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# Fine-scale movement of green turtles in modified foraging habitats

Submitted by

**Emily Grace Webster**

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# Statement of the Contribution of Others

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# Outputs produced during PhD candidature

## Peer-reviewed journal articles

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

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## Technical reports

Webster, E.G., Hamann, M., Limpus, C.J. (2022) Report on habitat use by green turtles tracked in the Wiggins Island area of Port Curtis 2021-2022. Report produced for Eco Logical Australia, August 2022, 23 pp.

Webster, E.G., Hamann, M., Limpus, C.J. (2020) Report on habitat use by green turtles tracked in the Wiggins Island area of Port Curtis 2019. Report produced for Eco Logical Australia, June 2020. 20 pp.

Webster, E.G., Hamann, M., Shimada, T. and Limpus, C.J. (2020) Chapter 4, Habitat use and site fidelity- analysis of 73 GPS satellite telemetry deployments 2010-2019. In Limpus, C.J. and FitzSimmons N.N. (2020) Increasing the understanding of the green turtle population in Port Curtis, 2016-2019. Brisbane: Department of Environment and Science, Queensland Government. Report produced for the Ecosystem Research and Monitoring Program Advisory Panel as part of Gladstone Ports Corporation Ecosystem Research and Monitoring Program, April 2021. 32 pp.

Limpus, C.J., Hamann, M. and Webster, E.G. (2020) DES aquatic threatened species program GBRMPA funded loggerhead turtle satellite telemetry: 2019-2020. Report produced for GBRMPA, August 2020. 7 pp.

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# Abstract

An understanding of habitat use by wildlife in space and time informs effective conservation, particularly where space and natural resources are shared by wildlife and humans. Developing this understanding requires establishing where animals are, why they move, what their resource requirements are and how they interact with threats. In coastal Queensland, threats to marine turtles include modification of coastal habitats to support the expansion of human populations, direct interactions between wildlife and human activities (e.g., vessels, infrastructure, fishing, marine debris), and impacts of climate change, such as increasing severity of weather events, affecting the physical and ecological characteristics of the environment. Since the 1980s satellite telemetry and other remote sensing data collection technologies have allowed monitoring of turtles in their in-water environments to elucidate their habitat use and inform management of these protected species.

For marine turtles globally, nesting females are the most well-studied cohort because finding and accessing nesting beaches to observe them is generally straightforward. Nonetheless, marine turtles spend most of their lives in water, and most of all, in foraging habitats. Several species, including the green turtle *Chelonia mydas,* have strong fidelity to foraging sites. Upon reaching a certain age and size, green turtles recruit to neritic foraging areas, and though home range size is somewhat variable across regions, typically turtles occupy confined foraging ranges across decades. Mature turtles then return to those areas between breeding migrations. There is evidence to suggest that individual turtles may persist in their foraging range irrespective of natural or anthropogenic disturbances and, if artificially displaced, will return to it. Foraging grounds are frequently inhabited by mixed sex and size cohorts. Thus, an ecological understanding of the foraging periods of green turtles and safeguarding of existing foraging habitats are important considerations for broader species management.

Satellite telemetry is among the more commonly adopted methods for studying marine turtles in water. However, satellite-linked GPS and ARGOS devices are costly, limiting attainable sample sizes, and often fail over time, which limits their ability to collect data over long periods. Consequently, obtaining enough data to make population-scale inferences regarding habitat use is a common challenge. This thesis investigates fine-scale movement of foraging green turtles using a large GPS tracking dataset consisting of a total 109 individuals across three study locations and spanning from 2010-2021 with an average tracking duration per turtle of 139 days. Using green turtles as a focal species, I discuss some of the challenges of conserving protected species in habitats that are susceptible to natural and human-mediated changes.

In Chapter 1 I provide a synthesis of the direct and indirect anthropogenic threats facing green turtles at a global scale. I introduce global research trends, highlighting that limitations in study methods contribute to a bias to study of nesting females, despite the importance of in-water life stages. Focussing on the genetic stocks residing in Queensland waters, I summarise the current state of knowledge about the threats and in-water ecology of green turtles. I introduce satellite telemetry as a potential tool to address some of the established knowledge gaps for the species and set out the conservation and research contexts in which my study sits.

My thesis provides evidence to reinforce that foraging site fidelity is a predominant strategy in coastal foraging aggregations and describes intraspecific variability in movement behaviour. To achieve this, in Chapter 2 I consolidated satellite tracks for 72 green turtles, collected by multiple entities over 8 years at seven sites within a large multi-commodity port contributing to an ecological monitoring initiative (the Port Curtis Ecosystem Research and Monitoring Program) that aims to minimize impacts of planned developments on the marine environment. I determined the minimum number of satellite-tracked green turtles required to represent spatial distribution patterns in the foraging ground and evaluated the factors underpinning differences in range size and site fidelity. I calculated the percentage overlap between pairs of seasonal range areas as a measure of short-term site fidelity. I conducted a mechanistic range shift analysis to detect significant deviations from range residency behaviour. Green turtles exhibited spatially confined ranges and remained faithful to their foraging area for periods of up to 260 days. Range size was significantly different between microhabitats and study years. Only 16 individuals (22% of tracked turtles) performed significant range shifts, indicating that occupied areas represent important habitats, and most turtles are unlikely to adjust their space-use in response to anthropogenic or natural disturbances. Although this dataset represents an atypically large sample of satellite tracked individuals, representative data were obtained at only two key sites. This study highlights the importance of evaluating clear objectives when sampling animals for satellite telemetry studies to obtain representation of sites, periods of interest, or age and sex cohorts.

While Chapter 2 determines that foraging green turtles are typically range residents, some individuals exhibited high mobility at either large or fine scales. In Chapter 3 of my thesis, I re-examine the tracking data from Port Curtis, including an additional 10 tags deployed there by CSIRO in 2010 (n=80) and report on five (6.25%) green turtles tracked to alternative foraging grounds further than 80 km away. I explore potential environmental cues that may explain long-range movements of these foraging individuals. In over 50 years of region-wide mark recapture programs and more recent satellite telemetry studies, less than 0.18% of recaptured individual green turtles, immature or adult, have been recorded using more than one foraging site. For the five tracked individuals, maximum displacement from deployment at the capture site exceeded that of any other non-breeding tracked turtles. I hypothesised that unstable habitat conditions, driven by frequent floods, may prompt a few individuals to risk relocation to a new site or forage across a broad area. The temporal coverage of our tracking dataset was insufficient to conclusively demonstrate a direct effect of flooding events on long-range movements. However, long-range movements appear in both this study and in unpublished tracking data from Great Sandy Strait in southern Queensland at the mouth of the Mary River. I did not detect changes in space-use by nonbreeding turtles in relation to the timing of major weather events at Port Curtis. Instead, extreme weather events, including floods, are linked to dietary shifts, poor health and uptake of inorganic pollutants by turtles, indicating they scarcely move in response to floods. In the last decade, the increased frequency of extreme weather has coincided with coastal infrastructural expansion. Understanding this changing landscape and the potential exacerbation of climate effects by anthropogenic activities is pertinent to managers at this and other coastal sites when considering thresholds for environmental compliance, sustainability of industrial practices and approaches to future development.

While Chapter 3 explores the potential environmental drivers of long-range movements of a few foraging turtles, Chapter 4 explores what might drive mobility at fine scales. Foraging animals move through the environment to satisfy their requirements for food, rest, reproduction, and risk avoidance. Understanding how these animals respond to changing environmental conditions can help to characterise favourable habitats and determine whether they might be motivated to depart when those habitats become unsuitable. In Chapter 4 I developed an analysis of 61 green turtle tracks from Port Curtis 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", at local scales. 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. I also determined that individuals within the green turtle foraging aggregation respond differently to environmental cues to move and hypothesised that a diversity of strategies within a foraging aggregation could confer its resilience to disturbance events. Chapter 4 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.

In Chapter 2 of my thesis, I established representative foraging distributions for Port Curtis at two monitored sites. In Chapter 4, I identified some of the environmental factors that encourage residency behaviour, associated with foraging and resting. A detailed foraging distribution of the species is not established at a regional scale. In Chapter 5 I develop telemetry-based habitat models with boosted regression trees to identify the environmental characteristics underpinning foraging habitat suitability for green turtles in the Great Barrier Reef region. I fit models to green turtle Fastloc GPS tracks from both modified (Port Curtis) and unmodified (Shoalwater Bay and sites settled to by post-nesting females from Raine Island) inshore foraging sites and using two types of pseudo-absences (background sampling and simulated correlated random walks). Different diet items and physical characteristics underpin turtle presence at modified compared to unmodified sites. I assess model performance by the ability to predict known foraging areas and compare the explanatory power (percent deviance explained) and predictive skill (Area Under the Curve) of the models. I then use the chosen model to predict potentially suitable foraging areas for green turtles in the Great Barrier Reef region. Between 2010 and 2022, the total area of suitable habitat declined, with nearshore areas becoming less suitable over time. 50% of the predicted suitable habitat fell within Habitat Protection Zones, and 19% in Marine National Park Zones of the Great Barrier Reef Marine Park. Identifying which biophysical drivers are most important to predict foraging habitat could inform modelling efforts in less data rich regions in Australia and overseas, noting however that extrapolation of models to other regions or times outside of the sampled environment may not be appropriate or reliable. Evaluating changes over time in habitat distribution provides insights into the degree to which broad-scale environmental changes and anthropogenic activities influence the condition or function of habitats, even within protected area boundaries.

Lastly, the General Discussion presents recommendations for future research and approaches to management of foraging green turtles in Queensland, supported by the findings from the data chapters. My thesis aims to target established knowledge gaps from the Port Curtis Ecosystem Research and Monitoring Programme and the Queensland Marine Turtle Conservation Strategy. Leveraging multiple freely available datasets in a data-rich region of the world, I contribute new information about the foraging ecology of the species. The approaches developed in this thesis can inform movement ecology studies for other species and in less data-rich parts of the world.

The overarching goal of this work is to develop a useful output for site managers. Our predictions of green turtle foraging habitat distribution imply that despite a high degree of protection within the Great Barrier Reef Marine Park, foraging habitats are susceptible to changes in both distribution and extent. Considering foraging site fidelity, substantial benefit is afforded to individual turtles that reside within protected area boundaries. However, due to the expansiveness

of the distribution of low-density foraging habitats in the region, future initiatives to safeguard foraging turtles should be geared towards maintaining functional habitats.

## Table of Contents

## List of Tables

# List of Figures

# List of Abbreviations

| | |
|---|---|
| AICc | Akaike's Information Criterion (correlated) |
| AIMS | Australian Institute of Marine Science |
| AKDE | Autocorrelated Kernel Density Estimate |
| ARS | Area Restricted Search |
| AUC | Area Under the Curve |
| BE | Boyne Estuary |
| BIA | Biologically Important Area |
| BOM | Australian Bureau of Meteorology |
| CCL | Curved Carapace Length |
| CI | Confidence Interval |
| CMR | Capture-mark-recapture |
| coef | Coefficient |
| CRW | Correlated Random Walk |
| CS | Coral Sea |
| CSIRO | Commonwealth Scientific and Industrial Research Organisation |
| DCCEEW | Department of Climate Change, the Environment, Energy and Water |
| DETSI | Queensland Department of Environment, Tourism, Science, and Innovation |
| df | Degrees of Freedom |
| EEZ | Exclusive Economic Zone |
| EFI | Ecology Fine Inorganics |
| ENSO | El Niño Southern Oscillation |
| EPBC Act | Environmental Protection and Biodiversity and Conservation Act |
| ERMP | Ecosystem Research and Monitoring Program |
| FGPS | Fastloc - Global Positioning System |
| GBR | Great Barrier Reef |
| GBRMP | Great Barrier Reef Marine Park |
| GBRMPA | Great Barrier Reef Marine Park Authority |
| GBRWHA | Great Barrier Reef World Heritage Area |
| GIS | Geographic Information System |
| GoC | Gulf of Carpentaria |
| GPC | Gladstone Ports Corporation |
| GPS | Global Positioning System |
| IUCN | International Union for Conservation of Nature |
| IUCN SSC | International Union for Conservation of Nature Species Survival Commission |
| JCU | James Cook University |
| LNG | Liquid Natural Gas |
| MKDE | Movement-based Kernel Density Estimate |
| MP | Movement Persistence model |
| MRSA | Mechanistic Range Shift Analysis |
| NCL | New Caledonia |
| nGBR | northern Great Barrier Reef genetic stock |
| PB | Pelican Banks |
| PTT | Platform Terminal Transmitter |
| QI | Quoin Island |
| QTCP | Queensland Turtle Conservation Project |

| | |
|---|---|
| RIRP | Raine Island Recovery Project |
| RMU | Regional Management Unit |
| SE | Standard Error |
| SELTMP | Social and Economic Long-Term Monitoring Program |
| sGBR | southern Great Barrier Reef genetic stock |
| ST | South Trees |
| TED | Turtle Excluder Device |
| TPR | True Positive Rate |
| TropWATER | Centre for Tropical Water and Aquatic Ecosystem Research |
| TSS | True Skill Statistic |
| UD | Utilisation distribution |
| VAN | Vanuatu |
| WB | Western Basin |
| WBDDP | Western Basin Dredging and Disposal Project |
| WCI | Wild Cattle Island |
| WI | Wiggins Island |

# Chapter 1: General introduction

Human populations increasingly encroach on wildlife and their habitats. Coastal habitats in particular face direct pressures from modification caused by expanding human activities, and indirect pressures from climate change (3), including changes to physical environmental characteristics such as temperature profiles (4–6), and ecological processes; food webs (7), water quality (5,8) and severe weather events (9–11). Effective and sustainable management of changing coastal habitats and their component biota requires a detailed understanding of the way animals use them (12,13). This includes answering questions such as: what characterises good habitat? What are the inhabitants' resource requirements? Where are the animals? How motile or faithful are they to these areas? And what prompts changes to their habitat use? Answers to these questions provide insight into how animals might respond to changing conditions including future population resilience. Detailed understanding of habitat use by animals can also be used to delineate the overlap between human activities and animals in space and time, as a first step in assessing risks to them from anthropogenic activities (14–16). Fortunately, continued technological advancements mean the collection of detailed spatio-temporal information on coastal wildlife and their habitats is increasingly efficient, accurate and frequent. For example, combining data streams from tracking devices that collect detailed information about the location and behaviour of wildlife in space and time, and environmental sensors, both remote and in situ, which provide information on habitat condition and change, can be used to draw ecological conclusions. These may include identifying environmental drivers of behaviour, habitat preferences or likely responses to environmental change. To achieve conservation outcomes, identifying knowledge gaps with conservation practitioners, and other stakeholders (in both the wildlife and the habitat) ensures that studies target questions that are key to management.

To explore the way wildlife uses increasingly modified coastal habitats, my thesis leverages a diverse range of data sources, including tracking data and remotely sensed data. I study the green turtle, *Chelonia mydas,* because they are residents to spatially constricted neritic foraging areas over decades, meaning that modifications to these habitats will likely affect their health, growth, and survival. In light of anthropogenic coastal expansion, upholding the ecological, cultural, and economic value of green turtles requires management of shared spaces. I examine how historical and new animal tracking and environmental datasets from multiple sources can be analysed to answer questions identified by state government, and a partnership between research and industry to inform effective management of a protected marine species in heavily modified foraging habitats.

## 1.1 Ecology and conservation of green turtles

### *1.1.1 Global research trends*

The current state of knowledge of marine turtle biogeography is coloured by geographical biases. Access to, and observation of, turtle nesting beaches is relatively uncomplicated compared to in-water habitats. This means that nesting females continue to be the most studied age and sex cohort represented in the sea turtle literature (17,18). Nesting beach studies contribute to an understanding of population trends (19–21), female breeding biology (e.g., 1,22–24), physiology (e.g., 25,26), embryology (e.g., 27), temperature dependent sex determination (e.g., 25,28), and adult and hatchling behaviour (e.g., 29,30). Some nesting populations are more extensively studied than others, namely sites close to human population centers and in developed countries (18). Knowledge of in-water biology including morphology, growth, physiology, diet, health, habitat selection and migrations of sea turtles is steadily growing, supported by new methods and technologies.

### *1.1.2 Global distribution*

The green turtle, *Chelonia mydas,* is circumglobally distributed in tropical, subtropical and temperate waters. This long-lived migratory species has a complex life history, utilising diverse foraging and breeding habitat at different life stages. Hatchlings and post-hatchlings inhabit pelagic oceanic waters, while larger juveniles to adults live in nearshore environments including seagrass meadows, algal pastures, coral and rocky reefs, estuaries, and rivers (31,32). Adults migrate up to thousands of kilometers to reach their natal breeding and nesting areas (33,34). The species is globally classified as endangered (35). Decades of illegal and legal harvest by humans for green turtle meat and eggs have led to declines of green turtle subpopulations in all ocean basins including at several of the historically largest and most important rookeries (36–38). The global trend for the species is declining, based on numbers of nesting females at index sites (35). Though some populations are showing significant recovery in response to protective legislation and conservation efforts, these efforts rely on an understanding of species biology, threats and trends in abundance (39). Species listings for marine turtles tend to rely on trends in the numbers of nesting females at index rookeries, and in many locations the size, composition and trends in abundance of known foraging aggregations has not been quantified.

### *1.1.3 Human-mediated threats to green turtles*

Climate change, in combination with the expansion of human populations, contributes to globally significant extinctions of megafauna (40). Climate change will alter the distribution of megafauna by reducing the availability of habitat and shelter, changing the distribution of food resources, and changing the physical environmental characteristics that influence their physiology

(41). Coastal species are at risk worldwide. Green turtles are particularly susceptible to these impacts. For example, increasing sand temperatures during incubation at nesting beaches have been shown to produce predominantly female hatchlings, while extreme temperatures can be lethal (42–44). Sea level rise contributes to loss of viable nesting habitat at existing nesting sites (45). Ocean acidification, runoff and increasing frequency of servere weather events (46,47), produce changes in marine food webs and changes to community composition and distribution of seagrass meadows (48,49) and coral reefs (50,51).

In addition, direct anthropogenic stressors on wildlife and their habitats reduce resilience to climate change impacts (26). Globally, the expansion of coastal development to accommodate elevated human population growth in coastal areas has led to increased overlap between human activities and wildlife habitats (52). Coastal development, which involves altering natural coastlines for residential, infrastructural, industrial, or agricultural construction, including by land clearing, dredging, land reclamation, or modification of waterbodies, typically generates increased terrestrial and chemical runoff to the detriment of water quality (53–56). Marine turtles are additionally susceptible to ingestion of and entanglement in marine debris introduced into the water column by human activities (57,58). Habitat degradation is identified as one of the primary threats to sea turtles (59).

Generally, there is a paucity of information in the published literature regarding the relationship between industry and marine turtles, especially in foraging environments. Industrial threats include artificial lighting, dredging, boat strike, oil spills, explosive oil platform removal and seismic programs (23,60). Rectifying this gap will take partnerships between industry, government, traditional owners, and research.

Marine turtles are caught incidentially in legal and illegal fishing operations, resulting in injury or direct mortality (61,62). Turtle excluder devices (TEDs) in trawl nets, developed in the 1970s and 1980s, are 97% effective in excluding turtles from trawling gear (63). Injury or death can also be caused by impact from the hull or propeller of moving commercial and recreational vessels, particularly in shallow habitats (64). Turtles may avoid areas with high vessel activity (65).

