data were analysed all together and separately for each stock. However, the Northwest Shelf stock was split into two because the two most northern rookeries of this stock (in the Kimberley region) are geographically isolated from those in the southern part (Pilbara region) and constitute separate management units. In addition, there is evidence to suggest genetic differentiation between at least one of the two Kimberley rookeries (Lacepede Islands) and the rest of the Northwest Shelf stock (FitzSimmons et al., 2018). Thus, the analysis was done separately for each of three groups: (a) Kimberley part of the Northwest Shelf stock (NWS stock-Kimberley, including Maret and Lacepede islands), (b) Pilbara part of the Northwest Shelf stock (NWS stock-Pilbara, i.e all rookeries south of Lacepede Is.) and (c) Scott-Browse stock (Table 1). We also combined NWS stock-Kimberley and Scott-Browse stocks for the analysis of post-nesting movements as both these stocks use the Kimberley region predominantly (Figure 1).

In order to identify spatial distribution and important areas (i.e. areas of high use of importance for life-history stages, such as breeding, migration and foraging and similar to the concept
defined for EBSAs and BIAs), we gridded the study area and calculated the time spent in each grid cell using the time-weighted tracks for each turtle for the entire track duration and for inter-nesting, foraging and migration behaviours separately using the R package trip (Sumner & Luque, 2015). Time spent was calculated using a 3 x 3 km square grid for inter-nesting and a 20 x 20 km square grid for migration and foraging. These grid cell sizes were selected based on the scale of the movements; very small (100 s of m to km) for inter-nesting and very large (100-1,000 s of km) for post-nesting and to be in line with grid cell sizes used for other turtle species distributions quantified in this region (Whittock et al., 2014, 2016).

We calculated the relative proportion of time spent per cell for each individual for each behaviour by dividing the time spent in each grid cell for each behaviour by the total track duration for each behaviour. All individual turtle time spent grids were then overlaid and the values in each grid cell were summed for all turtles combined and the values normalized to range between 0 and 1 to provide an occupancy index. We calculated the occupancy index for the entire track duration and for inter-nesting, foraging and migration behaviours separately, both at the scale of rookery (for inter-nesting only) and stock/sub-stock (NWS stock-Pilbara, NWS stock-Kimberley and Scott-Browse stock). Similarly, the number of turtles in each grid cell was also summed and then divided by the total number of turtles in the study (entire track and in each behavioural mode).

To represent spatial use for inter-nesting, migration and foraging, we ranked the summed grid cell values (both occupancy index and number of turtles) from largest to smallest and determined the spatial distribution as the cells encompassing the top 95% (for inter-nesting) and 75% (for migration, foraging and the entire track) of the cumulative frequency distribution based on the method described by Soanes et al. (2013) and akin to 75% and 95% utilization distributions. The 75% distribution was used instead of the 95% for foraging, migration and the entire track to exclude rare large migration events to the above) to assist with spatial planning and management of foraging green turtles. Each turtle’s individual 75% distribution was then overlaid on this map and we summed the number of turtles having their individual 75% distribution within each of the bounded areas. In order to understand the effect of grid size on this process, we repeated the process using a range of other grid sizes (5, 10, 50, 100 km).

We also calculated the proportion of the spatial distributions for each behaviour inside marine protected areas (MPAs), including Australian Marine Parks (Commonwealth areas), marine reserves (State waters) and Indigenous Protected Areas (www.environment.gov.au/land/nrs/science/capad). In addition, we calculated the proportion of the inter-nesting and foraging distributions inside spatial protections designated by the Commonwealth of Australia to protect green turtles: the Inter-nesting Habitat Critical 20 km radius around rookeries and the foraging BIAs. As the migratory movement of the green turtles appeared to overlap with the migratory corridor proposed by Pendoley et al. (2014) for flatback turtles (Notator depressus) from 4 rookeries in the Pilbara region, which also had a high proportion of overlap (46%) with humpback whales (Megaptera novaeangliae), we also calculated the proportion of the migration distribution that overlapped with this corridor and the proportion of the migratory corridor defined by Pendoley et al. (2014) inside MPA’s as above.

