



Intraspecific variability in flatback turtle habitat use: $\delta^{15}\text{N}$ as an indicator of foraging locations

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ABSTRACT: Identifying migration routes and key habitats is critical for the management and conservation of migratory species. Tracking and stable isotope analysis (SIA), particularly of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), are often used to study animal movements, with SIA particularly useful when animals move through isotopic gradients. Marine turtles are typically highly migratory, moving between nesting and foraging grounds often located 100s–1000s km apart. The flatback turtle *Natator depressus* is endemic to the Australian continental shelf. Satellite tracking ($n = 44$) and SIA ($n = 33$) of females nesting in eastern Queensland, Australia, were used to identify main foraging areas, describe intraspecific variation in the location of foraging areas, and determine if $\delta^{13}\text{C}$ and/or $\delta^{15}\text{N}$ values can be used to identify foraging regions. Although foraging grounds were widely dispersed, tracking identified 3 main foraging regions. SIA agreed with tracking, indicating foraging site fidelity. Generalized linear models and linear discriminant analysis (LDA) were used to estimate how well $\delta^{13}\text{C}/\delta^{15}\text{N}$ and nesting sites can perform as indicators of broad foraging regions and to predict foraging regions for turtles with no tracking data. $\delta^{15}\text{N}$ was a strong predictor of the foraging region. LDA correctly classified the foraging region of 94% of individuals and was suitable to predict foraging regions of untracked individuals. A strong negative linear relationship between turtle $\delta^{15}\text{N}$ and foraging latitude indicates the presence of a $\delta^{15}\text{N}$ isoscape along the eastern Queensland coast. This is the first demonstration of an isoscape for the region, which should be useful for studying and monitoring the habitat use of flatback turtles and other migratory species.

KEY WORDS: Flatback turtles · Foraging areas · Habitat use · Isoscape · Satellite tracking · Stable isotope analysis · Telemetry · Turtles

1. INTRODUCTION

Migrations shape the spatio-temporal distributions of numerous aquatic and terrestrial animal species, affecting a range of ecological processes and con-

necting well-distanced habitats and food webs (Polis et al. 1997, Holdo et al. 2011). Understanding migrations is therefore essential to understand broader ecological and evolutionary processes (e.g. Subalusky et al. 2017, Schmaljohann et al. 2022) and is often key for adequate

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species and/or ecosystem conservation and management (e.g. Walsh et al. 2020, Albers et al. 2023). For appropriate management of migratory species, it is critical to identify the habitats used, their relative importance, and the migration routes used to connect them.

Marine turtles are well-recognized migratory taxa that typically conduct large-scale migrations across habitats often separated by 100s–1000s km (e.g. Limpus et al. 1992, Becking et al. 2016, Ferreira et al. 2021). As a group, they are subjected to a range of human-induced impacts including fishing, vessel strikes, pollution, habitat loss and degradation, and climate change (Tomás et al. 2008, Wallace et al. 2011, Patrício et al. 2021). Information on marine turtle movement ecology and habitat use can therefore be useful to identify the stressors that operate throughout their life cycle and distributions, aiding in the development of appropriate management decisions and science-based conservation strategies (Hays & Hawkes 2018). Thus, it is important to identify the geographic distribution of the foraging areas of different populations and to assess the relative importance of the different foraging areas for turtles nesting across their range.

The flatback turtle *Natator depressus* is endemic to the Australian continental shelf and only breeds on the Australian coast (Walker & Parmenter 1990). The species is listed as Data Deficient under the IUCN Red List (Red List Standards & Petitions Subcommittee 1996) and as vulnerable and migratory by the Australian Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act 1999). Like other marine turtles, flatbacks migrate between nesting and foraging grounds (Thums et al. 2017). However, unlike the other species, flatback turtles do not have an oceanic life cycle stage (Hamann et al. 2011, Wildermann et al. 2017). They forage in subtidal inshore waters (Wildermann 2017), but little dietary data are available, with current information suggesting that adults and subadults are carnivorous and feed mostly on soft-bodied invertebrates such as soft corals, holothurians, and jellyfish (Zangerl et al. 1988, Limpus 2007). As with other marine turtles (e.g. loggerhead turtles *Caretta caretta* [Eder et al. 2012], leatherback turtles *Dermochelys coriacea* [Seminoff et al. 2012]), flatbacks show natal philopatry (FitzSimmons et al. 2020) and fidelity to nesting areas (Limpus 2007), and different females have different migration patterns and use different migration routes and foraging areas (Whitlock et al. 2016, Wildermann 2017). Their foraging grounds can be located 100s–1000s km from their nesting areas, and an individual can use 1 or more areas as foraging grounds (Limpus et al. 1984, Whitlock et al. 2016, Wildermann 2017).

Satellite tracking is commonly used to directly study animal migration, movement, and habitat use and is particularly useful for marine turtles, as they need to come to the surface to breathe. Stable isotope analysis (SIA) can also be useful to study movement and habitat use, because the stable isotope composition of a consumer's tissues provides time-integrated information on resource use. Indeed, since the stable isotope composition can differ between different types of primary producers and undergoes a predictable change as it is passed on to consumers, the stable isotope composition of a consumer gives time-integrated information on diet and/or habitat use. In the coastal environment, variations in baseline $\delta^{13}\text{C}$ values result mainly from differences in occurrence and extent of different habitats (e.g. seagrass beds, mangrove forests, intertidal areas), as the dominant producers in the different habitats are generally characterized by different $\delta^{13}\text{C}$ values. In the marine environment, baseline stable $\delta^{15}\text{N}$ values can vary spatially due to differences in nitrogen biogeochemistry between regions, including differences in nitrogen source (nitrate, fixed N_2 , ammonium) and nitrogen cycling pathways (nitrification, denitrification, remineralization, nitrate uptake, N_2 fixation by diazotrophs) in the water column and in the sediments (Montoya 2008, McMahon et al. 2013). At smaller spatial scales, there can be differences in $\delta^{15}\text{N}$ due to anthropogenic causes such as incorporation of sewage into coastal food webs (e.g. Connolly et al. 2013) or differences in urbanization (McClelland & Valiela 1997) or agricultural development levels (e.g. Anderson & Cabana 2005). Thus the stable isotope composition of a consumer can be used as a biogeochemical tag, but unlike electronic tracking that follows animal movements after tagging, it provides information on where the animal has been prior to sampling.