Green turtle meat and eggs were historically overharvested. Many of the world’s coastal communities still consume them, both legally and illegally. Some populations can recover from historical harvest (36,66), but determining whether or not consumptive use is sustainable is challenging, requiring evaluation of the social, economical and ecological contexts and scale at which the harvest occurs. Data about both turtle populations and the methods and amounts of consumptive use are insufficient in many places to evaluate this (17,67). In Australia, the commercial use was banned in the 1960s, and legal cultural Indigenous use occurs in northern Australia (68).

Diseases in coastal turtle populations are associated with reduced water quality from chemical and sediment runoff from river outflows, and natural seasonal fluctuations in temperature and rainfall (69,70). Common diseases in Australian green turtle populations include fibropapillomatosis, coccidiosis and “soft shell syndrome”. The risk of diseases and pathogens to many green turtle stocks in Australia is unknown (71).

### *1.1.4 RMUs and genetic stocks*

Because the species and its’ populations are geographically widespread, and individuals may traverse thousands of kilometers across jurisdictional boundaries in their post-hatchling stage and during breeding migrations, protections need to be enforced across jurisdictional boundaries (72). Addressing threats to marine turtles is additionally challenging because they are long-lived. The effect of threats at one life stage or in one habitat may not be immediately measurable; population-scale changes arising from threats may take decades to demonstrate an effect. Thus to facilitate conservation actions, a consistent global framework for identifying marine turtle populations was adopted by the the International Union for Conservation of Nature Species Survival Commission (IUCN SSC) in 2010, known as Regional Management Units [RMUs (73,74)]. RMUs are global organisational framework for sea turtle populations which are created based on available biogeographical information such as abundance, genetics and species distribution, and designed to guide species management and conservation (73). Each RMU can encompass multiple genetic populations. As an example, the southwestern Pacific RMU is made up of seven distinct genetic stocks of green turtle, including the northern and southern Great Barrier Reef (nGBR and sGBR) stocks. This is a potential challenge for species management because any changes to a genetic population that comprises relatively low proportions of the RMU, arising from local stressors or chance events, may not be represented in the RMU. For example, though both the Gulf of Carpentaria and Coral Sea stocks are within the southwestern Pacific RMU, their stock population dynamics, nesting and foraging patterns are not well understood. Development of representative management units for marine turtles requires understanding of fidelity to foraging sites, migratory routes and connectivity among green turtle populations.

Green turtle stocks are genetically distinct and considered to be functionally and demographically independent. Cohabitation by multiple genetic stocks is common at foraging grounds, and small amounts of genetic exchange occurs between stocks when males opportunistically mate with females at foraging grounds or along migratory pathways (75,76). However, generally, breeding distributions of genetic stocks are geographically cohesive.

Aligning the scale of jurisdictional boundaries and population units can be tricky. In Australia, several distinct stocks inhabit national waters, and many of these distribute beyond national waters at various life stages. The Australian federal government’s Biologically Important Areas (BIAs) for protected marine species are a national species-level framework that focus on identifying the distribution of important habitats to support decision making and conservation planning. They outline areas used, and when, for reproduction, feeding, migration and resting of marine species protected under the EPBC Act. BIAs are designated by nomination of areas of interest, which are assessed by a panel of subject matter experts and determined by the Department of Climate Change, Energy, the Environment and Water. The current BIA for green turtles does not include foraging areas.

## 1.2 Green turtles in the Great Barrier Reef region of Queensland, Australia

### *1.2.1 Population status, trend and conservation in Queensland*

The green turtle is classified as vulnerable in Queensland (Nature Conservation Act 1992) and Australia (Environment Protection and Biodiversity Conservation Act 1999, Department of Environment and Energy 2016). In Queensland, green turtles pertain to four distinct genetic stocks: sGBR and nGBR, the Coral Sea and the Gulf of Carpentaria stocks (Figure 1). Each stock is named for its localised nesting and courtship areas, but turtles from each stock forage at sites throughout the region.

The sGBR stock was historically depleted by the turtle soup trade 1860-1950, but is showing moderate recovery, and the nGBR stock is severely depleted and showing early stages of decline (71). Except for allowances of indigenous harvest by holders of Native Title rights, the species has been totally protected in Queensland since 1950 (77). Queensland’s capture-mark-recapture (CMR) program has coverage of foraging and breeding habitats for multiple breeding stocks over decades (78). Demography of the sGBR stock is well described. Queensland National Parks and Conservation Parks encompass 90% of sGBR nesting habitat and 97% of eastern Queensland coastal waters are within state or federal protected areas (79,80).

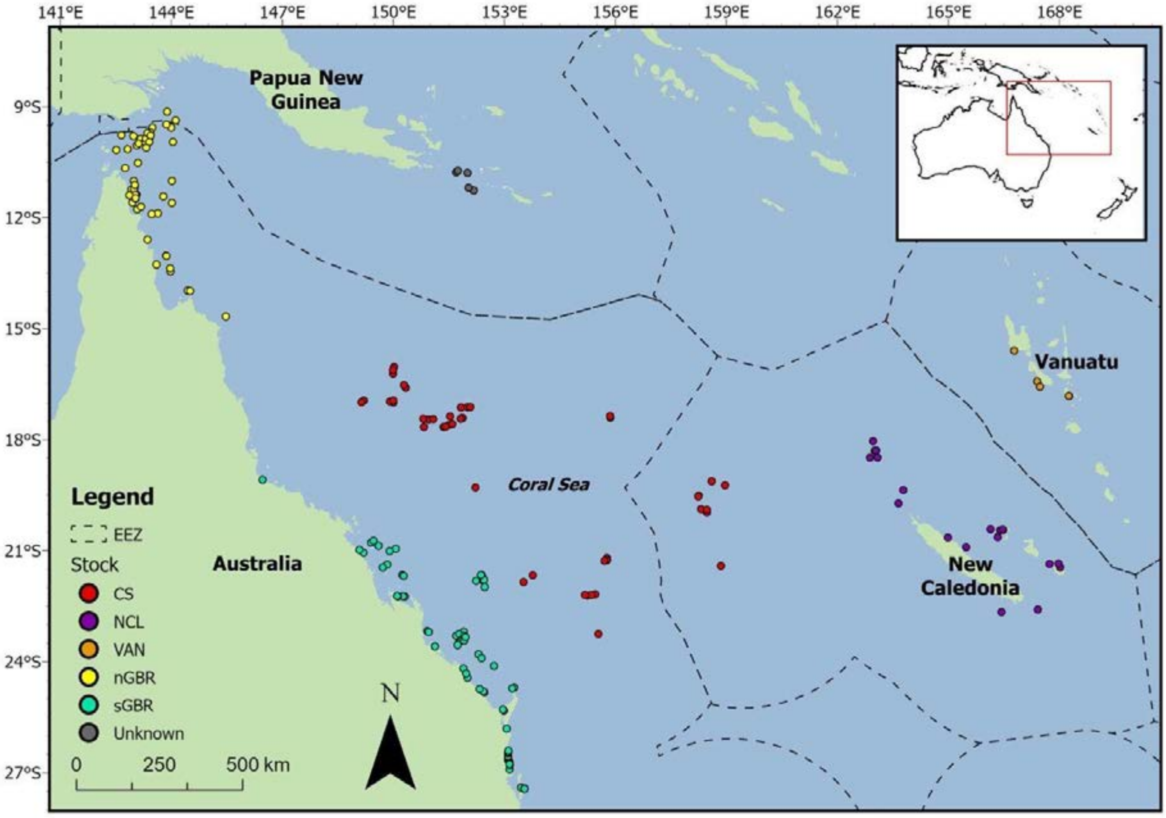
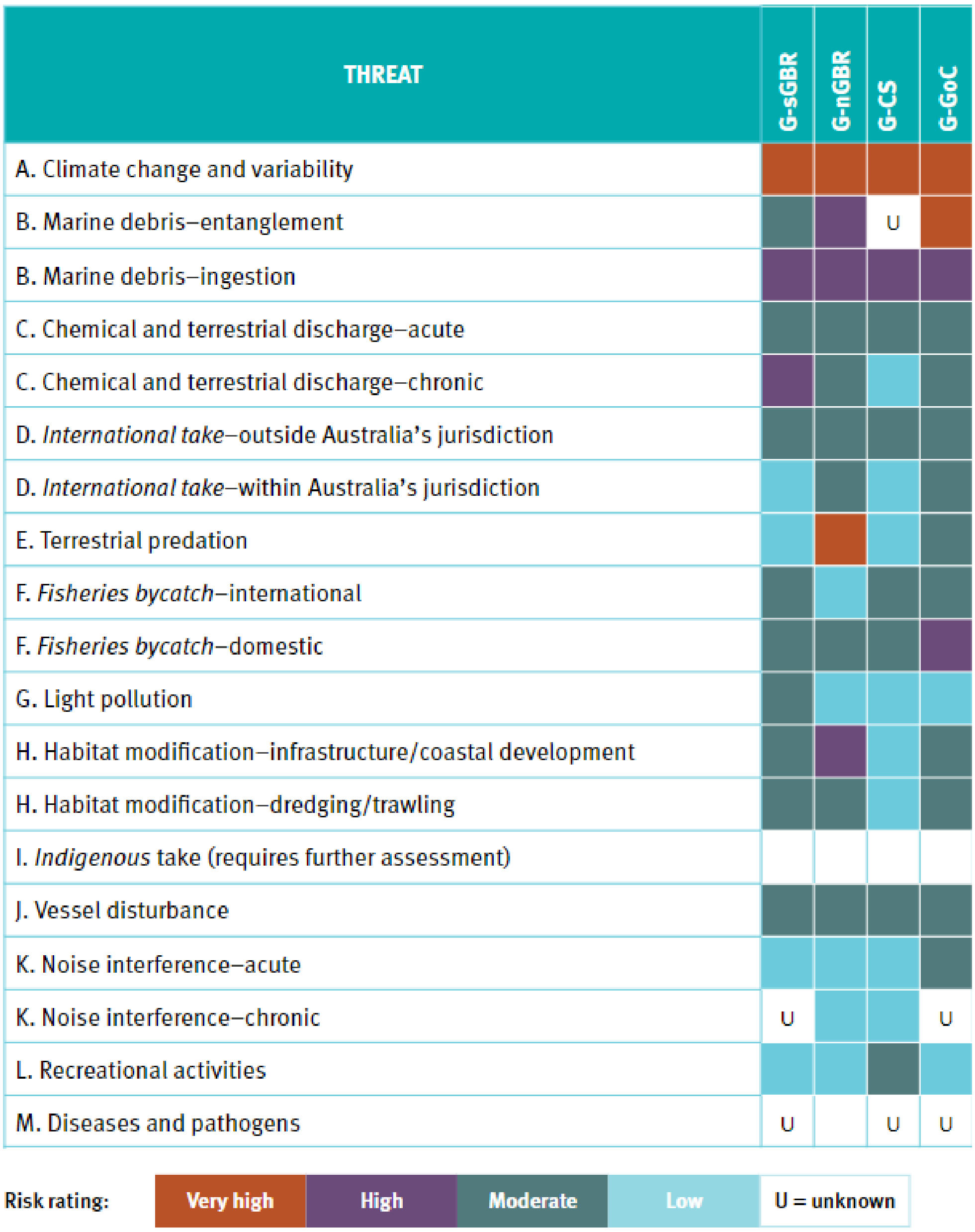


Figure 1 Distribution of known green turtle nesting sites coloured by genetic stocks, including stocks that occupy Queensland waters for foraging and migration. EEZ (exclusive economic zone); CS (Coral Sea); NCL (New Caledonia); VAN (Vanuatu); nGBR (northern Great Barrier Reef); sGBR (southern Great Barrier Reef) - figure also used in the IUCN Red List assessment for green turtles (81).

Climate change and variability present a very high risk to green turtles in Queensland (Figure 2). In Queensland, major flood events lead to dieback and mediate recovery of seagrasses and benthic sessile organisms (82–84). Bleaching events caused by thermal stress on the Great Barrier Reef, cyclones, flood plumes, algal blooms and ocean acidification are major concerns for coral reef habitats (85). In feeding grounds in Australia, other threats include indigenous harvest, marine debris entanglement and ingestion, boat strike and habitat degradation, both by infrastructural and coastal developments, and chronic chemical and terrestrial discharge (23,80,86,87). Indigenous harvest is unquantified but may represent a substantial cause of individual mortality for the sGBR and nGBR green turtle stocks (23). The relative threat and/or sustainability of Indigenous take of eggs and meat on green turtles in Australia is unknown. In Queensland, while diseases like green turtle fibropapillomatosis have at times caused concern, diseases are not generally regarded as a main issue. However, disease is the most important cause of stranding mortalities in inshore habitats, while human related impacts are attributed to only a small percentage of mortalities (69,88,89). In Queensland, most trap-based nets release green turtles alive, and the Queensland government is implementing bans on gill net fishing, meaning fishing-based impacts are less problematic in this region.



| THREAT | G-sGBR | G-nGBR | G-CS | G-GoC |
|---|---|---|---|---|
| A. Climate change and variability | 🟧 | 🟧 | 🟧 | 🟧 |
| B. Marine debris–entanglement | 🟩 | 🟪 | U | 🟧 |
| B. Marine debris–ingestion | 🟪 | 🟪 | 🟪 | 🟪 |
| C. Chemical and terrestrial discharge–acute | 🟩 | 🟩 | 🟩 | 🟩 |
| C. Chemical and terrestrial discharge–chronic | 🟪 | 🟩 | 🟦 | 🟩 |
| D. *International take*–outside Australia's jurisdiction | 🟩 | 🟩 | 🟩 | 🟩 |
| D. *International take*–within Australia's jurisdiction | 🟦 | 🟩 | 🟦 | 🟩 |
| E. Terrestrial predation | 🟦 | 🟧 | 🟦 | 🟩 |
| F. *Fisheries bycatch*–international | 🟩 | 🟦 | 🟩 | 🟩 |
| F. *Fisheries bycatch*–domestic | 🟩 | 🟩 | 🟩 | 🟪 |
| G. Light pollution | 🟩 | 🟦 | 🟦 | 🟦 |
| H. Habitat modification–infrastructure/coastal development | 🟩 | 🟪 | 🟦 | 🟩 |
| H. Habitat modification–dredging/trawling | 🟩 | 🟩 | 🟦 | 🟩 |
| I. *Indigenous* take (requires further assessment) | | | | |
| J. Vessel disturbance | 🟩 | 🟩 | 🟩 | 🟩 |
| K. Noise interference–acute | 🟦 | 🟦 | 🟦 | 🟩 |
| K. Noise interference–chronic | U | 🟦 | 🟦 | U |
| L. Recreational activities | 🟦 | 🟦 | 🟩 | 🟦 |
| M. Diseases and pathogens | U | | U | U |

Risk rating: 🟧 Very high 🟪 High 🟩 Moderate 🟦 Low U = unknown

Figure 2 Summarised risk assessment for Queensland green turtle stocks from page 12 of the Marine Turtle Conservation Strategy 2021-2031 (71); sGBR- southern Great Barrier Reef, nGBR- northern Great Barrier Reef, CS- Coral Sea, GoC- Gulf of Carpentaria

### *1.2.2 Green turtles foraging in Queensland*

Green turtles spend the majority of their lives in foraging areas yet these in-water life stages for the species are relatively under-studied compared to breeding stages. They are year-round residents in their foraging areas (87,90,91), and display high fidelity to them (92,93). Foraging areas provide habitat to green turtle aggregations from multiple genetic stocks (94) and are comprised of individuals from juvenile to adult life stages (77,95). These habitats provide refuge for resting and predator avoidance (96,97), and benthic and pelagic food resources which are required to meet the energetic requirements for breeding (98). Survival, health (89,99), reproductive output (100), and thus population viability depend on the condition of foraging habitats. Below I set out key concepts of the foraging ecology of green turtles as a precurser to understanding factors that may influence their distribution and movement during foraging.

#### 1.2.2.1 Recruitment

Oceanic, planktivorous post-hatchlings recruit to neritic development habitats as juveniles, and undergo a shift toward herbivory (31,101). Recruitment of green turtles to eastern Queensland inshore habitats occurs at size 40-50 cm at ~5-10 years of age (87,102,103). Once recruited to a feeding ground, individuals usually remain there, rather than moving between sites (92). Though generally percieved as predominantly herbivorous post-recruitment, carnivory has been documented for the species in large juveniles and adults in Moreton Bay (101,104) and Raine Island (105) among other locations. There is substantial spatial overlap between developmental and adult foraging grounds.

#### 1.2.2.2 Diet

Green turtle diet is highly variable across foraging sites, somewhat reflecting availability of food resources. In Queensland, green turtles are recorded as consuming a variety of seagrasses (*Halophila ovalis, Halodule uninervis, Zostera capricorni, Halophila spinulosa, Halodule pinifolia, Cymodocea serrulate, Thalassia temprichii, Enhalus acoroides)* and a range of red, brown, and green algae (77,101,102,106–109). At some sites, green turtles consume mangrove roots, fruits and cotelydons (*Rhizophera* and *Avicenia* sp.), though these usually contribute to relatively small proportions of the diet (110). Macroplankton (*ctenophora*, fish and crustaceans) can contribute substantially to an individual diet sample (102). Green turtles may adapt their diet in response to sub-optimal conditions or changes to forage availability. Prior *et al.* 2021 (111) demonstrated evidence of dietary shifts as juvenile turtles exploited different habitat types within the foraging ground. The ability of green turtles to either explore diverse food resources, or be stenophagous, suggests that they are “facultative herbivores” (106). For example, seagrasses dominate diets at seagrass meadows, but macroalgae dominate on algal pastures and rocky reefs such as Heron/Wistari Reefs (112), and parts of Port Curtis (111) and Moreton Bay (31). Turtles may select for young plants and species with higher nutritive values and lower lignin levels (90,106–108,113). *C. mydas* may return to cropped areas of seagrass and feed off nutritionally rich new regrowth (109,114,115). There appears to be no nutritive difference in seagrass compared to macroalgae for growth of green turtles (103). Access to shallow forage is facilitated at high tide (102,112). In Moreton Bay and Shoalwater Bay, turtles forage on macroalgae and mangroves along the banks, and move into deeper gutters and channels on the falling tide (77,110).

In general, the quality of available forage affects growth rates, age to maturity and reproductive output of the species (103). Females must aquire sufficient energetic reserves at foraging grounds to endure long-distance migration and egg production for breeding, taking at least 18 months (22,100) and up to several years to recover between migrations (116).

### *1.2.3 Foraging range*

Green turtles' foraging ranges vary geographically in size (117) and reflect the distribution and community composition of benthic dietary items (92). Foraging home ranges are small in most inshore Queensland foraging habitats, but can vary between smaller than one and greater than 100 km$^2$ (2,109,118,119). There is often substantial variability between the foraging ranges of green turtle individuals at a single site. Differences in size and position of foraging ranges relative to body size are attributed to differential metabolic requirements for some mixed age feeding aggregations (109).

### *1.2.4 Seasonality and diel patterns*

Exothermic marine turtles occupy limited temperature ranges (120,121) or compensate for temperature changes with shifting habitat use (122). Spatial shifts are more likely to occur in temperate regions, where variability in temperature is large (118,123).

Seasonally distinct foraging habitats reflect temporally variable food resources. Winter forage may be sparsely distributed (118,124), while summer forage may comprise of greater species richness. In Queensland, runoff following major weather events in the wet summer months can be detrimental to seagrasses and macroalgae.