2.5 | Effect of sample size on calculated spatial distributions

We assessed the effect of sample size on the spatial distribution extent for each behaviour using the 95% distribution using the R package SDLfilter (Shimada, 2019). Please see Shimada et al. (2020) for details but to summarize, we took the cell values of each turtle raster layer (i.e. relative proportion of time spent per cell) and for increasing sample size from 2 to the maximum number of individuals, we merged all areas identified by existing data (e.g. n-1 individuals) and calculated the proportion of time spent by an additional individual (n) over the collective area. We then calculated mean proportion of overlap for each sample size (2 to the maximum) from 1,000 random permutations. We considered an asymptote was attained once the mean proportion of overlap reached 0.95. After this point, the sample size was deemed sufficient to describe the general distribution of the population because on average a new additional individual will only spend 5% of time outside the identified area.

3 | RESULTS

3.1 | Effect of sample size on calculated spatial distributions

The plots of the cumulative proportion of overlap for the inter-nesting distribution for each rookery show that the asymptote was reached for all rookeries at n = 2-10 individuals sampled (see vertical dashed lines on Figure 2) except at the Montebello Islands (n = 5 turtles tagged) (Figure 2). The sample size was therefore adequate to describe the inter-nesting distribution at these nine sites. The cumulative proportion of overlap for migration was near to the asymptote (NWS stock-Pilbara with 0.83 overlap, and NWS stock-Kimberley/Scott-Browse stocks combined with 0.89
overlap) but the proportion of overlap for foraging (all stocks combined) was 0.59. Thus, the sample size was near to adequate for describing the migration distribution but not large enough to adequately quantify the extent of the foraging distributions (Figure 2).

### 3.2 Movement behaviour

Satellite tag deployments (all data combined) lasted between 19.5 and 537.5 days (median = 131.6 days) with a mean...
of 150.6 ± 95.7 days and mean total distance travelled of 804.6 ± 778.2 km (Table 1). Out of the 96 turtles, 19 remained resident at the rookery for the duration of their deployment. However, for 6 of the 19 resident turtles, the tracks were only of short duration (30.7 ± 10.3 days) and on examination of the end dates we concluded that these tracks represented inter-nesting behaviour only. Thus 13 out of 90 turtles (14%) showed non-migratory post-nesting behaviour (i.e. Type A3—local residence; turtles of a rookery that did not migrate and displayed post-nesting movements in the same or similar areas as inter-nesting). The 13 residents remained near their nesting sites at Rosemary Island (4), Ningaloo (3), Middle Island (2), Legendre Is (1), Scott Reef (1), Barrow Island (1) and Montebello islands (1) and had tracking durations of 173.0 ± 81.2 days.

Our calculation of inter-nesting area included 88 turtles, with the remaining eight switching to migratory behaviour and leaving the rookery immediately or shortly after tagging. Inter-nesting behaviour lasted for 43.7 ± 22.7 days on average after transmitters were deployed before turtles switched to migration behaviour, representing 38.5 ± 17.2% of the track duration.

After accounting for the short tracks (n = 6, ~30 day duration) and non-migratory turtles (13), our calculation of migration distribution included 77 turtles with an average duration of 18.5 ± 17.8 days spent in migration that represented 15.8 ± 17.5% of the track duration.