Since turtle epidermis has a turnover rate of >6 mo (e.g. Seminoff et al. 2007), the stable isotope composition of the epidermis of nesting females should integrate information on diet and habitat used over the previous few months, i.e. turtles sampled during their nesting season will provide information on the habitat and food assimilated while at their foraging grounds. Although no $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ isoscape has been identified for the eastern Queensland coast to date, if a relationship between the stable isotope composition of turtles and the location of foraging grounds (confirmed by satellite data) is identified, it will be possible to determine the location of the foraging grounds of untracked nesting females using stable isotopes (Zbinden et al. 2011). This method was used

successfully for marine turtles in other regions (e.g. Ceriani et al. 2012, Pajuelo et al. 2012b, Seminoff et al. 2012, Vander Zanden et al. 2015) but was not useful for loggerhead turtles *C. caretta* sampled along the Great Barrier Reef (GBR) (Coffee et al. 2020). Due to the low analytical cost of SIA, this approach allows for a much larger number of individuals to be sampled, in comparison to the more expensive satellite tagging. Moreover, stable isotope samples can be collected with little effort and by non-specialized personnel, making it a cost-effective technique that can be more widely used for monitoring. However, to our knowledge, no stable isotope-based studies are available for flatback turtles. This study aims to use satellite tracking and SIA of flatback turtles from the Australian eastern Queensland coast to (1) identify main foraging areas and (2) determine if SIA can be an indicator of the foraging locations of flatback turtles.

2. MATERIALS AND METHODS

2.1. Satellite tracking

Between 2009 and 2016, 44 female flatback turtles *Natator depressus* from 8 nesting beaches in eastern Queensland, Australia, were tagged using Argos-linked Fastloc GPS tags (Wildlife Computers) Fig. 1, (Table S1 in Supplement 1 at www.int-res.com/articles/suppl/n053p167_supp/, for all supplements). From north to south, the sites were Wunjunga (W [ID prefix]; 19.777° S, 147.616° E; n = 9), Halliday Bay (HB; 20.894° S, 148.990° E; n = 3), Ball Bay (BB; 20.907° S, 149.000° E; n = 1), Eimeo (E; 21.036° S, 149.180° E; n = 1), Blacks Beach (BIB; 21.044° S, 149.187° E; n = 1), Peak Island (PI; 23.342° S, 150.934° E; n = 2), Curtis Island (CI; 23.741° S, 151.300° E; n = 26), and Mon Repos (MR; 24.798° S, 152.443° E; n = 1) (Fig. 1). Tags were deployed using a harness designed for use on flatback turtles (Sperling & Guinea 2004). Satellite telemetry data from each turtle were acquired from the Wildlife Computers data portal (<https://my.wildlifecomputers.com/>). Turtle tracking data were initially filtered using the R (R Core Team 2022) package 'SDLfilter' to identify and remove spatial and temporal duplicates (Shimada 2016), and a data-driven filter (Shimada et al. 2012) was used to remove locations marked by biologically unlikely swimming speed ($> 7.6 \text{ km h}^{-1}$) and turning speeds ($> 1.8 \text{ km h}^{-1}$) using high-accuracy locations (quality index (qi) ≥ 3 ; excluding all Argos locations). The resulting tracks were then mapped using QGIS (QGIS Development Team

2022), and unrealistic fixes occurring on land (except for nesting sites) were manually removed.

To study habitat use, residency phases of each turtle track were extracted by identifying (stationary) home range phases and movement shifts using the segmentation-only procedure in the 'segclust2d' R package (Patin et al. 2020). The residency phases (i.e. excluding the nesting and travelling phases) were then used to estimate the distributions of foraging areas, using autocorrelated kernel density estimates (AKDEs) derived from continuous time movement models. This was done using the 'ctmm' package (Calabrese et al. 2016, Fleming & Calabrese 2017). A 10 m error prior was incorporated into the AKDEs to account for Fastloc GPS errors, and optimal weighting was used to account for temporal sampling biases (Fleming et al. 2018, preprint doi.org/10.1101/2020.06.12.130195). The Queensland coastline was used as a physical barrier for AKDE estimation. AKDEs were calculated for each individual turtle, and average population AKDEs were also computed for all turtles combined and for turtles tagged at Wunjunga, at Curtis Island, and at the remaining nesting sites, using the 'mean()' function in the 'ctmm' package. Details on model selection and other model parameters as well as overall (95% AKDEs) and core foraging area (50% AKDEs) sizes can be found in Table S2 in Supplement 1.

Overlaps of overall foraging areas (95% AKDEs) between turtle pairs and between groups of turtles were estimated using the Bhattacharyya coefficient using the 'ctmm' package (Winner et al. 2018). The similarities are expressed as coefficients ranging from 0 to 1, implying no shared area and identical distributions, respectively. Two turtles were excluded from the foraging area and overlap estimations as they either did not reach a stationary phase (HB-54531) or did not leave the nesting area (HB-154296) during the transmission phase (see Fig. S1 in Supplement 2 for tracks).

2.2. SIA

Stable isotope samples were obtained from female turtles nesting at Wunjunga (n = 18) and Curtis Island (n = 15) by collecting a 0.5 cm² epidermis sample from the fore flippers using a scalpel. In the laboratory, tissues were dried at 60°C for 48 h. Samples were then shaved into fine pieces with a scalpel, weighed, and encapsulated into tin capsules. Lipids were not removed, as lipid removal has no effect on marine turtle epidermis $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values (Vander Zanden et al. 2014, Bergamo et al. 2016). Moreover,