Green turtles are active during daylight hours (125). In Queensland, peaks in foraging activity occur at dawn and dusk (126,127). Individuals may use discrete areas in the day compared to at night, reflecting requirements for resting and predator avoidance. (125)(126,127)

### *1.2.5 Site fidelity*

Green turtles have strong seasonal and inter-annual fidelity to foraging sites (92,123,124,128–130). Green turtles may reside in a single foraging area between breeding migrations (109) and across decades (92,94). Individuals rarely shift between foraging sites (59,92,131) and return when artificially displaced (127,132). Individuals will bypass suitable habitats en route to their frequented habitats (92). The benefit of site familiarity is knowledge of seasonal changes, competitors and predation, likely to outweigh the risk of inhabiting unknown sites.

### *1.2.6 Navigation*

It is ultimately likely that sea turtles use a hierarchy of navigational cues (125,133). Geomagnetic cues might facilitate navigation during open ocean migrations with regional accuracy (134–136). Oceanic migrants are also likely to use coarse headings from solar cues (96).

Navigation in feeding grounds enables site fidelity, homing and the detection and acquisition of foraging resources. Within foraging grounds, sea turtles are unlikely to use geomagnetic cues that do not vary substantially on fine scales (127). Green turtles returning to their foraging grounds after being experimentally displaced, performed directional corrections two hours either side of sunrise, suggesting solar cues were instrumental in homing (125).

## 1.3 Tools of the trade – satellite telemetry

Satellite telemetry allows remote collection of biological data at high temporal resolution, facilitating study of in-water life stages of air-breathing marine animals. Satellite telemetry can contribute to the ecological information and species distributions underpinning the boundaries of Marine Protected Areas and management zones (79,137). For example, spatially or temporally-explicit restrictions on fishing and recreational vessels may target areas and times when marine turtles are susceptible to fisheries bycatch and boat strike (64,138). MPAs can be beneficial to sympatric species where range overlap exists (2,139,140). In addition, the effect of specific threats on the tracked animals can be deduced by making inferences about animal fates based on tracking data diagnostics (141,142). Lastly, integrated methodologies and data-sharing help to generate representative samples sizes from tracking data, and to situate the tracks in an ecological context (143,144).

For air-breathing marine animals, locations are acquired and transmitted when the animal is at the surface. ARGOS-linked PTTs (platform terminal transmitters) transmit data to polar-orbiting Argos satellites, which calculate location using Doppler shift and transmit the data remotely. Location accuracy depends on the number of Argos source satellites used to calculate a fix, and the number of signals transmitted. Data are attributed a quality index, where indices 0-3 require a minimum 4 uplinks (3 is accurate to <130m, 2 to 150-300m and 1 to 350-1000m) (145).

Fastloc GPS (FGPS) tags rapidly acquire GPS information from satellites and post-process this data to estimate an animals' position. The location is remotely transferred via the Argos network during a subsequent surfacing event. For locations calculated from > 4 satellites location accuracy is within tens of meters (146). Fastloc tags are more expensive than ARGOS tags, and are typically favoured for fine scale movement and habitat use studies (145,147).

### *1.3.1 Limitations*

Satellite transmitters are financially costly, constraining the sample size that can be attained with them. An artefact of this is that most satellite tracking studies target a single life history stage, at a local rather than population-scale. Researchers must also consider inherrent limitations in tracking data collection, namely that the amount of data received is limited by transmitter failure; battery exhaustion, animal mortality, premature detachment, biofouling, antenna breakage and failure of the saltwater switch (148,149). In addition, tracks provide only an instantaneous record reflecting short-term patterns.

Though attachment of tracking devices of appropriate size does not appear to influence growth, reproduction or survival of sea turtles (150), impact studies are required to determine whether telemetry data is representative of wild behaviour (151).

Utility of tracking data can be enhanced by incorporating information on the environmental and biological factors driving movement and distribution in analyses to generate ecologically relevant findings, overlaying spatial information with information of spatial extent of conservation concerns and emphasising stakeholder engagement in project conceptualisation to develop research that is impact-targeted (152).

## 1.4 Thesis rationale and significance

Protection of marine turtles in coastal habitats supports survivorship and health of turtles themselves but is also beneficial for the health and diversity of coastal ecosystems. Globally, habitat loss is argued to be the most threatening process to marine turtles (59). Turtles that demonstrate high fidelity to foraging areas may have limited resilience to alterations to their residential habitat (118). Understanding of space use, site fidelity and resource requirements is instrumental in evaluating resilience and responses of turtles to habitat changes.

The foraging distribution, particularly of sub-adults, of the nGBR, sGBR and Coral Sea green turtle stocks has not been established. Many important foraging sites may be unknown in both the shallow inshore region and coral reefs (76). Factors influencing fine-scale movement ecology in-water habitats vary regionally (e.g., diet and range size are variable in space and time, as established above). Regionally specific knowledge is missing in some areas, as well as an understanding of what mediates these geographical differences on a larger scale. Intra-specific behavioural variability represents a knowledge gap for foraging ecology for the species. Most importantly, the extent and relative impacts of climate change and anthropogenic pressures (e.g., in industry, exposure to toxicity) on foraging turtles and their habitats, are a challenge to elucidate.

In 2013, the Gladstone Ports Corporation (GPC) completed The Western Basin Dredging and Disposal Project (WBDDP). The project consisted of deepening and widening existing shipping channels in Port Curtis, as well as creating new channels, swing basins and berth pockets. To meet compliance requirements for the Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act), the GPC developed an Ecosystem Research and Monitoring Program (ERMP). The ERMP aims to monitor and manage marine environment of Port Curtis and Port Alma, mitigating potential impacts of the planned and future dredging projects on listed threatened and migratory species and the values of the Great Barrier Reef World Heritage Area (GBRWHA). One specific objective listed under the ERMP is to increase the understanding of green turtle habitat use in the Port Curtis and Port Alma region, using satellite telemetry. When I commenced my PhD candidature, this study had already commenced as a collaboration between James Cook University, Queensland Department of Environment, Tourism, Science, and Innovation, and the Gladstone Port Authority. Sixty-three Green turtles were captured and tracked with FGPS for the ERMP between 2010-2018. During my candidature I deployed a further 10 tags in 2019, and 10 in 2021, funded by Ecological Australia, to help address the objectives of the ERMP.

In addition to addressing the objectives of the ERMP I wanted my thesis to synthesise data into information that could be used for the applied management of green turtles. Tracking data contributes to an understanding of space-use by animals that can be translated into policy in the form of spatial or temporal restrictions of use. In Queensland, a region which affords greater than average protection to sea turtle habitats and where sea turtle populations have been well studied over decades, high quality tracking data can provide strength in advice to policy by determining the extent of interactions between sea turtles and specific threats. To do this, satellite tracks must be representative of a range of sex and age classes, and high-quality environmental data must be available. To broaden the extent of my PhD research to the Great Barrier Reef region, I supplemented the ERMP tracking data with green turtle tracks collected by CSIRO in Port Curtis, JCU TropWATER in Shoalwater Bay and tracks of post-nesting females from Raine Island, as well as multiple freely-available environmental datasets for Chapters 5 and 6. I wanted to enhance the utility of my research by targeting knowledge gaps for the management of the species on a regional scale identified in (71):

- Development of fine-scale mapping and modelling tool to identify and assess the quality of current and potential refugial foraging habitat

- Identify important inshore, shallow foraging grounds
- Recording changes over time in foraging habitat, especially in relation to climate change impacts
- Assess the risk to those areas that are not currently protected and consider the most appropriate mechanisms to ensure protection
- Increasing understanding of the risk to specific turtle stocks from projected climate impacts, including mangrove die-off and increasing frequency of severe weather

Collaboration with stakeholders (Queensland DETSI, GPC, DCCEEW) is key to ensuring their needs are addressed and that findings are presented to them in a useable format (153).

## 1.5 Thesis outline

### *1.5.1 Aims*

The overarching objective of this thesis was to investigate fine-scale movement of foraging green turtles using a large GPS tracking dataset. Specifically, the thesis focusses on three aims:

1. To establish foraging ranges and quantify site fidelity of foraging green turtles
2. To investigate the drivers of their distribution and fine-scale movements
3. To characterise suitable foraging habitat and create dynamic estimates of foraging distribution in the Great Barrier Reef

### *1.5.2 Structure*

In **Chapter 1**, I provide a general introduction to establish the ecological and conservation context in which my thesis is situated, and outline the rationale for my research objectives. I explain general concepts in foraging ecology for the species, current population trends, and threats. I explore how satellite telemetry may be used to target existing knowledge gaps and inform conservation measures.

**Chapter 2** quantifies site fidelity of foraging green turtles and calculates the minimum representative sample sizes from the tracking data. I calculate the seasonal foraging ranges of individual turtles and determine the amount of overlap in turtle space use in successive seasons. I evaluate whether life history traits (size, sex, age) and capture location are related to range size. I conduct a mechanistic range shift analysis to identify range residents and describe several distinct movement patterns exhibited by individual turtles in the foraging aggregation. Associated publication:

> Webster, E.G., Hamann, M., Shimada, T., Limpus, C. and Duce, S. (2022). Space-use patterns of green turtles in industrial coastal foraging habitat: Challenges and opportunities

for informing management with a large satellite tracking dataset. Aquatic Conservation: Marine and Freshwater Ecosystems, 32(6), 1041–1056. https://doi.org/10.1002/aqc.3813

**Chapter 3** is an exploratory work investigating the potential causes of long-range departures from a foraging site of a few tracked turtles. In light of the fidelity trait established in Chapter 2, I discuss habitat changes arising from servere weather events and periods of intensive human use as potential disturbances which may have impacted the movement strategy of a few idividuals.

**Chapter 4** examines the environmental drivers of changes in fine-scale movement behaviour. It identifies periods of local residency and transitting, and establishes a set of dynamic environmental characteristics that are associated with the duration of residency and the likelihood of transitioning between the two behaviours. Associated publication:

Webster, E.G., Duce, S., Hamann, M., Murray, N., Shimada, T., Limpus, C. (2024). Should I stay or should I go? The influence of environmental conditions on green turtle residnece time and outward transit in foraging areas. Marine Biology 171, 144. https://doi.org/10.1007/s00227-024-04450-1

In **Chapter 5** I develop a telemetry-based habitat model for foraging green turtles in the inshore Great Barrier Reef region. I use a suite of freely-available spatial and spatio-temporal datasets and a machine learning approach to first characterise suitable foraging habitat (via telemetry-based habitat modelling), and use the model to create predictions of suitable habitat at two timepoints. I evaluate the amount of suitable habitat in protected Great Barrier Reef zones and designated port areas, and compare the distribution of suitable habitat over time.

In **Chapter 6** I summarise the key findings from Chapters 2-5 in the context of the regional and global state of knowledge about green turtles. I evaluate the implications of my contribution in a conservation context and provide suggestions for future directions for this work.

# Chapter 2: Home ranges, site fidelity, diversity of movement strategies

**Published manuscript:**

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

## 2.1 Abstract

Increasing overlap between anthropogenic activities and wildlife can lead to problematic human–wildlife interactions. To manage these, an understanding of animal space-use patterns, with sufficient temporal and spatial detail is required. Satellite telemetry can provide such detailed data; however, the cost of tracking units places a significant limitation on sample size. Satellite tracks for 72 green turtles were consolidated through collaboration with multiple entities over 8 years at seven sites within a large industrial port contributing to an ecological monitoring initiative to minimize impacts of planned developments. This study aims to determine the minimum number of satellite-tracked green turtles required to represent spatial distribution patterns in the foraging ground and to evaluate factors underpinning differences in distribution and site fidelity metrics to inform appropriate management strategies.

An autocorrelated kernel density estimator was used to construct 95% utilization distributions for individual turtles during each calendar season. Percentage overlap between pairs of seasonal utilization distributions was calculated as a measure of short-term site fidelity. Mechanistic range shift analysis was applied to detect significant deviations from range residency behaviour. Green turtles exhibited spatially confined ranges and remained faithful to their foraging area for periods of up to 260 days. Range size was significantly different between microhabitats and study years. Only 16 individuals (22% of tracked turtles) performed significant range shifts, indicating that occupied areas represent important habitats, and most turtles are unlikely to adjust their space-use in response to anthropogenic or natural disturbances. Although this dataset represents an atypically large sample of satellite tracked individuals, representative data were obtained at only two key sites. This study highlights the importance of evaluating clear objectives when sampling animals for satellite telemetry studies to obtain representation of sites, periods of interest, or age and sex cohorts.

## 2.2 Introduction

Growing human populations increasingly encroach upon natural ecosystems (e.g., 52,154–157), with urban spread and industrialization contributing to diverse impacts on adjacent environments (158–162 among others). Shallow inshore habitats represent nurseries (163–165) and developmental or foraging grounds (166,167) for many marine animals (168). Altering these habitats can therefore have repercussions for the reproductive output of species, trophic interactions and ecosystem health, and extend beyond the specific sites of the disturbance (168,169).

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

Representative utilization distribution modelling with tracking data may elucidate core habitat areas for the management of ongoing, and planned developments, or human activities that may interact with protected wildlife including charismatic marine megafauna such as green turtles (*Chelonia mydas*) (2,64,118,144,153,170,171). Green turtles inhabit shallow inshore habitats at multiple life stages (77,80,87) and some populations (including the southern Great Barrier Reef stock) are increasing in size (20,23,36,71,80). Coupled with coastal urban and industrial expansion, this is likely to lead to increased frequency of interactions between turtles and humans (69,172). There is a paucity of information on the overlap between turtles and coastal infrastructure including industry in Queensland.

High fidelity and the tendency of green turtles to return to their foraging areas when displaced or following breeding migrations, may limit their resilience to local disturbances such as human development and extreme weather events (92,127). In low density foraging areas where individuals of multiple age and size classes share habitat and show prominent residency, the protection of a few key sites at pertinent times is likely to confer considerable long-term conservation benefits (171,173,174). Identification of these sites and periods should consider habitat requirements for individuals at several life history stages and dynamic oceanographic and biological processes that characterize variations in resource availability including rainfall events, tidal flow regimes, senescence and reproduction of primary producers.

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

## 2.3 Methods

### *2.3.1 Study site*

Port Curtis (Figure 3) sits within the boundary of the Great Barrier Reef World Heritage Area. It is Queensland's largest multi-commodity port, and the fifth largest in Australia by cargo tonnage and exemplifies the overlap between large-scale industrial activities and marine life. The port infrastructure consists of eight main wharf centres containing 20 wharves and supporting coal, Liquefied Natural Gas, grain, aluminium, cement and alumina export, and import of bauxite, among others (175). It also hosts commercial and recreational fishing vessels and transport for tourism to the Capricorn Bunker group of islands. Port Curtis includes extensive intertidal areas and is a known habitat for six species of marine turtles (175). Study of habitat use by marine turtles in Port Curtis began in 2009 in response to planned dredging and expansion of port infrastructure to accommodate a growing demand for vessel operations. Queensland Department of Environment, Tourism, Science and Innovation and university collaborators have monitored the demographics, population dynamics, health and habitat use of green turtle foraging populations in the port since 2010 (175). Green turtles in Port Curtis predominantly belong to the Southern Great Barrier Reef genetic stock (76,80).

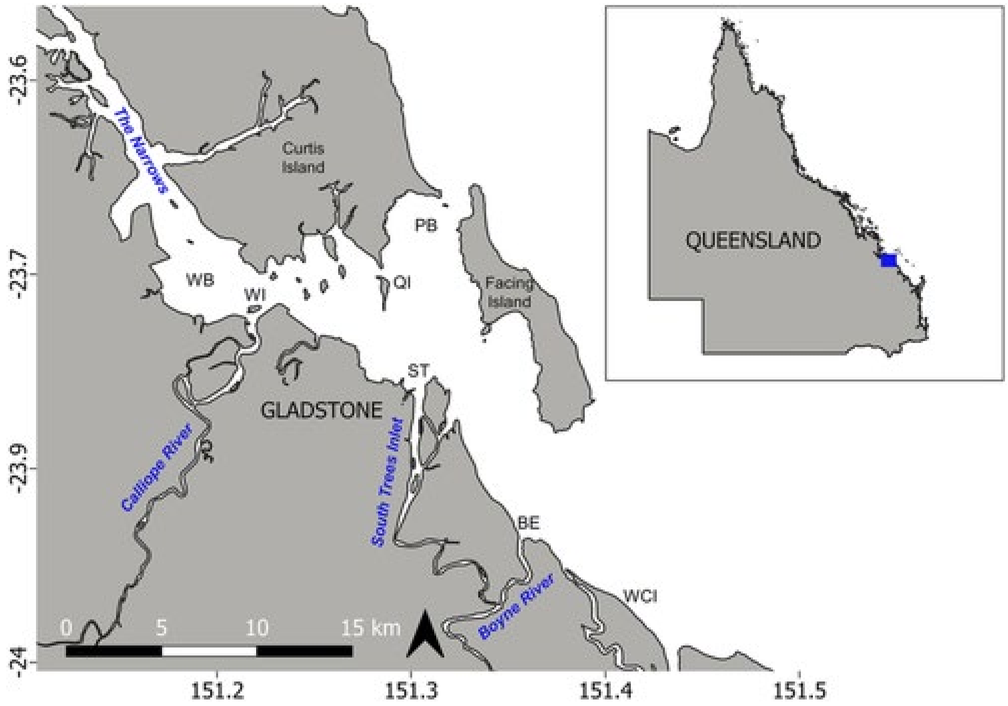


Figure 3 Map of Queensland with insert showing Port Curtis study sites monitored by Queensland Department of Environment, Tourism, Science and Innovation: Pelican Banks (PB), Western Basin (WB), Wiggins Island (WI), Quoin Island (QI), South Trees (ST), Boyne Estuary (BE) and Wild Cattle Island (WCI)

The abundance and extent of seagrasses in Port Curtis has declined since 2005 due to increasing frequency of major weather events (176) and the consequences for marine turtles are of concern. Major flooding caused by tropical cyclone Yasi in 2011 and ex-tropical cyclone Oswald in 2013 was linked to record numbers of strandings of both green turtles and dugongs in Port Curtis (177,178). Similarly, green turtles in Port Curtis had poorer body condition than at other coastal foraging sites in Queensland following the 2010 and 2011 flood events (89,179). Another major flood event occurred in 2017. Repeated flood disturbance may lead to long-term loss of seagrass meadows, affecting the health, survivorship and reproduction of foraging turtles (180).

Port Curtis comprises seven broadly defined study areas for green turtle monitoring (Figure 3): the Pelican Banks (PB) intertidal seagrass flats (primarily *Zostera muelleri* with some *Halophila ovalis*, *H. decipiens* and *Halodule uninervis*) beside the outflows through the channel between Curtis and Facing Islands; the Western Basin (WB) characterized by turbid water with patchy seagrass cover (H. ovalis and Z. muelleri capricorni); the Wiggins Island (WI) intertidal flats fed by outflows from the Calliope River; Quoin Island (QI) intertidal rocky reef and mangrove habitats; South Trees (ST) intertidal and subtidal flats; Wild Cattle Island (WCI) subtidal adjacent to outflows from Colosseum Creek; and the intertidal flats adjacent to the Boyne Estuary (BE).