All turtles that migrated exhibited Type A1 strategy with oceanic and/or coastal movements to neritic foraging sites (Figure 1b; Figures S1–S3), except for one turtle from Scott Reef that displayed Type B (pelagic) movements prior to swimming towards the mainland and switching to Type A1 movements (Figure S1). Most of the turtles with A1 strategy displayed coastal movements (77%, n ± 59) (Figure S1), with the remainder (23%, n = 18) displaying oceanic movements (Figure S1a). Although some turtles used areas far from the coast, i.e. crossing the Joseph Bonaparte Gulf and Gulf of Carpentaria (Figures S1 and S2), this was not considered true oceanic migration. All turtles departing the only oceanic rookery at Scott Reef (n = 13) had a short period of oceanic swimming as they transited over deeper waters to reach the continental shelf (Figure 1; Figure S1b). Five turtles from coastal rookeries also exhibited oceanic movement including one turtle from each of Barrow Island and Montebello Islands swimming to the Rowley Shoals, one turtle migrating from Middle Island to the island of Sumba in Indonesia, and two turtles from the Lacepede Islands moving towards coastal waters off the Kimberley region and the Northern Territory (Figure S1a). Turtles from NWS stock (Pilbara and Kimberley sub-stocks) migrated mostly in a northeasterly direction from the rookery, but some (34%) also migrated south-west or south (Figure 1). All turtles from the Scott Reef rookery migrated to mainland Australia and followed the northwestern and northern Australian coast (Figure 1). Two turtles (both from NWS stock) left the Australian Exclusive Economic Zone (EEZ) into Indonesian waters (Sumba Island) and Papua New Guinea travelling 2,390 and 3,157 km respectively (Figure S1). Other notable migrations were from Barrow Island to the Cobourg Peninsula, Northern Territory (2,683 km) and from the Maret Islands to the Torres Strait in Queensland (2,418 km). The total distance travelled during migration between rookery and foraging areas was shortest for NWS stock-Pilbara (60–2,683 km, median = 306 km) followed by NWS stock-Kimberley (103–3,157 km, median = 733 km) and longest for Scott-Browse (479–2,308 km, median = 1,025 km) (Table 1). This matched the duration of the migration with 12 ± 14 days for NWS stock-Pilbara, 21 ± 20 days for NWS stock-Kimberley and 29 ± 18 days for Scott-Browse stock. Turtles from Scott-Browse were the slowest (42 ± 7 km/day) whereas turtles from NWS stock-Kimberley had the fastest movement rate 48 ± 26 km/day (Table 1).

Turtles tracked from the NWS stock-Pilbara remained mostly within Western Australia and the Pilbara region (91%) resulting in little mixing with the other stocks, whereas turtles tracked from NWS stock-Kimberley and Scott Reef were mixed along the Kimberley coast and migrated into other states and territories in Australia (Figure 1a; Figure S3). After accounting for the short tracks (6) and a further 7 tags that stopped transmitting during the migration we had a sample size of 83 for calculating foraging distribution. Turtles spent 109.4 ± 87.7 days (58.6 ± 23.8% of their time) in this behavioural mode until the tags stopped transmitting. Most turtles had only one foraging ground but 14 turtles (17%) had 2 with short periods of transit behaviour (3.2 ± 1.9 days) between them. No re-migration to a rookery was recorded.

3.3 | Turtle distribution

3.3.1 | Inter-nesting

Higher values of occupancy index and high overlap of turtles per grid cell occurred adjacent to nesting beaches for all rookeries (Figure 3; Figure S2). The area of use (95% distribution) for each site varied between 52.4 and 618.2 km² when calculated with the occupancy index, and between 78.5 and 1,890.3 km² when calculated with the number of turtles (Table 2). Using the depth of the water column obtained from bathymetry data underlying the inter-nesting locations from SSM tracks, inter-nesting turtles occupied mostly shallow waters (median depth = 9 m, range = 4–62 m) (Table 2), with the 95% distribution bounded by the 20 m bathymetric contour (Figure 3). Location data from turtles nesting at Scott Reef had the highest mean depth during inter-nesting (61.9 ± 167.4 m), although the 50% distribution (for both occupancy index and number of turtles) was located in shallow waters inside the lagoon (Figure 2c,d, indicated in red and yellow on the map). The higher mean depth for locations of inter-nesting turtles at Scott Reef is likely explained by a large range in values of bathymetry as demonstrated by the very high standard deviation of the mean, with the median (22 m) being perhaps more representative in this case where the distribution of the data was highly skewed. This is likely explained by the position of Scott Reef at the continental shelf edge, with deep water (>400 m) close to the rookery (3–4 km distance).
3.3.2 | Migration

During migration, the occupancy index was predictably low for all stocks due to the directed nature of migratory movements with high speeds (>40 km/day) and, consequently, less time spent in individual grid cells (Figure 4; Figures S4 and S5). As a result of the low occupancy, the migration distribution based on the number of turtles overlapping in a grid cell is potentially more informative than the occupancy index for highlighting hotspot areas (Figure 4; Figures S4 and S5). In the NWS-Kimberley stock, grid cells with higher occupancy (occupancy index > 0.5) and overlap of migrating turtles (> 40%) were often associated with areas near rookeries where many turtles are departing at similar times. However, the migration distributions also indicated other areas of high overlap of turtles, such as around Dampier Archipelago for the NWS stock-Pilbara (Figure 4a,b) and between the Maret Islands and Bougainville Peninsula for the NWS stock-Kimberley and Scott-Browse stocks (Figure 4c,d; Figure S5), highlighting these regions as potential areas for protection.

