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Should I stay or should I go? The influence of environmental conditions on green turtle residence time and outward transit in foraging areas

Emily G. Webster[1] · Stephanie Duce[1] · Mark Hamann[1] · Nicholas Murray[1] · Takahiro Shimada[2] · Colin Limpus[2]

Abstract

Foraging animals move through the environment to satisfy their requirements for food, rest, reproduction and risk-avoidance. Understanding how animals respond to changing environmental conditions can help to characterise favourable habitat and determine whether they might be motivated to depart when those habitats become unsuitable. Foraging green turtles are typically residents that scarcely move in response to environmental changes or disturbances. Some individuals though, exhibit high mobility at fine scales. We developed an analysis of Fastloc GPS tracks of 61 green turtles using cox regression models and generalised linear mixed models to investigate the influence of a suite of environmental characteristics on the length of residence time and probability of turtles transitioning between two behavioural modes, "stay" or "go". Decisions to move ("go") were influenced by short-term changes in the local environmental conditions. Individuals were more likely to "stay" when temperature increased during their stay and were more likely to "go" when turbidity decreased, and they entered deeper habitats. This result implies that foraging and resting ("staying") primarily occurs in benthic, shallow, warm habitats, while transit ("going") is facilitated in deeper, clear water. We also determined that individuals within the green turtle foraging aggregation respond differently to environmental cues to move and hypothesise that a diversity of strategies within a foraging aggregation could confer its resilience to disturbance events. Our study provides new evidence of the factors influencing movements in green turtles and can aid in predicting how they may respond to future changes and enhance risk mitigation efforts through dynamic and adaptive planning.

Abbreviations

AICc	Second order Akaikes Information Criterion for small samples
AIMS	Australian Institute of Marine Science
ARS	Area restricted search
BoM	Australian Bureau of Meteorology
CCL	Curved carapace length
CSIRO	Commonwealth scientific and industrial research organisation
DESI	Queensland Department of Environment, Science and Innovation
EHP	Queensland Department of Environment and Heritage Protection (now DESI)
EPBC Act	Environment Protection and Biodiversity Conservation Act
FGPS	Fastloc Global Positioning System
GBR4	EReefs Great Barrier Reef 4 km resolution model
GLMM	Generalised linear mixed model
GPC	Gladstone Ports Corporation
JCU	James Cook University
LNG	Liquid natural gas
MKDE	Movement-based kernel density estimate
PTT	Platform terminal transmitter
QLD	Queensland
QTCP	Queensland Turtle Conservation Program
UD	Utilisation distribution

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✉ Emily G. Webster
Emily.webster1@my.jcu.edu.au

1 College of Science and Engineering, James Cook University, 1 James Cook Drive, Douglas, QLD 4811, Australia

2 Queensland Department of Environment, Science and Innovation, 41 Boggo Road, Dutton Park, QLD 4102, Australia

Introduction

Decisions about if, and when, to move are guided by an animal's environment and internal cues. The tendency to remain in a defined area can be described as residency and can confer familiarity to local resources that fulfil physiological needs, withstanding temporary fluctuations in those resources. This is true too for species exhibiting long-distance migration behaviour, whereby animals revisit multiple familiar habitats to meet their requirements for specific activities such as foraging and breeding. Between migrations, relocation to an unfamiliar location is risky as a new location may not be viable long-term. Thus, residency is advantageous in unpredictable conditions if the risk of changing sites is high (Switzer 1993).

Green turtles (*Chelonia mydas*) are classified as endangered globally (Seminoff 2023), and vulnerable under Queensland state (Nature Conservation Act 1992) and Australian (Environmental Protection and Biodiversity Conservation Act 1999) legislation. In their inshore foraging grounds, unpredictable natural disturbances occur, which can impact the quality or quantity of food available. For example, outflow from floods following extreme weather events transports excess suspended sediment into the water column. Sediment then occludes light and can settle to smother benthic prey species inhibiting productivity (McCormack et al. 2013; Coles et al. 2012; Rasheed et al. 2014). Floods and resulting erosion also contribute to the loss of rhizomes and the seed bank, impacting recovery time of aquatic vegetation (Campbell and McKenzie 2004; Preen and Marsh 1995). Forbes et al. (1996) documented green turtles switching to less nutritious diet items when preferred diet was not available. Thus, deleterious weather can lead to long term nutritional loss for the megafauna that consume benthic organisms (Bauer et al. 2011; Limpus and Nicholls 2000). These events can affect the long-term viability of foraging habitat yet, rather than prompting displacement of foraging turtles, turtles have been found to stay at the expense of their health and reproductive output (Flint et al. 2015). Understanding this behaviour underpins the viability of turtle populations because the tendency to stay in one place may be maladaptive given the globally increasing frequency of severe weather events (IPCC 2012; Milly et al. 2002; Ummenhofer and Meehl 2017).

Green turtles are generally faithful to their foraging sites (Shimada et al. 2019, 2016a; Webster et al. 2022; Limpus et al. 1992), often remaining at a site for months or years (Limpus et al. 2005). Individuals who depart frequently return to these sites following displacement by people and post-breeding migrations (Shimada et al. 2019). However, while residency predominates in many green turtle foraging aggregations, satellite tracking studies have revealed that individual strategies are context-dependent and may be characterised by multiple behaviours (Webster et al. 2022). A recent satellite tracking study of 72 turtles in Port Curtis on the Queensland coast found they may inhabit several discrete local areas consecutively or alternately, perform short forays away from and returning to their site of choice, or more rarely, depart the area, resettling elsewhere (Webster et al. 2022).

The drivers of fine-scale green turtle movements, in contrast to residency in a single location, have typically been related to the predictable, cyclical changes that characterise inshore foraging grounds as well as life history. For example, seasonal and diel temperature cycles and temperature at depth play a role in behavioural thermoregulation in some green turtle foraging aggregations (Crear et al. 2016; Read et al. 1996; Madrak et al. 2016; Blumenthal et al. 2010; Chambault et al. 2016; Musick and Limpus 1997). Though the species is tolerant of a range of temperatures (Chambault et al. 2016), as ectotherms, green turtles typically demonstrate fidelity to foraging sites where temperatures are stable (Musick and Limpus 1997). Similarly, temperature and rainfall patterns dictate growth and senescence of primary producers (Holloway-Adkins and Dennis 2017; Reisser et al. 2013), which are a key diet item for green turtles at non-reef neritic foraging grounds (e.g., seagrasses, algae, mangrove leaves and fruits) (Forbes 1996, 1993; Bjorndal 1997; Arthur et al. 2008; Prior et al. 2016). Green turtles in Bermuda show increased local movement between foraging areas coinciding with periods of low food availability, attributed to increased foraging effort (Meylan et al. 2022). Green turtle activity cycles (Christiansen et al. 2017; Petit et al. 2020), physiology (Hazel 2009; Hazel et al. 2009; Senko et al. 2010) and orientation (Shimada et al. 2016b) are often linked to diel patterns, and tides provide intermittent access to intertidal habitat and can facilitate passive transport of foraging green turtles (Switzer 1993; McCormack et al. 2013; Coles et al. 2012; Madrak et al. 2016; Shimada et al. 2016b). Despite these probable interactions, little is known about how diel or seasonal changes in microhabitats influence residency and patterns of movement.