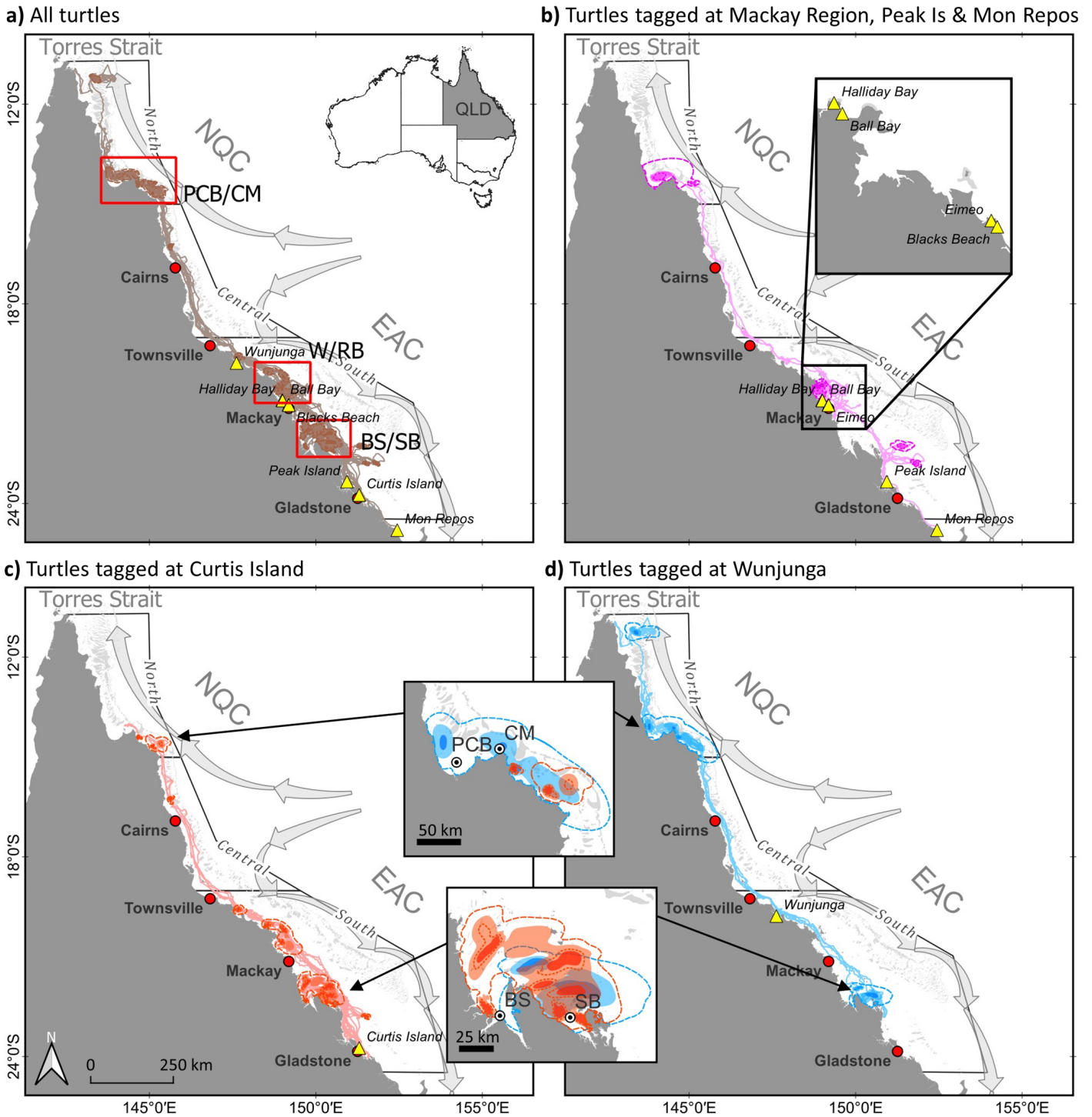


Fig. 1. Flatback turtle tracks and mean foraging areas for (a) all turtles ($n = 42$); (b) turtles tagged at Halliday Bay, Ball Bay, Eimeo, Blacks Beach, Peak Island, and Mon Repos ($n = 7$); (c) turtles tagged at Curtis Island ($n = 26$); and (d) turtles tagged at Wunjunga ($n = 9$). Yellow triangles indicate tagging sites; red circles represent main cities. Mean 95% autocorrelated kernel density estimations (AKDEs) (lighter shades, representing the overall foraging areas) and 50% AKDEs (darker shades, representing the core foraging areas), including 95% CIs for 95% AKDEs (dotted lines for lower bounds and dashed lines for higher bounds of CIs) are shown. Overlapping areas of Curtis Island (red) and Wunjunga (blue) turtles (c,d) are shown in the zoomed-in rectangles. Main foraging areas are indicated by rectangles in (a); PCB/CM: Princess Charlotte Bay/Cape Melville region; W/RB: Whitsundays/Repulse Bay region; BS/SB: Broad Sound/Shoalwater Bay region. Grey arrows show main currents; NQC: North Queensland Current; EAC: East Australian Current. QLD: Queensland

with the exception of 1 individual, epidermis C:N ratios were lower than 3.5, the minimum value suggested for lipid extraction or mathematical correction of $\delta^{13}\text{C}$ values (Post et al. 2007). Samples were analysed at the University of California Davis Stable Isotope Facility (USA) using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer. Results are expressed as per mil (‰) deviations from standards, as defined by: $\delta^{13}\text{C}/\delta^{15}\text{N} = [(R_{\text{sample}} / R_{\text{reference}}) - 1] \times 10^3$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$ for carbon and ${}^{15}\text{N}/{}^{14}\text{N}$ for nitrogen. Result precision was $\pm 0.1\text{‰}$ ($\pm\text{SD}$) for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, calculated from standards.

Turtle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were compared between individuals sampled at the 2 sites with a *t*-test for $\delta^{15}\text{N}$ and the non-parametric Mann-Whitney rank sum test for $\delta^{13}\text{C}$ (given that the distributions of $\delta^{13}\text{C}$ values were not normal). Small size-corrected standard ellipse area (SEA_C ; a measure of niche width) was calculated for turtles from each site using the R package 'SIBER' (stable isotope Bayesian ellipses in R; Jackson et al. 2011) and the standard ellipse area (SEA) positions in the $\delta^{13}\text{C}/\delta^{15}\text{N}$ space compared. The overlap between the 2 SEAs (a measure of niche overlap) was also computed, as the proportion of the overlapped area in relation to the sum of the non-overlapping area of the 2 SEAs, so that for 2 completely separated ellipses, the overlapping area is 0% and for coincidental ellipses, 100%. SEA sizes were compared using the Bayesian standard ellipse area (SEA_B) (Jackson et al. 2011).

2.3. Turtles with both stable isotope and tracking data

For turtles with both stable isotope and tracking data available ($n = 16$; 11 from Curtis Island and 5 from Wunjunga), $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were related to the location of the main foraging grounds (i.e. 95% AKDEs) using a generalized linear model (GLM). Since the eastern Queensland coastline is long, spanning $\sim 17.5^\circ$ of latitude, and flatback turtles used a relatively narrow (typically < 40 km wide) corridor along the coastline, for each turtle, the latitudinal location (in decimal degrees) of the centroid of its foraging ground was used as an indicator of foraging area location. GLMs were therefore computed to identify the effects of tagging site, the centroid of the latitude of the main foraging area, and the westward distance between the main foraging area and the shoreline on $\delta^{13}\text{C}$ and on $\delta^{15}\text{N}$ values (separately). This was done using the 'glm' function in R, with the most parsimo-

nous model selected based on Akaike's information criterion (AIC) (Zuur et al. 2007). To help visualize the relationships (or lack thereof) between each of the explanatory variables and $\delta^{13}\text{C}/\delta^{15}\text{N}$ values, scatterplots were constructed, and regression analysis was used when a linear relationship was apparent, to describe the relationship between variables. Finally, linear discriminant analysis (LDA) was used to estimate how well turtle $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and tagging site can be used as indicators of broad foraging regions (confirmed by tracking) and to predict the foraging regions for turtles with no tracking data. This was done using the 'lda' function from the R package 'MASS' v.7.3-58.1 (Venables & Ripley 2002). Three foraging regions were considered: North (north of 15°S), Central (between 15 and 19°S), and South (south of 19°S) (see Fig. 1), corresponding approximately to the area north of Cape Flattery, the area between Cape Flattery and Townsville, and the area south of Townsville, respectively. These subdivisions were based on the circulation patterns that arise from the 2 main currents that affect the study area: the North Queensland Current (NQC) and the East Australia Current (EAC). These currents enter the GBR from the Coral Sea as residual flows, flowing northwards from $\sim 15^\circ\text{S}$ (NQC) and southwards from $\sim 19^\circ\text{S}$ (EAC) (Choukroun et al. 2010, Andutta et al. 2013) (see Fig. 1). Between these latitudes is a transition zone of weak flow (Choukroun et al. 2010).

