

RESEARCH ARTICLE

Space-use patterns of green turtles in industrial coastal foraging habitat: Challenges and opportunities for informing management with a large satellite tracking dataset

Emily G. Webster¹  | Mark Hamann¹  | Takahiro Shimada²  | Colin Limpus² | Stephanie Duce¹ 

¹College of Science and Engineering, James Cook University, Townsville, QLD, Australia

²Queensland Department of Environment and Science, Brisbane, QLD, Australia

Correspondence

Emily G. Webster, College of Science and Engineering, James Cook University, Townsville, QLD, Australia.

Email: emily.webster1@my.jcu.edu.au

Funding information

GHD Group; GISERA Marine Project; Gladstone Ports Corporation (partially funded by the Ecosystem Research and Monitoring Program); James Cook University; Orica Limited; Queensland Department of Environment and Science (formerly Department of Environment and Heritage Protection); Shell's QGC Business, Australia Pacific LNG and Santos GLNG; The Centre for Tropical Water and Aquatic Ecosystem Research (TropWATER)

Abstract

1. Increasing overlap between anthropogenic activities and wildlife can lead to problematic human–wildlife interactions. To manage these, an understanding of animal space-use patterns, with sufficient temporal and spatial detail is required. Satellite telemetry can provide such detailed data; however, the cost of tracking units places a significant limitation on sample size.
2. Satellite tracks for 72 green turtles were consolidated through collaboration with multiple entities over 8 years at seven sites within a large industrial port contributing to an ecological monitoring initiative to minimize impacts of planned developments.
3. This study aims to determine the minimum number of satellite-tracked green turtles required to represent spatial distribution patterns in the foraging ground and to evaluate factors underpinning differences in distribution and site fidelity metrics to inform appropriate management strategies.
4. An autocorrelated kernel density estimator was used to construct 95% utilization distributions for individual turtles during each calendar season. Percentage overlap between pairs of seasonal utilization distributions was calculated as a measure of short-term site fidelity. Mechanistic range shift analysis was applied to detect significant deviations from range residency behaviour.
5. Green turtles exhibited spatially confined ranges and remained faithful to their foraging area for periods of up to 260 days. Range size was significantly different between microhabitats and study years. Only 16 individuals (22% of tracked turtles) performed significant range shifts, indicating that occupied areas represent important habitats, and most turtles are unlikely to adjust their space-use in response to anthropogenic or natural disturbances.
6. Although this dataset represents an atypically large sample of satellite tracked individuals, representative data were obtained at only two key sites.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2022 The Authors. *Aquatic Conservation: Marine and Freshwater Ecosystems* published by John Wiley & Sons Ltd.

7. This study highlights the importance of evaluating clear objectives when sampling animals for satellite telemetry studies to obtain representation of sites, periods of interest, or age and sex cohorts.

KEYWORDS

coastal management, continuous time movement models, habitat use, marine turtle, range, satellite telemetry, site fidelity, utilization distribution

1 | INTRODUCTION

Growing human populations increasingly encroach upon natural ecosystems (e.g. Halpern et al., 2015; Venter et al., 2016; Watson et al., 2016; Taylor-Brown et al., 2019; Harfoot et al., 2021), with urban spread and industrialization contributing to diverse impacts on adjacent environments (Lutcavage et al., 1997; Neumann et al., 2015; Mentaschi et al., 2018; Prosser et al., 2018; Todd et al., 2019 among others). Shallow inshore habitats represent nurseries (Beck et al., 2001; Sheaves, Baker & Johnston, 2006; Cheminée et al., 2021) and developmental or foraging grounds (Seitz et al., 2006; Coles et al., 2007) for many marine animals (Seitz et al., 2014). Altering these habitats can therefore have repercussions for the reproductive output of species, trophic interactions and ecosystem health, and extend beyond the specific sites of the disturbance (Seitz et al., 2014; Macura et al., 2019).

Minimizing impact to marine species requires knowledge of their spatial distributions and how these change over time. For wild animals, distribution information can be ascertained from tracking data. However, the cost of fine-scale tracking typically imposes a major limitation on the number of animals that can be tracked. Therefore, tracks collected may fail to represent larger population-scale patterns. Evaluating representativity is pertinent for deriving population-level inferences from the tracking data, particularly in an applied management context.

Representative utilization distribution modelling with tracking data may elucidate core habitat areas for the management of ongoing, and planned developments, or human activities that may interact with protected wildlife including charismatic marine megafauna such as green turtles (*Chelonia mydas*) (Blumenthal et al., 2006; Godley et al., 2008; Scott et al., 2012; Gredzens et al., 2014; Shimada et al., 2016a; Shimada et al., 2017; Hays et al., 2019). Green turtles inhabit shallow inshore habitats at multiple life stages (Limpus, Couper & Read, 1994; Limpus et al., 2005; Limpus, Paramenter & Chaloupka, 2013) and some populations (including the southern Great Barrier Reef stock) are increasing in size (Chaloupka & Limpus, 2001; Chaloupka et al., 2008; Limpus, 2008; Limpus, Paramenter & Chaloupka, 2013; Department of Environment and Science, 2021). Coupled with coastal urban and industrial expansion, this is likely to lead to increased frequency of interactions between turtles and humans (Hazel & Gyuris, 2006; Flint et al., 2017a). There is a paucity of information on the overlap between turtles and coastal infrastructure including industry in Queensland.

High fidelity and the tendency of green turtles to return to their foraging areas when displaced or following breeding migrations, may limit their resilience to local disturbances such as human development and extreme weather events (Shimada et al., 2016b; Shimada et al., 2020). In low density foraging areas where individuals of multiple age and size classes share habitat and show prominent residency, the protection of a few key sites at pertinent times is likely to confer considerable long-term conservation benefits (Scott et al., 2012; Schofield et al., 2013; Hays et al., 2021). Identification of these sites and periods should consider habitat requirements for individuals at several life history stages and dynamic oceanographic and biological processes that characterize variations in resource availability including rainfall events, tidal flow regimes, senescence and reproduction of primary producers.

To inform appropriate management strategies for protected green turtles in a large industrial port, this study addresses four research objectives: (i) to determine the minimum number of green turtles required to represent population scale distribution patterns at each study site and year; (ii) to delineate representative areas used by tracked foraging green turtles and assess potential factors underpinning green turtle distributions including site, time, and turtle maturity, sex and size; (iii) to quantify individual fidelity to sites, an important species trait that may implicate resilience of green turtles to changes in resource availability and local threats; and (iv) to examine evidence of deviation from site fidelity behaviour by identifying significant range shifts.

2 | METHODS

2.1 | Study Site

Port Curtis (Figure 1) sits within the boundary of the Great Barrier Reef World Heritage Area. It is Queensland's largest multi-commodity port, and the fifth largest in Australia by cargo tonnage and exemplifies the overlap between large-scale industrial activities and marine life. The port infrastructure consists of eight main wharf centres containing 20 wharfs and supporting coal, Liquefied Natural Gas, grain, aluminium, cement and alumina export, and import of bauxite among others (Gladstone Ports Corporation, 2019). It also hosts commercial and recreational fishing vessels and transport for tourism to the Capricorn Bunker group of islands. Port Curtis includes extensive intertidal areas and is known habitat for six species of

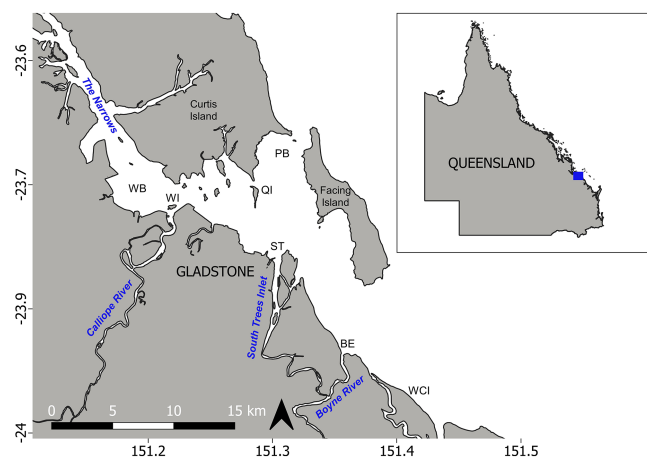


FIGURE 1 Map of Queensland with insert showing Port Curtis study sites monitored by Queensland Department of Environment and Science: Pelican Banks (PB), Western Basin (WB), Wiggins Island (WI), Quoin Island (QI), South Trees (ST), Boyne Estuary (BE) and Wild Cattle Island (WCI)

marine turtle (Gladstone Ports Corporation, 2019). Study of habitat use by marine turtles in Port Curtis began in 2009 in response to planned dredging and expansion of port infrastructure to accommodate a growing demand for vessel operations. Queensland Department of Environment and Science and university collaborators have monitored the demographics, population dynamics, health and habitat use of green turtle foraging populations in the port since 2010 (Gladstone Ports Corporation, 2019). Green turtles in Port Curtis predominantly belong to the Southern Great Barrier Reef genetic stock (Limpus, Paramenter & Chaloupka, 2013; FitzSimmons & Limpus, 2014).

The abundance and extent of seagrasses in Port Curtis has declined since 2005 due to increasing frequency of major weather events (Bryant et al., 2013) and the consequences for marine turtles are of concern. Major flooding caused by tropical cyclone Yasi in 2011 and ex-tropical cyclone Oswald in 2013 was linked to record numbers of strandings of both green turtles and dugongs in Port Curtis (Meager & Limpus, 2014; Flint et al., 2017b). Similarly, green turtles in Port Curtis had poorer body condition than at other coastal foraging sites in Queensland following the 2010 and 2011 flood events (Limpus et al., 2012; Flint et al., 2015). Another major flood event occurred in 2017. Repeated flood disturbance may lead to long-term loss of seagrass meadows, affecting the health, survivorship and reproduction of foraging turtles (Flint et al., 2017b).