Green turtle movements during foraging have also been attributed to life history traits and intraspecific interactions. On larger scales, ontogeny is associated with a dietary shift when young turtles recruit to neritic habitats and transition from pelagic to benthic food sources (Arthur et al. 2008; González Carman et al. 2012; Quiñones et al. 2022; Cardona et al. 2010). The developmental migration hypothesis suggests that juvenile turtles occupy shallow developmental foraging habitat, and as subadults approaching sexual maturity move to other benthic 'adult' foraging grounds (Chambault et al.

2018; Siegwalt et al. 2020; Bolten 2003; Limpus and Fitzsimmons 2020). However, while this is well described in the northern Atlantic (Siegwalt et al. 2020; Seminoff et al. 2006), there are only a few records of developmental migration in eastern Australia (Limpus et al. 2005; Limpus and Fitzsimmons 2020; Limpus et al. Unpublished dataset (QTCP, Limpus pers. Comm.)). Developmental migrations manifest on large scales ranging tens to thousands of km, though true distances are only known for a few populations (Heithaus 2013). In contrast, fine-scale movements can occur within a foraging site, driven by ontogenetic differences. Juveniles may move to utilise a variety of habitat types as they exhibit high plasticity in their diet. Similarly, despite previously being considered predominantly benthic herbivores, the relative contribution of pelagic prey animals to the diet of adult green turtles is not well quantified and may be reflected in mobility (Meylan et al. 2011; Chambault et al. 2018). In eastern Australia, most foraging aggregations comprise of mixed size classes thus, ontogenetic differences may manifest in cohorts exploiting different habitats within an aggregation. For example, smaller turtles comprise a larger proportion of foraging aggregations than adults within structured habitat where they have protection from predation, such as on coral reefs (Seminoff et al. 2006; Luschi et al. 2003) and in shallow mangrove edges (Pillans et al. 2021). Turbid habitat may also provide protection from predators (Limpus et al. 1994). Small turtles can also occupy small pools and shallow gutters at low tide while bigger turtles need to move into deeper waters (Limpus et al. 2005; Herzfeld et al. 2004). Finally, there is likely to be some variability in individual responses to cues to move within a foraging aggregation, because of differing requirements and behaviours of different age cohorts, sexes, and sizes. Intraspecific behavioural variability presents a significant gap in our knowledge of the foraging ecology of the species.

To investigate potential biophysical drivers of residence and movement behaviours of green turtles and provide new evidence in the west Pacific of fundamental factors influencing their spatial ecology, we developed an analysis of the satellite tracks of green turtles at a well-known inshore foraging site in Port Curtis, Queensland. Understanding which factors elicit a movement response will improve upon existing estimates of spatio-temporal distributions, to include information on how turtles respond to local scale changes. Refining our understanding of distribution in space and time provides key information for targeted and adaptive management of this species. Therefore, this study aims to identify the drivers influencing the duration of residency periods in foraging green turtles, identify those drivers responsible for whether foraging green turtles commence residency or transit outward, and investigate the influence of tides and diel cycles on turtles' staying or going.

Methods

Study site

Port Curtis (Fig. 1) in central Queensland is a large multi-commodity port that sits within the Great Barrier Reef World Heritage Area. The shallow-inshore harbour is fed with outlets from the Calliope and the Boyne rivers, South Trees Inlet and the Narrows. The input of sediment loads and poor connection with the offshore region results in appreciable sediment concentrations within the estuary which become negligible seaward of Facing Island. Current flow within the harbour is predominantly tidal and the water column is well mixed (Chambault et al. 2020). The intertidal and subtidal habitats include seagrass, mangroves and macroalgae, soft and hard corals, mud, sand, gravel, rock, and dredged channels (Shimada et al. 2012).

Tracking data collection

We collected Fastloc-GPS (FGPS) tracks of 61 green turtles at Port Curtis. These are detailed in Webster et al. (2022), including only those turtles tracked between December 2010 and April 2019. The dataset consists of 22 females (18 adults, 4 subadults), 27 males (19 adults, 8 subadults and 2 juveniles) and 12 individuals of unidentified sex (9 subadults and 3 juveniles), which ranged between 42.1 and 116.6 cm in curved carapace length. Fastloc-GPS (FGPS) were configured to transmit every 30 min and provided locations and timestamps of turtles with relatively high spatial accuracy (estimated mean error 47.1 m when derived from > 3 satellites) (Dujon et al. 2014; Shimada et al. 2012).

We filtered the tracking data to remove duplicates, spurious locations based on unrealistic travel speeds, and locations on land using the SDLfilter R package (Shimada et al. 2012). We included only FGPS locations derived from at least four source satellites, and ARGOS location classes 1, 2 and 3. The mean accuracy of the FGPS locations is < 50 m (Webster et al. 2022), substantially finer than the spatial resolution of the environmental data (Table 1). Error of ARGOS location classes 1,2,3 is estimated between 250 and 1500 m pre-filtering. The data-driven filter (SDLfilter) considers each location's preceeding and succeeding location. This means that unrealistic points are removed, and the accuracy of the post-filtered ARGOS data is higher than we would otherwise expect from raw equivalent location classes. We also removed locations with a net displacement greater than 140 km from the turtles' release
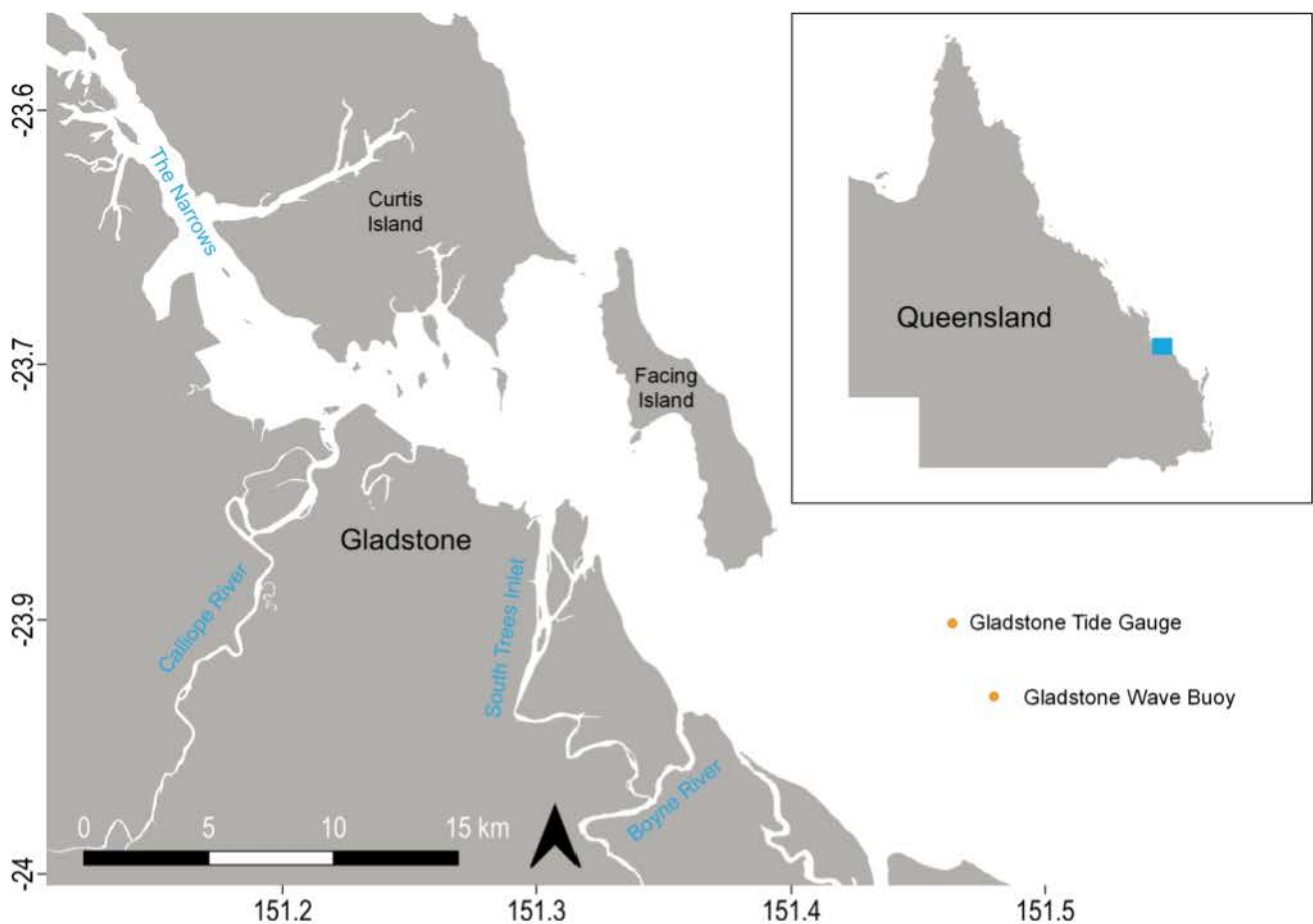
Fig. 1 Site map of Port Curtis showing position in central Queensland, location of major freshwater outflows and the location of Gladstone Tide Gauge and Wave Buoy