3. RESULTS

3.1. Satellite tracking

Flatback turtles were tracked for 55 to 586 d (Table S1). Following nesting, individuals migrated up to ~ 1300 km to their foraging areas, typically moving within ~ 40 km from the coast. Foraging grounds were dispersed along a ~ 1500 km shoreline, from Shoalwater Bay in the south (22.1°S) to Torres Strait in the north (11.2°S) (Fig. 1). In general, foraging habitats were within 30 km of the coast (Fig. 1), but 4 individuals (W-141758, BIB-108471, PI-96774, PC-134199) used more offshore foraging areas, 70 to 120 km off the coast (Fig. S2 in Supplement 2). Distances from nesting to foraging grounds were highly variable, with some individuals (e.g. BB-120641 and PI-96776) foraging in areas adjacent to their nesting grounds, while others (e.g. CI-141742 and CI-141759) moved > 1000 km (see Fig. S2). Moreover, foraging area sizes varied greatly among individuals, with 95% AKDEs varying from 60 km^2 for CI-141739 to 3907 km^2 for CI-54528 (Table S2).

All 26 turtles tagged at Curtis Island moved north (Fig. 1c, Fig. S2). Most ($n = 16$; or 62%) moved to the Broad Sound/Shoalwater Bay region and nearby islands area, 5 (19%) moved to the Whitsundays/Repulse Bay region, and 3 (11%) moved ~1200 km north, to the area off Cape Melville. Of the 9 turtles tagged in Wunjunga, 5 moved north, including 1 (W-141758) that moved >1000 km to a foraging area at the tip of Cape York and 4 that moved ~700 km to the area around Princess Charlotte Bay/Cape Melville (Fig. 1d, Fig. S2). The other 4 individuals moved ~415 km south, to the Broad Sound/Shoalwater Bay region. Of the 6 turtles tagged in the Mackay region (Halliday Bay, Ball Bay, Eimeo, and Blacks Beach), 2 moved >900 km north (one to Princess Charlotte Bay and the other to Cape Melville), 1 moved ~320 km south to the Capricorn and Bunker Group, 1 moved to a foraging area only ~35 km north, 1 did not reach a stationary phase, and the last turtle did not leave the nesting area during the transmission phase (Figs. S1 & S2). Of the 2 turtles tagged at Peak Island, one moved ~130 km northwest offshore and the other moved to the Whitsundays/Repulse Bay region. The turtle tagged the furthest south, at Mon Repos, moved ~600 km north to the Whitsundays region (Repulse Bay) (Fig. S2).

There was a wide range in overall foraging (95% AKDEs) overlaps between pairs of turtles, even among turtle pairs tagged at the same site (e.g. for turtles

tagged at Curtis Island, Bhattacharyya coefficients ranged from 0.00 to 0.87; Supplement 3). However, the vast majority of overall foraging area overlaps were low: 0.0 for 85% of turtle pairs and <0.1 for 94%. Only for 21 of the turtle pairs (2.4%) were the Bhattacharyya coefficients >0.5, suggesting some overlap. This shows that, in general, the different turtles forage in different specific areas, even if they move to the same overall region (see Fig. 1). The overall foraging area overlap between the groups of turtles tagged at Curtis Island and Wunjunga was 0.36 (95% CI: 0.26–0.48).

Tracking data show 3 broad foraging areas (Fig. 1), with 45% of the tracked turtles using the Broad Sound/Shoalwater Bay region, 21% in the area between the Princess Charlotte Bay and Cape Melville region, and 19% in the Whitsundays/Repulse Bay region. The remaining 14% of the turtles used other foraging areas, spread over the eastern Queensland coast (Figs. 1 & 2, Fig. S2).

3.2. SIA

Turtle epidermis $\delta^{13}\text{C}$ values ranged from -17.7 to -10.3‰ (Table 1, Fig. 3), with no significant differences between the 2 sampling sites (Mann-Whitney rank sum test, $p > 0.05$). Regarding $\delta^{15}\text{N}$, turtles from Curtis Island had higher $\delta^{15}\text{N}$ values than turtles from

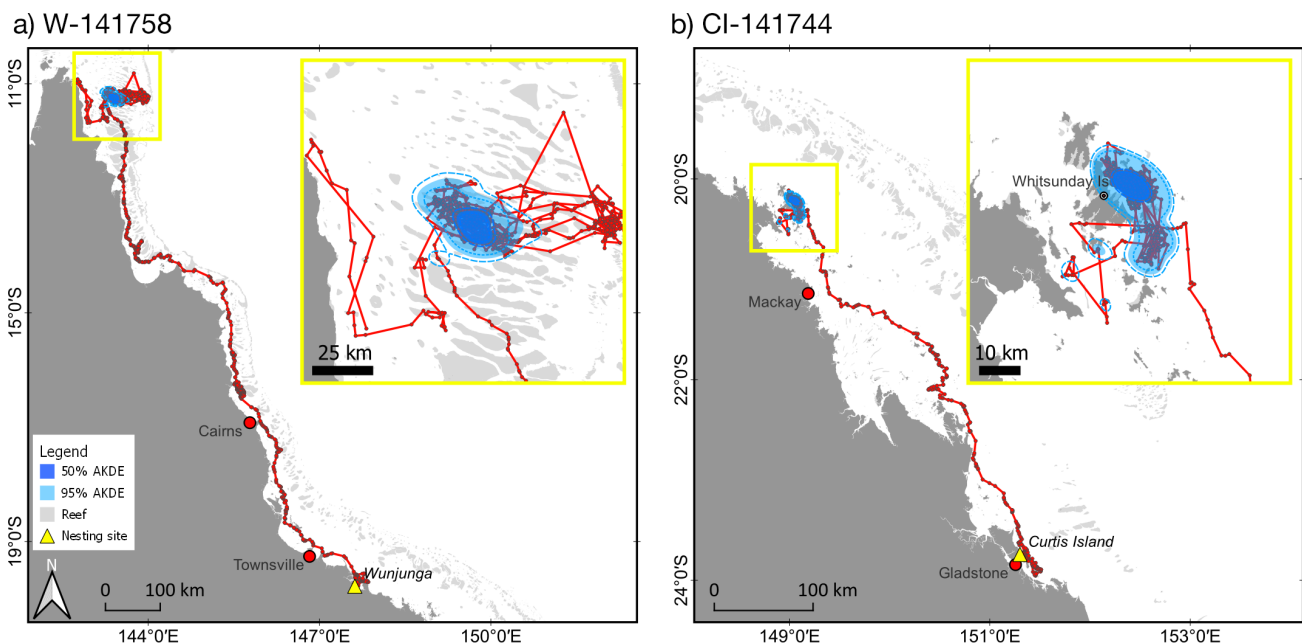


Fig. 2. Overall foraging areas (95% autocorrelated kernel density estimations [AKDEs]), core foraging areas (50% AKDEs), and tracks (red lines) of (a) a flatback turtle tagged at Wunjunga and (b) a flatback turtle tagged at Curtis Island. Yellow rectangles show zoomed-in area of foraging areas. For the remaining individuals, see Fig. S2 in Supplement 2