3.3.3 | Foraging

Foraging turtles were largely concentrated in shallow waters (median of 9 m, ranging from 1 to 104.5 m) although the two turtles with foraging behaviour at Rowley Shoals located near the 300 m bathymetric contour used deeper water (82.6 ± 18.4 m) (Figures 1 and 5c,f). The 75% foraging distribution constituted multiple, discrete grid cells of medium to high occupancy (occupancy index > 0.5) but low overlap of turtles (<6% of foraging turtles) in nearshore waters of islands and the mainland. Given the difficulty of seeing detail of the distribution at the scale of use (Figure 1), we present the distribution at a range of smaller scale sections of the coast (Figure 5). The calculated area was...
TABLE 2  Area size in km² of the 50% (shown for comparison with other studies) and 95% inter-nesting distribution for each rookery based on occupancy index and number of turtles (N). Mean depth of the water column (±SD) obtained from bathymetry data underlying inter-nesting locations of SSM tracks for each rookery is also shown.

| Stock                      | N  | 50% index of occupancy | 95% index of occupancy | 50% N turtles | 95% N turtles | Mean depth (m) |
|----------------------------|----|-------------------------|-------------------------|---------------|---------------|----------------|
| NWS stock-Pilbara          |    |                         |                         |               |               |                |
| Legendre Is                | 4  | 17.6                    | 52.8                    | 70.4          | 220.2         | 7.9 ± 8.8      |
| Rosemary Is                | 6  | 8.8                     | 158.4                   | 149.6         | 563.2         | 8.7 ± 7.6      |
| Middle Is                  | 10 | 17.5                    | 87.8                    | 61.4          | 237.0         | 3.5 ± 3.9      |
| Barrow Is                  | 9  | 43.9                    | 281.2                   | 149.4         | 597.5         | 13.9 ± 10.5    |
| Muiron Is                  | 6  | 8.7                     | 52.4                    | 61.1          | 227.0         | 4.9 ± 4.2      |
| Ningaloo Reef              | 7  | 8.7                     | 69.8                    | 52.3          | 78.5          | 17.0 ± 7.9     |
| Montebello Is              | 10 | 70.4                    | 193.7                   | 176.1         | 484.2         | 8.5 ± 10.2     |
| NWS stock-Kimberley        |    |                         |                         |               |               |                |
| Lacepede Is                | 10 | 18.0                    | 197.7                   | 188.7         | 737.0         | 4.7 ± 4.3      |
| Maret Is                   | 19 | 45.5                    | 618.2                   | 327.3         | 1,890.3       | 31.3 ± 14.6    |
| Scott-Browse stock         |    |                         |                         |               |               |                |
| Scott Reef                 | 12 | 9.1                     | 145.7                   | 82.1          | 783.0         | 61.9 ± 167.4   |

FIGURE 4  Migration distributions for the NWS stock-Pilbara zoomed to the 75% distribution (black contour) (a–b) and NWS stock-Kimberley and Scott-Browse stocks combined (c–d) using the occupancy index (a and c) and the percentage of migrating turtles per grid cell (b and d). Grey lines indicate bathymetric contours 50, 200, 1,000 m.