Port Curtis comprises seven broadly defined study areas for green turtle monitoring (Figure 1): the Pelican Banks (PB) intertidal seagrass flats (primarily *Zostera muelleri* with some *Halophila ovalis*, *H. decipiens* and *Halodule uninervis*) beside the outflows through the channel between Curtis and Facing Islands; the Western Basin (WB) characterized by turbid water with patchy seagrass cover (*H. ovalis* and *Z. muelleri capricorni*); the Wiggins Island (WI) intertidal flats fed by outflows from the Calliope River; Quoin Island (QI) intertidal rocky reef and mangrove habitats; South Trees (ST) intertidal and subtidal

flats; Wild Cattle Island (WCI) subtidal adjacent to outflows from Colosseum Creek; and the intertidal flats adjacent to the Boyne Estuary (BE).

2.2 | Turtle capture and processing

In each of the study years (2010–2019) green turtles were captured as part of regular monitoring activities by either rodeo (Limpus, 1978) or intercepted with blocking nets as they moved off shallow flats on the falling tide (Limpus et al., 2017). A GPS location was recorded for each capture. All captured individuals were taken to the Gladstone Marina for processing. Weight and curved carapace length (CCL) were recorded, and external body condition was examined. Where trained personnel were present, sex and breeding status was determined by laparoscopy and/or ultrasonography (Limpus, Couper & Read, 1994; Limpus et al., 2005). Turtles were marked with two uniquely numbered titanium flipper tags (as per Limpus et al., 1992). For satellite tag attachment, algae, flaking scute material and epifauna were removed from the anterior portion of the carapace, which was roughened using sandpaper and cleaned with acetone. The tag was glued across the first and second vertebral scutes with a Sika anchorfix 3 + 2-part epoxy. Before becoming touch-dry this first attachment was reinforced with fibreglass tape and epoxy around the borders of the tag, extending onto the adjacent costal scutes. The tag and attachment were then painted with antifoul paint and allowed to set overnight. Turtles were released the next day from either their capture site, or at a location between the Gladstone Marina and the capture site. Capture of turtles, transmitter attachment and data collection for this programme were approved by either the JCU Animal Ethics Committee or the Department of Agriculture and Fisheries Ethics Committee and conducted within an approved Queensland Government project.

Sampling in Port Curtis was conducted opportunistically until 2018. From 2010 to 2018, most captures occurred on the Pelican Banks, where conditions were favourable for catching (clear and shallow water). Initial results from tracked turtles (Shimada et al., 2016a; Hamann et al., 2017; Pillans et al., 2021) indicated that they mostly remain in the area in which they were captured, and that tracking a few turtles does not reflect space-use in the wider port. Subsequent emphasis was placed on the capture and tracking of individuals at other sites closer to ongoing and planned development operations. For this reason, and the variability of funding for tracking studies year-to-year (Appendix A), only small samples of turtles were obtained from WCI, ST, BE and QI for the present study.

2.3 | Transmitter configuration and data filter

Wildlife computers (Redmond, WA, USA) SPLASH10 or Sirtrack (Havelock North, NZ) Fastloc GPS tags were used in all study years (Appendix A). Only Fastloc GPS fixes were retained due to their relatively high location accuracy (Shimada et al., 2012; Dujon,

Lindstrom & Hays, 2014). The first 24 hours were removed from each individual's track to account for acclimation or homing behaviour (Shimada et al., 2016b). For outlier removal, locations with residual error values of greater than 30, or from less than four source satellites were removed. Additionally, the SDLfilter package in the R software (Shimada et al., 2012) was used to exclude spurious locations determined by maximum travel speeds and turning angles. Spatial and temporal duplicates in the data and locations above the high tide line were also excluded (Shimada et al., 2016b). Fastloc GPS locations screened with the SDLfilter data driven filter had a mean accuracy of 47.1 m when derived from >3 satellites (Shimada et al., 2012); a similar mean data accuracy was assumed for the current tracking data.

2.4 | Optimal sample sizes

The minimum number of individuals required to represent the distribution of green turtles at each site and year was estimated with the SDLfilter package (Shimada et al., 2021). This method calculates the probability of each randomly selected individual's (1^{st} – i^{th}) utilization distribution (UD) being within areas used by (merged 100% UD of) other individuals (1^{st} – $(i-1)$). The merged 100% UD was chosen to minimize the impact of potential under-estimation of coverage areas caused by the tight association of the estimated UD with the highly accurate GPS locations. The mean probability and cumulative areas corresponding to each number of tracked individuals is determined through bootstrapping and a rational function is fitted to these mean probabilities to estimate an asymptotic curve relative to sample sizes (i.e. number of tracked individuals). The minimum sample size is determined as the number of individuals required to reach 95% of the estimated asymptote of the mean overlap probabilities. For this analysis, the UD was estimated from entire tracks of individuals with a movement-based kernel density estimator in the R package adehabitatHR (Calenge, 2006). The movement-based kernel density estimator was selected for its ability to deal with entire tracks (up to 260 days) with low computation cost.

2.5 | Utilization distribution estimation

Location error estimates from Dujon, Lindstrom & Hays (2014) encompassing the 95th percentile of filtered data from fixed trials were used to calibrate the filtered data according to location classes defined by the number of source satellites (Table 1). Error calibration accounts for location error in utilization distribution estimation (Fleming et al., 2019). For each individual, continuous time movement models were fitted for each calendar season of the tracking period in the ctmm R package (Fleming & Calabrese, 2021). Several residual maximum likelihood-based models were fitted with the ctmm.select() function, and models with lowest Akaike' information criterion (AIC) were selected for timeseries kriging (Fleming et al., 2016) to produce UD from weighted autocorrelated kernel density estimates (AKDEs) for each season with the akde() function (Fleming & Calabrese, 2021).

TABLE 1 Estimated root mean square user equivalent range error (m) with 95% confidence intervals (CIs) of Fastloc GPS based on number of satellites used to acquire relocations in Dujon, Lindstrom & Hays (2014) dataset. Estimated with the ctmm package in the R software

Number of Satellites	Low 95% CI	Estimate	High 95% CI
4	760.66	937.02	1,113.03
5	585.78	630.75	675.67
6	396.12	421.24	446.35
7	365.28	384.67	404.05
8	152.94	159.14	165.34
9	12.66	13.19	13.71
10	11.42	12.45	13.47
11	9.31	10.67	12.03

Contours delineating 50% and 95% volume of the AKDE represent the area where it would be expected to find the animal with 50% and 95% chance. Home range estimation for discrete time periods can be used to describe the distribution of range residents but is not meaningful for migratory or nomadic individuals (Börger et al., 2020). Effective sample sizes in the AKDE are proportional to the number of times an animal crosses their home range in the sampled period (Fleming et al., 2019). The AKDE generated from tracks with small effective sample size is likely to underestimate home range area and confidence intervals will be unacceptably large. Thus, AKDEs obtained from effective sample sizes fewer than six were discarded (Fleming et al., 2019). The ctmm approach accounts for autocorrelation (Fleming & Calabrese, 2017), missing and irregular data (Fleming et al., 2018), small effective sample sizes (Fleming et al., 2019), and location error (Fleming et al., 2020).

2.6 | Fidelity and range shifts

The degree of overlap of AKDE between consecutive seasons was calculated with the overlap() function for each individual in the ctmm package and used as a measure of individual site fidelity. Individual tracks were too short to allow calculation of overlap across years. Significant range shifts were identified with mechanistic range shift analysis (MRSA) in the R package MARCHER (Gurarie & Cheraghi, 2017). The MRSA performs a likelihood ratio test to compare movement models for an animal's location data with and without a simulated range shift. Animals without significant range shifts were considered range residents. Generalized linear mixed models (Appendix B) were constructed in the R package glmmTMB (Brooks et al., 2017) to assess covariates of significant differences in the size of the seasonal 95% UD area, pairwise overlap of seasonal UD and for significant range shifts. The covariates assessed were individual maturity, size (CCL), sex, capture site and capture year, with individual included as a random factor. Several combinations of predictor variables were tested for each response variable based on the study objectives and the ability of generalized linear mixed models

to meet model assumptions and converge given unequal sample sizes across categories. Significant covariates were identified by selecting the best ranking model based on AIC corrected for small sample sizes (AICc). Model fits were validated with residual diagnostics tests, tests for zero inflation, dispersion and temporal autocorrelation in the DHARMA package in R (Hartig, 2021). A limitation of the study design is that tracks with significant range shifts are not reflected in the overlap metrics, as UD's derived from tracks with small effective sample sizes were removed. This reduced the sample of individuals with UD's showing little seasonal overlap.

3 | RESULTS

3.1 | Transmitter performance

Between 2010 and 2019, 73 green turtles were deployed with satellite tags and data were received from 72 individuals. This included 39 adults (19 male and 20 female) and 34 immatures (12 male, 10 female, 12 sex not determined). CCL was between 85.6 and 116.6 cm for adults and 42.1 and 99.7 cm for immatures. The tracking duration was between 41 and 397 days (mean \pm SE = 136 ± 7), and a mean \pm SE of 5.7 ± 0.5 locations per day were received per individual, although the amount of data steadily decreased throughout the tracking periods. Slightly fewer locations were received during the day (locations between sunrise and sunset, 49.4%) than at night (locations before sunrise and after sunset, 50.6%) overall.

3.2 | Optimal sample sizes

The minimum number of individuals required to reach 95% of the estimated asymptote of mean overlap probabilities was 21 (Figure 2a). For each study site separately, representative sample sizes (x) were only obtained for turtles captured at two of the seven study sites, the Pelican Banks ($x = 12$ individuals, Figure 2b) and Wiggins Island ($x = 3$ individuals, Figure 2c). At the Pelican Banks site, representative sample sizes were obtained for all three maturity classes: juveniles ($x = 3$, Figure 3a), sub-adults ($x = 3$, Figure 3b) and adults ($x = 12$, Figure 3c). All of the tracked turtles at Wiggins Island were immature individuals. When considering discrete study periods, representative samples were obtained in 2010 ($x = 2$), 2013 ($x = 8$), 2015 ($x = 3$) and 2019 ($x = 3$). In these years, individuals were captured at one or two sites. During years in which representative samples were not achieved (2014, 2016 and 2018) a few individuals were sampled from each of three or more sites, and the mean overlap probability of their UD's did not reach 95% of the estimated asymptote.