### 2.3.2 *Turtle capture and processing*

In each of the study years (2010–2019) green turtles were captured as part of regular monitoring activities by either rodeo (181) or intercepted with blocking nets as they moved off shallow flats on the falling tide (91). A GPS location was recorded for each capture. All captured individuals were taken to the Gladstone Marina for processing. Weight and curved carapace length (CCL) were recorded, and external body condition was examined. Where trained personnel were present, sex and breeding status was determined by laparoscopy and/or ultrasonography (77,87). Turtles were marked with two uniquely numbered titanium flipper tags, as per Limpus *et al.* 1992 (182). For satellite tag attachment, algae, flaking scute material and epifauna were removed from the anterior portion of the carapace, which was roughened using sandpaper and cleaned with acetone. The tag was glued across the first and second vertebral scutes with a Sika anchorfix 3 + 2-part epoxy. Before becoming touch-dry this first attachment was reinforced with fibreglass tape and epoxy around the borders of the tag, extending onto the adjacent costal scutes. The tag and attachment were then painted with antifoul paint and allowed to set overnight. Turtles were released the next day from either their capture site, or at a location between the Gladstone Marina and the capture site. Capture of turtles, transmitter attachment and data collection for this programme were approved by either the JCU Animal Ethics Committee or the Department of Agriculture and Fisheries Ethics Committee and conducted within an approved Queensland Government project.

Sampling in Port Curtis was conducted opportunistically until 2018. From 2010 to 2018, most captures occurred on the Pelican Banks, where conditions were favourable for catching (clear and shallow water). Initial results from tracked turtles (118,119,183) indicated that they mostly remain in the area in which they were captured, and that tracking a few turtles does not reflect space-use in the wider port. Subsequent emphasis was placed on the capture and tracking of individuals at other sites closer to ongoing and planned development operations. For this reason, and the variability of funding for tracking studies year-to-year (Appendix 1), only small samples of turtles were obtained from WCI, ST, BE and QI for the present study.

### *2.3.3 Transmitter configuration and data filter*

Wildlife computers (Redmond, WA, USA) SPLASH10 or Sirtrack (Havelock North, NZ) Fastloc GPS tags were used in all study years (Appendix 1). Only Fastloc GPS fixes were retained due to their relatively high location accuracy (146,147). The first 24 hours were removed from each individual's track to account for acclimation or homing behaviour (125). For outlier removal, locations with residual error values of greater than 30, or from less than four source satellites were removed. Additionally, the SDLfilter package in the R software (147) was used to exclude spurious locations determined by maximum travel speeds and turning angles. Spatial and temporal duplicates in the data and locations above the high tide line were also excluded (125). Fastloc GPS locations screened with the SDLfilter data driven filter had a mean accuracy of 47.1 m when derived from >3 satellites (147); a similar mean data accuracy was assumed for the current tracking data.

### *2.3.4 Optimal sample sizes*

The minimum number of individuals required to represent the distribution of green turtles at each site and year was estimated with the SDLfilter package (184). This method calculates the probability of each randomly selected individual's ($1^{st}$–*i*th) utilization distribution (UD) being within areas used by (merged 100% Uds of) other individuals [$1^{st}$–(*i*−1)]. The merged 100% UD was chosen to minimize the impact of potential under-estimation of coverage areas caused by the tight association of the estimated Uds with the highly accurate GPS locations. The mean probability and cumulative areas corresponding to each number of tracked individuals is determined through bootstrapping and a rational function is fitted to these mean probabilities to estimate an asymptotic curve relative to sample sizes (i.e., number of tracked individuals). The minimum sample size is determined as the number of individuals required to reach 95% of the estimated asymptote of the mean overlap probabilities. For this analysis, the Uds were estimated from entire tracks of individuals with a movement-based kernel density estimator in the R package adehabitatHR (185). The movement-based kernel density estimator was selected for its ability to deal with entire tracks (up to 260 days) with low computation cost.

### *2.3.5 Utilisation distribution estimation*

Location error estimates from (146) encompassing the $95^{th}$ percentile of filtered data from fixed trials were used to calibrate the filtered data according to location classes defined by the number of source satellites (Table 1). Error calibration accounts for location error in utilization distribution estimation (186). For each individual, continuous time movement models were fitted for each calendar season of the tracking period in the ctmm R package (187). Several residual maximum likelihood-based models were fitted with the ctmm.select() function, and models with lowest Akaike' information criterion (AIC) were selected for timeseries kriging (188) to produce Uds from weighted autocorrelated kernel density estimates (AKDEs) for each season with the akde() function (187). Contours delineating 50% and 95% volume of the AKDE represent the area where it would be expected to find the animal with 50% and 95% chance. Home range estimation for discrete time periods can be used to describe the distribution of range residents but is not meaningful for migratory or nomadic individuals (189). Effective sample sizes in the AKDE are proportional to the number of times an animal crosses their home range in the sampled period (186). The AKDE generated from tracks with small effective sample size is likely to underestimate home range area and confidence intervals will be unacceptably large. Thus, AKDEs obtained from effective sample sizes of fewer than six were discarded (186). The ctmm approach accounts for autocorrelation (190), missing and irregular data (191), small effective sample sizes (186), and location error (192).

Table 1 Estimated root mean square user equivalent range error (m) with 95% confidence intervals (CIs) of Fastloc GPS based on number of satellites used to acquire relocations in (146) dataset. Estimated with the ctmm package in the R software

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

### *2.3.6 Fidelity and range shifts*

The degree of overlap of AKDE between consecutive seasons was calculated with the overlap() function for each individual in the ctmm package and used as a measure of individual site fidelity. Individual tracks were too short to allow calculation of overlap across years. Significant range shifts were identified with mechanistic range shift analysis (MRSA) in the R package MARCHER (193). The MRSA performs a likelihood ratio test to compare movement models for an animal's location data with and without a simulated range shift. Animals without significant range shifts were considered range residents. Generalized linear mixed models (Appendix 2) were constructed in the R package glmmTMB (194) to assess covariates of significant differences in the size of the seasonal 95% UD area, pairwise overlap of seasonal Uds and for significant range shifts. The covariates assessed were individual maturity, size (CCL), sex, capture site and capture year, with individual included as a random factor. Several combinations of predictor variables were tested for each response variable based on the study objectives and the ability of generalized linear mixed models to meet model assumptions and converge given unequal sample sizes across categories. Significant covariates were identified by selecting the best ranking model based on AIC corrected for small sample sizes (AICc). Model fits were validated with residual diagnostics tests, tests for zero inflation, dispersion and temporal autocorrelation in the DHARMa package in R (195). A limitation of the study design is that tracks with significant range shifts are not reflected in the overlap metrics, as UDs derived from tracks with small effective sample sizes were removed. This reduced the sample of individuals with Uds showing little seasonal overlap.

## 2.4 Results

### *2.4.1 Transmitter performance*

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

### *2.4.2 Optimal sample sizes*

The minimum number of individuals required to reach 95% of the estimated asymptote of mean overlap probabilities was 21 (Figure 4a). For each study site separately, representative sample sizes (x) were only obtained for turtles captured at two of the seven study sites, the Pelican Banks (x = 12 individuals, Figure 4b) and Wiggins Island (x = 3 individuals, Figure 4c). At the Pelican Banks site, representative sample sizes were obtained for all three maturity classes: juveniles (x = 3, Figure 3a), sub-adults (x = 3, Figure 5b) and adults (x = 12, Figure 5c). All of the tracked turtles at Wiggins Island were immature individuals. When considering discrete study periods, representative samples were obtained in 2010 (x = 2), 2013 (x = 8), 2015 (x = 3) and 2019 (x = 3). In these years, individuals were captured at one or two sites. During years in which representative samples were not achieved (2014, 2016 and 2018) a few individuals were sampled from each of three or more sites, and the mean overlap probability of their Uds did not reach 95% of the estimated asymptote.

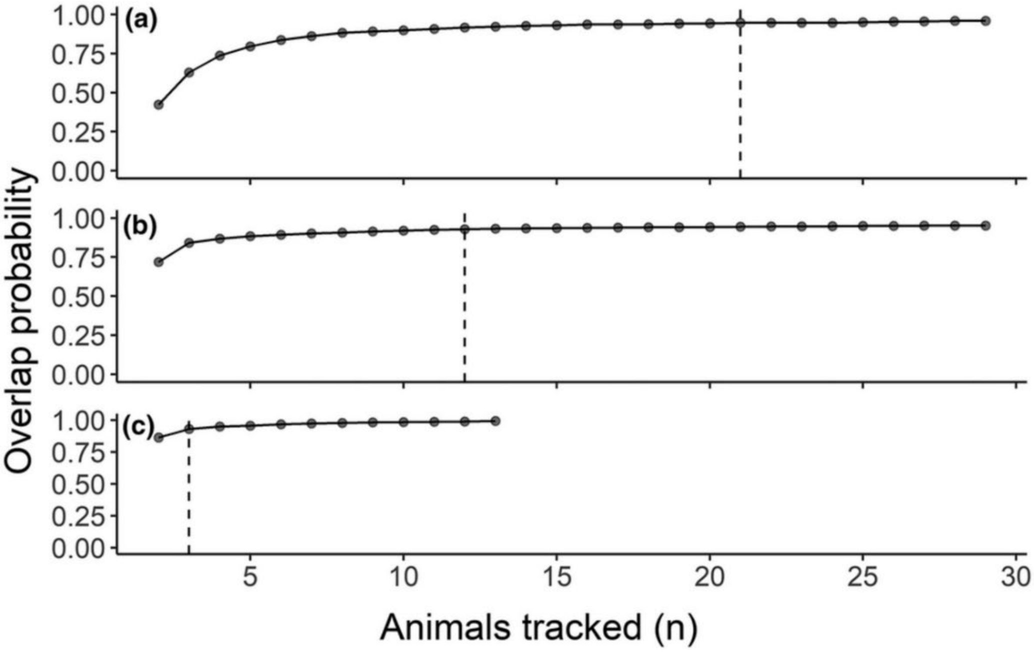


Figure 4 Mean probability of individual's 95% utilization distributions (from movement-based kernel density estimation from entire tracks of green turtles) occurring within the collective UD, based on the number of animals tracked (n). The number of individuals required to reach 95% of the estimated asymptote (dotted vertical line), implies the number of tracks considered representative at (a) all sites, (b) Pelican Banks and (c) Wiggins Island

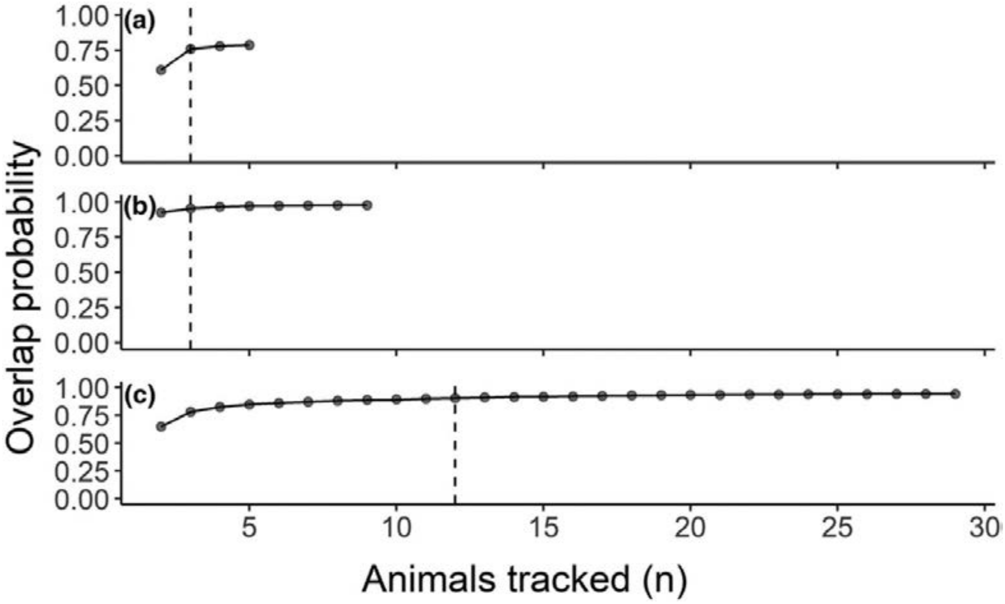


Figure 5 Mean probability of individual's 95% utilization distributions (from movement-based kernel density estimation from entire tracks of green turtles) occurring within the collective UD, based on the number of animals tracked (n). The number of individuals required to reach 95% of the estimated asymptote (dotted vertical line), implies the number of tracks considered representative for (a) juveniles, (b) sub-adults and (c) adults

### *2.4.3 Utilisation distributions*

Tags yielded enough data to generate seasonal UDs for 41, 22, 13 and 34 individuals in spring, summer, autumn and winter respectively (maximum three and median two seasons per individual). An Ornstein–Uhlenbeck Foraging (OUF, Ouf or OUΩ) anisotropic model was selected as the model with the lowest AIC for all seasonal subsets of the tracking data. The OUF incorporates positional and velocity autocorrelation and the tendency of animals to remain in a restricted area (range residency). Ouf is a special case of the OUF where the position and velocity autocorrelation time scales are equal, which is probably an effect of artificially restricting the tracking period to seasonal subsets of the data. OUΩ specifies a model with oscillatory range crossings. A subset of individual’s distributions estimated for three successive calendar seasons is depicted in Figure 6. Utilization distribution areas are summarized in Table 2. Turtles generally had spatially confined ranges with median seasonal UDs of 9.4 (0.07–288.0) km$^2$. The best ranking model for predicting UD size included study site as the only predictor. Utilization distributions were significantly larger at the PB compared to Wiggins Island ($z = -3.11$, $P = 0.002$), QI ($z = -3.15$, $P = 0.002$), ST ($z = -2.51$, $P = 0.012$) and Western Basin ($z = -2.15$, $P = 0.032$; Figure 7a). The two next best ranked models included both site and either season or study year as predictors. Season did not significantly affect UD area (Table 3; Figure 7b, Appendix 2). Turtles tracked in 2019 had smaller ranges than those tracked in the reference year, 2010 ($z = -2.996$, $P = 0.003$; Figure 7c). In the lower ranked models, there was no evidence of influence of sex or size of individuals on the size of their UD (Table 3; Appendix 2).

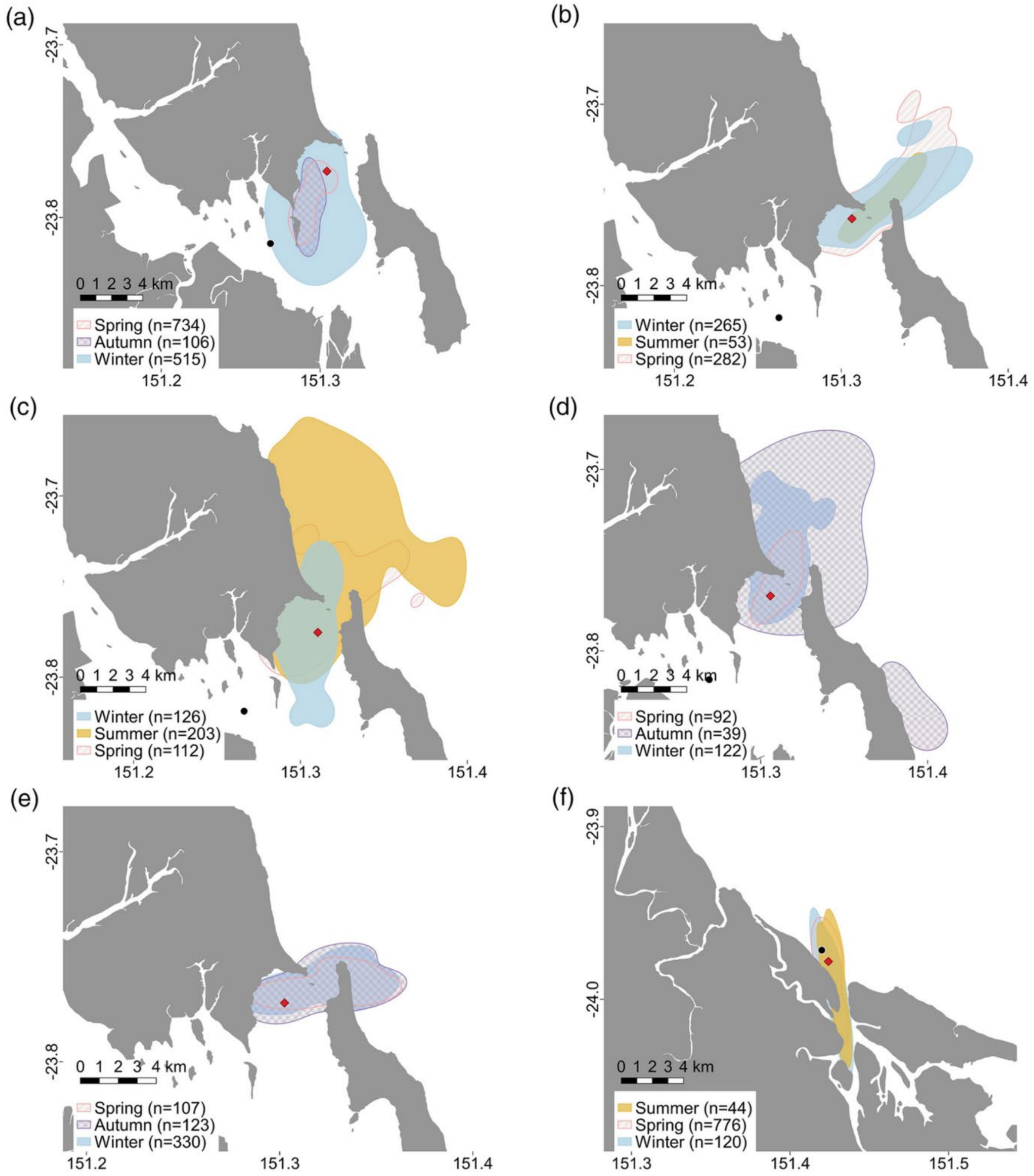


Figure 6 Seasonal 95% utilization distributions for green turtles (a) adult male QA13938 (2014), (b) adult female QA58221 (2015), (c) adult female QA43123 (2015), (d) adult female QA45524 (2014), unsexed subadult QA45601 (2014) and (f) subadult male QA86247 (2018) showing capture site (red diamond) and release site (black circle). ‘n’ refers to number of relocations used to generate each UD. For ease of visualization scale varies across figures