FIGURE 5  Foraging distributions (all data combined) off Shark Bay (a, d), from near Exmouth up to Dampier Archipelago (b, e); from Port Hedland to Broome (c, f), Kimberley and Scott Reef (g, j), Cobourg Peninsula and Tiwi Islands (h, k), and Gulf of Carpentaria and Torres Strait (i, l). a–c and g–i show foraging distributions calculated using the occupancy index, d–f and j–l show foraging distributions calculated using the percentage of foraging turtles per grid cell; Black contours indicate the 75% distribution contours and grey lines are bathymetric contours (10, 50, 100 and 200 m).
considerably larger when using number of turtles than using occupancy (69,122 km$^2$ and 23,798 km$^2$, respectively), likely because the occupancy distribution was influenced by the many discrete, small foraging areas with high occupancy that were used by only one or low numbers of individuals (Figure 5a–c, g, h). Whereas the 75% foraging distribution using number of turtles indicated all grid cells used by 1 or more turtles irrespective of the intensity in which areas were used resulting in a larger extent. Given this, and that our distribution is likely to be an underestimate (based on our sample size analysis), we considered the distribution using the number of turtles per grid cell as a more conservative measure of the overall spatial distribution of foraging turtles. The 75% foraging distribution included Shark Bay, a near continuous polygon from Ningaloo to Roebuck Bay, the southern (Buccaneer Archipelago and Adele Island) and northern Kimberley (off the Bougainville Peninsula) and one site in the Northern Territory (Tiwi Islands and Cobourg Peninsula). To assist with management, we identified 13 geographical areas (Figure S6) that made up the 75% distribution where multiple turtles from either one or both stocks co-occurred (Table 3; Figure S7, Table S1). The size of grid used for the calculation of foraging distribution did not have a strong influence on the identification of these foraging areas although it clearly has an influence on the size of the area (Figure S8). Almost all foraging regions defined with a 20 km grid cell were also identified with increasing and decreasing grid sizes, with the exception of Rowley Shoals that was not identified with a 50 or 100 km grid (Figure S8).

The 95% inter-nesting distribution (occupancy index) had the largest overlap (40.2%) with protected areas (Figure 6b, c), followed by the 75% foraging distribution (number of turtles, 34.4%) (Figure 6e, f; Table S2). During migration, 22.2% of the 75% migration distribution for the NWS stock-Pilbara and 34.4% of the combined 75% migration distribution for the NWS stock-Kimberley and Scott-Browse stock were inside protected areas (Figure 6d; Table S2). There was a reasonable match between the spatial extent of the 95% inter-nesting distribution (occupancy index and number of turtles) and the Inter-nesting Habitat Critical Areas (defined as a 20 km buffer around known rookeries) for the Lacepede Islands, Maret Islands and Scott Reef (Figure 6; Table S2). Although the 95% inter-nesting distribution for the NWS stock-Pilbara rookeries was encompassed by the 20 km buffer, it was much smaller (Figure 6). We identified a large overlap (40.4%) between the 75% migration distribution for the NWS stock-Pilbara and the migratory corridor (75% kernel distribution) proposed by Pendoley et al. (2014) (Figure 6d). The proposed migratory corridor also had a 17.7% overlap with the 75% migration distribution for the NWS stock-Kimberley and Scott-Browse stocks combined (Figure 6). The migration corridor proposed by Pendoley et al. (2014) had a 33.1% overlap with existing Australian Marine Parks (Commonwealth) and 3.1% with State-managed reserves (Table S2). The 75% foraging distribution overlapped with existing foraging BIAs recognized by the Australian Government in Western Australia in the Barrow Group, Dampier Archipelago, Port Hedland and Roebuck Bay, but there was only 5% overlap overall (Figure 6; Table S2). Some of the designated foraging BIAs were not validated by our analysis (e.g. Joseph Bonaparte Gulf although it encompasses some of the migration distribution from WA to NT) and many of the foraging areas quantified in this study are not formally recognized as BIAs (Figure 6e, f).

Interactive maps of the distributions delimited here can be accessed in the North West Atlas (https://northwestatlas.org/nwa/nws2s-megaflora).

|                  | NWS stock-Pilbara | NWS stock-Kimberley | Scott-Browse |
|------------------|------------------|---------------------|--------------|
| Shark Bay        | 4                |                     |              |
| Exmouth /Ningaloo| 11               |                     |              |
| Barrow Group     | 6                |                     |              |
| Dampier Archipelago | 7            |                     |              |
| Mundabullangana   | 4                |                     |              |
| Port Hedland     | 5                | 1                   |              |
| Eighty Mile Beach| 6                | 2                   | 2            |
| Rowley Shoals    | 1                | 1                   |              |
| Roebuck Bay      | 1                | 2                   |              |
| Adele Is         | 1                | 1                   |              |
| Buccaneer        | 2                |                     |              |
| Bougainville     | 5                | 1                   |              |
| Tiwi/Cobourg     | 1                | 7                   | 5            |

**TABLE 3** Number of individual turtles (calculated using the 75% foraging distribution of each individual turtle) from each rookery and stock/sub-stock at each region along the coast (see Figure 5). Outlined rows indicate areas used for foraging by all stocks/sub-stocks.
Compiling and analysing a large satellite tracking dataset allowed us to quantify the spatial extent of inter-nesting for a representative portion of adult female green turtles from Western Australian rookeries (n = 10) comprising 2 genetic stocks. We have provided the first spatial data on the areas used post-nesting, identifying two main migratory corridors (Pilbara and Kimberley) to many disparate, primarily neritic foraging areas dispersed throughout inshore waters along the northwestern Australian coastline. Despite some limitation with sample size, our quantification of foraging distribution provides more robust data to support spatial management and conservation of green turtles at local and regional scales than is currently available.