Table 1. Range and mean \pm SD (in parentheses) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (in ‰) and C:N ratios of turtles sampled at each site. Small size-corrected standard ellipse area (SEA_C , in ‰²) and 95% credible intervals of the Bayesian standard ellipse area (SEA_B ; in brackets) are also indicated

Site	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C:N	SEA_C	n
Curtis Island	−16.9 to −10.3 (−15.0 \pm 1.6)	11.8–15.2 (13.4 \pm 0.9)	2.9–3.2 (3.1 \pm 0.1)	4.7 (2.4–7.4)	15
Wunjunga	−17.7 to −12.7 (−15.8 \pm 1.1)	11.2–13.9 (12.4 \pm 0.8)	2.9–3.3 (3.1 \pm 0.1)	3.0 (1.6–4.4)	18

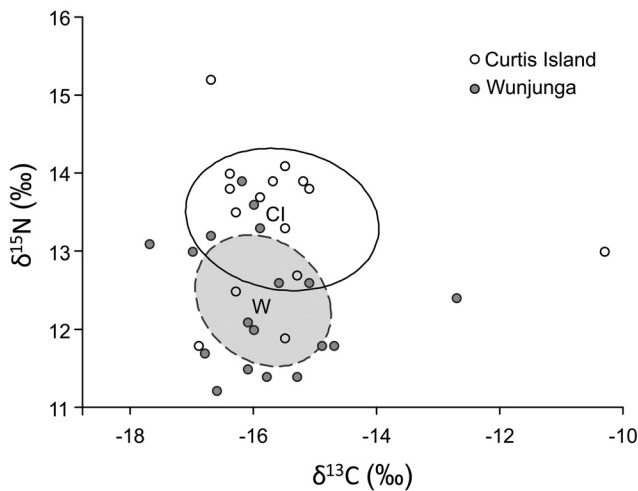


Fig. 3. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and standard ellipses of turtles sampled at Wunjunga (W) and Curtis Island (CI)

Wunjunga (t -test, $p < 0.01$) (Table 1, Fig. 3). The SEA_C of Curtis Island turtles was larger than that of Wunjunga turtles (Table 1, Fig. 3), but there was considerable overlap between the 95% credibility intervals of SEA_B from the 2 sites (Table 1), suggesting the difference was not significant. The SEA overlap was only 15%. Twenty-one percent of the Curtis Island SEA overlapped with the Wunjunga SEA, while 34% of the Wunjunga turtles' SEA overlapped with that of Curtis Island (see Fig. 3).

3.3. Turtles with both satellite tracking and stable isotope data

For 16 flatback turtles, both stable isotope and tracking data were available. As with the overall tagging dataset, the foraging locations of these individuals ranged from Shoalwater Bay in the south to Torres Strait in the north. For $\delta^{13}\text{C}$, the most parsimonious GLM identified the distance of the main foraging location to the shoreline as the sole factor explaining $\delta^{13}\text{C}$, although its coefficient was not significant

($t = 1.496$, $p = 0.159$). Accordingly, regression analysis did not detect a relationship between these variables (Fig. 4). For $\delta^{15}\text{N}$, the most parsimonious GLM found that turtle $\delta^{15}\text{N}$ values depend only on the latitude of the main foraging area ($t = -7.844$, $p < 0.001$), and regression analysis confirmed a significant negative relationship between these variables ($R^2 = 0.75$, $p < 0.001$; Fig. 4). When the identified relationship was used to estimate latitude

of foraging area for untracked turtles (foraging latitude ($^\circ$) = $-3.04 \times \delta^{15}\text{N} + 20.76$) and results compared with tracking information, data suggest that flatback turtles use mostly the Broad Shoal/Shoalwater Bay, the Whitsundays/Repulse Bay, and the Princess Charlotte Bay/Cape Melville areas as foraging grounds (Fig. 5).

LDA confirmed that $\delta^{15}\text{N}$ was the main predictor of the foraging region of nesting flatback turtles. Linear discriminant 1 explained 98% of the variance (Fig. 6), with $\delta^{15}\text{N}$ being the best discriminant variable, with a coefficient of linear discriminant of -1.4 . $\delta^{13}\text{C}$ and tagging site had coefficients closer to 0 (-0.1 and 0.5 , respectively). The model correctly attributed the main foraging region to 15 of the 16 flatback turtles, resulting in a model accuracy of 94%. The only incorrect classification was a turtle that foraged in the Central region that was attributed to the South region. When the model was applied to the $\delta^{15}\text{N}$ values of turtles with no tracking data, it classified 1 Curtis Island individual as foraging in the North region and 5 in the South region. For Wunjunga turtles, it classified 7 individuals as foraging in the North region, 1 in the Central region, and 5 in the South region (Fig. 6). Overall, when considering both tracked and untracked turtles, results suggest that most (68.8%) Curtis Island turtles forage in the South region, 12.5% in the Central region, and 18.8% in the North region. For turtles sampled at Wunjunga, results suggest that the North is the most important foraging region, with 61.1% of the stable isotope-sampled turtles assigned to that region, while 33.3% were assigned to the South region and 5.6% to the Central region (Fig. 6).

4. DISCUSSION

The combined use of tracking and SIA was useful to ascertain flatback turtle movement and habitat use patterns. Following nesting, tracked turtles migrated up to ~ 1300 km to widely dispersed forag-