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

| **Year** | **Site** | **n** | **CCL (mm)** | **Days Tracked (±SE)** | **FGPS Locations (±SE)** | **n seasonal UDs generated** | **Mean seasonal 95% UD area (km$^2$ [95% CI])** | **Mean seasonal overlap (% [95% CI])** |
|---|---|---|---|---|---|---|---|---|
| 2010 | Pelican Banks | 5 | 87.6 (51.3–104.4) | 204.4 ± 13.6 | 554 ± 146 | 8 | 54.4 [28.3, 89.9] | 58.7 [46.8,70.7] |
| 2013 | Pelican Banks | 10 | 85.1 (42.1–111.0) | 116.3 ± 32.8 | 526 ± 101 | 13 | 35.6 [21.5, 53.2] | 81.9 [69.7, 91.8] |
|  | Wiggins Island | 3 | 47.7 (46–49.1) | 58.3 ± 5.9 | 286 ± 59 | 3 | 19.4 [9.7, 32.8] | NA |
| 2014 | Boyne River | 1 | 116.6 | 202.0 | 859 | 3 | 2.6 [2.0, 3.2] | 78.2 [65.9, 88.9] |
|  | Pelican Banks | 10 | 94.1 (63.1–110.9) | 144.3 ± 14.8 | 576 ± 193 | 19 | 27.9 [16.6, 42.8] | 84.0 [72.1, 91.9] |
|  | Quoin Island | 1 | 50.2 | 260.0 | 249 | 1 | 0.2 [0.1, 0.4] | NA |
| 2015 | Pelican Banks | 11 | 91.0 (77.8–108.2) | 156.9 ± 10.2 | 561 ± 48 | 20 | 27.1 [19.0, 36.9] | 81.8 [72.6, 89.4] |
| 2016 | Boyne River | 1 | 94.7 | 126.0 | 682 | 1 | 32.1 [20.1, 46.7] | NA |
|  | Pelican Banks | 10 | 100.3 (92.9–114.6) | 129.3 ± 13.1 | 489 ± 126 | 10 | 12.6 [9.5, 16.2] | 95.0, [88.5, 98.9] |
|  | Western Basin | 4 | 98.6 (85.3–108.7) | 120.0 ± 22.6 | 868 ± 120 | 9 | 4.3 [3.2, 5.5] | 95.3, [89.8, 98.3] |
| 2017 | Pelican Banks | 3 | 82.2 (75.7–94.6) | 182 ± 46.7 | 494 ± 388 | 4 | 21.4 [15.9, 27.8] | 67.1, [54.4, 79.3] |
| 2018 | Pelican Banks | 1 | 77.2 | 189.0 | 753 | 1 | 5.0 [3.7, 6.7] | NA |

| Year | Site | n | CCL (mm) | Days Tracked (±SE) | FGPS Locations (±SE) | n seasonal UDs generated | Mean seasonal 95% UD area (km$^2$ [95% CI]) | Mean seasonal overlap (% [95% CI]) |
|---|---|---|---|---|---|---|---|---|
| | South Trees | 5 | 79.8 (67.2–98.0) | 138.2 ± 18.5 | 806 ± 64 | 5 | 5.3 [4.0, 6.8] | 64.8, [54.3, 71.6] |
| | Wild Cattle Island | 2 | 81.4 (71.5–91.3) | 115.0 ± 1.0 | 894 ± 59 | 5 | 14.3 [8.2, 22.4] | 79.2, [62.1, 91.2] |
| 2019 | Wiggins Island | 10 | 64.2 (45.1–99.0) | 172.8 ± 17.2 | 1,114 ± 189 | 8 | 4.5 [3.0, 6.3] | 47.6, [35.9, 60.3] |

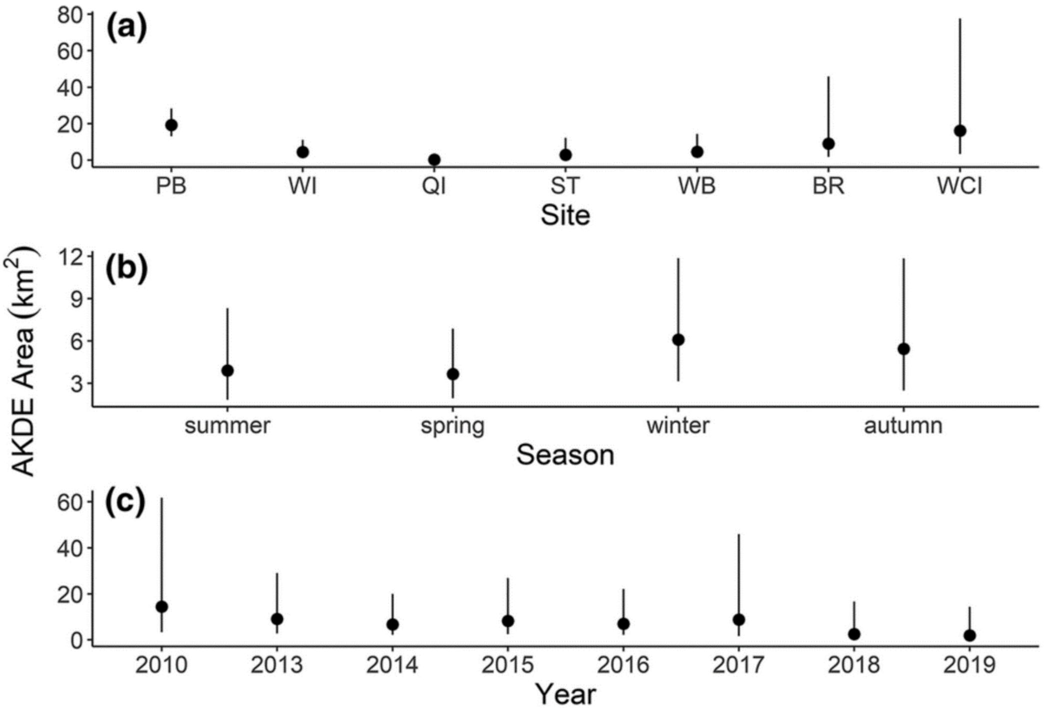


Figure 7 Estimated marginal means (±95%CI) of seasonal 95% utilization distribution area from selected generalized linear mixed models by (a) site, (b) season and (c) year as given by the first, second and third best fitting models respectively

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

| **Response, distribution and link function** | **Model rank** | **Fixed effects** | **Estimate** | **SE** | **Z** | ***P*** |
|---|---|---|---|---|---|---|
| UD area (γ distribution with log link function) | 1st | Intercept (PB) | 16.596 | 0.201 | 82.51 | <2e−16 |
| | | Site:WI | −1.544 | 0.497 | −3.11 | 0.002* |
| | | Site:QI | −4.321 | 0.373 | −3.15 | 0.002* |
| | | Site:ST | −1.917 | 0.764 | −2.51 | 0.012* |
| | | Site:WB | −1.365 | 0.636 | −2.15 | 0.032* |
| | | Site:BR | −0.698 | 0.892 | −0.78 | 0.434 |
| | | Site:WCI | −0.109 | 0.868 | −0.13 | 0.900 |
| | 2nd | Intercept (Season:Summer, Site:PB) | −16.44 | 0.285 | −57.6 | <2e−16 |
| | | Season:Spring | −0.061 | 0.287 | −0.21 | 0.832 |
| | | Season:Winter | 0.440 | 0.329 | 1.34 | 0.182 |
| | | Season:Autumn | 0.330 | 0.427 | 0.77 | 0.440 |
| | | Site:WI | −1.479 | 0.497 | −2.97 | 0.003* |
| | | Site:QI | −4.493 | 1.396 | −3.22 | 0.001* |
| | | Site:ST | −1.693 | 0.768 | −2.20 | 0.027* |
| | | Site:WB | −1.534 | 0.649 | −2.36 | 0.018* |
| | | Site:BR | −0.796 | 0.887 | 0.90 | 0.368 |
| | | Site:WCI | 0.003 | 0.857 | 0.00 | 0.998 |
| | 3rd | Intercept (Year:2010, Site:PB) | 17.078 | 0.624 | 27.359 | <2e−16 |
| | | Year:2013 | −0.377 | 0.760 | −0.496 | 0.620 |
| | | Year:2014 | −0.679 | 0.732 | −0.929 | 0.353 |
| | | Year:2015 | 0.471 | 0.732 | −0.644 | 0.520 |
| | | Year:2016 | −0.612 | 0.803 | −0.763 | 0.446 |
| | | Year:2017 | −0.388 | 0.988 | −0.392 | 0.695 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | Year:2018 | −1.639 | 1.514 | −1.082 | 0.279 |
| | | Year:2019 | −1.821 | 1.280 | −1.423 | 0.152 |
| | | Site:WI | −0.644 | 0.982 | −0.655 | 0.512 |
| | | Site:QI | −4.123 | 1.435 | −2.873 | 0.004* |
| | | Site:ST | −0.763 | 1.572 | −0.486 | 0.627 |
| | | Site:WB | −1.235 | 0.796 | −1.550 | 0.212 |
| | | Site:BR | −0.531 | 0.942 | −0.564 | 0.573 |
| | | Site:WCI | 1.049 | 1.625 | 0.645 | 0.519 |
| | 4th | Intercept (Sex:F) | 16.099 | 0.299 | 53.78 | <2e−16 |
| | | Sex:I | −0.219 | 0.257 | −0.17 | 0.862 |
| | | Sex:M | 0.181 | 0.403 | 0.45 | 0.654 |
| | | Scale (CCL) | 0.419 | 0.343 | 1.22 | 0.221 |
| | | SexI:scale (CCL) | 0.005 | 0.727 | 0.01 | 0.995 |
| | | SexM:scale (CCL) | 0.636 | 0.545 | 1.17 | 0.242 |
| UD overlap (β distribution with logit link function) | 1st | Intercept (Year:2010) | 0.353 | 0.545 | 0.647 | 0.517 |
| | | Year:2013 | 1.194 | 0.705 | 1.693 | 0.090 |
| | | Year:2014 | 1.370 | 0.640 | 2.140 | 0.032* |
| | | Year:2015 | 1.194 | 0.844 | 1.855 | 0.064 |
| | | Year:2016 | 2.300 | 0.681 | 3.380 | <0.001* |
| | | Year:2017 | 0.311 | 1.097 | 0.284 | 0.777 |
| | | Year:2018 | 0.572 | 0.716 | 0.799 | 0.425 |
| | | Year:2019 | −0.4433 | 1.0862 | −0.408 | 0.683 |
| | 2nd | Intercept (Site:PB) | 1.564 | 0.213 | 7.346 | 2.05e−13 |
| | | Site:WI | −1.654 | 1.055 | −1.569 | 0.117 |
| | | Site:ST | −0.787 | 0.766 | −1.03 | 0.304 |
| | | Site:WB | 1.178 | 0.622 | 1.894 | 0.058 |
| | | Site:BR | −0.364 | 0.978 | −0.372 | 0.710 |
| | | Site:WCI | −0.523 | 0.740 | −0.706 | 0.480 |
| | 3rd | (Intercept SEASONS AutumnXSummer) | 0.727 | 0.703 | 1.034 | 0.301 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | SEASONS AutumnXSpring | 0.862 | 0.811 | 1.062 | 0.288 |
| | | SEASONS AutumnXWinter | 1.472 | 0.782 | 1.883 | 0.060 |
| | | SEASONS SpringXSummer | 0.671 | 0.748 | 0.897 | 0.369 |
| | | SEASONS SpringXWinter | −1.190 | 1.208 | −0.985 | 0.325 |
| | | SEASONS SummerXWinter | 0.562 | 0.861 | 0.653 | 0.513 |
| | 4th | Intercept (Maturity:SA) | 1.573 | 0.246 | 6.406 | 1.49e−10 |
| | | Maturity:J | 0.068 | 0.843 | 0.081 | 0.936 |
| | | Maturity:A | −0.176 | 0.402 | −0.437 | 0.662 |
| | 5th | Intercept (Sex:F) | 1.468 | 0.290 | 5.058 | 4.24e−7 |
| | | Sex:I | 1.585 | 1.348 | 1.176 | 0.240 |
| | | Sex:M | −0.109 | 0.432 | −0.252 | 0.801 |
| | | Scale (CCL) | 0.371 | 0.331 | 1.123 | 0.261 |
| | | SexI:scale (CCL) | 0.408 | 0.733 | 0.556 | 0.579 |
| | | SexM:scale*CCL | −0.950 | 0.680 | −1.398 | 0.162 |
| Range shift (binomial distribution with logit link function) | 1st | (Intercept) | −0.763 | 0.978 | −0.779 | 0.436 |
| | | SEASONS | 0.085 | 0.419 | 0.203 | 0.839 |

### 2.4.4 *Fidelity and range shifts*

Fidelity to site was calculated as the degree of overlap ±95% confidence interval between seasonal UDs for an individual. This ranged between 35.9% and 99.6%, with a mean of 81.6% (Figure 8). Range residents, defined as individuals who did not perform significant range shifts, made up 77.8% of tracked individuals. The highest ranked model included study year as the only predictor and individual as a random factor (Figure 8). Seasonal ranges in 2016 and 2014 had significantly more overlap than in the reference year 2010 (z = 2.14, P = 0.032 and z = 3.38, P < 0.001 respectively). In lower ranked models, season pair, site, sex and size covariates did not significantly affect seasonal range overlap (Table 3; Appendix 2).

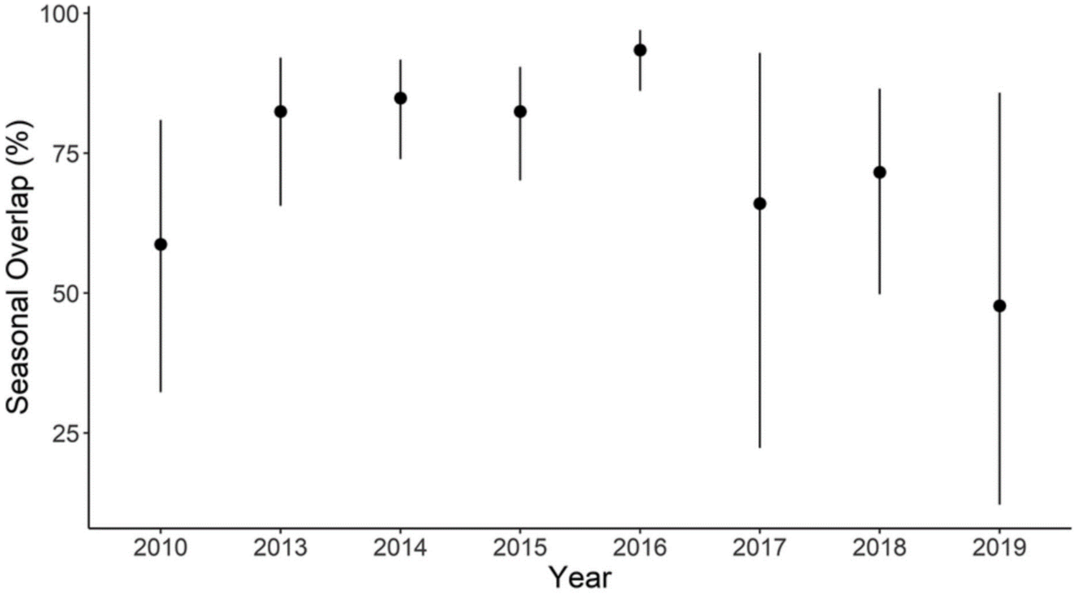


Figure 8 Estimated marginal means (±95%CI) from best ranked generalized linear mixed model of overlap between seasonal pairs of 95% utilization distributions with study year as the only predictor

Significant range shifts, unrelated to resettlement at the capture site, were detected for 16 individuals. Breeding migrations were included as significant range shifts according to MRSA, with maximum displacements of 139.5 and 97.1 km (n = 2). Non-breeding range shifts occurred over a mean period of 4.0 (0.2–22.1) days. A maximum displacement of 153.5 km from the initial fix was recorded for the non-breeding adult female QA66526 over 7 days in November 2016. Figure 9 depicts four individuals as examples of range residency (a, b), periodic range shift (c, d), forays or discrete loop trips (e, f) and breeding migration (g, h). No significant covariates of range shift were detected.

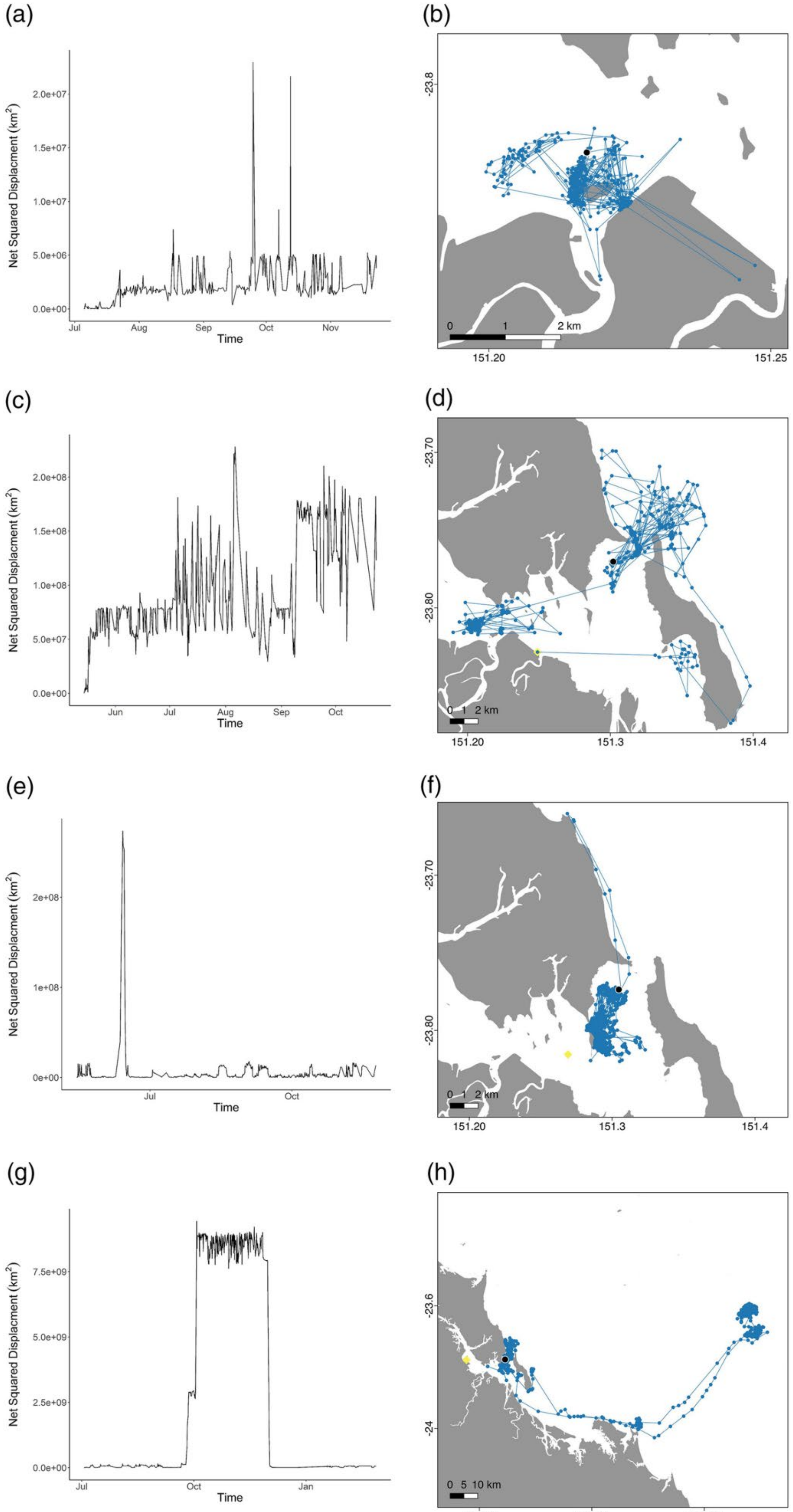

(a)
Net Squared Displacment (km$^2$)
2.0e+07
1.5e+07
1.0e+07
5.0e+06
0.0e+00
Jul
Aug
Sep
Oct
Nov
Time
(b)
-23.8
0
1
2 km
151.20
151.25
(c)
Net Squared Displacment (km$^2$)
2.0e+08
1.5e+08
1.0e+08
5.0e+07
0.0e+00
Jun
Jul
Aug
Sep
Oct
Time
(d)
-23.70
-23.80
0 1 2 km
151.20
151.3
151.4
(e)
Net Squared Displacment (km$^2$)
2e+08
1e+08
0e+00
Jul
Oct
Time
(f)
-23.70
-23.80
0 1 2 km
151.20
151.3
151.4
(g)
Net Squared Displacment (km$^2$)
7.5e+09
5.0e+09
2.5e+09
0.0e+00
Jul
Oct
Jan
Time
(h)
-23.6
-24
0 5 10 km
151.20
151.60
152.00

Figure 9 Net displacement of green turtles throughout the tracking period showing movement paths of (a, b) juvenile male QA84342, (c, d) adult male QA36875, (e, f) adult male QA13938 and (g, h) adult male K93087. Respectively, these individuals displayed range residency, significant range shift, looping behaviour and breeding migration. For ease of visualization the scale of the axes varies between plots

## 2.5 Discussion

### *2.5.1 Minimum representative sample sizes*

The minimum number of tracked green turtles required to represent spatial distribution patterns at the foraging grounds were determined to be between 3 and 21, depending on the study site, study year and maturity group (Figures 4 and 5). Typically, sample sizes in animal telemetry studies are small because of the high cost of tracking devices (144,149,196). In this study, long-term monitoring, facilitated by financial support from industry, enabled the collection of an atypically large tracking dataset (72 individuals). Importantly, this study has identified green turtle distributions that can be considered representative of the space used by foraging turtles at two monitored sites. Turtles are unlikely to depart from these areas and if removed artificially, tend to return there (127). Modification of these key areas is likely to impact the survival of the individuals that occupy them. Nevertheless, representativity was not attained at five of seven sites, nor for 3 of the 8 study years. Fewer individuals were required to represent space-use at particular sites than for the entire study area, implying that greater sampling effort is required for studies if they occur over larger areas or time frames. Similarly, fewer individuals were representative of a particular maturity cohort than for the group overall, thus population studies require sampling of multiple cohorts. Collectively, this demonstrates that if the research is being conducted to understand current or future impacts of habitat change there is a need to explicitly outline marine wildlife management objectives such as identifying specific sites (development footprints) and periods of interest, prior to commencement of tracking studies, particularly where individuals display spatially confined behaviours. This is necessary to draw ecologically meaningful conclusions from the tracking data.