Our results show that the existing delineation of a 20 km radius around green turtle rookeries as an inter-nesting buffer in the Recovery Plan for Marine Turtles in Australia (Commonwealth of Australia, 2017) encompassed the inter-nesting distribution we defined here, supporting its effectiveness in protecting nesting green turtles. For the NWS stock-Pilbara rookeries, the 95% distribution area was, however, considerably smaller than the 20 km buffer.

The migration patterns we found were in accordance with a review of turtle migration strategies by Godley et al. (2008) suggesting there are 4 general strategies, with green turtles showing two of these: Type A1; oceanic and/or coastal movement to neritic foraging grounds and Type A3; local residence. We found a Type A1 movement pattern for the majority of WA turtles (86%) and 14% Type A3 as has been found for green turtles nesting at the Cocos Keeling Islands (Whiting et al., 2008). Even turtles from the Scott-Browse stock nesting on Sandy Islet at Scott Reef (an oceanic atoll at the edge of the Australian continental shelf) showed mostly Type 1 movement, as has also been found for other oceanic islands such as the Galapagos Islands and Ascension Island (Godley et al., 2002; Hays et al., 2002; Seminoff et al., 2008). These oceanic island nesters often perform directed movement crossing oceanic regions to reach foraging grounds in mainland coastal locations despite apparent availability of foraging habitat at these islands or potentially other locations along the way (Hays et al., 2002; Shimada et al., 2019). Indeed, we found only 1–3 individuals that had movement behaviour classified as foraging on route to foraging grounds, with the majority having only one main foraging ground.

However, in contrast to green turtles in Galapagos and Ascension islands that migrate over extensive (thousands of km) oceanic areas (Hays et al., 2002; Seminoff et al., 2008), the migratory behaviour of green turtles in Western Australia was largely dominated by less extensive movements (804.6 ± 778.2 km) and mostly coastal routes, with many even resident (14%), although some large distances (>2,000 km) and oceanic movements were recorded. This may be related to the fact that the majority of the studied rookeries were on the continental shelf, relatively close to the mainland shore. This predominance of coastal travel was also observed for green turtles in the Mediterranean Sea (Godley et al., 2002), Equatorial Guinea (Mettler et al., 2019) and Costa Rica (Blanco et al., 2012) with the distribution of foraging habitat availability and quality (Christiansen et al., 2017) a suggested reason for this migration strategy. Regional oceanographic setting and ocean currents also play a significant role in hatching dispersal and are thought to largely determine adult foraging grounds (Gaspar et al., 2012; Hays et al., 2010; Scott et al., 2014). The dispersal of simulated particles from different locations along the coast of Western Australia showed that release locations on wide continental shelves, as is present on most of the Northwest Shelf, resulted in particles being retained on the shelf (Robson et al., 2017).

We broadly identified two migratory corridors, one used by the NWS stock-Pilbara and another used by the NWS stock-Kimberley and the Scott-Browse stock with some overlap at the northern and southern extents respectively (Figures 4 and 6). We also identified areas within each corridor that might be acting as bottlenecks with a high proportion of migrating turtles overlapping in a narrow section along the nearshore, particularly near the Dampier Archipelago in the Pilbara (41% of NWS stock-Pilbara migrating turtles) and between the Maret Islands and Bougainville Peninsula in the North Kimberley (47% NWS stock-Kimberley and Scott-Browse stock migrating turtles). These locations of overlap are likely driven by preference for the shortest migration route around the coast. The corridor along the Pilbara coast and the southern end of the Kimberley corridor also overlapped (40% and 18% respectively) with the spatial extent and location of a migratory corridor used by multiple marine fauna species (Figure 6d; Pendoley et al., 2014). Given the importance of these corridors in connecting breeding and foraging grounds, Pendoley et al. (2014) proposed the creation of a new MPA based on this multi-species coastal corridor. Our results provide further support for this notion (noting that 36% was included in existing MPAs) and the use of the corridors defined here to potentially designate further Habitat Critical Areas for green turtles and other turtle species.