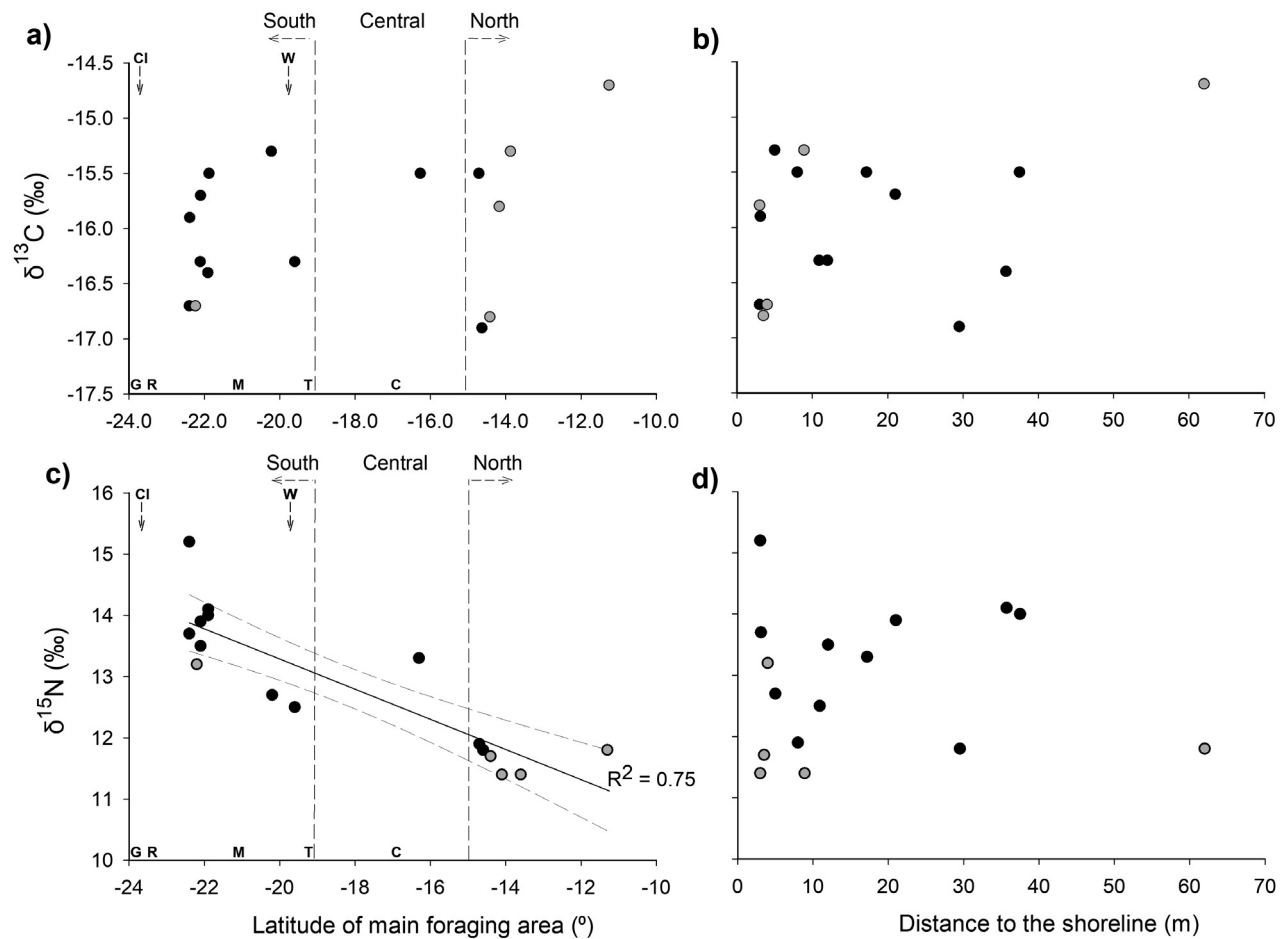


Fig. 4. Relationship between the (a,c) centroid of the latitude of the main foraging area and (b,d) distance to the shoreline on flatback turtle (a,b) $\delta^{13}\text{C}$ and (c,d) $\delta^{15}\text{N}$ values. Black points: turtles sampled at Curtis Island (CI); grey points: turtles sampled at Wunjunga (W). A significant relationship between latitude of main foraging area and $\delta^{15}\text{N}$ values was present: $\delta^{15}\text{N} = -0.25 \times \text{foraging latitude} + 8.36$ ($R^2 = 0.75$, $p < 0.001$; indicated by black line, with dashed lines showing the 95% confidence bands). Foraging regions (South, Central, North) and latitudes of the tagging locations (CI and W) are also indicated (top), along with the latitudes of the coastal cities along the study area (from south to north; G: Gladstone; R: Rockhampton; M: Mackay; T: Townsville; C: Cairns)

ing areas. As with flatbacks tagged in the state of Western Australia (Pendoley et al. 2014, Whittock et al. 2016, Thums et al. 2018) and in the Torres Strait (Hamann et al. 2015), individuals nesting in one area foraged in a number of different sites (Wildermann 2017; this study). Tracking identified 3 main foraging regions: around the Broad Sound/Shoalwater Bay area in the south, in the Whitsundays/Repulse Bay region, and between Cape Flattery and Princess Charlotte Bay further north. Although in general turtles tagged in the southern locations tended to use more southern foraging areas, there was an overlap in foraging areas between turtles tagged at the 2 main sites (Wunjunga and Curtis Island).

Stable isotope results agreed well with tracking data. For example, the variability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

values of turtles sampled at Curtis Island and Wunjunga shows that individuals from the same nesting beach used different foraging grounds. Stable isotope data also confirmed the overlap in foraging area between turtles tagged at the different sites, as although $\delta^{15}\text{N}$ values of Wunjunga turtles were lower than those of Curtis Island turtles, there was considerable overlap.

Although $\delta^{13}\text{C}$ was not a useful indicator of foraging locations, the variability in $\delta^{13}\text{C}$ values found for turtles at both sites suggests that the different individuals rely on food webs based on isotopically distinct producers, or at least based on different contributions of isotopically distinct producers. Coastal planktonic producers have lower $\delta^{13}\text{C}$ values, typically between -22 and -19‰ (Clementz & Koch 2001, Frisch et al.

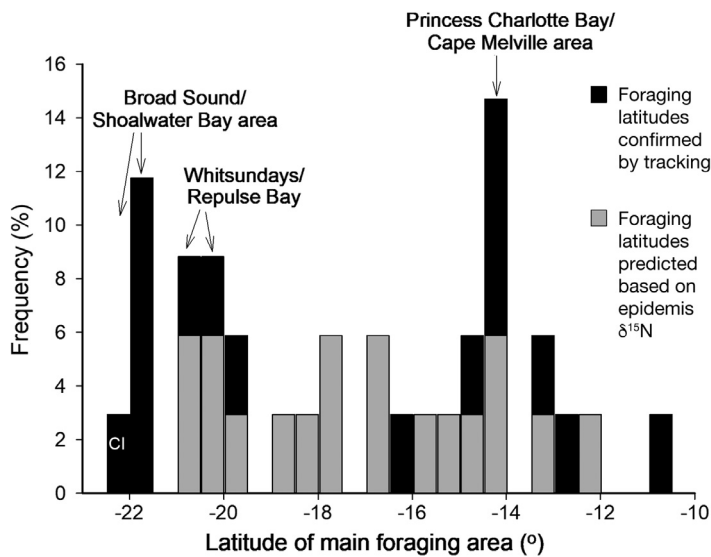


Fig. 5. Latitudes of the main foraging area of flatback turtles. Black bars: latitudes confirmed by tracking; grey bars: latitudes predicted based on epidermis $\delta^{15}\text{N}$ values, using the equation: foraging latitude ($^{\circ}$) = $-3.04 \times \delta^{15}\text{N} + 20.76$

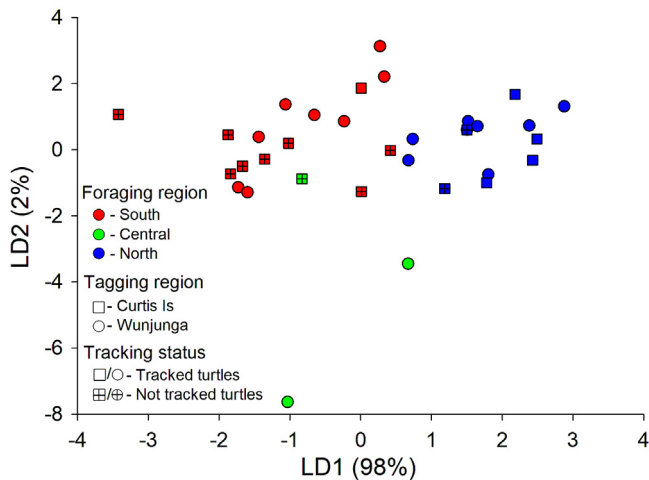


Fig. 6. Linear discriminant analysis for foraging region based on flatback turtle $\delta^{13}\text{C}$ values, $\delta^{15}\text{N}$ values, and tagging site. Numbers in brackets are the proportion of the variance explained by each linear discriminant (LD)