3.3 | Utilization distributions

Tags yielded enough data to generate seasonal UD's for 41, 22, 13 and 34 individuals in spring, summer, autumn and winter

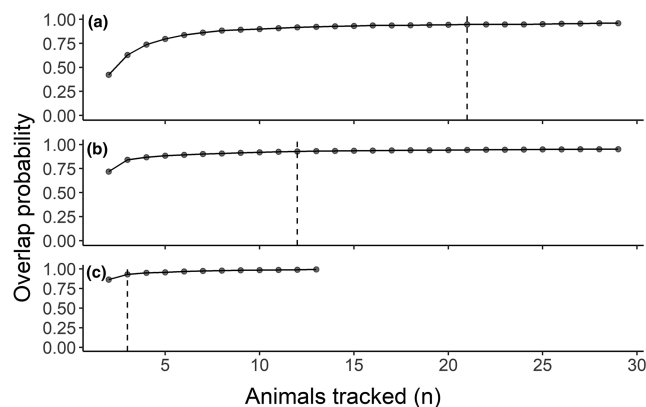


FIGURE 2 Mean probability of individual's 95% utilization distributions (from movement-based kernel density estimation from entire tracks of green turtles) occurring within the collective UD, based on the number of animals tracked (n). The number of individuals required to reach 95% of the estimated asymptote (dotted vertical line), implies the number of tracks considered representative at (a) all sites, (b) Pelican Banks and (c) Wiggins Island

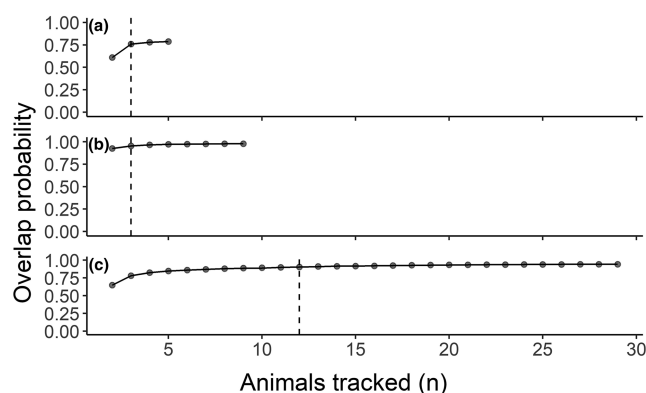


FIGURE 3 Mean probability of individual's 95% utilization distributions (from movement-based kernel density estimation from entire tracks of green turtles) occurring within the collective UD, based on the number of animals tracked (n). The number of individuals required to reach 95% of the estimated asymptote (dotted vertical line), implies the number of tracks considered representative for (a) juveniles, (b) sub-adults and (c) adults

respectively (maximum three and median two seasons per individual). An Ornstein-Uhlenbeck Foraging (OUF, OUF or OU Ω) anisotropic model was selected as the model with the lowest AIC for all seasonal subsets of the tracking data. The OUF incorporates positional and velocity autocorrelation and the tendency of animals to remain in a restricted area (range residency). OUF is a special case of the OUF where the position and velocity autocorrelation time scales are equal, which is probably an effect of artificially restricting the tracking period to seasonal subsets of the data. OU Ω specifies a model with oscillatory range crossings. A subset of individual's distributions estimated for three successive calendar seasons is depicted in Figure 4. Utilization distribution areas are summarized in Table 2.

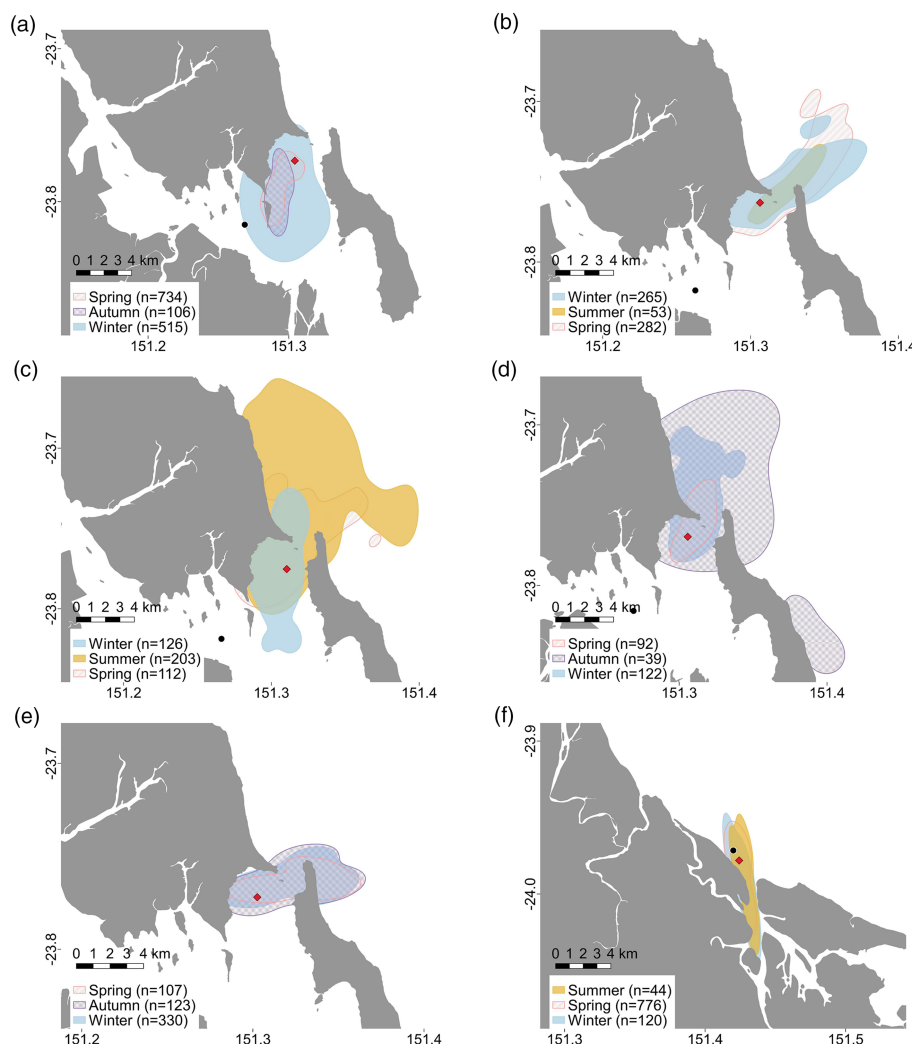


FIGURE 4 Seasonal 95% utilization distributions for green turtles (a) adult male QA13938 (2014), (b) adult female QA58221 (2015), (c) adult female QA43123 (2015), (d) adult female QA45524 (2014), (e) unsexed subadult QA45601 (2014) and (f) subadult male QA86247 (2018) showing capture site (red diamond) and release site (black circle). 'n' refers to number of relocations used to generate each UD. For ease of visualization scale varies across figures

Turtles generally had spatially confined ranges with median seasonal UD of 9.4 (0.07–288.0) km². The best ranking model for predicting UD size included study site as the only predictor. Utilization distributions were significantly larger at the PB compared to Wiggins Island ($z = -3.11$, $P = 0.002$), QI ($z = -3.15$, $P = 0.002$), ST ($z = -2.51$, $P = 0.012$) and Western Basin ($z = -2.15$, $P = 0.032$; Figure 5a). The two next best ranked models included both site and either season or study year as predictors. Season did not significantly affect UD area (Table 3; Figure 5b, Appendix B). Turtles tracked in 2019 had smaller ranges than those tracked in the reference year, 2010 ($z = -2.996$, $P = 0.003$; Figure 5c). In the lower ranked models, there was no evidence of influence of sex or size of individuals on the size of their UD (Table 3; Appendix B).

3.4 | Fidelity and range shifts

Fidelity to site was calculated as the degree of overlap $\pm 95\%$ confidence interval between seasonal UD for an individual. This ranged between 35.9% and 99.6%, with a mean of 81.6%

(Figure 6). Range residents, defined as individuals who did not perform significant range shifts, made up 77.8% of tracked individuals. The highest ranked model included study year as the only predictor and individual as a random factor (Figure 6). Seasonal ranges in 2016 and 2014 had significantly more overlap than in the reference year 2010 ($z = 2.14$, $P = 0.032$ and $z = 3.38$, $P < 0.001$ respectively). In lower ranked models, season pair, site, sex and size covariates did not significantly affect seasonal range overlap (Table 3; Appendix B).

Significant range shifts, unrelated to resettlement at the capture site, were detected for 16 individuals. Breeding migrations were included as significant range shifts according to MRSA, with maximum displacements of 139.5 and 97.1 km ($n = 2$). Non-breeding range shifts occurred over a mean period of 4.0 (0.2–22.1) days. A maximum displacement of 153.5 km from the initial fix was recorded for the non-breeding adult female QA66526 over 7 days in November 2016. Figure 7 depicts four individuals as examples of range residency (a, b), periodic range shift (c, d), forays or discrete loop trips (e, f) and breeding migration (g, h). No significant covariates of range shift were detected.