site, corresponding to known breeding migrations of two tracked turtles.

Data analysis

We used the residence time method with Lavielle partitioning (Shimada et al. 2016b; Barraquand and Benhamou 2008; Lavielle 2005) to partition each turtle's track into segments of distinct behaviours in the adehabitatLT R package (Calenge et al. 2023). GPS data from air-breathing marine animals are irregular in time, determined by whether the duration of surfacing events of the animal are long enough for the satellite tags to acquire a fix. Unless conditions are optimum, the lag between successive fixes will be longer than the tag's configured interval. Transmission rates often decrease over the life of the tag, due to biofouling impeding successful transmission. Various approaches to behavioural partitioning exist e.g., state-space modelling, hidden Markov models). Because of irregularity in our data, the temporal resolution we were able to achieve using state-space modelling was > 12 h. Therefore, we chose the residence time

method for its ability to provide an estimate of latency to move at each tracked location, and to retain high temporal resolution of tracking data. The residence time method calculates the time taken for the animal to enter and leave a circle with a predefined radius centered around each satellite tracked location, allowing for forward and backward crossing of the circle within a set time range. We defined a radius of 300 m and a maximum time a turtle can leave and re-enter the circle, while still being considered as 'resident' to that area, of 3 h. The scale of the radius was selected by testing several inputs, with 300 m providing a suitable balance between detailed analysis and a reliable result (Barraquand and Benhamou 2008). Mean residence time is assumed to increase in intensively used areas (Barraquand and Benhamou 2008), thus we employed Lavielle partitioning of the turtle tracks based on mean residence time (Shimada et al. 2016b). We identified two distinct behavioural modes from the segmentation, area restricted search (ARS) characterised by high mean residence time indicating intensive use of an area for foraging or resting, and transit with lower mean residence time and directed or transitory movement.

Table 1 Metadata for selected covariates including data source, spatial and temporal resolution, examples of influence on green turtle movement and method by which the selected covariate was appended to the tracking data

Covariate	Source	Spatial resolution	Temporal resolution	Examples of relationship to green turtle movement	Append method
Temperature (°C)	eReefs coupled hydrodynamic-biogeochemical model, with the most recent catchment forcing: GBR4_H2p0_B3p1_Cq3b, values at −0.5 m depth (CSIRO, DESI, AIMS and BoM, (Herzfeld et al. 2004))	4 km	Daily	● Thermoregulation (Madrak et al. 2016) ● Tolerance of a range of temperatures (Chambault et al. 2016) ● Juveniles have fidelity to feeding sites where temperature is stable (Musick and Limpus 1997) ● Previously found to have no effect due to small temperature range at Port Curtis (Shimada et al. 2016a)	Custom R script to query the eReefs server, extracting a value of each of the variables at −0.5 m depth, the nearest latitude and longitude, and matching date
Salinity (‰)				● Chronically high values would affect primary producers, but at this study site runoff moves out of the harbour away from the seagrass beds (Shimada et al. 2016a) ● Green turtle tolerance of a range of values (Chambault et al. 2016)	
Turbidity (Secchi depth in m)				● Counterintuitively, as turbidity increases, Secchi depth decreases ● Chronically high values of turbidity would affect primary producers, but at this study site sediment from runoff moves out of the harbour away from the seagrass beds (Shimada et al. 2016a)	
Seagrass nitrogen (concentration of nitrogen biomass in seagrass per m^2)				● Represents a foraging resource (Lamont et al. 2015; Hays et al. 2018; Seminoff et al. 2002)	
Bathymetry (m)	Project 3D-GBR (Beaman 2017)	100 m	Static	Related to benthic habitat, structure and food availability (Whiting and Miller 1998)	Extracted from raster pixel each location falls within

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Table 1 (continued)

Covariate	Source	Spatial resolution	Temporal resolution	Examples of relationship to green turtle movement	Append method
Tide height (m)	Gladstone tide gauge (Australian Bureau of Meteorology and Queensland Department of Transport and Main Roads, https://www.data.qld.gov.au/datas et/gladstone-tide-gauge-near-real-time-data/resource/7337fa8d-31f9-4056-a669-820c27e33f6a)	–	10 min	Tides provide intermittent access to intertidal habitat, passive transport (Pillans et al. 2021; Whiting and Miller 1998; Senko et al. 2019; Brooks et al. 2009) In Port Curtis currents are primarily tidal	Estimated at each location accounting for differences in time between tide readings at gauge and location with the depthfilter function of the SDLfilter R package
Tide phase	Calculated from Gladstone tide gauge data (above)	–	1 h	Tides provide intermittent access to intertidal habitat, passive transport (Pillans et al. 2021; Whiting and Miller 1998; Senko et al. 2019; Brooks et al. 2009) In Port Curtis currents are primarily tidal	Identified high and low tides from 10 min tide readings from the Gladstone tide gauge (above) with the HL.NL() function from the VulnToolkit R package (Hill and Anisfeld 2021). We assigned four tide phases; high and low tide were defined as being within 1 h of the high and low tides respectively, outgoing tides were between high and low, and incoming tides were between low and high
Time of day	From timestamp of Fastloc-GPS locations	–	1 s	Related to activity cycles, physiology (Hazel 2009; Hazel et al. 2009; Senko et al. 2010) and visual navigation cues (Shimada et al. 2016b)	Assigned categories to each tracked location; sunrise and sunset inclusive of 1 h either side of sunrise and sunset time respectively, night as between sunset and sunrise, and daylight as between sunrise and sunset Sunrise and sunset times were obtained with the getSunlightTimes() function in the R suncalc (Thieurmel et al. 2022) package
Season	From timestamp of Fastloc-GPS locations	–	3 months	Reflects growth and senescence of primary producers (Holloway-Adkins and Dennis 2017), rain and temperature (Reisser et al. 2013) cycles	Assigned each tracking location with a calendar season
Significant wave height (average of the highest one third of the wave heights in a 30-min wave record, m)	Gladstone wave buoy (Queensland Department of Environment, Science and Innovation and Gladstone Ports Corporation)	Point	Daily	High waves may cause physical damage to shallow primary producers, and cause sediment resuspension	Measured significant wave height extracted at the nearest timestamp