### *2.5.2 Factors underpinning distribution and site fidelity*

The main factors underpinning differences in the size of green turtles' utilization distributions in Port Curtis were study site and year. Turtles at the Pelican Banks study site used larger areas than those at other sites (Figure 7). This may reflect the diversity, abundance, health and distribution of benthic dietary items (92,197). The larger UDs of Pelican Banks turtles could indicate low quality or patchy food resources (198). Alternatively, larger turtles that use the shallow water habitats of Pelican Banks may have limited access to grazing patches as they become exposed at low tide. Large and small turtles appear to take advantage of a variety of intertidal habitats as they have been observed moving off the flats into the deeper subtidal channels on the falling tide (77,80,110).

Turtles occupying other nearby sites may be exploiting other, smaller seagrass patches, or a variety of food items supported by intertidal and estuarine conditions, including macroalgae and epifauna growing on artificial substrates and rock walls, as well as mangrove roots and fruits upstream of river outflows (80,111). Foraging areas of green turtles align closely with the distribution of required resources for foraging and resting (197) or unique suites of environmental conditions (118,199). Although most animals exhibited short-term fidelity to foraging sites, differences in range sizes between study sites and years implies that larger numbers of tracked individuals, from a diverse range of micro-habitats are required to sufficiently represent the distribution of turtles at specific sites and periods of interest. No systematic, significant differences in UD size were detected across seasons, although at other green turtle foraging grounds larger winter than summer ranges may be an artefact of thermoregulatory behaviours, or adaptation to seasonal changes in resource availability (118,122).

Interannual differences were found in site fidelity (seasonal UD overlap metrics, Figure 7c). These may reflect changing resource distribution following major flood seasons. The availability of food resources for green turtles is related to rainfall events, with dry years supporting good forage and wet years providing poor forage and contributing to lower reproductive output in subsequent seasons (100). In years of poor forage, turtles may expand their space-use to obtain sufficient forage, or exploit alternative food resources (92,111,118). Overall, a high degree of seasonal overlap in space-use (35.9–99.6%, mean = 81.6%) and few (n = 16) individuals shifting between sites is further indication of fidelity to foraging sites. The tendency of green turtles to remain in one area when other apparently suitable foraging habitat is available, may reflect a ‘low risk’ strategy (92,133,198), the relative advantage of remaining in a familiar area compared to switching to an unknown one. Alternatively, non-ideal environmental conditions in other areas could be deterring turtles from shifting their distributions. The effect of physical environmental parameters on primary producers and consequently green turtles’ space-use is beyond the scope of this study. Further study with this dataset will focus on the environmental correlates of foraging range size and movement of tracked turtles.

This study highlights the diversity of space-use patterns performed by green turtles at inshore foraging grounds. From 72 individuals four different patterns of behaviour were identified including, range residency over several months (n = 48) or after delayed resettlement at the capture sites (n = 9, up to 12 days post-release), range shifts (n = 16) including forays and breeding migrations. Individuals differed in the scales of their maximum displacement from the point of capture (1.9–153.5 km) and size of seasonal 95% UDs (median = 9.4, 0.08–288.0 km$^2$). Such diversity of space-use patterns has also been noted in the north-west Pacific (143), eastern Mediterranean

(200,201) and Indian Ocean (199,201), which may be related to plasticity of foraging strategies (97). This diversity of space-use patterns poses a challenge for identifying appropriate management strategies for minimizing impacts to turtles. Nevertheless, 78% of tracked animals in this study displayed range residency and high fidelity, which is consistent with other characterizations of this species as having long-term fidelity to foraging sites, spanning decades (e.g., 92,118). This suggests that when representative sample sizes are obtained, the distribution information for these animals provides a realistic boundary delineating the habitat of the majority of individuals at the site.

### *2.5.3 Study implications and informing management*

The space-use patterns outlined in this study should be considered when devising approaches to mitigate the impact of planned developments on green turtles. Turtle distribution information from tracking studies can be used to assess spatial and temporal overlap with specific risks to turtles. In Moreton Bay, utilization distribution modelling aided the implementation of Go-Slow Zones in shallow foraging habitat of green and loggerhead turtles and dugong to reduce the rate of recreational vessel strikes (64). Risk of direct loss of habitat is assessed as being very high for foraging green turtles in Port Curtis (202). Mitigation of environmental stress from human activities may involve modifying operational practices for port infrastructure, potential sources of contamination from discharge and vessel management plans that overlap with turtle spatio-temporal distributions. Protections to key foraging habitats can also be beneficial to sympatric species such as seagrasses and dugongs (2,108,203). The distributions of foraging turtles outlined in this study will also serve as a backboard for evaluating resource requirements for this foraging aggregation by determining environmental characteristics that favour turtle occurrence, or ‘suitable’ environmental conditions through resource selection analysis and assessing changes in extent and location of ‘suitable’ habitats over time. Mitigation of detrimental anthropogenic impacts on a single green turtle foraging ground can be beneficial for multiple life stages, sexes and even breeding stocks. The trait of green turtles to remain faithful to foraging sites implies that irreparable local modifications to foraging habitat can impact fitness and survival of resident animals. Translating space-use patterns into protective regulations contributes to green turtles’ ability to acquire energy stores required for successful reproduction – and population viability for this species.

## 2.6 Acknowledgments

This project is the result of many years of ongoing monitoring at Port Curtis which involved deployment of tags (funding details given in Appendix 1) by various organizations, industry partners and volunteers. Research activities were facilitated by Queensland Turtle Conservation Project with Department of Environment, Tourism, Science and Innovation Aquatic Threatened Species Unit with assistance from Gidargil Land and Sea Rangers and funded by the Gladstone Ports Corporation through their Ecosystem Research and Monitoring Programme, Queensland Department of Environment, Tourism, Science and Innovation, James Cook University, The Centre for Tropical Water and Aquatic Ecosystem Research, Shell's QGC Business, Australia Pacific LNG, and Santos GLNG. Shell's QGC Business, Australia Pacific LNG and Santos GLNG purchased 10 tags deployed in 2019 and provided research funds for fieldwork and the analysis of these data. Open access publishing facilitated by James Cook University, as part of the Wiley – James Cook University agreement via the Council of Australian University Librarians.

## 2.7 Appendices

Appendix 1 Summary of Sirtrack (92) and wildlife computers SPLASH-10 satellite transmitter models deployed on green turtles in Port Curtis and funding sources 2010–2019. All transmitters were equipped with Fastloc GPS, and no individual was tracked twice in the study period

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

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

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

*Abbreviation: CCL, curved carapace length*

# Chapter 3: Space-use and long-range movements of green turtles in coastal foraging habitat following large flood events

## 3.1 Abstract

Extreme weather events are occurring with increasing frequency and intensity globally, impacting natural environments and wildlife populations. On tropical coasts, storms and cyclones impact the primary producer biomass of benthic organisms, affecting the organisms that consume them. Green turtles (*Chelonia mydas*) in the western Pacific recruit to inshore foraging grounds at approximately 10 years of age (23). Predominantly, individuals retain long-term fidelity to these discrete locations for foraging. In over 50 years of region-wide mark recapture programs and more recent satellite telemetry studies, less than 0.18% of recaptured individual green turtles, immature or adult, have been recorded using more than one foraging site. In this study, we examine a large (n=80) long-term satellite tracking dataset and report on five (6.25%) resident green turtles tracked to alternative foraging grounds further than 80 km away. For these five individuals, net displacement from deployment at the capture site exceeded that of any other non-breeding turtles tracked in this study. We hypothesised that chronic declines in habitat conditions, driven by frequent floods, may prompt a few individuals to risk relocation to a new site or forage across expanded areas. Though the temporal coverage of our tracking dataset was insufficient to conclusively demonstrate a direct effect of flooding events on long-range movements, we discuss our results in comparison with unpublished data on green turtle movements exceeding 25km at other inshore foraging sites in Queensland, with respect to whether or not these sites receive substantial freshwater input from major rivers following flood events. We did not detect changes in space-use by nonbreeding turtles in relation to the timing of major weather events at Port Curtis. Instead, extreme weather events, including floods, are linked to dietary shifts, poor health and uptake of inorganic pollutants by turtles, indicating that they scarcely move in response to floods. In the last decade, the increased frequency of extreme weather has coincided with coastal infrastructural expansion. Understanding this changing landscape and the potential exacerbation of climate effects by anthropogenic activities is pertinent to managers at this and other coastal sites when considering thresholds for environmental compliance, sustainability of industrial practices and approaches to future development.

## 3.2 Introduction

The behaviour and survival of wildlife is influenced by the dynamic environmental and anthropogenic conditions that shape their habitat. If resources are degraded, an animal may endure imperfect conditions or risk relocation to another site (92). Site fidelity confers familiarity with resources available to the animal in the habitat and its long-term viability (204). Therefore, rather than relocating, an animal may endure temporarily adverse conditions for foraging (205).

For marine turtles, enduring sub-optimal foraging conditions may be facilitated by their slow ectothermic metabolic rate and fat stores (205). Green turtles (*Chelonia mydas*) of the Southern Great Barrier Reef (sGBR) genetic stock show long-term fidelity to neritic foraging areas and spatially confined foraging ranges, which they generally adhere to up to and beyond reaching maturity (92,118,128). This is supported by multiple lines of evidence; first, if individual green turtles are relocated from their residential foraging areas, they will return there (127). Second, the Queensland Government has led a capture-mark recapture program for sea turtle species residing in Queensland waters for over 50 years (206). In this program, no *Chelonia mydas* individuals marked at breeding and later resighted in foraging grounds in this period have been sighted in more than one foraging site (92). Third, published Queensland Turtle Conservation Program satellite tracks included six green turtles returning from breeding to the same foraging areas they had previously used (92) and fourth, records of turtles tagged while foraging and resighted in more than one foraging ground are very rare. For example, at Shoalwater Bay from 2000-2004, three of 1779 (0.17%) recaptured green turtles had been previously recorded in another foraging area (87). All three were immature individuals, and the movement was speculated to be consistent with the developmental migration hypothesis (93,207), whereby immature turtles approaching sexual maturity transfer from shallow developmental foraging habitat to other benthic 'adult' foraging grounds. Similarly, at Moreton Bay between 1990-1992, just one of 826 (0.12%) captured individuals had been previously captured in another feeding area, at Heron Island ~490 km away (90). Aside from breeding, developmental migration and dispersal, green turtles' long-distance movements are atypical (205).

Long-range movements of a few foraging individuals are reported in Pillans et al. 2021 (183) and unpublished data (T. Shimada, unpublished data, 2024). A possible explanation may be localised declines in foraging habitat conditions. Many sGBR green turtles inhabit shallow inshore foraging habitats (23,90,126). These habitats can support turtle aggregations comprised of multiple life stages, sexes and distinct genetic stocks (23,80). La Niña years, characterised by floods, cyclones and increased freshwater runoff into coastal foraging areas, influence the quality and quantity of seagrass. Inshore coastal areas receive sediment-rich flood waters following extreme weather events. Excess suspended sediment occludes light, inhibiting the primary productivity of aquatic vegetation (176,208,209), which can be detrimental to populations of megafauna that consume primary producers as food (100,116). For example, la Niña years are associated with inhibited acquisition of energy stores required for breeding, resulting in fewer adult females coming into breeding after two years (100). Reduced food availability could potentially drive departure or expansion of foraging ranges in search of better forage [e.g., >25 km from the foraging ground, (109)], or turtles may persist at sites and endure reduced food availability (103).

At several inshore foraging sites in Queensland, record numbers of stranded, primarily herbivorous, green turtles and dugongs occurred in 2011 following two major flood events and the influence of tropical cyclone Yasi (89,178). These floods delivered sediment-rich water into most of the Great Barrier Reef World Heritage Area south of Cairns. The majority of green turtles captured in the Cleveland Bay area after this time had poor body condition and were feeding on red algae, where seagrass had previously dominated their diets (210). In January 2013, ex-tropical cyclone Oswald produced the largest flood event recorded for central Queensland (the Calliope and Boyne Rivers) in a decade (211). The outflows from this flood significantly lowered conductivity, raised turbidity at inshore sites, and elevated metalloid and nutrient loads in the water column (212). Extensive floods occurred again in the state’s southeast in 2017 (211) and in the summer of 2021/22 (213). In general, flood events along the coastlines are a primary cause of seagrass degradation globally (214).

In light of the reported relationships between large floods and the diet and health of inshore foraging turtles (89,177,179), our present study aims to ascertain whether behavioural changes were evident for satellite-tracked green turtles following major flood events occurring during the tracked period. This study investigates physical changes in foraging habitat post-flood as a potential driver of large displacement (>25 km) of a few tracked turtles. We expected that a flood response would be evidenced by expanded range areas or increased distances of exploratory movement by green turtles in the months following major rainfall events. Our results provide insight into the resilience of species inhabiting coastal ecosystems to extreme weather events, particularly when simultaneously impacted by anthropogenic habitat modifications.

## 3.3 Methods

Between 2010 and 2019, green turtles were deployed with satellite transmitters in Port Curtis (Figure 10) according to the protocol described by Limpus *et al.* 2001 (215). Port Curtis is a major multi-commodity port in central Queensland and supports some of the most expansive seagrass meadows in the region. It receives outflows from the Boyne, Calliope and Fitzroy Rivers and Baffle Creek. This study combines datasets collected from satellite transmitters deployed by CSIRO in 2013 [n=10, (183)] and collaborative Queensland Department of Environment, Tourism, Science, and Innovation (DETSI) and James Cook University projects 2010-2019 [n=70, (216)]. Turtles were captured in shallow foraging areas as part of regular long-term monitoring trips either via turtle rodeo or intercepted with blocking nets as they moved off the intertidal flats on the falling tide (95). We received Fastloc GPS locations from tracked turtles. Data were filtered to remove locations triangulated from fewer than four satellites [mean accuracy of 40 m for the retained points (147)], locations on land, spatial and temporal duplicates and spurious locations determined from unrealistic travel speeds and turning angles with the SDLfilter package in the R software (147). We removed each individual's first 24 hours of tracking data to account for post-release acclimation behaviour (127).

To determine the timing of major flood events, we obtained river discharge data from the Australian Bureau of Meteorology Water Data (BOM 2021) at four sites upstream of outflows into Port Curtis: Calliope at Castlehope, Fitzroy at the Gap, Milton on the Boyne and Mimdale on Baffle Creek (Figure 10B) for 2010-2020. Flood pulses were identified as dates on which daily discharge exceeded 8000 $m^3 sec^{-1}$ at the Fitzroy station or 1500 $m^3 sec^{-1}$ at the Calliope. To examine environmental characteristics following floods, turbidity and salinity data (BOM 2021) were obtained at two sites where most of the turtles were captured; the Wiggins Island intertidal flats (-23.772031 S, 151.303866 E, Figure 10A) which represent the inner harbour and receive outflows from the Calliope River and; the Pelican Banks intertidal and subtidal seagrass meadows (-23.810899 S, 151.218047 E, Figure 10A) which represent the outer harbour.

To evaluate changes in space use by turtles following flood events, we calculated 95% utilisation distributions (UDs) from autocorrelated kernel density estimates (AKDE) with the akde() command of the ctmm package in the R software (217) for three-month bins of the tracking data as per Webster *et al.* 2022 (216). We visually examined the area of the 95% UD for individuals who met assumptions of range-residency [effective sample sizes, proportional to number of range crossings was >6, (186)], against identified periods of major flooding. We also compared AKDE area in years post-flood (2011, 2013, 2015, 2017) to other years with generalised linear mixed models. We removed one outlier of a large AKDE area obtained from an individual (tag number 126273) whose track did not meet model assumptions of range residency by variogram assessment (218).

To assess the relationship between long-range movements and flood events, we calculated daily distance as the sum of linear distances between successive relocations in each calendar day for all tracked individuals, using the adehabitatLT package in R (185). This was done to standardise distances across irregular intervals between tracked locations. The difference between daily distance and mean daily distance for all tracked turtles over the entire study period was plotted along a timeseries. Positive deviations occur when the turtle travels further than the mean daily distance, while negative deviations occur when the turtle travelled less than the mean daily distance. We also calculated the maximum displacement for each individual as the distance between the initial retained fix and the furthest point from that fix in their track.

## 3.4 Results

Major flood peaks occurred in December 2010, January 2013, February 2015 and March 2017 (Figure 11A) at Baffle Creek, the Boyne, Calliope and Fitzroy discharge stations. Following these dates there were rapid declines in salinity (Figure 11B) and Secchi depth (increased turbidity) at both Wiggins Island and Pelican Banks. This was most evident at the Wiggins Island site, likely because of its proximity to outflows from the Calliope River (Figure 10A). AKDE area ranged between 0.07-166.8 $km^2$ (median 8.56 $km^2$). The five largest AKDE area values occurred between September 2013 and February 2014 (n=4) and June-August 2010 (n=1). There was no obvious pattern between timing of flood peaks and the size of the AKDE area (Figure 11D), and the AKDE area was not significantly larger in flood vs non-flood years (z=1.6, p=0.11). The number of individual turtles whose tracks coincided with the identified flood peaks (n=5 in Dec 2010, 0 in Jan 2013, 13 in Feb 2015 and 12 in Mar 2017) was too small to examine fine-scale turtle movement during the flood events (Figure 11D).