TABLE 2 Summary of tracked green turtles by year and site of capture showing number of Fastloc GPS relocations received, mean 95% utilization distribution (UD) area, tracking period and percentage overlap of seasonal UD's

Year	Site	n	CCL (mm)	Days Tracked (\pm SE)	FGPS Locations (\pm SE)	n seasonal UD's generated	Mean seasonal UD area (km ² [95% CI])	Mean seasonal overlap (% [95% CI])
2010	Pelican Banks	5	87.6 (51.3–104.4)	204.4 \pm 13.6	554 \pm 146	8	54.4 [28.3, 89.9]	58.7 [46.8, 70.7]
2013	Pelican Banks	10	85.1 (42.1–111.0)	116.3 \pm 32.8	526 \pm 101	13	35.6 [21.5, 53.2]	81.9 [69.7, 91.8]
	Wiggins Island	3	47.7 (46–49.1)	58.3 \pm 5.9	286 \pm 59	3	19.4 [9.7, 32.8]	NA
2014	Boyne River	1	116.6	202.0	859	3	2.6 [2.0, 3.2]	78.2 [65.9, 88.9]
	Pelican Banks	10	94.1 (63.1–110.9)	144.3 \pm 14.8	576 \pm 193	19	27.9 [16.6, 42.8]	84.0 [72.1, 91.9]
	Quoin Island	1	50.2	260.0	249	1	0.2 [0.1, 0.4]	NA
	Pelican Banks	11	91.0 (77.8–108.2)	156.9 \pm 10.2	561 \pm 48	20	27.1 [19.0, 36.9]	81.8 [72.6, 89.4]
2016	Boyne River	1	94.7	126.0	682	1	32.1 [20.1, 46.7]	NA
	Pelican Banks	10	100.3 (92.9–114.6)	129.3 \pm 13.1	489 \pm 126	10	12.6 [9.5, 16.2]	95.0 [88.5, 98.9]
	Western Basin	4	98.6 (85.3–108.7)	120.0 \pm 22.6	868 \pm 120	9	4.3 [3.2, 5.5]	95.3 [89.8, 98.3]
	Pelican Banks	3	82.2 (75.7–94.6)	182 \pm 46.7	494 \pm 388	4	21.4 [15.9, 27.8]	67.1 [54.4, 79.3]
2018	Pelican Banks	1	77.2	189.0	753	1	5.0 [3.7, 6.7]	NA
	South Trees	5	79.8 (67.2–98.0)	138.2 \pm 18.5	806 \pm 64	5	5.3 [4.0, 6.8]	64.8 [54.3, 71.6]
	Wild Cattle Island	2	81.4 (71.5–91.3)	115.0 \pm 1.0	894 \pm 59	5	14.3 [8.2, 22.4]	79.2 [62.1, 91.2]
	Wiggins Island	10	64.2 (45.1–99.0)	172.8 \pm 17.2	1,114 \pm 189	8	4.5 [3.0, 6.3]	47.6 [35.9, 60.3]

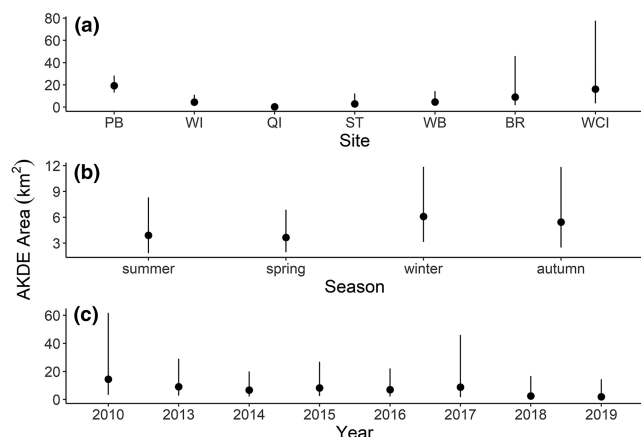


FIGURE 5 Estimated marginal means ($\pm 95\%$ CI) of seasonal 95% utilization distribution area from selected generalized linear mixed models by (a) site, (b) season and (c) year as given by the first, second and third best fitting models respectively

4 | DISCUSSION

4.1 | Minimum representative sample sizes

The minimum number of tracked green turtles required to represent spatial distribution patterns at the foraging grounds were determined to be between 3 and 21, depending on the study site, study year and maturity group (Figures 2 and 3). Typically, sample sizes in animal telemetry studies are small because of the high cost of tracking devices (Godley et al., 2008; Hays & Hawkes, 2018; Sequeira et al., 2019). In this study, long-term monitoring, facilitated by financial support from industry, enabled the collection of an atypically large tracking dataset (72 individuals). Importantly, this study has identified green turtle distributions that can be considered representative of the space used by foraging turtles at two monitored sites. Turtles are unlikely to depart from these areas and if removed artificially, tend to return there (Shimada et al., 2016b). Modification of these key areas is likely to impact the survival of the individuals that occupy them. Nevertheless, representativity was not attained at five of seven sites, nor for 3 of the 8 study years. Fewer individuals were required to represent space-use at particular sites than for the entire study area, implying that greater sampling effort is required for studies if they occur over larger areas or time frames. Similarly, fewer individuals were representative of a particular maturity cohort than for the group overall, thus population studies require sampling of multiple cohorts. Collectively, this demonstrates that if the research is being conducted to understand current or future impacts of habitat change there is a need to explicitly outline marine wildlife management objectives such as identifying specific sites (development footprints) and periods of interest, prior to commencement of tracking studies, particularly where individuals display spatially confined behaviours. This is necessary to draw ecologically meaningful conclusions from the tracking data.

4.2 | Factors underpinning distribution and site fidelity

The main factors underpinning differences in the size of green turtles' utilization distributions in Port Curtis were study site and year. Turtles at the Pelican Banks study site used larger areas than those at other sites (Figure 5). This may reflect the diversity, abundance, health and distribution of benthic dietary items (Hart et al., 2017; Shimada et al., 2020). The larger UD of PB turtles could indicate low quality or patchy food resources (Snape et al., 2018). Alternatively, larger turtles that use the shallow water habitats of Pelican Banks may have limited access to grazing patches as they become exposed at low tide. Large and small turtles appear to take advantage of a variety of intertidal habitats as they have been observed moving off the flats into the deeper subtidal channels on the falling tide (Limpus, Couper & Read, 1994; Limpus & Limpus, 2000; Limpus, Paramenter & Chaloupka, 2013). Turtles occupying other nearby sites may be exploiting other, smaller seagrass patches, or a variety of food items supported by intertidal and estuarine conditions, including macroalgae and epifauna growing on artificial substrates and rock walls, as well as mangrove roots and fruits upstream of river outflows (Limpus, Paramenter & Chaloupka, 2013; Prior, Booth & Limpus, 2016). Foraging areas of green turtles align closely with the distribution of required resources for foraging and resting (Hart et al., 2017) or unique suites of environmental conditions (Christiansen et al., 2017). Although most animals exhibited short-term fidelity to foraging sites, differences in range sizes between study sites and years implies that larger numbers of tracked individuals, from a diverse range of micro-habitats are required to sufficiently represent the distribution of turtles at specific sites and periods of interest. No systematic, significant differences in UD size were detected across seasons, although at other green turtle foraging grounds larger winter than summer ranges may be an artefact of thermoregulatory behaviours, or adaptation to seasonal changes in resource availability (Read, Grigg & Limpus, 1996; Shimada et al., 2016a).

Interannual differences were found in site fidelity (seasonal UD overlap metrics, Figure 5c). These may reflect changing resource distribution following major flood seasons. The availability of food resources for green turtles is related to rainfall events, with dry years supporting good forage and wet years providing poor forage and contributing to lower reproductive output in subsequent seasons (Limpus & Nicholls, 2000). In years of poor forage, turtles may expand their space-use to obtain sufficient forage, or exploit alternative food resources (Prior, Booth & Limpus, 2016; Shimada et al., 2016a; Shimada et al., 2020). Overall, a high degree of seasonal overlap in space-use (35.9–99.6%, mean = 81.6%) and few ($n = 16$) individuals shifting between sites is further indication of fidelity to foraging sites. The tendency of green turtles to remain in one area when other apparently suitable foraging habitat is available, may reflect a 'low risk' strategy (Schofield et al., 2010; Snape et al., 2018; Shimada et al., 2020), the relative advantage of remaining in a familiar area compared to switching to an unknown one. Alternatively, non-ideal environmental conditions in other areas could be deterring turtles

TABLE 3 Outputs from generalized linear mixed models for determining effect of biophysical covariates on 95% utilization distribution (UD) area, seasonal UD overlap and range shift. Models were selected on the basis of lowest corrected Akaike's Information Criterion