Table 1 (continued)

Covariate	Source	Spatial resolution	Temporal resolution	Examples of relationship to green turtle movement	Append method
Sex (male, female or unidentified)	Laparoscopy during capture (Queensland Department of Environment, Science and Innovation)	–	–	Movement may occur in response to life history cues or intraspecific interactions (Arthur et al. 2008; González Carman et al. 2012; Cardona et al. 2010; Meylan et al. 2011; Chambault et al. 2018; Siegwalt et al. 2020; Bolten 2003)	
Maturity (juvenile, sub-adult or adult)	Laparoscopy during capture (Queensland Department of Environment, Science and Innovation)	–	–	Plasticity of behavioural strategies in juveniles, cohorts exploiting different resources	
Size (curved carapace length)	Measured during capture (Queensland Department of Environment, Science and Innovation)	–	–	Plasticity of behavioural strategies in juveniles, cohorts exploiting different resources	

We determined that a track with data gaps longer than 72 h should be treated as independent tracks, which were partitioned separately. We assessed the frequency distribution of the number of transitions between ARS and transit among the turtles to ascertain whether individuals could be categorised as 'stayers' or 'goers'. We also examined the monthly displacement of individuals, by summing the values of net squared displacement between each tracked location and the turtles release location for each tracked month.

To assess the potential drivers of turtle residence and movement behaviour we conducted a broad literature search and selected environmental covariates that appeared in multiple peer-reviewed research articles as having influenced green turtle distribution, movement, or home range size (Table 1). For example, Blumenthal et al. (2010) found that foraging juvenile turtles move to thermoregulate. Therefore, we obtained a data layer representing surface water temperature for inclusion in the subsequent modelling stage of our analysis (Table 1). In subsequent analyses we tested for pairwise correlations between the covariates and removed one covariate from further analysis wherever a correlation was greater than 0.7. We selected bathymetry (Beaman 2017), temperature, salinity, turbidity (Secchi depth), estimated seagrass nitrogen (*Zostera*, *halophila* and deep seagrass as separate covariates) (Baird et al. 2020; Herzfeld et al. 2016), chlorophyll a (Baird et al. 2020; Herzfeld et al. 2016), tide height (Australian Bureau of Meteorology and Queensland Department of Transport and Main Roads), significant wave height (DESI coastal data system wave buoy) and time of day as covariates of interest (Table 1). Note that we used variables derived from the eReefs model estimated at 0.5 m depth.

We constructed the covariate dataset by appending the value of each covariate pixel to its corresponding track locations. For static variables such as bathymetry, we appended the pixel value at the location of the track record. For dynamic variables, we extracted the pixel values at the location that were closest in time to the track location. For significant wave height and tide height time series data, we appended the value closest in time to the tracked location, adjusting tide data to account for differences in time between tide readings at the gauge and the location using the SDLfilter R package (Shimada et al. 2012). The wave buoy and tide gauge were at up to 160 km straight line distance from the furthest tracked location.

What influences the duration of residency periods (stay)

To investigate environmental conditions that may influence residence time in foraging turtles we developed a cox regression model that determines the effect of a set of environmental covariates on the duration of ARS. We calculated four predictors from the selected environmental

covariates for each ARS segment (a) the mean), (b) peak values (min and max), and (c) changes over time ('delta'). The 'delta' values were calculated as the difference between the first and last values of each covariate in a segment and represent the overall change in condition that a turtle experienced during a segment. We coded each ARS segment as being ARS to transit or ARS-censored, whereby there was no data in the subsequent segment to determine what the turtle did next.

To investigate the effects of the environmental covariates on the duration of ARS we constructed cox regression models. We created a separate cox regression model for each of mean, min, max and delta covariate predictors. This allowed us to avoid including any two predictors ('mean', 'delta', 'minimum', 'maximum') from the same environmental covariate that were correlated with each other in a single model (e.g., mean temperature and maximum temperature were correlated but not included in the same model). Within these groupings, we ran a separate model for every environmental covariate and built up a final model by including those covariates with the highest explanatory power until the inclusion of additional covariates no longer improved the model fit (AICc). We included a frailty term for turtle ID in each model. The frailty term indicates that the effect of the covariates on the duration of ARS varies among the individuals. Cox regression is a semi-parametric method used to determine the effect of a treatment or set of covariates on the time until an outcome occurs, such as survival or death in the context of medical research. The regression coefficient relates to a hazard ratio, or the rate at which the outcome occurs amongst the study subjects. In our study we defined the outcome as the turtle ending ARS according to our track segmentation. If the hazard ratio was close to one, then the covariate had no effect on the duration of ARS, if it was greater than one it was associated with reduced duration of ARS, and if less than one it was associated with increased duration of ARS. We examined diagnostic residual plots to test the assumptions of cox regression: proportional hazards, influential cases and linearity (Fox and Weisberg 2002).

What prompts a turtle to settle or leave?

We selected the locations at the transition between ARS and transit segments (leaving)- coded as 1, and transit and ARS (settling)- coded as 0. We calculated the difference in the value of the environmental covariates between these selected locations and the previous day in the animal's trajectory (the 'change in' value) as well as the difference between the first and last values of each covariate in the segment, 'delta', preceding the change point. The 'change in' values were included as covariates to determine whether cues to leave included short-term changes in conditions experienced by the turtle, which are not represented when data were aggregated into the 'delta' value of longer segments. We tested for pairwise correlations and removed a covariate from further analysis when correlation was greater than 0.7. We built generalised linear mixed effects models with a binomial response in glmmTMB (Brooks et al. 2017) to evaluate the influence of each of the covariates in determining whether an animal initiated or terminated ARS, and combined covariates with the highest explanatory power into the final model until the addition of further covariates no longer improved the model fit (AICc). We tested for linearity and extreme values in the predictors by examining diagnostic plots with the DHARMa simulateResiduals() function (Hartig 2022). We also conducted Fishers F-tests to compare the variability of predictor values at the ARS to transit (leaving), compared to transit to ARS (settling) transition points.

Tidal and diel cycles

To test for effects of tides and the diel cycle, which operate on finer than daily temporal scales, we appended one of four time of day classes (sunrise, sunset, day and night, Table 1) and one of four tide phases (high, low, outgoing, incoming) to the locations at the transition between ARS and transit segments (refer to Table 1). We developed a generalised linear mixed effects model with a binomial response representing transition points (0—settling, 1—moving) in glmmTMB. We assessed model assumptions against diagnostic plots with the DHARMa simulateResiduals() function (Hartig 2022). Our analysis focused on testing time of day, tide phase, season, sex, size and age class as potential fixed effects and included turtle ID as a random effect to account for potentially different responses of individual turtles to the fixed effects. We selected the model with lowest Akaike Information Criterion and tested the overall significance of the fixed effects with a Type-II Wald Chi-square test using the function Anova in R.