The mean daily distance travelled by non-breeding green turtles was 3.11 km (±0.04 km SE). Of 80 individuals, five (6.25%) departed Port Curtis and resettled at an alternative foraging location. All five were originally captured at the Pelican Banks site (Table 4) and tracking duration was between two and eight months. Of these five individuals, four were mature adults (three female and one male), and one was a large pubescent female. Three of these individuals departed the Pelican Banks within 12 months of the January 2013 flood and one within 12 months of the February 2015 flood. The fifth individual performed a long-range movement in October 2016, not coinciding with any identified post-flood period. These five individuals reached maximum net displacements between 89.6 and 242.5 km from the site where they were released. The maximum daily distance travelled by these five individuals ranged from 26.1-110.4 km (Figure 10B, Table 4). Other non-breeding individuals (Figure 10B) reached maximum displacements of 1.6-50.2 km (median 8.2 km) from their initial position and travelled maximum daily distances of 3.4-38.5 (median 11.47) km. Daily distances for non-breeding green turtles were generally small in the inner and outer harbours, except where part of long-range travel trajectories (Figure 10C). High daily distances were also achieved by some individuals during short forays (Figure 10B).

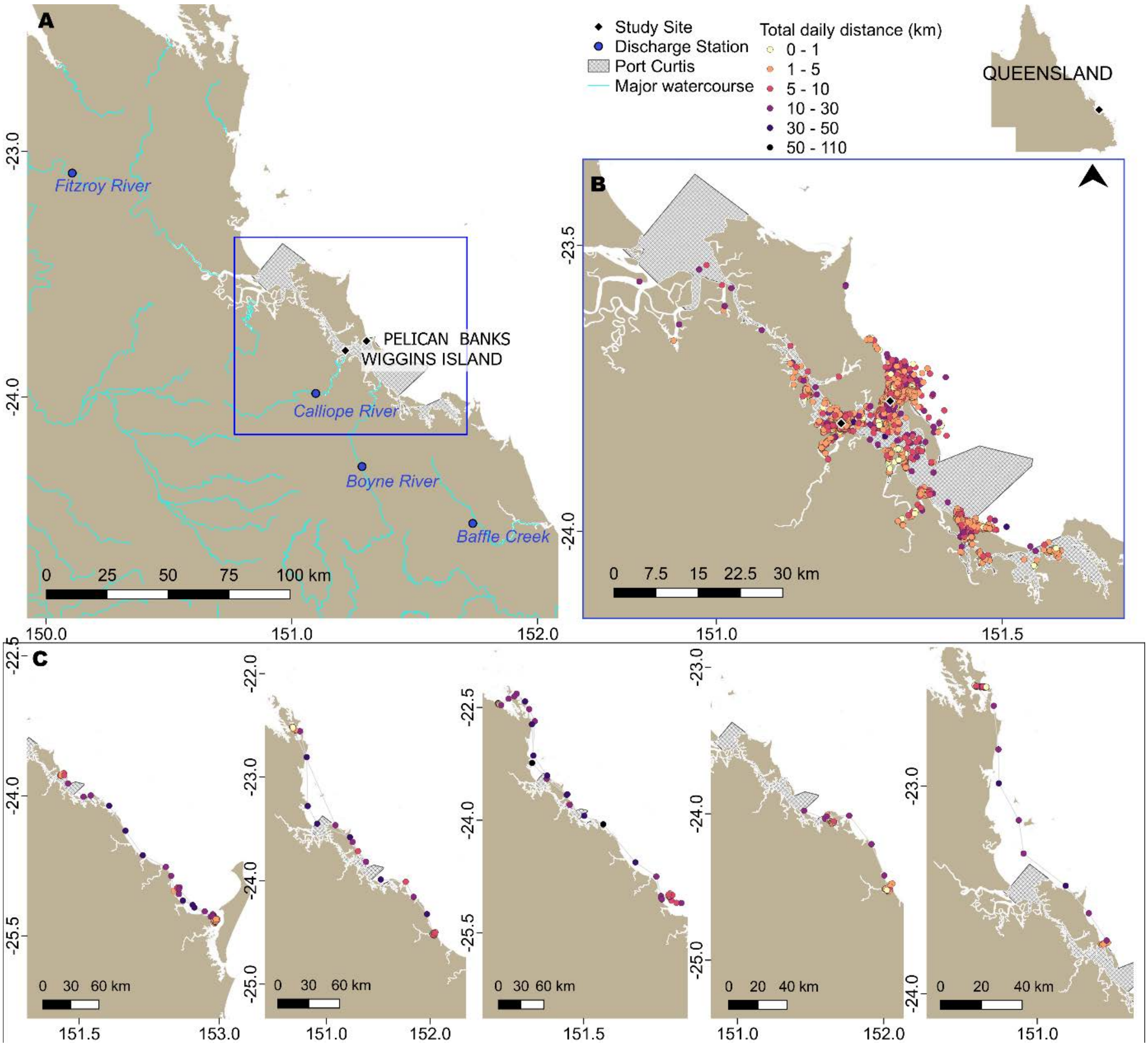


Figure 10 Site map showing A) locations of discharge stations and study sites within Port Curtis with the insert B) FGPS locations of non-breeding tracked green turtles (n=75) between 2010-2019, C) FGPS locations and paths of tracked individuals that resettled at alternative foraging sites >25 km from Port Curtis (tag numbers 126273, 126274, 131869, 149090, 157935 respectively), coloured by total distance travelled in each calendar day.

Table 4 Capture and deployment information, and timing and duration of long-range movements of five satellite-tracked green turtles that resettled at alternative foraging sites >25 km from Port Curtis

| Satellite tag | CCL (mm) | Sex | Maturity | Capture Location | Deploy Date | Date of long-range movement | Linear distance and direction of long-range movement (km) |
|---|---|---|---|---|---|---|---|
| 126273 | 101.6 | F | SA | Pelican Banks | 2 May 2013 | 17-31 May 2013 | 271 S |
| | | | | | | 18 Dec 2013 | 55 N |
| | | | | | | 3 Jan 2014 | 55 S |
| 126274 | 113.8 | F | A | Pelican Banks | 3 May 2013 | 3-8 May 2013 | 182 N |
| | | | | | | 23 July -14 Aug 2013 | 313 S |
| 131869 | 96.2 | F | A | Pelican Banks | 7 Nov 2013 | 8-14 Nov 2013 | 240 N |
| | | | | | | 17-28 Jan 2014 | 435 S |
| 149090 | 94.1 | M | A | Pelican Banks | 13 Jul 2015 | 13-14 Jul 2015 | 39 S |
| | | | | | | 2-12 Aug 2015 | 84 S |
| 157935 | 97.3 | F | A | Pelican Banks | 10 Oct 2016 | 5-12 Nov 2016 | 162 N |

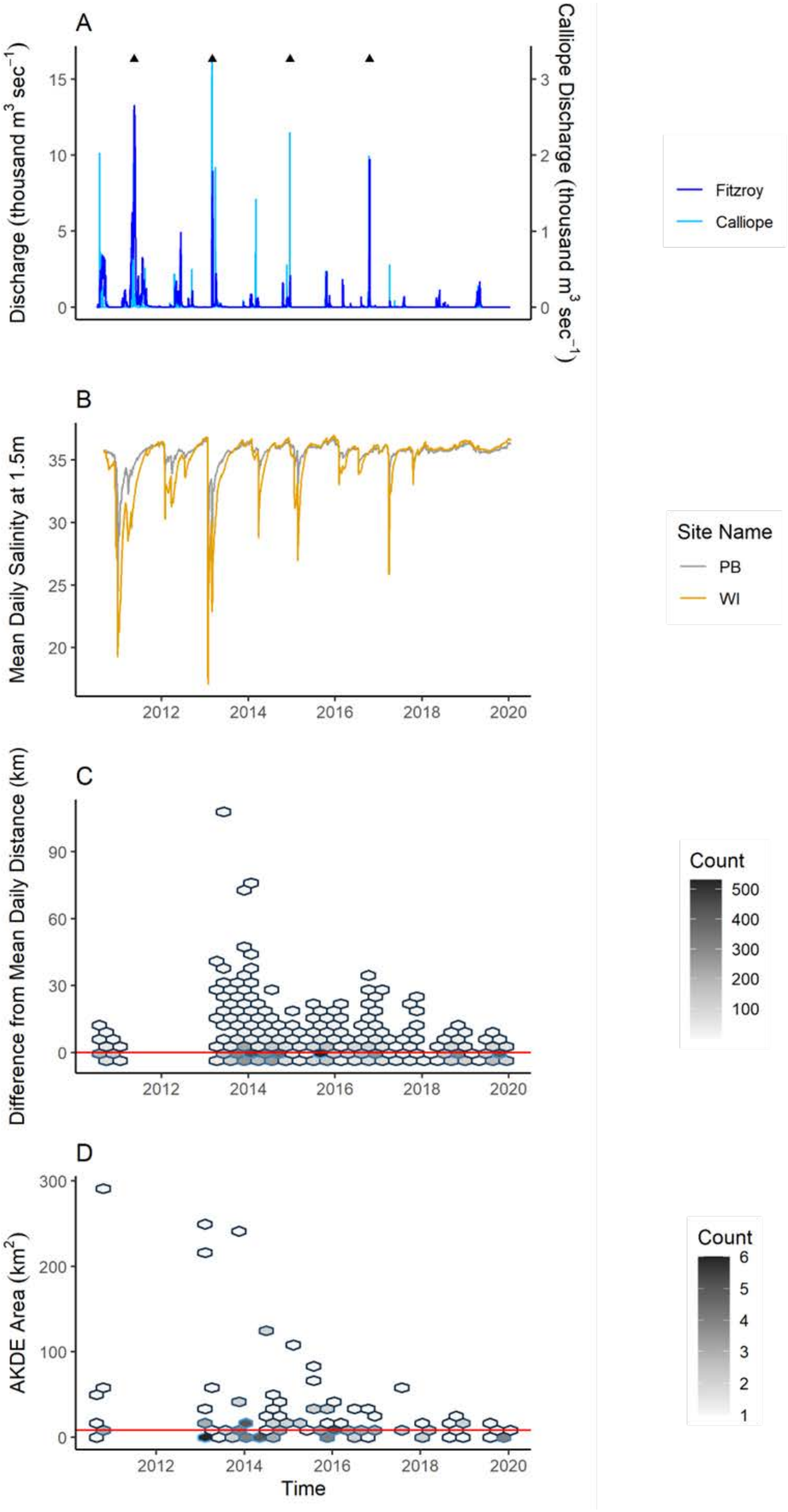

A
Discharge (thousand $m^3$ $sec^{-1}$)
0
5
10
15
Calliope Discharge (thousand $m^3$ $sec^{-1}$)
0
1
2
3
Fitzroy
Calliope
B
Mean Daily Salinity at 1.5m
20
25
30
35
2012
2014
2016
2018
2020
Site Name
PB
WI
C
Difference from Mean Daily Distance (km)
0
30
60
90
2012
2014
2016
2018
2020
Count
500
400
300
200
100
D
AKDE Area ($km^2$)
0
100
200
300
2012
2014
2016
2018
2020
Time
Count
6
5
4
3
2
1

Figure 11 For the study period 2010-2020: A) discharge from Fitzroy and Calliope Rivers showing major flood peaks (black triangles), B) salinity at 1.5m depth as measured at the Wiggins Island and Pelican Banks sites, C) difference between daily distance (sum of linear distances between each point recorded by individual per day) and the mean daily distance for all individuals for the study period (red line at 3.11 km), coloured by count (unique combinations of day-individual in each distance band) to indicate sampling distribution, D) area of 95% Utilisation Distribution from Autocorrelated Kernel Density Estimates for each individual binned over 3-month periods of the track, coloured by sample size (unique individuals in AKDE area band for each 3 month period; red line is the median AKDE area at 8.56 km$^2$)

## 3.5 Discussion

We identified four major flood peaks 2010-2020, which were followed by drops in salinity and increases in turbidity at two key monitored sites. Despite the floods' influence on the physical characteristics of the shallow inshore environment, there was no obvious deviation from the median calculated range size (AKDE) of tracked green turtles during or after the flood events (Figure 11), apart from large outliers in 2010 and 2013. The AKDE metric does not capture long range movements of individuals, as we removed non-range residents (individuals with small effective sample sizes or by variogram assessment) from this part of the analysis. Our study, therefore, does not identify strong evidence of relationship between extreme flood pulses and marine turtle space use.

Decades of persistence of megaherbivores at the site is a testament to their resilience to flood events. Green turtle growth rates are site dependent and reflect local environmental stochasticity and resultant food stock dynamics (103). For example, in Queensland foraging grounds, growth rates slow during extended ENSO periods featuring low sea surface temperatures and declines in macroalgal diversity and biomass (20,88). At Port Curtis, the body condition (ratio of carapace length to weight) of turtles captured within the 2011 flood plume footprint of the Boyne Estuary was poorer than those captured at other coastal foraging sites in Queensland, with chronic malnutrition as the primary diagnosis (179). This is evidence that during sub-optimal foraging conditions, green turtles persist at a site to the detriment of their body condition. Similarly, there is no evidence that green turtles, unlike dugongs, were spatially displaced by seagrass decline following the 2021/22 floods in Hervey Bay (213,219)

Nevertheless, five individuals travelled from the Pelican Banks to resettle at alternative foraging grounds >80km away. The timing of these departures coincides with the 12-month period in which seagrass dieback occurs following floods (82,220) for the identified flood events in 2013 (n=3 of 5) and 2015 (n=1 of 5). We discard developmental migration (93,207) as a potential explanation, which has been pointed to in previous records of long-distance movement during foraging (129) because the tracked individuals in our study were adults or large subadults (183). While shorter daily distances are characteristic of foraging or resting states (Figure 10B), except for short forays from foraging sites, the daily distances travelled by these five animals indicate directed travel behaviour (Figure 10C) over several days, similar to the travel speeds of migrating turtles (96).

We speculate two possible explanations for the observed behaviour:

1. A disturbance prompted long-range departures from Pelican Banks:

In the 10 years since tracking studies commenced, operations in the port have included expansion and deepening of existing shipping channels, the creation of new berth pockets and weirs, and in-filling land with dredge spoil (175). The average number of commercial vessels accessing the port has increased steadily since 2010 (221). This includes temporarily elevated vessel traffic in 2012 and 2013 associated with the construction of the Wiggins Island Coal Terminal and three Liquid Natural Gas facilities on the southern end of Curtis Island (222–224). Possible impacts of shipping activity include vessel strike, disturbance from noise and vibration, sediment resuspension disturbing habitats, fuel, oil or chemical spills (225). The five turtles that relocated to alternative foraging areas were all initially captured at Pelican Banks, outside of the footprint of dredge operations for the 2013 developments, which are likely to have elevated turbidity (i.e., 226). Because they inhabit shallow habitats, the mortality of green turtles by commercial and recreational vessel strikes is the highest among sea turtle species in Queensland (227). Whether boat traffic elicits a behavioural disturbance in green turtles is rarely documented. Boat presence and frequency of passing had no effect on the foraging or travelling time of sympatric dugongs inhabiting shallow inshore habitats (227). However, there is insufficient evidence to link the frequency of long-range departures with the timing of port operations. Similarly, green turtles tracked during major events such as cyclones, detonation experiments or planned constructions have been found not to alter their movement behaviour in response to those discrete events (M. Hamann, unpublished data, 2024 & 228). There is, therefore, limited evidence to suggest that this kind of behaviour could be attributed to discrete instances of anthropogenic disturbance.

2. Instability in habitat conditions prompted a few individuals to risk relocation to a new foraging site

Repeated flood events, in combination with increased pollutant loads of runoff likely led to declined habitat conditions by reducing the extent and diversity of seagrasses and their resilience to further environmental and anthropogenic disturbances in Port Curtis (176). Port Curtis, once a large expanse of seagrass, has shown a declining trend in biomass and cover alongside other coastal intertidal seagrass sites of the Great Barrier Reef (1999-2011) (229). At Pelican Banks, seagrass is the primary diet item for green turtles, while individuals occupying Wiggins Island also consume mangrove roots and shoots, algae, and zooplankton. This could explain why long-range movement was not evident in turtles caught and tracked from Wiggins Island. Analogously, green turtles were not observed in Brewers Bay for several weeks after Hurricane Irma removed shallow seagrass beds (230). Port Curtis' seagrass decline is well documented, and seagrasses are yet to return to pre-2011 flood conditions (176,209). The impact of seagrass decline on marine megaherbivores is evidenced by stranding rates of dugong post 2011 floods (99,177). Though dugong can exploit alternative food resources (231), unlike ectothermic green turtles, they cannot temporarily arrest their energy consumption and may be less resilient to prolonged food shortages (213,219,232). Therefore, relocation to alternative seagrass beds by dugongs is likely to precede algal feeding.

In Sandy Strait, approximately 250 km south of Port Curtis, long-distance movements of satellite-tracked foraging green turtles were recorded at a higher rate than in the present study (five of seven). These were all adult females. These individuals foraged across areas exceeding 30 km end to end (T. Shimada, unpublished data, 2024 & 118). Turtles at Sandy Strait have previously been shown to respond to seasonal temperature changes by expanding their habitat use in summer months (118). Like Port Curtis, the area receives freshwater input from a major river, the Mary, impacting the stability of seagrass resources. In comparison, of the green turtles tracked at Moreton Bay, Shoalwater Bay and Cardwell, none of which are impacted by major river outflows, three (adults, 2 female 1 male) of 29, one (adult male) of 15 and zero of five respectively, foraged over an expanded area (i.e., > 25 km across). At these sites green turtles did not achieve foraging ranges comparatively expansive to the maxima for individuals at Port Curtis and Sandy Strait [121.7 and 126.5 km$^2$ respectively (118)]. The tracking durations of the five individuals at Port Curtis that showed long range displacements were short (two to eight months), and we cannot be certain that turtles did not return to Port Curtis after the cessation of tracking. Thus, it is possible that those individuals were also foraging across an expanded range. A potential explanation is that adult turtles have learnt experience. During their life, performing exploratory forays, as described at Port Curtis (216), whether in response to poor habitat condition or otherwise, turtles may become aware of alternative foraging locations that they can return to when needed.

In general, green turtles show high fidelity to foraging areas, across decades, and under deteriorating conditions, but in our study, we present data indicating that turtles can relocate. Although our study is limited to a small number of turtles that relocated (n=5 of 80 tracked turtles), Pillans *et al.* 2021 (183) similarly reported unprecedented departure of green turtles from the Pelican Banks site during the 2013 study period based on acoustic telemetry. However, to determine whether chronic habitat change drives long-range foraging relocation in green turtles, behavioural, movement, and habitat quality data are needed overlapping pertinent flood periods and from other sites across their geographic range. Given the expense of satellite tracking, the difficulty of predicting floods and the logistical challenges of monitoring turtle behaviour and habitat quality these data are limited globally.

Ultimately, this study contributes to the evidence that long-range departures followed a period of intensive human and natural disturbance, leading to long-term habitat change. In degraded foraging habitat the advantages of long-term site familiarity conferred to resident herbivores by fidelity may be compromised, justifying the risk of moving to an unknown site for a few individuals.