2014), while benthic producers such as seagrass (Hemminga & Mateo 1996, Clementz & Koch 2001), coral (Heikoop et al. 2000), and microphytobenthos (Abrantes et al. 2015) are characterized by higher $\delta^{13}\text{C}$, typically greater than -15‰ . While for most of the individuals analysed $\delta^{13}\text{C}$ values were between -17.7 and -14.7‰ , suggesting different levels of reliance on both planktonic and benthic food webs, for 2 individuals (1 from Curtis Island and 1 from Wunjunga), $\delta^{13}\text{C}$ values were $>13\text{‰}$, suggesting a major

reliance on benthic producers. Unfortunately, those 2 individuals were not fitted with satellite transmitters.

Unlike with $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ analysis was useful to track flatback turtle foraging locations. Since the stable isotope composition gives information on resource use before sampling and tracking gives information on where the animal moves to after tagging, the significant relationship between epidermis $\delta^{15}\text{N}$ values and latitude of main foraging location suggests that the $\delta^{15}\text{N}$ values of turtles sampled at the nesting grounds reflect the food consumed at the foraging grounds and that flatback turtles return to the same region after nesting. Fidelity to foraging areas has been reported for both the eastern (Shimada et al. 2020) and western (Whitlock et al. 2016) Australian flatbacks.

Flatback turtle $\delta^{15}\text{N}$ was useful to assign foraging regions to nesting turtles and to determine the proportion of nesting individuals that used the different foraging regions. Indeed, LDA agreed with tracking data, in that most Curtis Island turtles forage in the South region, while most Wunjunga turtles forage in the North region. The Central region seems to be the least used. Note, however, that only 5 Wunjunga turtles had both tracking and stable isotope data and that few of the turtles with both stable isotope and tracking data foraged in the Central region. There could therefore be some error in the assignment of foraging areas to turtles from the Central region. A larger sampling size of turtles sampled by the 2 techniques would make the predictive power of LDA stronger. Ideally, data should be collected from other nesting regions across their nesting range and over multiple years, to account for temporal variability in the contribution of turtles that forage in the different regions to the breeding cohort because, as shown for green turtles *Chelonia mydas* (Bradshaw et al. 2017), the importance of the different foraging areas may vary among years.

The significant relationship between the latitude of the main foraging ground and turtle $\delta^{15}\text{N}$ values indicates that there is a $\delta^{15}\text{N}$ isoscape along the eastern Queensland coast and that this relationship is useful to infer the foraging region of flatback turtles at a regional level. This gradient could be a result of differences in ecology and/or oceanography between the southern and northern sections of the GBR. North of $\sim 18^{\circ}\text{S}$, the continental shelf is narrow and covered by reef matrix, leading to a shallow (<30 m deep) and relatively narrow (<20 km wide) lagoonal area, whereas southwards of $\sim 18^{\circ}\text{S}$, the continental shelf becomes increasingly wider, with reef mostly present on the outer part of the shelf, leading to the widening of the GBR lagoon (to ~ 150 km), with some areas reaching down to

130 m depth (Beaman 2020). One of the consequences of these differences in oceanography is that although seagrass is abundant throughout the GBR lagoon, seagrass cover is greater in the northern sections (Carter et al. 2021). However, since seagrass is characterized by relatively high $\delta^{13}\text{C}$ values (for our latitude range, seagrass $\delta^{13}\text{C}$ values of $-9.6 \pm 2.7\%$ [n = 40] are reported [Hemminga & Mateo 1996]), the lack of a relationship between latitude and turtle $\delta^{13}\text{C}$ suggests that differences in seagrass cover are not responsible for the observed $\delta^{15}\text{N}$ pattern.

Spatial differences in $\delta^{15}\text{N}$ values at the base of the food web can arise due to differences in availability and utilization of the different nitrogen sources (e.g. marine nitrate, fixed N_2 , ammonium) and differences in the biogeochemical processes both in the water column and in the sediments (Montoya 2008, McMahon et al. 2013). In the oligotrophic waters of the GBR, nitrogen enters the food webs mainly through inputs from catchment runoff and through N_2 fixation by diazotrophs, particularly *Trichodesmium* spp. (Messer et al. 2017, Blondeau-Patissier et al. 2018, Ani et al. 2023). In the GBR, *Trichodesmium* blooms are more frequent, larger, and longer lasting in the southern sections than in the north (Blondeau-Patissier et al. 2018, Ani et al. 2023), meaning their importance to the GBR lagoon food web likely increases as we move southwards. However, N_2 fixation leads to organic matter with relatively low $\delta^{15}\text{N}$ (approx. -2 to -1% ; Carpenter et al. 1997, Montoya et al. 2002), suggesting that the N_2 fixation process is not responsible for the observed increase in turtle $\delta^{15}\text{N}$ values with latitude.

It is possible that the observed north–south gradient in turtle $\delta^{15}\text{N}$ is, at least in part, a result of differences in $\delta^{15}\text{N}$ in the other major source of nitrogen for the GBR: nitrogen in catchment runoff. Along our study area, there is a latitudinal gradient in anthropogenic impact. Increases in river runoff $\delta^{15}\text{N}$ and, consequently, primary producer $\delta^{15}\text{N}$ due to anthropogenic impacts (measured based on population size and levels of industry, tourism, and agriculture) in adjacent catchments are well documented (e.g. Kendall et al. 2007, Jones et al. 2018). Differences in baseline $\delta^{15}\text{N}$ are then propagated up the food webs, making $\delta^{15}\text{N}$ values useful to identify foraging regions. Within our study area, most cities (Gladstone, Rockhampton, Mackay, and Townsville) are located south of latitude 19.2°S , while the region north of Cairns (16.9°S) is mostly undeveloped. Since urban wastewater is characterized by high $\delta^{15}\text{N}$ values (Costanzo et al. 2001, Cole et al. 2004, Risk et al. 2009), higher $\delta^{15}\text{N}$ values in turtles that forage in the southern loca-

tions could be a result of proximity to urbanization. Extensive agriculture also takes place in the southern region, in contrast to the northern region, where natural forest is still abundant (McCloskey et al. 2021), and river plumes also occur more frequently in the southern part of the coastline (to $\sim 18.3^\circ\text{S}$, Petus et al. 2014), facilitating the delivery of organic matter and pollutants to the GBR lagoon (Devlin et al. 2012).