Delineation of ARS vs transit habitats

Habitats where ARS occurs are likely to contain essential resources for foraging and resting while transit may have less specific requirements. We therefore created two movement-based kernel density estimates [MKDE in adehabitatHR (Shimada et al. 2019; Benhamou 2011; Calenge 2016)] for every turtle using (1) only ARS and (2) transit locations, yielding MKDEs that delineated where the turtles spent most time performing these two functionally different behaviours. We created an average of the ARS, and of the transit kernels (probability distributions) of all the turtles, with each independent track having equal weight. MKDE produces a utilisation distribution (UD) representing density

of use, for example, an animal can be expected to be found within its 95% UD contour 95% of the time (Benhamou 2011).

Results

We found that turtles varied in the number of behavioural transitions (i.e., between ARS and transit) they exhibited over the time they were tracked. Among 61 turtles, our track segmentation detected a mean of 10.3 transitions throughout their track (range 2–29). All individuals exhibited both behavioural modes and we did not detect any bimodality in the number of behavioural shifts exhibited by turtles, nor monthly displacement of the turtles, indicating that individuals could not be grouped into "stayers" and "goers" (Fig. S1). ARS segments had a mean duration of 21.6 days (range 0–126.2 days) and transit of 33 days (0–96.9 days) (Fig. S1).

Drivers of the duration of residence time

None of the 'mean' environmental covariates significantly affected the duration of ARS segments when tested alone. Changes in the environmental covariates temperature and *halophila* nitrogen over time ('delta'), both had a significant effect on the duration of ARS when tested alone ($\chi^2 = 8.42$, p < 0.01; $\chi^2 = 5.93$, p < 0.05 respectively). However, there was a significant interaction between these two variables ($\chi^2 = 11.96$, p < 0.001; Table S1, Fig. 2) when both were included in a combined model, meaning that the effect of ('delta') temperature on duration of ARS is reduced by the effect of the ('delta') *halophila* nitrogen. Extreme peaks (maximum or minimum) in turbidity and depth led to shorter ARS segments. Extreme peaks (maximum or minimum) in significant wave height and tide height resulted in longer ARS (Table S1, Fig. 2). Milder (higher 'minimum') peak values of *Zostera* seagrass nitrogen resulted in shorter ARS segments (Table S1, Fig. 2). Each of the four combined models (mean, delta, minimum, maximum) also included a significant frailty term for turtle ID. There was no effect of sex, maturity, or size of the turtles on the duration of ARS.

Drivers to settle or leave

A turtle transitioning to transit (leaving) compared to ARS (settling) was significantly positively influenced by change (since the previous day) in Secchi depth (turbidity), depth and negatively influenced by delta (difference between the start and end of the behavioural segment) temperature (Table S2, Fig. 3). Change in depth, which is a static condition, can be interpreted as changes experienced by the animal because they are moving through a heterogenous

environment. Our variable selection process for the GLMM highlighted change in *halophila* seagrass nitrogen as an influential covariate on the probability of leaving but with no statistical significance. The variability of the 'change in', and 'delta' values of temperature, turbidity, salinity, seagrass nitrogen (*Zostera*, *halophila* and deep), chlorophyll a, and depth covariates was higher at transit to ARS transition points (i.e., when turtles decided to settle in a location) compared to the ARS to transit points (i.e., when turtles decided to leave) (Table S3). This was also true for change in significant wave height, but not for delta significant wave height. This may reflect that during transit segments, turtles traverse longer distances and a wider range of habitats and conditions than during ARS.

Tidal and diel cycles

Time of day significantly influenced whether turtles transitioned from ARS to transit, compared to transit to ARS ($\chi^2 = 20.84$, df = 3, P < 0.001). Turtles were more likely to transition from ARS to transit at sunrise or at night compared to during daylight (Fig. 4, Table S4). There was no significant effect of tide phase ($\chi^2 = 0.34$, df = 3, P = 0.95) though movement away from a resident area was somewhat more probable at low tide (Fig. 5). Season, sex, age class and their interactions did not influence the probability of outward transit.

Delineation of ARS vs transit habitats

There was substantial overlap in the areas used for ARS and transit (Fig. 5). However, the averaged ARS UD was considerably smaller in area (50%UD = 9.08 km², 95%UD = 100.79 km²) than that of transit (50% = 174.28 km², 95% = 192.36 km²) (Fig. 5). The ARS 95% UD identified several discrete patches, including some that were not identified in the transit 95% UD, whereas the transit 95% UD indicated more ubiquitous use of the space. Most of the high ARS density areas (ARS 50% UD) coincided with some known intertidal and subtidal seagrass distribution, but also included river mouths and mangrove edges.

Discussion

Our results imply that decisions to move are influenced by short-term (i.e., days) changes in the conditions experienced by the animal. Rather than detecting thresholds of the environmental covariates that prompt staying or moving, we determined that turtles were more likely to stay when delta temperature increased and were more likely to initiate outward transit when turbidity decreased, and they entered deeper habitats. This suggests that ARS activities such as
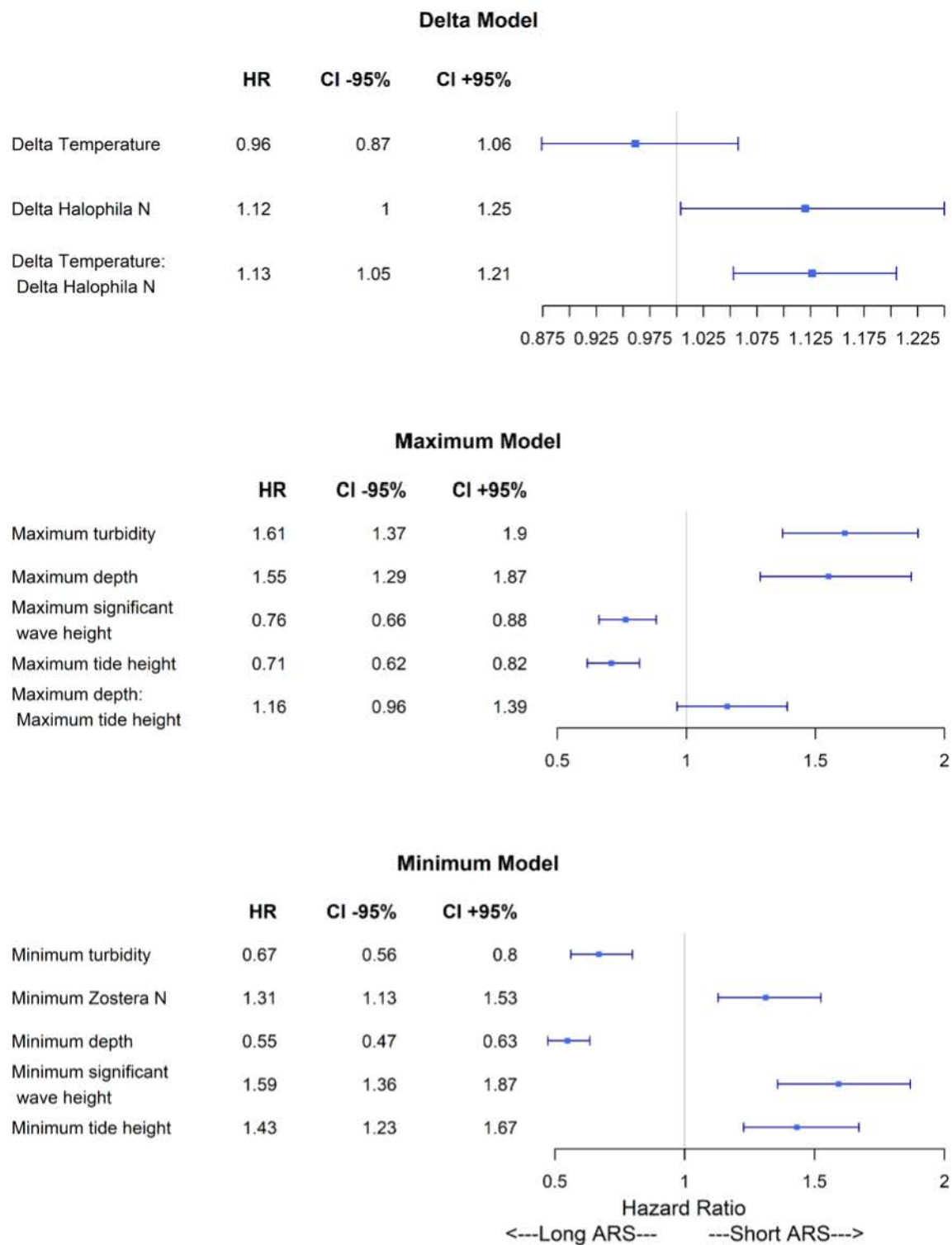
Delta Model