Although many of the foraging areas that we define have been previously documented in the literature (Dethmers et al., 2010; Heithaus et al., 2008; Pendoley, 2005; Preen et al., 1997; Prince et al., 2012; Richards et al., 2006) and in unpublished sources and through flipper tag recoveries, this is the first time the area used for foraging has been quantified. The foraging extent we calculated can be used to guide the designation of habitat critical areas for foraging, particularly off Eighty Mile Beach and Tiwi Is/Cobourg Peninsula where both stocks co-occurred and areas that had the highest number of turtle use (Exmouth/Ningaloo and the Dampier Archipelago). Some foraging grounds used by 1–2 tracked turtles, such as in Sumba, Indonesia, at Scott Reef, in the Gulf of Carpentaria and Torres Strait were not included in the 75% foraging distribution we calculated. This may be due to the limitation of our sample size, and a larger sample size and samples from additional rookeries and stocks not represented here (e.g. Browse Island, Cassini Island, Ashmore Reef), might have allowed the analysis to pick up these foraging grounds. For example, flipper tags from green turtles tagged at Northwest Shelf rookeries have been recovered in Arnhem Land and Gulf of Carpentaria (Prince, 1998; DBCA unpublished data) and genetic mixed stock analysis shows that Northwest Shelf turtles are also...
found in the Gulf of Carpentaria and Indonesia (Dethmers, 2010; Dethmers et al., 2010; Jensen, 2010; Joseph et al., 2014).

Our analysis showed relatively low (compared to our sample size of 96) overlap of foraging turtles (max – 6%) which may suggest high availability of foraging habitat in our study region (i.e. inshore waters of much of northern Australia). However, our analysis indicated that despite our large sample size, it was still insufficient for calculating the total distribution over our large study area. This is likely because our sample size is still considerably small when compared to the expected population size of green turtles in Western Australia. For example, Dethmers et al. (2006) estimated the population of female green turtles in the Northwest Shelf stock alone to be approximately ~125,000 individuals. Increasing the sample size of tracked nesting females on the studied rookeries and deploying at rookeries not yet sampled may decrease this limitation. It is also likely a significant portion of other Australian stocks (Ashmore Reef, Gulf of Carpentaria) and international green turtle stocks forage in Australia and mix with the Northwest Shelf stock at foraging grounds (Dethmers et al., 2010). Deploying transmitters on turtles on the foraging grounds, including males and juveniles, combined with further genetic analysis may also be useful for increasing our ability to determine the total foraging distribution (reach the asymptote in the cumulative overlap curve) and to identify important mixed or single stock foraging areas. In addition, species distribution models and habitat suitability models may also be useful for documenting suitable foraging habitat for green turtles (e.g. Hawkes et al., 2007; Pikesley et al., 2013), and thus potentially being able to account for the uncertainty (lack of an asymptote in our cumulative probability curve) in the extent of the foraging distribution presented here. Despite these limitations, the broad geographical distribution we defined is still extremely valuable, as it is the first quantitative analysis of green turtle distribution at the stock scale and is a marked improvement on the previous data deficient methods. Importantly, our analysis of sample size is rarely undertaken and provides additional context with which to interpret the results.

Around 98% of the tracked turtles remained in Australian waters. Although our assessment of sample size precludes us from extrapolating this to the stock scale, it does suggest that a large portion of Australian green turtle stocks remain within Australian waters (only 2/96 left the Australian EEZ), and therefore, conservation and management strategies for this sub-population (at least for females) will correspond primarily to actions at the national scale. However, the total proportion of female green turtles leaving the Australian EEZ and foraging in international jurisdictions is likely to be greater than our estimated 2%. Thus, inter-jurisdictional management with neighbouring countries may be necessary to ensure full protection for Australian green turtle stocks; however, more data are needed to determine the necessity for such actions.