Response, distribution and link function	Model rank	Fixed effects	Estimate	SE	Z	P
UD area (γ distribution with log link function)	1 st	Intercept (PB)	16.596	0.201	82.51	<2e-16
		Site:WI	-1.544	0.497	-3.11	0.002*
		Site:QI	-4.321	a.373	-3.15	0.002*
		Site:ST	-1.917	0.764	-2.51	0.012*
		Site:WB	-1.365	0.636	-2.15	0.032*
		Site:BR	-0.698	0.892	-0.78	0.434
		Site:WCI	-0.109	0.868	-0.13	0.900
	2 nd	Intercept (Season:Summer, Site:PB)	-16.44	0.285	-57.6	<2e-16
		Season:Spring	-0.061	0.287	-0.21	0.832
		Season:Winter	0.440	0.329	1.34	0.182
		Season:Autumn	0.330	0.427	0.77	0.440
		Site:WI	-1.479	0.497	-2.97	0.003*
		Site:QI	-4.493	1.396	-3.22	0.001*
		Site:ST	-1.693	0.768	-2.20	0.027*
		Site:WB	-1.534	0.649	-2.36	0.018*
		Site:BR	-0.796	0.887	0.90	0.368
		Site:WCI	0.003	0.857	0.00	0.998
	3 rd	Intercept (Year:2010, Site:PB)	17.078	0.624	27.359	<2e-16
		Year:2013	-0.377	0.760	-0.496	0.620
		Year:2014	-0.679	0.732	-0.929	0.353
		Year:2015	0.471	0.732	-0.644	0.520
		Year:2016	-0.612	0.803	-0.763	0.446
		Year:2017	-0.388	0.988	-0.392	0.695
		Year:2018	-1.639	1.514	-1.082	0.279
		Year:2019	-1.821	1.280	-1.423	0.152
		Site:WI	-0.644	0.982	-0.655	0.512
		Site:QI	-4.123	1.435	-2.873	0.004*
		Site:ST	-0.763	1.572	-0.486	0.627
		Site:WB	-1.235	0.796	-1.550	0.212
		Site:BR	-0.531	0.942	-0.564	0.573
		Site:WCI	1.049	1.625	0.645	0.519
	4 th	Intercept (Sex:F)	16.099	0.299	53.78	<2e-16
		Sex:I	-0.219	0.257	-0.17	0.862
		Sex:M	0.181	0.403	0.45	0.654
		Scale (CCL)	0.419	0.343	1.22	0.221
		SexI:scale (CCL)	0.005	0.727	0.01	0.995
		SexM:scale (CCL)	0.636	0.545	1.17	0.242
UD overlap (β distribution with logit link function)	1st	Intercept (Year:2010)	0.353	0.545	0.647	0.517
		Year:2013	1.194	0.705	1.693	0.090
		Year:2014	1.370	0.640	2.140	0.032*
		Year:2015	1.194	0.844	1.855	0.064
		Year:2016	2.300	0.681	3.380	<0.001*
		Year:2017	0.311	1.097	0.284	0.777
		Year:2018	0.572	0.716	0.799	0.425
		Year:2019	-0.4433	1.0862	-0.408	0.683

(Continues)

TABLE 3 (Continued)

Response, distribution and link function	Model rank	Fixed effects	Estimate	SE	Z	P
	2nd	Intercept (Site:PB)	1.564	0.213	7.346	2.05e−13
		Site:WI	−1.654	1.055	−1.569	0.117
		Site:ST	−0.787	0.766	−1.03	0.304
		Site:WB	1.178	0.622	1.894	0.058
		Site:BR	−0.364	0.978	−0.372	0.710
		Site:WCI	−0.523	0.740	−0.706	0.480
	3rd	(Intercept SEASONS AutumnXSummer)	0.727	0.703	1.034	0.301
		SEASONS AutumnXSpring	0.862	0.811	1.062	0.288
		SEASONS AutumnXWinter	1.472	0.782	1.883	0.060
		SEASONS SpringXSummer	0.671	0.748	0.897	0.369
		SEASONS SpringXWinter	−1.190	1.208	−0.985	0.325
		SEASONS SummerXWinter	0.562	0.861	0.653	0.513
	4th	Intercept (Maturity:SA)	1.573	0.246	6.406	1.49e−10
		Maturity:J	0.068	0.843	0.081	0.936
		Maturity:A	−0.176	0.402	−0.437	0.662
	5th	Intercept (Sex:F)	1.468	0.290	5.058	4.24e−7
		Sex:I	1.585	1.348	1.176	0.240
		Sex:M	−0.109	0.432	−0.252	0.801
		Scale (CCL)	0.371	0.331	1.123	0.261
		SexI:scale (CCL)	0.408	0.733	0.556	0.579
		SexM:scale*CCL	−0.950	0.680	−1.398	0.162
Range shift (binomial distribution with logit link function)	1st	(Intercept)	−0.763	0.978	−0.779	0.436
		SEASONS	0.085	0.419	0.203	0.839

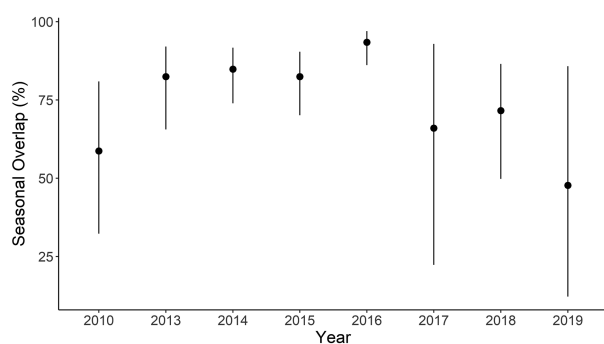


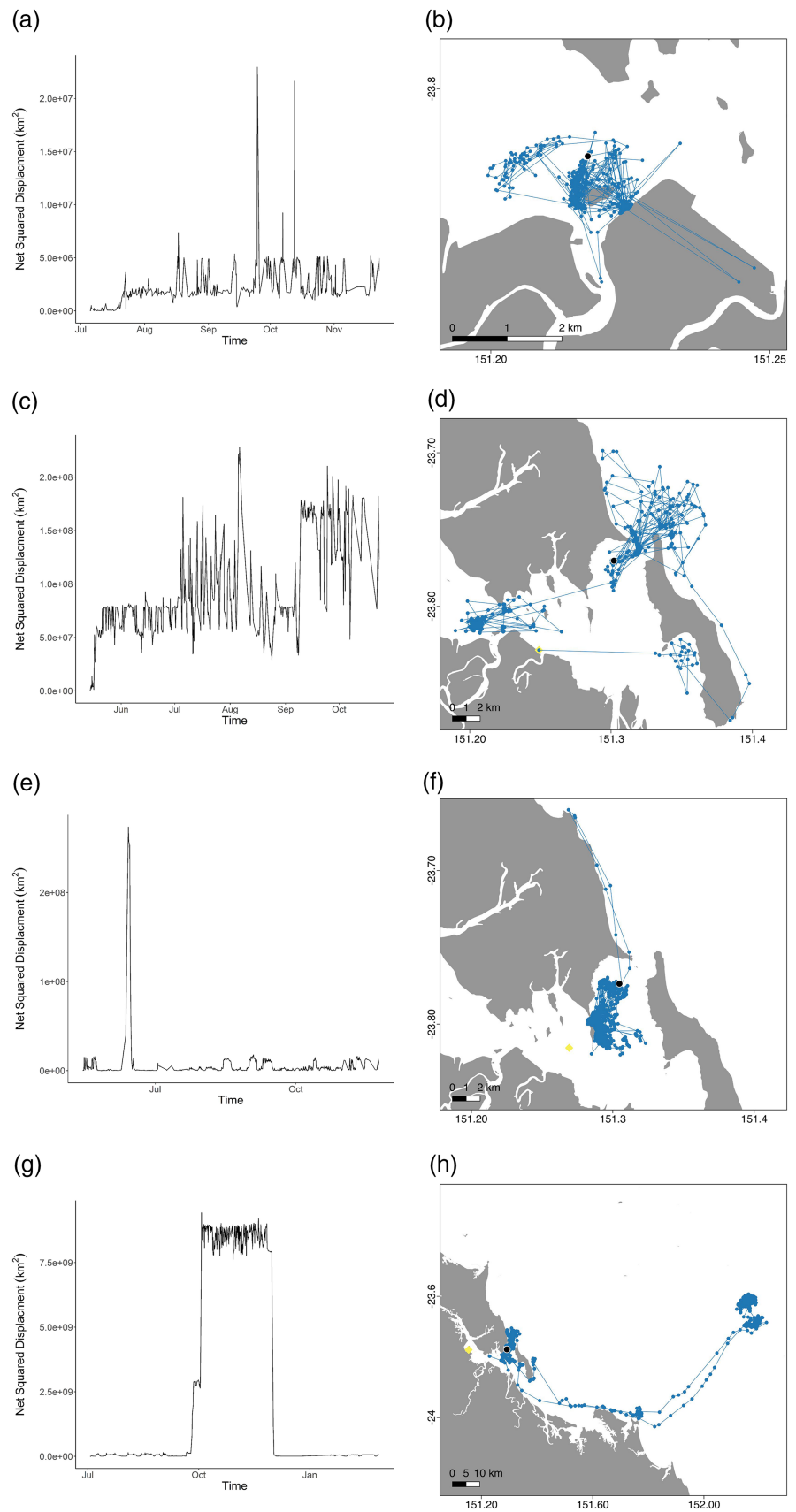
FIGURE 6 Estimated marginal means ($\pm 95\%$ CI) from best ranked generalized linear mixed model of overlap between seasonal pairs of 95% utilization distributions with study year as the only predictor

from shifting their distributions. The effect of physical environmental parameters on primary producers and consequently green turtles' space-use is beyond the scope of this study. Further study with this dataset will focus on the environmental correlates of foraging range size and movement of tracked turtles.

This study highlights the diversity of space-use patterns performed by green turtles at inshore foraging grounds. From

72 individuals four different patterns of behaviour were identified including, range residency over several months ($n = 48$) or after delayed resettlement at the capture sites ($n = 9$, up to 12 days post-release), range shifts ($n = 16$) including forays and breeding migrations. Individuals differed in the scales of their maximum displacement from the point of capture (1.9–153.5 km) and size of seasonal 95% UD (median = 9.4, 0.08–288.0 km²). Such diversity of space-use patterns has also been noted in the north-west Pacific (Hatase et al., 2006), eastern Mediterranean (Hochscheid et al., 1999) and Indian Ocean (Christiansen et al., 2017; Chambault et al., 2020), which may be related to plasticity of foraging strategies (Thomson et al., 2018). This diversity of space-use patterns poses a challenge for identifying appropriate management strategies for minimizing impacts to turtles. Nevertheless, 78% of tracked animals in this study displayed range residency and high fidelity, which is consistent with other characterizations of this species as having long-term fidelity to foraging sites (spanning decades, e.g. Shimada et al., 2016a; Shimada et al., 2020). This suggests that when representative sample sizes are obtained, the distribution information for these animals provides a realistic boundary delineating the habitat of the majority of individuals at the site.