	HR	CI -95%	CI +95%
Delta Temperature	0.96	0.87	1.06
Delta Halophila N	1.12	1	1.25
Delta Temperature: Delta Halophila N	1.13	1.05	1.21

0.875 0.925 0.975 1.025 1.075 1.125 1.175 1.225

Maximum Model

	HR	CI -95%	CI +95%
Maximum turbidity	1.61	1.37	1.9
Maximum depth	1.55	1.29	1.87
Maximum significant wave height	0.76	0.66	0.88
Maximum tide height	0.71	0.62	0.82
Maximum depth: Maximum tide height	1.16	0.96	1.39

0.5   1   1.5   2

Minimum Model

	HR	CI -95%	CI +95%
Minimum turbidity	0.67	0.56	0.8
Minimum Zostera N	1.31	1.13	1.53
Minimum depth	0.55	0.47	0.63
Minimum significant wave height	1.59	1.36	1.87
Minimum tide height	1.43	1.23	1.67

0.5   1   1.5   2

Hazard Ratio

<---Long ARS---   ---Short ARS--->

Fig. 2 Hazard ratios (blue square) from Cox proportional hazards models showing effects of most influential environmental covariates on duration of ARS segments. Horizontal lines are 95% confidence intervals. Any horizontal line that crosses the grey vertical line (the line of null effect) does not have a statistically significant result. The higher the hazard ratio the higher the likelihood of an ARS segment ending (being shorter in duration) i.e., a hazard ratio of > 1 indicates that per unit increase in the covariate, the likelihood of ARS ending is that many times higher (shorter ARS segments). Conversely, a hazard ratio of less than 1 indicates lower likelihood of end of ARS (longer ARS segments). The 'delta' model predictors represent the change over time in the environmental covariates during an ARS segment, while the predictors in the 'minimum' and 'maximum' models represent peak values of those covariates during the segment. The x axis has been scaled to optimise visualisation in each panel separately

Fig. 3 Combined logistic regression model showing the partial effects of the most influential covariates, change in turbidity (Secchi depth), change in Halophila seagrass nitrogen, change in depth (no effect) and delta temperature, on probability of outward travel, showing partial residuals
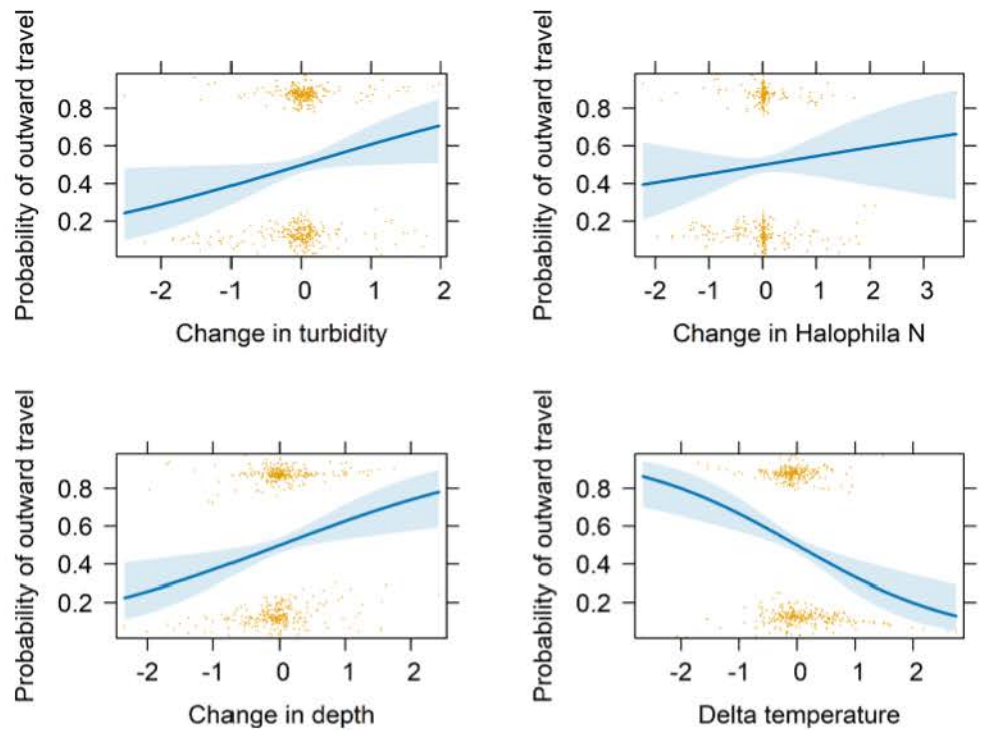
Fig. 4 Fixed effects of generalised linear mixed model comparing probability of outward travel ($\pm$ SE) across time-of-day periods and tide phases
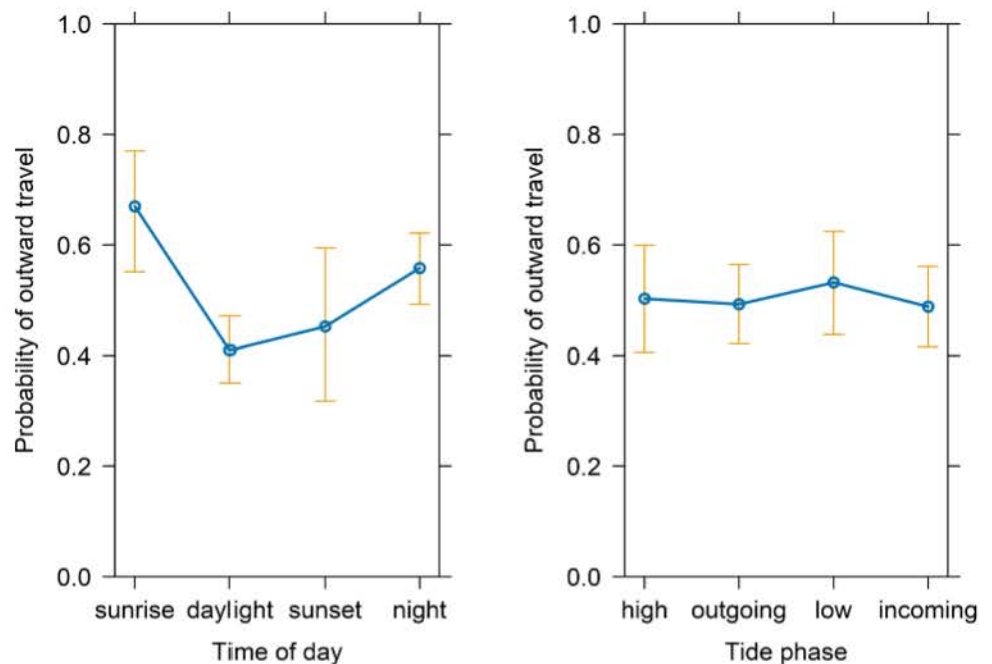
foraging and resting are cued when turtles enter primarily benthic, shallow, warm habitats, while travel is facilitated in deeper, clear water. We determined that all the selected covariates representing changes in conditions experienced by the turtles prior to switching behaviours were more