Upon entering the GBR, nutrients and other soluble materials of terrestrial origin are estimated to reside within the GBR lagoon for >1 mo to 1 yr, remaining close to the coast and moving north or south, depending on the entry location (Luick et al. 2007). These residency periods are long relative to the development times of tropical plankton, meaning any spatial differences in the stable isotope composition of imported material will be incorporated into the local food webs, up to higher trophic level species (Abrantes et al. 2013). From the other side, oceanic waters entering the GBR are estimated to remain within the lagoon for 3–5 mo (Andutta et al. 2013). This time frame, again, allows for the stable isotope composition of living organisms to change to reflect any spatial differences in nutrient stable isotope composition and/or environmental conditions. In the GBR, some chemicals transported from adjacent catchments, including contaminants, have been detected in green turtle tissues, with latitudinal differences in chemical profiles reflecting adjacent land use activities (Villa et al. 2017, Dogruer et al. 2018, Gallen et al. 2019). This supports the hypothesis that differences in $\delta^{15}\text{N}$ values of material transported from the adjacent terrestrial environment are reflected in our flatback turtle tissues, particularly as both green and flatback turtles feed on coastal benthic food webs.

It could also be argued that the latitudinal differences in turtle $\delta^{15}\text{N}$ values resulted from differences in flatback turtle trophic position, as $\delta^{15}\text{N}$ values are often used as trophic level indicators (Post 2002). However, although not well studied, the diet (and, consequently, trophic position) of flatback turtles is likely consistent across the soft-bottom habitats where they forage, meaning it is unlikely that differences in turtle trophic level are driving the observed latitudinal pattern.

Although marine isoscapes have been used to identify turtle foraging grounds in several regions including the northwestern Atlantic (Ceriani et al. 2012, Pajuelo et al. 2012a), the Gulf of Mexico (Vander Zanden et al. 2015), northwestern Africa (Eder et al. 2012), and the Mediterranean Sea (Bradshaw et al. 2017), to date, no latitudinal isoscape has been identified for the eastern Queensland coast. Three studies

(to our knowledge) have previously used SIA to study turtle foraging locations along the eastern Australian coast. In Coffee et al. (2020), no relationship between the latitude of foraging areas and epidermis $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values of nesting loggerhead turtles was detected, despite the sampled turtles using foraging grounds distributed throughout ~2000 km of the Queensland coast, which included the latitudes of the present study. This discrepancy could occur because loggerhead turtles forage over a wider range of habitats, including coral and rocky reefs, seagrass beds, and sandy/muddy areas (Limpus 2008), and have broad and generalized diets (Thomson et al. 2012), feeding on both benthic and pelagic food webs (Casale et al. 2008, Peckham et al. 2011). Since different habitats and/or food webs can have different baseline $\delta^{13}\text{C}$ and/or $\delta^{15}\text{N}$, even if there is an isoscape in a particular habitat type, the averaged stable isotope composition of loggerhead turtles could make it difficult to detect the presence of that potential isoscape. Unlike loggerhead turtles, flatback turtles feed on more specific habitats (inshore subtidal soft-bottom habitats) (Limpus 2007, Wildermann 2017), with available dietary data suggesting they rely on food webs mostly based on benthic primary producers (Zangerl et al. 1988, Limpus 2007, Wildermann 2017). Therefore, flatback tissues would more easily reflect an isoscape of benthic habitats, if such an isoscape is present. Note, however, that in Coffee et al. (2020), only 3 of the loggerhead turtles sampled foraged in the northern GBR, 3 others in the southern GBR, and 9 further south in subtropical eastern Australia, and those had variable $\delta^{15}\text{N}$ values (10.2–12.2‰ in the northern GBR, 8.5–10.5‰ in the southern GBR, 7.4–13.8‰ in subtropical eastern Australia) (Coffee et al. 2020). It is possible that larger sample sizes could have led to the identification of a relationship between latitude of foraging area and $\delta^{15}\text{N}$ values. In another study, green turtles nesting at Raine Island (northern GBR) had generally lower $\delta^{15}\text{N}$ values than green turtles nesting at Heron Island, > 1500 km away in the southern GBR (Coffee 2020), a result that could reflect the presence of a $\delta^{15}\text{N}$ isoscape, in agreement with the present study. In a different approach, the third study (Pearson et al. 2019) used barnacle growth rates and $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of shells of commensal barnacles to predict foraging regions of green and loggerhead turtles. Barnacle shell $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values reflect the water temperature and salinity conditions at the time of deposition, with minimal contribution from diet. There were differences between turtles foraging in northern and southern Queensland, which were explained as resulting from the lati-

tudinal gradient in temperature and from the salinity gradient between estuarine and marine environments. This method could also be useful to study flatback turtle foraging regions in the future.

5. CONCLUSION

The combined use of satellite tracking and SIA was useful to identify the relative importance of the different foraging regions to nesting flatback turtles. Importantly, this study identified a $\delta^{15}\text{N}$ isoscape in eastern Australia, which allows for flatback turtle foraging regions to be inferred based on $\delta^{15}\text{N}$ values, with potential management and conservation applications. For example, this approach can be useful to monitor changes or trends in the relative importance of the different foraging regions, information that could be useful to prioritize areas to be protected or to identify/quantify the impacts of weather events such as cyclones or human activities like shipping, trawling, and port developments. Flatback turtles are presently monitored at index nesting beaches (Department of Environment and Science 2021), so the incorporation of stable isotope sampling at those beaches could be a valuable add-on to monitor changes in foraging area use. Although SIA leads to a less accurate delimitation of foraging areas than tracking (Bradshaw et al. 2017), the technique can be particularly useful, as the low cost of analyses allows for a large number of turtles to be sampled. Egg yolk sampling (e.g. Hatase et al. 2002, Ceriani et al. 2014) or analysis of commensal barnacle shells (Pearson et al. 2019, 2020) could also be considered in future studies, for easier and less invasive sampling. This study was the first to identify a $\delta^{15}\text{N}$ isoscape in eastern Australia, an isoscape that can be beneficial for studying and monitoring the habitat use of not only flatback turtles but also other migratory species along the eastern Australian coast (e.g. bull sharks *Carcharhinus leucas* [Heupel et al. 2015], spotted mackerel *Scomberomorus munroi* [Begg et al. 1997]). It would be highly beneficial if comprehensive baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value data, at appropriate spatial and temporal scales, were available for the region and for the overall Australian coast.

Acknowledgements. This project was funded by World Wide Fund for Nature (WWF) and corporate partner Factorie. Research was conducted under permit SA 2021/11/808. We thank the Queens Beach Action Group, Gudjuda Reference Group Aboriginal Corporation, Giringun Aboriginal Corporation, and WWF for their help in data collection.

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Editorial responsibility: Alistair Hobday (Guest Editor),
Hobart, Tasmania, Australia
Reviewed by: M. D. Ramirez and 1 anonymous referee

Submitted: March 30, 2023
Accepted: November 9, 2023
Proofs received from author(s): February 5, 2024