FIGURE 7 Net displacement of green turtles throughout the tracking period showing movement paths of (a, b) juvenile male QA84342, (c, d) adult male QA36875, (e, f) adult male QA13938 and (g, h) adult male K93087. Respectively, these individuals displayed range residency, significant range shift, looping behaviour and breeding migration. For ease of visualization the scale of the axes varies between plots



4.3 | Study implications and informing management

The space-use patterns outlined in this study should be considered when devising approaches to mitigate the impact of planned developments on green turtles. Turtle distribution information from tracking studies can be used to assess spatial and temporal overlap with specific risks to turtles. In Moreton Bay, utilization distribution modelling aided the implementation of Go-Slow Zones in shallow foraging habitat of green and loggerhead turtles and dugong to reduce the rate of recreational vessel strikes (Shimada et al., 2017). Risk of direct loss of habitat is assessed as being very high for foraging green turtles in Port Curtis (Eco Logical Australia, 2019). Mitigation of environmental stress from human activities may involve modifying operational practices for port infrastructure, potential sources of contamination from discharge and vessel management plans that overlap with turtle spatio-temporal distributions. Protections to key foraging habitats can also be beneficial to sympatric species such as seagrasses and dugongs (André, Gyuris & Lawler, 2005; Gredzens et al., 2014; Zeh et al., 2016). The distributions of foraging turtles outlined in this study will also serve as a backboard for evaluating resource requirements for this foraging aggregation by determining environmental characteristics that favour turtle occurrence, or 'suitable' environmental conditions through resource selection analysis and assessing changes in extent and location of 'suitable' habitats over time. Mitigation of detrimental anthropogenic impacts on a single green turtle foraging ground can be beneficial for multiple life stages, sexes and even breeding stocks. The trait of green turtles to remain faithful to foraging sites implies that irreparable local modifications to foraging habitat can impact fitness and survival of resident animals. Translating space-use patterns into protective regulations contributes to green turtles' ability to acquire energy stores required for successful reproduction – and population viability for this species.

ACKNOWLEDGEMENTS

This project is the result of many years of ongoing monitoring at Port Curtis which involved deployment of tags (funding details given in Appendix A) by various organizations, industry partners and volunteers. Research activities were facilitated by Queensland Turtle Conservation Project with Department of Environment and Science Aquatic Threatened Species Unit with assistance from Gidargil Land and Sea Rangers and funded by the Gladstone Ports Corporation through their Ecosystem Research and Monitoring Programme, QLD Department of Environment and Science, James Cook University, The Centre for Tropical Water and Aquatic Ecosystem Research, Shell's QGC Business, Australia Pacific LNG, and Santos GLNG. Shell's QGC Business, Australia Pacific LNG and Santos GLNG purchased 10 tags deployed in 2019 and provided research funds for fieldwork and the analysis of these data. Open access publishing facilitated by James Cook University, as part of the Wiley - James Cook University agreement via the Council of Australian University Librarians.

[Correction added on 3 June 2022, after first online publication: CAUL funding statement has been added.]

CONFLICT OF INTEREST

The authors have no competing financial interests nor other sources of conflict of interest to disclose.

DATA AVAILABILITY STATEMENT

Data available on request due to third party restrictions.

ORCID

Emily G. Webster  <https://orcid.org/0000-0002-0949-9851>

Mark Hamann  <https://orcid.org/0000-0003-4588-7955>

Takahiro Shimada  <https://orcid.org/0000-0002-3364-5169>

Stephanie Duce  <https://orcid.org/0000-0002-3225-3315>

REFERENCES

- André, J., Gyuris, E. & Lawler, I.R. (2005). Comparison of the diets of sympatric dugongs and green turtles on the Orman Reefs, Torres Strait, Australia. *Wildlife Research*, 32(1), 53–62. <https://doi.org/10.1071/WR04015>
- Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M. et al. (2001). The Identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates: A better understanding of the habitats that serve as nurseries for marine species and the factors that create site-specific variability in nursery quality will improve conservation and management of these areas. *Bioscience*, 51(8), 633–641. [https://doi.org/10.1641/0006-3568\(2001\)051\[0633:TICAMO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2)
- Blumenthal, J.M., Solomon, J., Bell, C., Austin, T., Ebanks-Petrie, G., Coyne, M.S. et al. (2006). Satellite tracking highlights the need for international cooperation in marine turtle management. *Endangered Species Research*, 2, 51–61. <https://doi.org/10.3354/esr002051>
- Börger, L., Fieberg, J., Horne, J.S., Rachlow, J.L., Calabrese, J.M. & Fleming, C.H. (2020). Animal home ranges: Concepts, uses, and estimation. In: D.L. Murray, B.K. Sandercock (Eds.) *Population Ecology in Practice*. 1st Hoboken, NJ: Wiley-Blackwell, pp. 315–328.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C. W., Nielsen, A. et al. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2), 378–400. <https://doi.org/10.32614/RJ-2017-066>
- Bryant, C., Rasheed, M., Davies, J., Carter, A., Sankey, T. & Tol, S. (2013). *Long term seagrass monitoring in the port Curtis Western basin: Quarterly seagrass assessments and permanent transect monitoring progress report November 2009 to 2012*. TropWATER, James Cook University.
- Calenge, C. (2006). The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197(3–4), 516–519. <https://doi.org/10.1016/j.ecolmodel.2006.03.017>
- Chaloupka, M.Y., Bjørndal, K.A., Balazs, G.H., Bolten, A.B., Ehrhart, L.M., Limpus, C.J. et al. (2008). Encouraging outlook for recovery of a once severely exploited marine megaherbivore. *Global Ecology and Biogeography*, 17(2), 297–304. <https://doi.org/10.1111/j.1466-8238.2007.00367.x>
- Chaloupka, M.Y. & Limpus, C.J. (2001). Trends in the abundance of sea turtles resident in Southern Great Barrier Reef waters. *Biological Conservation*, 102(3), 235–249. [https://doi.org/10.1016/S0006-3207\(01\)00106-9](https://doi.org/10.1016/S0006-3207(01)00106-9)
- Chambault, P., Dalleau, M., Nicet, J.B., Mouquet, P., Ballorain, K., Jean, C. et al. (2020). Contrasted habitats and individual plasticity drive the