variable at the transition between transit to ARS (settling) compared to ARS to transit segments (moving), indicating that turtles traversed more space and a variety of conditions during transit compared to ARS.
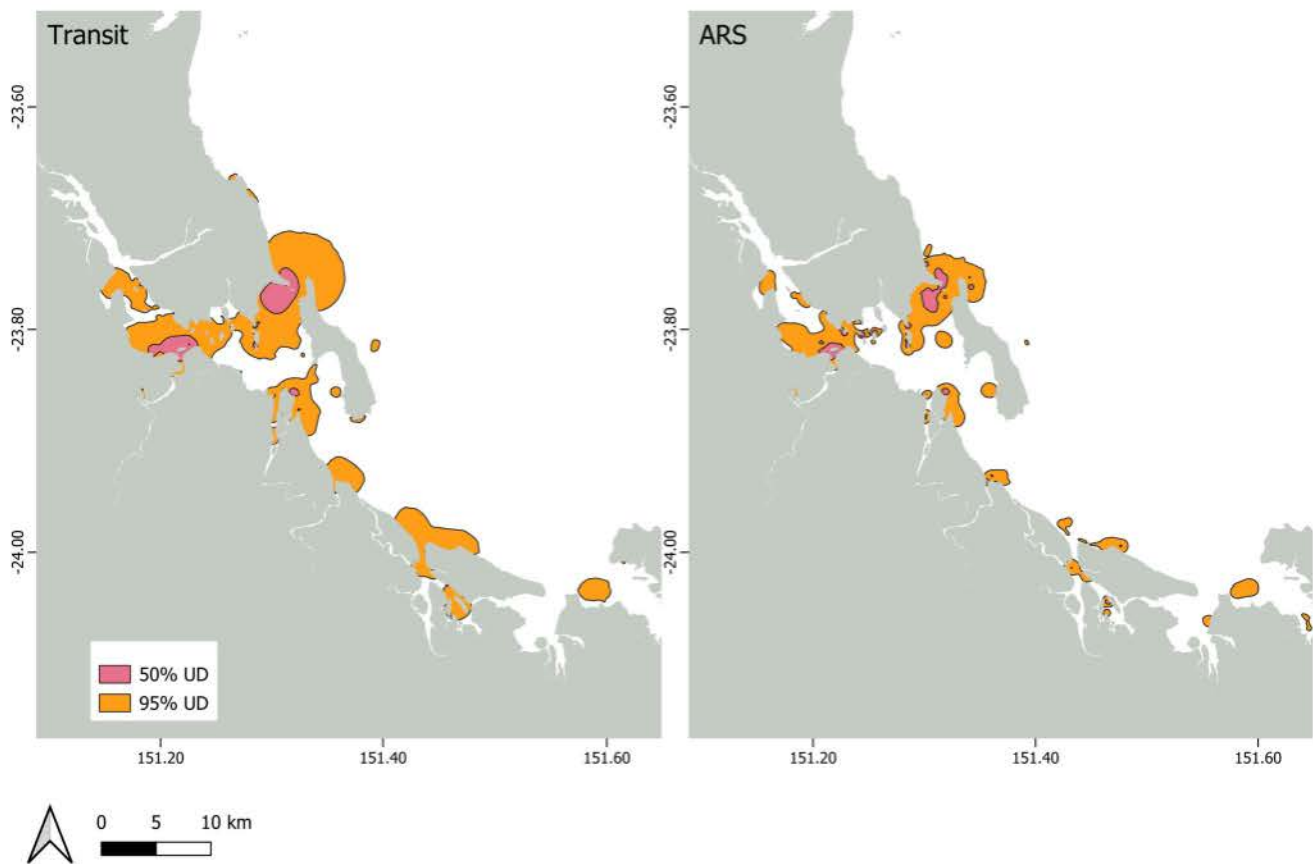
Fig. 5 Map of probability density of occurrence from movement-based kernel density estimates from locations classified as transit (left panel) and ARS (right panel), averaged for all the tracked turtles, outlining the 50% and 95% utilisation distributions

Temperature

Our results indicated that duration of ARS segments was most influenced by temperature, turbidity, and depth. Green turtles seek to occupy warm waters to maintain optimal body temperature (Limpus and Nicholls 2000) and they stayed longer when there was an increase in the temperature they experienced during the ARS segment.

Turbidity

Peaks in turbidity (when the minimum turbidity experienced was very clear or the maximum turbidity experienced was very turbid) were associated with shorter ARS segments. Consistently, our logistic regression demonstrated that when the turbidity decreased throughout the ARS segment (i.e. the water became clearer), the probability of outward transit increased. This suggests that moderately turbid water did not invoke a movement response (Chambault et al. 2020). Similarly, East Pacific green turtles, who consume substantial invertebrate prey, are known to remain foraging in very highly turbid waters. Shallow turbid waters can also support seagrass abundance (Shimada 2015).

Depth

Peaks in depth (moving through very deep or very shallow areas) were associated with short ARS, indicating that ARS habitats are predominantly shallow, but when water is too shallow, for example in intertidal areas which are inaccessible at low tide, turtles must move away. The significant influence of change in depth on transition between ARS and transit indicates that the turtle was passing through a changing depth profile as they were leaving the ARS or transit area.

Time of day

We determined that turtles were more likely to initiate outward travel at sunrise compared to other times of day. Sunrise may represent a visual navigational cue that can be used by turtles for homing and orientation at local scales and facilitate their movement (Limpus et al. 1992; Shimada

et al. 2016b). Similarly, shallow foraging may be preferred during the day, when the risk of being visually identified by potential predators is high, whereas moving through deeper habitats under the cover of darkness is facilitated at night.

We expected to find a strong positive relationship between ARS duration and seagrass nitrogen (concentration in biomass per m^2), however our results showed that an increase in *halophila* seagrass nitrogen discouraged turtles from remaining in ARS and when minimum *Zostera* seagrass nitrogen was low, ARS was long. There was no association between the duration of ARS and deep seagrass variables. The strong spatial relationship between turtle distributions and the extent of seagrass meadows that has been reported elsewhere over large spatial scales (Hays et al. 2018), is not reflected in any apparent association between ARS and seagrass nitrogen biomass in this study. It is notable also that seagrass in the area is often sparse when present, which, in combination with the turbid conditions, inhibits its detection by remote sensing. Thus, representing the distribution of these inshore seagrasses at fine temporal and spatial scales is a major challenge. Nevertheless, our results suggest the turtles tracked in this study area utilised seagrass to differing extents, with macroalgae, mangrove fruits and invertebrate prey items available as alternative food sources (Prior et al. 2016; Limpus and Limpus 2000). Even turtles that reside primarily over known seagrass beds are likely to have multiple diet items contributing to their food intake. We were not able to acquire spatio-temporal data on the availability of these food resources for this analysis. In particular, the distribution of pelagic and benthic invertebrate prey has not been included. Rather than there being clear boundaries between microhabitats, there is likely substantial spatial overlap between benthic food sources for green turtles, including algae, invertebrates, and seagrass. Additionally, in Port Curtis, the availability of different seagrasses is not spatially ubiquitous. *Halophila* spp. dominate in subtidal areas, while *Zostera* and other taxa (e.g., *Halodule uninervis*) occur in interspersed intertidal patches (Erftemeijer and Robin Lewis 2006).