The overlap between green turtle movements and MPAs (Australian and State/Territory), indicated a relatively high protection that currently exists for the satellite tagged turtles in this study. For example, both the foraging distribution off Eighty Mile Beach and the proposed migratory corridor (Pendoley et al., 2014) largely overlap with the MPAs in that area (Commonwealth, State and Indigenous). However, the zoning of MPAs does vary greatly in relation to the activities allowed, from fully closed to open to general use or recreational activities (diving/snorkelling tourism, recreational fishing and navigation). National Parks, Sanctuary and Recreational Use zones within Australian marine protected areas (Commonwealth and State-managed) are closed to commercial activities such as commercial fishing and aquaculture. Some types of commercial fishing may be allowable with authorization in Special Purpose and Habitat Protection zones ([https://parksausralia.gov.au/marine/parks/] (Figure 6). Unsurprisingly perhaps, given that the BIAs were not based on quantitative analysis, our results show that the foraging BIAs are largely underestimating and missing important foraging areas for green turtles in Western Australia (only 5% overlap). Although the inter-nesting buffer (20 km radius around rookeries) did overlap with some of the foraging areas, especially on the southern Pilbara coast, these protections are likely to be focussed on the nesting season rather than year round.

Our study highlights the value of compiling and analysing multiple tracking datasets for the delineation of distribution and BIA/EBSA for marine turtles to assist with assessing and mitigating impacts of industrial development and other pressures in the region. Our results have shown that the foraging distribution of green turtles from two stocks in Western Australia expands throughout northwest and northern Australian coastal waters, including the Northern Territory and Queensland. Some turtles also crossed into international EEZs of Indonesia (n = 2) and Papua New Guinea (n = 1) potentially exposing them to additional threats from illegal harvest (Joseph et al., 2014; Pilcher et al., 2008). This suggests that a future analysis of satellite tracking data would benefit from the incorporation of data from those areas, with tracking datasets for this species in existence more broadly in the Indian Ocean and Southeast Asia (Hays et al., 2018). The inclusion of these datasets would allow for a more complete picture with the potential to offer further insights into the movement ecology of this threatened and migratory species, as has been shown for other similar collaborative studies (e.g Fossette et al., 2014; Hazen et al., 2017; Hindell et al., 2016, 2020).

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

Existing tracking data compiled in this study can be made available upon request with consent from data owners. Data from new satellite transmitter deployments included in this study (n = 20) have been made available at Zoatrack (https://zoatrack.org/projec ts/534) and the Australian Institute of Marine Science Data Centre at: https://www.aims.gov.au/nw-shoals-to-shore/threatened-speci es-of-the-north-west.

ORCID

Luciana C. Ferreira  https://orcid.org/0000-0001-6755-2799

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BIOSKETCH

The research team includes a broad group comprised of research scientists, conservation managers and environmental consultants based largely in Australia. The main focus of our research is the ecology of threatened marine megafauna (especially marine turtles) and specifically distribution, movement and identification of important areas to assist management and conservation. The team have authored and co-authored over 300 publications between them, much of which has been instrumental in informing policy and regulation on marine turtle and other threatened species management in Australasia and more broadly. The team includes members of the IUCN Marine Turtle Specialist Group (https://www.iucn-mtsg.org/) with key involvement in the Australian marine turtle recovery process (https://www.environment.gov.au/marine/publications/recovery-plan-marine-turtles-australia-2017) and the National Environmental Science Program (NESP, https://www.nespmarine.edu.au/theme/theme -threatened-and-migratory-species). The research was led by the Australian Institute of Marine Science (Ferreira and Thums), the top-ranked research institution in the field of marine and freshwater biology (2015–2019) and co-led by the Marine Science Program (NESP, https://www.nespmarine.edu.au/theme/ theme -threatened-and-migratory-species). The research team includes members of the IUCN Marine Turtle Specialist Group (https://www.iucn-mtsg.org/) with key involvement in the Australian marine turtle recovery process (https://www.environment.gov.au/marine/publications/recovery-plan-marine-turtles-australia-2017) and the National Environmental Science Program (NESP, https://www.nespmarine.edu.au/theme/theme -threatened-and-migratory-species). The research was led by the Australian Institute of Marine Science (Ferreira and Thums), the top-ranked research institution in the field of marine and freshwater biology (2015–2019) and co-led by the Marine Science Program at the Department of Biodiversity, Conservation and Attractions (DBCA, Whiting, Fossette, Tucker).

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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