- fine scale movements of juvenile green turtles in coastal ecosystems. *Movement Ecology*, 8, 1. <https://doi.org/10.1186/s40462-019-0184-2>
- Cheminée, A., Le Direach, L., Rouanet, E., Astruch, P., Goujard, A., Blanfuné, A. et al. (2021). All shallow coastal habitats matter as nurseries for Mediterranean juvenile fish. *Scientific Reports*, 11(1), 14631. <https://doi.org/10.1038/s41598-021-93557-2>
- Christiansen, F., Esteban, N., Mortimer, J.A., Dujon, A.M. & Hays, G.C. (2017). Diel and seasonal patterns in activity and home range size of green turtles on their foraging grounds revealed by extended Fastloc-GPS tracking. *Marine Biology*, 164, 10. <https://doi.org/10.1007/s00227-016-3048-y>
- Coles, R.G., McKenzie, L.J., Rasheed, M.A., Mellors, J.E., Taylor, H., Dew, K. et al. (2007). Status and trends of seagrass habitats in the great barrier reef world heritage area. Marine and Tropical Sciences Research Facility, Reef and Rainforest Research Centre Limited.
- Department of Environment and Science. (2021). *Marine turtle breeding and migration atlas*. Available at: <https://apps.information.qld.gov.au/TurtleDistribution/> [Accessed 13 September 2021]
- Dujon, A.M., Lindstrom, R.T. & Hays, G.C. (2014). The accuracy of Fastloc-GPS locations and implications for animal tracking. *Methods in Ecology and Evolution*, 5(11), 1162–1169. <https://doi.org/10.1111/2041-210X.12286>
- Eco Logical Australia. (2019). *Cumulative impact assessment – Gatcombe and Golding cutting channel duplication EIS*. Brisbane, Australia: Eco Logical Australia Pty Ltd.
- FitzSimmons, N.N. & Limpus, C.J. (2014). Marine turtle genetic stocks of the Indo-Pacific: Identifying boundaries and knowledge gaps. *Indian Ocean Marine Turtle Newsletter*, 20, 2–18.
- Fleming, C.H. & Calabrese, J.M. (2017). A new kernel density estimator for accurate home-range and species-range area estimation. *Methods in Ecology and Evolution*, 8(5), 571–579. <https://doi.org/10.1111/2041-210X.12673>
- Fleming, C.H. & Calabrese, J.M. (2021). ctmm: Continuous-time movement modeling. R Package. Version 0.6.0. Available at: <https://CRAN.R-project.org/package=ctmm>
- Fleming, C.H., Drescher-Lehman, J., Noonan, M.J., Akre, T.S.B., Brown, D.J., Cochrane, M.M. et al. (2020). A comprehensive framework for handling location error in animal tracking data (preprint). *bioRxiv*. <https://doi.org/10.1101/2020.06.12.130195>
- Fleming, C.H., Fagan, W.F., Mueller, T., Olson, K.A., Leimgruber, P. & Calabrese, J.M. (2016). Estimating where and how animals travel: An optimal framework for path reconstruction from autocorrelated tracking data. *Ecology*, 97(3), 576–582. <https://doi.org/10.1890/15-1607.1>
- Fleming, C.H., Noonan, M.J., Medici, E.P. & Calabrese, J.M. (2019). Overcoming the challenge of small effective sample sizes in home-range estimation. *Methods in Ecology and Evolution*, 10(10), 1679–1689. <https://doi.org/10.1111/2041-210X.13270>
- Fleming, C.H., Sheldon, D., Fagan, W.F., Leimgruber, P., Mueller, T., Nandintsetseg, D. et al. (2018). Correcting for missing and irregular data in home-range estimation. *Ecological Applications*, 28(4), 1003–1010. <https://doi.org/10.1002/eap.1704>
- Flint, J., Flint, M., Limpus, C.J. & Mills, P.C. (2017a). Status of marine turtle rehabilitation in Queensland. *PeerJ*, 5, e3132. <https://doi.org/10.7717/peerj.3132>
- Flint, J., Flint, M., Limpus, C.J. & Mills, P.C. (2017b). The impact of environmental factors on marine turtle stranding rates. *PLoS ONE*, 12(8), e0182548. <https://doi.org/10.1371/journal.pone.0182548>
- Flint, M., Eden, P.A., Limpus, C.J., Owen, H., Gaus, C. & Mills, P.C. (2015). Clinical and pathological findings in green turtles (*Chelonia mydas*) from Gladstone, Queensland: Investigations of a stranding epidemic. *EcoHealth*, 12(2), 298–309. <https://doi.org/10.1007/s10393-014-0972-5>
- Gladstone Ports Corporation. (2019). *Port of Gladstone*. Available at: <https://www.gpcl.com.au/port-of-gladstone> [Accessed 1 February 2021]
- Godley, B.J., Blumenthal, J.M., Broderick, M.S., Coyne, M.S., Godfrey, M.H., Hawkes, L.A. et al. (2008). Satellite tracking of sea turtles: Where have we been and where do we go next? *Endangered Species Research*, 4(1–2), 3–22. <https://doi.org/10.3354/esr00060>
- Gredzens, C., Marsh, H., Fuentes, M.M.P.B., Limpus, C.J., Shimada, T. & Hamann, M. (2014). Satellite tracking of sympatric marine megafauna can inform the biological basis for species co-management. *PLoS ONE*, 9(6), e98944. <https://doi.org/10.1371/journal.pone.0098944>
- Gurarie, E. & Cheraghi, F. (2017). *marcher: Migration and range change estimation in R*. R package. version 0.0-2. Available at: <https://CRAN.R-project.org/package=marcher>
- Halpern, B., Frazier, M., Potapenko, J., Casey, K., Koenig, K., Longo, C. et al. (2015). Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nature Communications*, 6(1), 7615. <https://doi.org/10.1038/ncomms8615>
- Hamann, M., Limpus, C.J., Shimada, T. & Preston, S. (2017). *Final report on green turtle habitat use in port Curtis 2014 to 2017*. Gladstone Ports Corporation's Ecosystem Research and Monitoring Program.
- Harfoot, M.B.J., Johnston, A., Balmford, A., Burgess, N.D., Butchart, S.H. M., Dias, M.P. et al. (2021). Using the IUCN Red List to map threats to terrestrial vertebrates at global scale. *Nature Ecology & Evolution*, 5(11), 1510–1519. <https://doi.org/10.1038/s41559-021-01542-9>
- Hart, K.M., Iverson, A.R., Benschoter, A.M., Fujisaki, I., Cherkiss, M.S., Pollock, C. et al. (2017). Resident areas and migrations of female green turtles nesting at Buck Island Reef National Monument, St. Croix, US Virgin Islands. *Endangered Species Research*, 32, 89–101. <https://doi.org/10.3354/esr00793>
- Hartig, F. (2021). DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R Package Version 0.4.3. Available at: <https://CRAN.R-project.org/package=DHARMa>
- Hatase, H., Sato, K., Yamaguchi, M., Takahashi, K. & Tsukamoto, K. (2006). Individual variation in feeding habitat use by adult female green sea turtles (*Chelonia mydas*): Are they obligately neritic herbivores? *Oecologia*, 149(1), 52–64. <https://doi.org/10.1007/s00442-006-0431-2>
- Hays, G.C., Bailey, H., Bograd, S.J., Bowen, W.D., Campagna, C., Carmichael, R.H. et al. (2019). Translating marine animal tracking data into conservation policy and management. *Trends in Ecology & Evolution*, 34(5), 459–473. <https://doi.org/10.1016/j.tree.2019.01.009>
- Hays, G.C. & Hawkes, L.A. (2018). Satellite tracking sea turtles: Opportunities and challenges to address key questions. *Frontiers in Marine Science*, 5, 432. <https://doi.org/10.3389/fmars.2018.00432>
- Hays, G.C., Mortimer, J.A., Rattray, A., Shimada, T. & Esteban, N. (2021). High accuracy tracking reveals how small conservation areas can protect marine megafauna. *Ecological Applications*, 31(7), e02418. <https://doi.org/10.1002/eap.2418>
- Hazel, J. & Gyuris, E. (2006). Vessel-related mortality of sea turtles in Queensland, Australia. *Wildlife Research*, 33(2), 149–154. <https://doi.org/10.1071/WR04097>
- Hochscheid, S., Godley, B.J., Broderick, A.C. & Wilson, R.P. (1999). Reptilian diving: Highly variable dive patterns in the green turtle *Chelonia mydas*. *Marine Ecology Progress Series*, 185, 101–112. <https://doi.org/10.3354/meps185101>
- Limpus, C.J. (1978). Exploration north: Australia's wildlife from desert to reef. In: H.J. Lavery (Ed.) *The Reef*. Richmond, Victoria: Richmond Hill Press, pp. 187–222.
- Limpus, C.J. (2008). *A biological review of Australian marine turtles, 2. Green turtle Chelonia mydas (Linnaeus)*. Brisbane, Australia: Queensland Environmental Protection Agency.
- Limpus, C.J., Couper, P.J. & Read, M. (1994). The green turtle, *Chelonia mydas* in Queensland: Population structure in a warm temperate feeding area. *Memoirs of the Queensland Museum*, 35(1), 139–154.