The primary producers that contribute to the diet of inshore green turtles experience natural fluctuations in health and distribution with seasonal variation in temperature and rainfall. Turbidity and physical disturbances from winds and waves exceeding critical thresholds for extended periods are detrimental to these primary producer communities (Erftemeijer and Robin Lewis 2006; Benham et al. 2019; Limpus et al. 2013). For this reason, we expected ARS segments to be shorter when turbidity and significant wave height (mean values) were high, however we did not detect any pattern relating to the mean values of any input covariates and the duration of ARS. We suspect that given the dynamic nature of the site, mean values over the timescale of an ARS segment may not be indicative of site condition,

which is established over longer periods. Therefore, the changes that prompt movement may be occurring on finer temporal scales than the length of ARS segments, and cues arising from low minima, high maxima or change over time are lost when the data are aggregated into means.

The significant frailty terms in our analyses of a broad suite of environmental cues known to influence turtle movement indicated that individuals within the aggregation respond differently to cues to move. Because we did not detect any relationship between age (37 adults, 21 subadults and 5 juveniles), sex (22 females, 22 males and 12 unidentified sex) or size (42.1–116.6 cm CCL) and behaviour, we cannot attribute these differences to life history contexts. It is unclear whether these differences are inherent traits of individuals or plasticity of responses to cues, however there was no evidence of bimodality in the number of behavioural shifts or the mean displacement of the tracked turtles which would suggest cohorts of 'movers' and 'stayers'. However, as the animals were sampled at several micro-habitats throughout the Port and in different study years, all the turtles experienced different sets of conditions during their tracking period. This may mask the effects of specific local conditions on the subset of tracked turtles experiencing them. For example, though tides did not appear to affect the probability of outward transit, anecdotally a subset of the tracks demonstrated movements highly correlated to tides (Pillans et al. 2021). Tidal change is likely unimportant for outward transit during neap tides, and where core areas used by turtles are sufficiently deep to allow them to remain at low tide. Individual turtles that forage at different sites within the harbour have been found to have differing dietary preferences (Limpus and Fitzsimmons 2020; Pillans et al. 2021; Limpus et al. 2013). Whether dietary differences represent inherent inter-individual differences cannot be determined because different diet items were not uniformly available for the tracked turtles in space or time. A diversity of strategies within a green turtle foraging aggregation may indicate resource partitioning, with some turtles utilizing different habitats and their associated foraging resources (e.g., mangrove edges, intertidal or subtidal seagrass, pelagic prey animals). These habitats would each require differing movement patterns to exploit their resources, for example intermittent access to intertidal seagrasses is facilitated at high tide. Similarly, foraging dichotomy has been observed in loggerhead turtles (McClellan et al. 2010). There may be different drivers for different types of movement. Examples of contexts that shape differing strategies include turtles that revisit a preferred refuge site apart from the location of their forage. This represents a movement between feeding and resting or predator avoidance. In this example, our analysis would have detected the turtle as having short ARS and transit segments, even though they were resident to a single area. Turtles performing short forays from a primary foraging site

may be undertaking exploratory movement of the broader area, prior to long-range departures from the site, consistent with the developmental migration hypothesis. It is likely that this employment of a diversity of strategies contributes to the resilience of populations to dynamic conditions because boom and bust of a particular resource does not uniformly affect the aggregation. The next step to untangling intraspecific behavioural differences could be to investigate the consequences or advantages of different behavioural strategies on growth rate, survival, breeding rates and emigration rates, however we were not able to address this with the present dataset.

This study highlights the utility of employing multiple freely available datasets (eReefs, Queensland government and Gladstone Ports Corporation meters) to enhance the outcomes of research findings. The strength of our results is constrained by the margins of error of the input covariate data including outputs of the eReefs model. The size of the error margin differs for each covariate. We acknowledge this as a limitation in our study but retained these inputs as the best currently available at this spatial and temporal scale. The data we extracted from the GBR4 model has 4 km pixels, at daily resolution. Our analysis assumes that the daily resolution is fine enough to capture variations in environmental conditions that occur on the timescale of changes between the ARS and transit segments, and that transit movements are large enough to traverse grid cells. The analyses presented here assumed that turtle occurrence corresponded with surface conditions at each location and time, though we acknowledge that turtles occupy three-dimensional environments. Additionally, this study does not encompass all potential sources of disturbance that may prompt a turtle to move. For example, at low tide, subtidal water in the harbour may be less than 3 m deep, providing limited refuge from recreational vessel traffic. During fieldwork, we observed that turtles in shallow water moved when a passing vehicle churned the bottom. These fine-scale movements were not captured in our analysis. Anthropogenic drivers of movement may also include hunting of turtles in shallow areas (Limpus pers. Comm.).

Understanding when and where turtles are likely to move in relation to current environmental conditions enables extrapolation of how they may respond to future changes and enhances our ability to assess and manage risk (Dalleau et al. 2019). For example, the probability of outward travel is highest at sunrise, at which time human activity (i.e., recreational boating) is typically higher than at night. We determined that though there was substantial overlap between ARS and transit areas, the transit UDs were larger in area. More movement over larger areas at sunrise may mean turtles are more likely to traverse and interact with human activities. Importantly, individuals may differ in their response to environmental conditions, with some remaining in place while others move. Turtles do not always move in response to disturbances, particularly when there is a delay in how that disturbance affects the quality of their habitat (Lamont et al. 2021). If foraging habitats become degraded and turtles do not adapt, populations may be affected [e.g., less females will come into breeding, juvenile growth rates will be constrained, foraging turtles may be emaciated and in poor health resulting in increments of strandings (Meager 2016; Meager and Limpus 2014)]. Nevertheless, foraging site fidelity is considered a favourable strategy under unpredictable environmental conditions (Switzer 1993). This study identified core areas for ARS and demonstrated that transit is occurring in and around these core areas. Turtles may be moving between intensively used areas when conditions at one location are less favourable for foraging and resting or for predator avoidance. Being able to identify areas and times of high use is important because pressures on turtles are not uniformly distributed in space and time (MacDonald et al. 2013). Having an improved understanding of the spatio-temporal patterns of these animal's behaviour can be used to minimize their exposure to risks through dynamic and adaptive planning. For example, this study established that some individuals will likely move when turbidity is very high, and temperature drops. Implementation of temporary go-slow zones with buffers around ARS habitats following major flood events or during planned dredging could reduce the exposure of turtles to recreational vessel strike.

Conclusion

Green turtles in foraging grounds experience cues to move that include changes in the temperature, turbidity conditions they experience and depths they move through. Individuals within foraging aggregations respond differently to these cues. A diversity of movement strategies might improve the populations' resilience to dynamic conditions. This study highlights how local scale changes might affect the suitability of foraging habitat for turtles, and how they may respond to future changes, which can inform implementation of dynamic adaptive management interventions.

Declarations

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