- Limpus, C.J., FitzSimmons, N.N., Finlayson, K., Harmonn, C., McKinnon, A., Sergeev, J.M. et al. (2017). *Increase the understanding of the green turtle population in port Curtis*. Queensland Department of Environment and Heritage Protection.
- Limpus, C.J. & Limpus, D.J. (2000). Mangroves in the diet of *Chelonia mydas* in Queensland, Australia. *Marine Turtle Newsletter*, 89, 13–15.
- Limpus, C.J., Limpus, D.J., Arthur, K.E. & Parmenter, C.J. (2005). *Monitoring of green turtle population dynamics in Shoalwater Bay: 2000–2004*. Queensland Environmental Protection Agency and the Great Barrier Reef Marine Park Authority.
- Limpus, C.J., Limpus, D.J., Savage, M. & Shearer, D. (2012). *Health assessment of green turtles in south and Central Queensland following extreme weather impacts on coastal habitat during 2011*. Queensland Department of Environment and Heritage Protection.
- Limpus, C.J., Miller, J.D., Parmenter, C.J., Reimer, D., McLachlan, N. & Webb, R. (1992). Migration of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles to and from eastern Australian rookeries. *Wildlife Research*, 19(3), 347–357. <https://doi.org/10.1071/WR9920347>
- Limpus, C.J. & Nicholls, N. (2000). ENSO Regulation of Indo-Pacific green turtle populations. In: G.L. Hammer, N. Nicholls, C. Mitchell (Eds.) *Applications of Seasonal Climate Forecasting in Agricultural and Natural Ecosystems*. Dordrecht: Springer Netherlands, pp. 399–408.
- Limpus, C.J., Parmenter, C.J. & Chaloupka, M. (2013). Monitoring of coastal sea turtles: Gap analysis 2. Green turtles, *Chelonia mydas*, in the Port Curtis and Port Alma region. Gladstone Ports Corporation's Ecosystem Research and Monitoring Program.
- Lutcavage, M.E., Plotkin, P., Witherington, B. & Lutz, P.L. (1997). Human impacts on sea turtle survival. In: P.L. Lutz, J.A. Musick (Eds.) *The Biology of Sea Turtles, volume I*. Boca Raton, FL: CRC Press, pp. 387–409.
- Macura, B., Byström, P., Airoldi, L., Eriksson, B.K., Rudstam, L. & Støttrup, J.G. (2019). Impact of structural habitat modifications in coastal temperate systems on fish recruitment: A systematic review. *Environmental Evidence*, 8(1), 14. <https://doi.org/10.1186/s13750-019-0157-3>
- Meager, J.J. & Limpus, C.J. (2014). Mortality of inshore marine mammals in eastern Australia is predicted by freshwater discharge and air temperature. *PLoS ONE*, 9(4), e94849. <https://doi.org/10.1371/journal.pone.0094849>
- Mentaschi, L., Voudoukas, M.I., Pekel, J.F., Voukouvalas, E. & Feyen, L. (2018). Global long-term observations of coastal erosion and accretion. *Scientific Reports*, 8(1), 12876. <https://doi.org/10.1038/s41598-018-30904-w>
- Neumann, B., Vafeidis, A.T., Zimmermann, J. & Nicholls, R.J. (2015). Future coastal population growth and exposure to sea-level rise and coastal flooding - a global assessment. *PLoS ONE*, 10(3), e0118571. <https://doi.org/10.1371/journal.pone.0118571>
- Pillans, R.D., Fry, G.C., Haywood, M.D.E., Rochester, W., Limpus, C.J., Patterson, T. et al. (2021). Residency, home range and tidal habitat use of Green Turtles (*Chelonia mydas*) in Port Curtis, Australia. *Marine Biology*, 168(6), 88. <https://doi.org/10.1007/s00227-021-03898-9>
- Prior, B., Booth, D.T. & Limpus, C.J. (2016). Investigating diet and diet switching in green turtles (*Chelonia mydas*). *Australian Journal of Zoology*, 63(6), 365–375. <https://doi.org/10.1071/ZO15063>
- Prosser, D.J., Jordan, T.E., Nagel, J.L., Seitz, R.D., Weller, D.E. & Whigham, D.F. (2018). Impacts of coastal land use and shoreline armoring on estuarine ecosystems: An Introduction to a special issue. *Estuaries and Coasts*, 41(S1), 2–18. <https://doi.org/10.1007/s12237-017-0331-1>
- Read, M.A., Grigg, G.C. & Limpus, C.J. (1996). Body temperatures and winter feeding in immature green turtles, *Chelonia mydas*, in Moreton Bay, southeastern Queensland. *Journal of Herpetology*, 30(2), 262–265. <https://doi.org/10.2307/1565520>
- Schofield, G., Dimadi, A., Fossette, S., Katselidis, K.A., Koutsoubas, D., Lilley, M.K.S. et al. (2013). Satellite tracking large numbers of individuals to infer population level dispersal and core areas for the protection of an endangered species. *Diversity and Distributions*, 19(7), 834–844. <https://doi.org/10.1111/ddi.12077>
- Schofield, G., Hobson, V.J., Fossette, S., Lilley, M.K.S., Katselidis, K.A. & Hays, G.C. (2010). BIODIVERSITY RESEARCH: Fidelity to foraging sites, consistency of migration routes and habitat modulation of home range by sea turtles. *Diversity and Distributions*, 16(5), 840–853. <https://doi.org/10.1111/j.1472-4642.2010.00694.x>
- Scott, R., Hodgson, D.J., Witt, M.J., Coyne, M.S., Adnyana, W., Blumenthal, J.M. et al. (2012). Global analysis of satellite tracking data shows that adult green turtles are significantly aggregated in Marine Protected Areas. *Global Ecology and Biogeography*, 21(11), 1053–1061. <https://doi.org/10.1111/j.1466-8238.2011.00757.x>
- Seitz, R.D., Lipcius, R.N., Olmstead, N.H., Seebo, M.S. & Lambert, D.M. (2006). Influence of shallow-water habitats and shoreline development on abundance, biomass, and diversity of benthic prey and predators in Chesapeake Bay. *Marine Ecology Progress Series*, 326, 11–27. <https://doi.org/10.3354/meps326011>
- Seitz, R.D., Wennhage, H., Bergström, U., Lipcius, R.N. & Ysebaert, T. (2014). Ecological value of coastal habitats for commercially and ecologically important species. *ICES Journal of Marine Science*, 71(3), 648–665. <https://doi.org/10.1093/icesjms/fst152>
- Sequeira, A.M.M., Heupel, M.R., Lea, M.A., Eguiluz, V.M., Duarte, C.M., Meekan, M.G. et al. (2019). The importance of sample size in marine megafauna tagging studies. *Ecological Applications*, 29(6), e01947. <https://doi.org/10.1002/eap.1947>
- Sheaves, M., Baker, R. & Johnston, R. (2006). Marine nurseries and effective juvenile habitats: An alternative view. *Marine Ecology Progress Series*, 318, 303–306. <https://doi.org/10.3354/meps318303>
- Shimada, T., Jones, R., Limpus, C.J., Groom, R. & Hamann, M. (2016a). Long-term and seasonal patterns of sea turtle home ranges in warm coastal foraging habitats: Implications for conservation. *Marine Ecology Progress Series*, 562, 163–179. <https://doi.org/10.3354/meps11972>
- Shimada, T., Jones, R., Limpus, C.J. & Hamann, M. (2012). Improving data retention and home range estimates by data-driven screening. *Marine Ecology Progress Series*, 457, 171–180. <https://doi.org/10.3354/meps09747>
- Shimada, T., Limpus, C.J., Hamann, M., Bell, I., Esteban, N., Groom, R. et al. (2019). Fidelity to foraging sites after long migrations. Dryad, Dataset. <https://doi.org/10.5061/dryad.j6q573n8j>
- Shimada, T., Limpus, C.J., Hamann, M., Bell, I., Esteban, N., Groom, R. et al. (2020). Fidelity to foraging sites after long migrations. *Journal of Animal Ecology*, 89(4), 1008–1016. <https://doi.org/10.1111/1365-2656.13157>
- Shimada, T., Limpus, C.J., Jones, R. & Hamann, M. (2017). Aligning habitat use with management zoning to reduce vessel strike of sea turtles. *Ocean and Coastal Management*, 142, 163–172. <https://doi.org/10.1016/j.ocecoaman.2017.03.028>
- Shimada, T., Limpus, C.J., Jones, R., Hazel, J., Groom, R. & Hamann, M. (2016b). Sea turtles return home after intentional displacement from coastal foraging areas. *Marine Biology*, 163(8), 1–14. <https://doi.org/10.1007/s00227-015-2771-0>
- Shimada, T., Thums, M., Hamann, M., Limpus, C.J., Hays, G.C., FitzSimmons, N.N. et al. (2021). Optimising sample sizes for animal distribution analysis using tracking data. *Methods in Ecology and Evolution*, 12(2), 288–297. <https://doi.org/10.1111/2041-210X.13506>
- Snape, R.T.E., Bradshaw, P.J., Broderick, A.C., Fuller, W.J., Stokes, K.L. & Godley, B.J. (2018). Off-the-shelf GPS technology to inform marine protected areas for marine turtles. *Biological Conservation*, 227, 301–309. <https://doi.org/10.1016/j.biocon.2018.09.029>
- Taylor-Brown, A., Booth, R., Gillett, A., Mealy, E., Ogbourne, S.M., Polkinghorne, A. et al. (2019). The impact of human activities on

- Australian wildlife. *PLoS ONE*, 14(1), e0206958. <https://doi.org/10.1371/journal.pone.0206958>
- Thomson, J.A., Whitman, E.R., Garcia-Rojas, M.I., Bellgrove, A., Ekins, M., Hays, G. et al. (2018). Individual specialization in a migratory grazer reflects long-term diet selectivity on a foraging ground: Implications for isotope-based tracking. *Oecologia*, 188(2), 429–439. <https://doi.org/10.1007/s00442-018-4218-z>
- Todd, P.A., Heery, E.C., Loke, L.H.L., Thurstan, R.H., Kotze, D.J. & Swan, C. (2019). Towards an urban marine ecology: Characterizing the drivers, patterns and processes of marine ecosystems in coastal cities. *Oikos*, 128(9), 1215–1242. <https://doi.org/10.1111/oik.05946>
- Venter, O., Sanderson, E., Magrath, A., Allan, J.R., Beher, J., Jones, K.R. et al. (2016). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications*, 7(1), 12558. <https://doi.org/10.1038/ncomms12558>
- Watson, J.E.M., Jones, K.R., Fuller, R.A., Marco, M.D., Segal, D.B., Butchart, S.H.M. et al. (2016). Persistent disparities between recent rates of habitat conversion and protection and implications for future global conservation targets. *Conservation Letters*, 9(6), 413–421. <https://doi.org/10.1111/conl.12295>
- Zeh, D.R., Heupel, M.R., Hamann, M., Limpus, C.J. & Marsh, H. (2016). Quick Fix GPS technology highlights risk to dugongs moving between protected areas. *Endangered Species Research*, 30, 37–44. <https://doi.org/10.3354/esr0072>

How to cite this article: Webster, E.G., Hamann, M., Shimada, T., Limpus, C. & Duce, S. (2022). Space-use patterns of green turtles in industrial coastal foraging habitat: Challenges and opportunities for informing management with a large satellite tracking dataset. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 32(6), 1041–1056. <https://doi.org/10.1002/aqc.3813>

APPENDIX A: Summary of Sirtrack (Shimada et al., 2019) and wildlife computers SPLASH-10 satellite transmitter models deployed on green turtles in Port Curtis and funding sources 2010–2019. All transmitters were equipped with Fastloc GPS and no individual was tracked twice in the study period

Year	n	Tag Type	Deployed by	Funding Source
2010	5	Sirtrack Fastloc	GHD	GHD
2013	10	SPLASH10-F-296A and SPLASH10-F-296C	CSIRO	GISERA Marine project
2013	13	SPLASH10-F-296A and SPLASH10-F-297A	EHP + JCU	ORICA
2014	12	SPLASH10-F-296A	JCU	GPC
2015	11	SPLASH10-F-297A	JCU	GPC
2016	11	SPLASH10-F-297A	JCU	GPC
2017	3	SPLASH10-F-297A	EHP	EHP
2018	4	SPLASH10-BF-344E	JCU Seagrass (Michael Rasheed)	TropWater (JCU)
2018	2	SPLASH10-BF-297B	EHP	EHP
2018	2	SPLASH-10-F-334D	EHP	Shell's QGC Business, Australia Pacific LNG and Santos GLNG
2019	10	SPLASH10-F-385	DES + JCU	Shell's QGC Business, Australia Pacific LNG and Santos GLNG

APPENDIX B: Corrected Akaike Information Criterion (AICc) and delta R^2 values for generalized linear mixed models evaluating predictors of utilization distribution (UD) area, seasonal overlap and range shift

Response	Model	AICc	Marginal R^2	Conditional R^2	df
AREA	UD Area ~ Sex * scale (CCL) + (1 ID)	3903.7	0.16	0.71	8
	UD Area ~ Season + Site + (1 ID)	3896.4	0.25	0.70	12
	UD Area ~ Year + Season + (1 ID)	3909.7	0.17	0.67	13
	UD Area ~ Year + Site + (1 ID)	3896.9	0.26	0.72	16
	UD Area ~ Site + (1 ID)	3891.0	0.24	0.71	9
OVERLAP	Overlap ~ Maturity + (1 ID)	-64.0	NA	NA	5
	Overlap ~ Scale (CCL)*Sex + (1 ID)	-60.0	NA	NA	8
	Overlap ~ Sex + (1 ID)	-62.8	NA	NA	5
	Overlap ~ Site + (1 ID)	-70.8	NA	NA	8
	Overlap ~ Year + Seasons + (1 ID)	-63.9	NA	NA	15
	Overlap ~ Seasons + (1 ID)	-64.9	NA	NA	9
	Overlap ~ Scale (CCL) + (1 ID)	-63.6	NA	NA	4
	Overlap ~ Year + (1 ID)	-73.4	NA	NA	10
SHIFT	Shift ~ Year + (1 ID)	104.9	0.82	0.82	9
	Shift ~ Sex*scale (CCL) + (1 ID)	101.1	<0.01	0.93	7
	Shift ~ Season	101.3	<0.01	0.03	3

Abbreviation: CCL, curved carapace length.