# Chapter 4: Environmental drivers of local movement and residency

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Webster, E.G., Duce, S., Hamann, M., Murray, N., Shimada, T., Limpus, C. (2024). Should I stay or should I go? The influence of environmental conditions on green turtle residence time and outward transit in foraging areas. Marine Biology 171, 144. https://doi.org/10.1007/s00227-024-04450-1

## 4.1 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 habitats 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.

## 4.2 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 (204).

Green turtles (*Chelonia mydas*) are classified as endangered globally (35), 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 (176,208,209). Floods and resulting erosion also contribute to the loss of rhizomes and the seed bank, impacting recovery time of aquatic vegetation (82,233). Forbes *et al.* (106) 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 (100,116). 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 (89). 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 (11,234,235).

Green turtles are generally faithful to their foraging sites (92,118,128,216), often remaining at a site for months or years (87). Individuals who depart frequently return to these sites following displacement by people and post-breeding migrations (92). 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 (216). 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 (216).

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 (122,129,236–239). Though the species is tolerant of a range of temperatures (239), as ectotherms, green turtles typically demonstrate fidelity to foraging sites where temperatures are stable (129). Similarly, temperature and rainfall patterns dictate growth and senescence of primary producers (240,241), which are a key diet item for green turtles at non-reef neritic foraging grounds (e.g., seagrasses, algae, mangrove leaves and fruits) (31,101,106,111). Green turtles in Bermuda show increased local movement between foraging areas coinciding with periods of low food availability, attributed to increased foraging effort (242). Green turtle activity cycles (199,243), physiology (65,126,244) and orientation (125) are often linked to diel patterns, and tides provide intermittent access to intertidal habitat and can facilitate passive transport of foraging green turtles (125,176,204,208,237). 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 (31,245–247). 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 (32,91,93,207). However, while this is well described in the northern Atlantic (93,248), there are only a few records of developmental migration in eastern Australia (C. Limpus, unpublished data, 2022 & 87,91). Developmental migrations manifest on large scales ranging tens to thousands of km, though true distances are only known for a few populations (249). 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 (207,250). 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 (248,251) and in shallow mangrove edges (183). Turbid habitat may also provide protection from predators (77). Small turtles can also occupy small pools and shallow gutters at low tide while bigger turtles need to move into deeper waters (87,252). 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.

## 4.3 Methods

### *4.3.1 Study site*

Port Curtis (Figure 12) 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 (201). The intertidal and subtidal habitats include seagrass, mangroves and macroalgae, soft and hard corals, mud, sand, gravel, rock, and dredged channels (147).

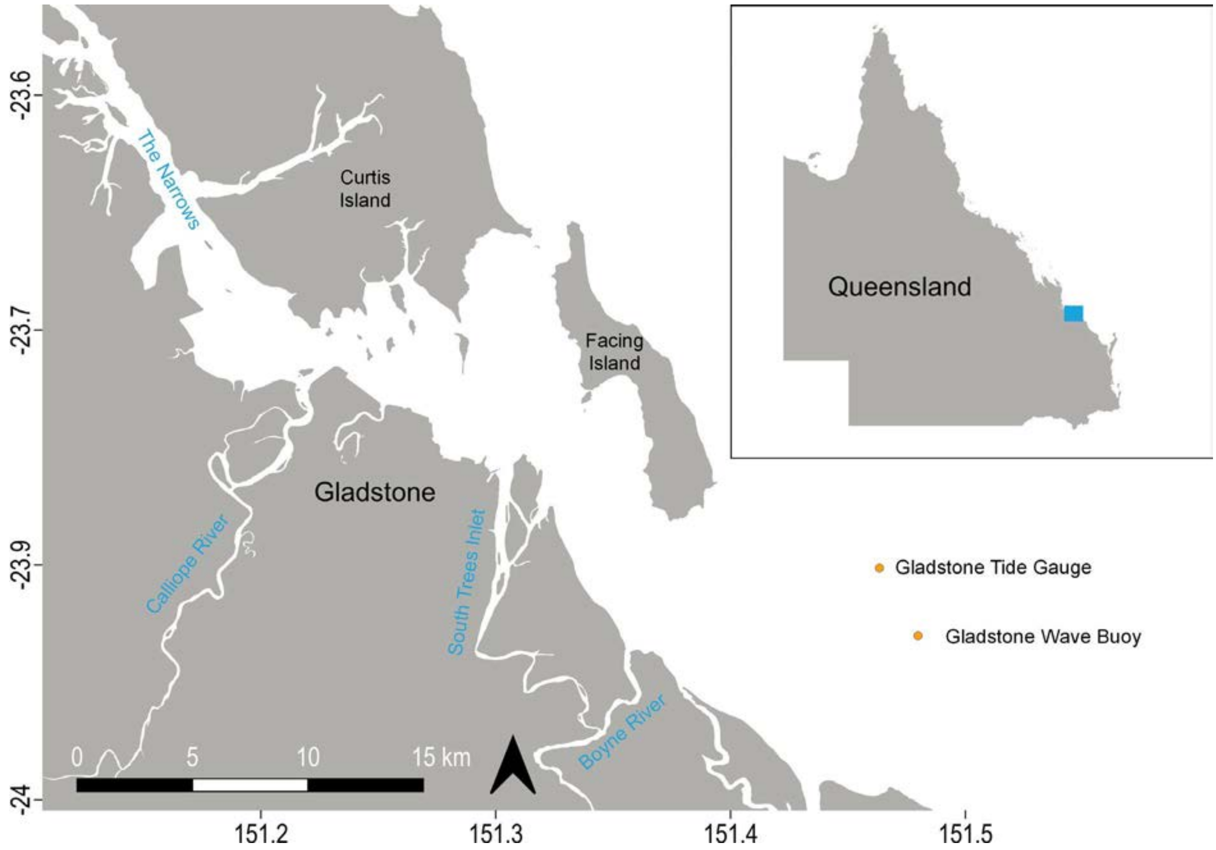


Figure 12 Site map of Port Curtis showing position in central Queensland, location of major freshwater outflows and the location of Gladstone Tide Gauge and Wave Buoy

### *4.3.2 Tracking data collection*

We collected Fastloc GPS (FGPS) tracks of 61 green turtles at Port Curtis. These are detailed in (216), 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) (146,147)

We filtered the tracking data to remove duplicates, spurious locations based on unrealistic travel speeds, and locations on land using the SDLfilter R package (147). 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 (216), substantially finer than the spatial resolution of the environmental data (Table 5). 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 preceding 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 site, corresponding to known breeding migrations of two tracked turtles.

### *4.3.3 Data analysis*

We used the residence time method with Lavielle partitioning (125,253,254) to partition each turtle's track into segments of distinct behaviours in the adehabitatLT R package (255). 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 (253). Mean residence time is assumed to increase in intensively used areas (253), thus we employed Lavielle partitioning of the turtle tracks based on mean residence time (125). 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. 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 5). For example, Blumenthal *et al.* 2010 (238) 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 5). 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 (256), temperature, salinity, turbidity (Secchi depth), estimated seagrass nitrogen (*Zostera*, *Halophila* and deep seagrass as separate covariates) (257,258), chlorophyll a (257,258), tide height (Australian Bureau of Meteorology and Queensland Department of Transport and Main Roads), significant wave height (DETSI coastal data system wave buoy) and time of day as covariates of interest (Table 5). 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 (147). The wave buoy and tide gauge were at up to 160 km straight line distance from the furthest tracked location.

Table 5 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 ($^{o}$C) | eReefs coupled hydrodynamic-biogeochemical model, with the most recent catchment forcing: GBR4_H2p0_B3p1_Cq3b, values at -0.5m depth (CSIRO, DETSI, AIMS and BoM, [52]) | 4 km | Daily | ● Thermoregulation (237).<br>● Tolerance of a range of temperatures (239).<br>● Juveniles have fidelity to feeding sites where temperature is stable (129).<br>● Previously found to have no effect due to small temperature range at Port Curtis (118). | 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 (118).<br>● Green turtle tolerance of a range of values (239). | |

| Covariate | Source | Spatial resolution | Temporal resolution | Examples of relationship to green turtle movement | Append method |
|---|---|---|---|---|---|
| Turbidity (Secchi depth in m) | | | | ● Counterintuitively, as turbidity increases, Secchi depth decreases.<br>● 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 (118). | |
| Seagrass nitrogen (concentration of nitrogen biomass in seagrass per $m^2$) | | | | ● Represents a foraging resource (59,259,260). | |
| Bathymetry (m) | Project 3D-GBR (256) | 100 m | Static | Related to benthic habitat, structure and food availability (109). | Extracted from raster pixel each location falls within |
| Tide height (m) | Gladstone tide gauge (Australian Bureau of Meteorology and Queensland Department of Transport and Main Roads, https://www.data.qld.gov.au/dataset/gladstone-tide-gauge-near-real-time-data/resource/7337fa8d-31f9-4056-a669-820c27e33f6a) | - | 10 minutes | Tides provide intermittent access to intertidal habitat, passive transport (109,151,183,261).<br>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 (147). |

| **Covariate** | **Source** | **Spatial resolution** | **Temporal resolution** | **Examples of relationship to green turtle movement** | **Append method** |
|---|---|---|---|---|---|
| Tide phase | Calculated from Gladstone tide gauge data (above) | - | 1 hour | Tides provide intermittent access to intertidal habitat, passive transport (109,151,183,261).<br>In Port Curtis currents are primarily tidal. | Identified high and low tides from 10 minute tide readings from the Gladstone tide gauge (above) with the HL.NL() function from the VulnToolkit R package (262). We assigned four tide phases; high and low tide were defined as being within one hour 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 second | Related to activity cycles, physiology (65,126,244) and visual navigation cues (125). | Assigned categories to each tracked location; sunrise and sunset inclusive of 1 hour 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 (263) package. |

| Covariate | Source | Spatial resolution | Temporal resolution | Examples of relationship to green turtle movement | Append method |
|---|---|---|---|---|---|
| Season | From timestamp of Fastloc GPS locations | - | 3 months | Reflects growth and senescence of primary producers (240), rain and temperature (241) 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-minute wave record, m) | Gladstone wave buoy (Queensland Department of Environment, Tourism, 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. |
| Sex (male, female or unidentified) | Laparoscopy during capture (Queensland Department of Environment, Tourism, Science, and Innovation) | - | - | Movement may occur in response to life history cues or intraspecific interactions (31,32,93,207,245–247,250). | |
| Maturity (juvenile, sub-adult or adult) | Laparoscopy during capture (Queensland Department of Environment, Tourism, Science, and Innovation) | - | - | Plasticity of behavioural strategies in juveniles, cohorts exploiting different resources. | |
| Size (curved carapace length) | Measured during capture (Queensland Department of Environment, Tourism, Science, and Innovation) | - | - | Plasticity of behavioural strategies in juveniles, cohorts exploiting different resources | |

### *4.3.4 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 (264).

### *4.3.5 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 (194) 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 (265). 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.

### *4.3.6 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 5) and one of four tide phases (high, low, outgoing, incoming) to the locations at the transition between ARS and transit segments (refer to Table 5). 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 (265). 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.

### *4.3.7 Delineation of ARS vs transit habitats*

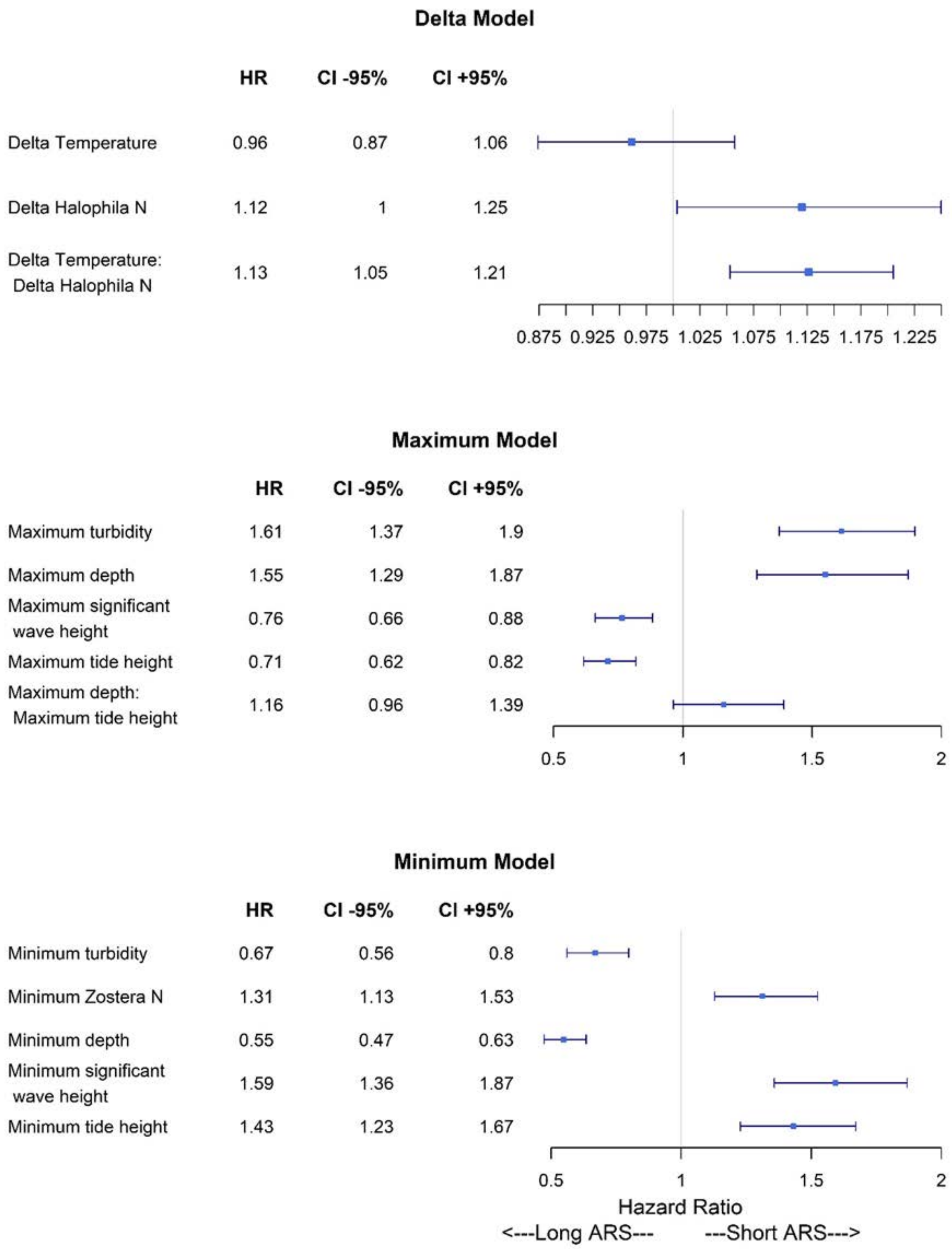
Habitats where ARS occurs are likely to contain essential resources for foraging and resting while there may be fewer habitat requirements to use an area for transit. We therefore created two movement-based kernel density estimates [MKDE in adehabitatHR (92,185,266)] for every turtle using (1) only ARS 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 (266).

## 4.4 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" (Appendix 7). ARS segments had a mean duration of 21.6 days (range 0-126.2 days) and transit of 33 days (0-96.9 days) (Appendix 7).

### *4.4.1 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 of temperature and *Halophila* nitrogen over time ('delta'), both had a significant effect on the duration of ARS when tested alone ($\chi2=8.42$, $p<0.01$; $\chi2=5.93$, $p<0.05$ respectively). However, there was a significant interaction between these two variables ($\chi2=11.96$, $p<0.001$; Appendix 3, Figure 13) 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 (Appendix 3, Figure 13). Milder (higher 'minimum') peak values of *Zostera* seagrass nitrogen resulted in shorter ARS segments (Appendix 3, Figure 13). 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.



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 |

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 |

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 |

Figure 13 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

### *4.4.2 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 (Appendix 4, Figure 14). 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 transit 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) (Appendix 5). 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.

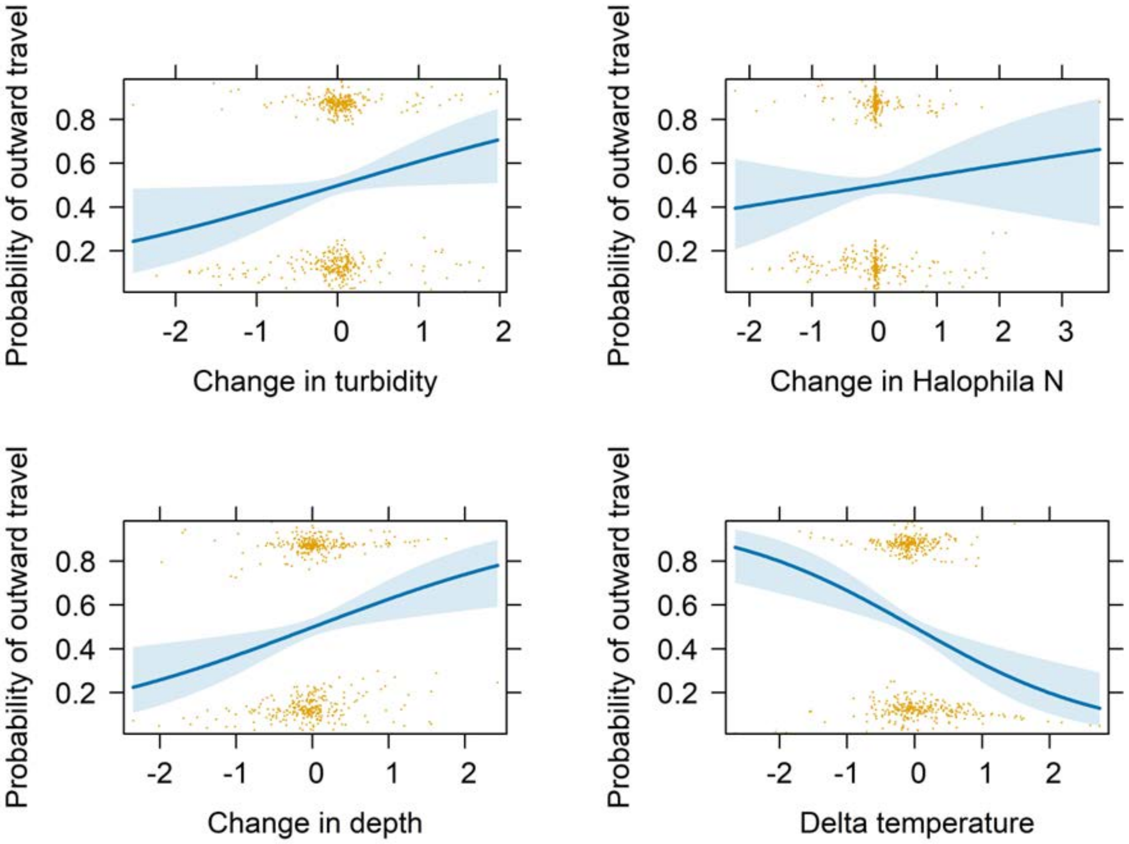


Figure 14 Combined logistic regression model showing the partial effects of the most influential covariates, change in turbidity (Secchi depth), change in *Halophila* seagrass nitrogen, change in depth (no effect) and delta temperature, on probability of outward travel, showing partial residuals

### ***4.4.3 Tidal and diel cycles***

Time of day significantly influenced whether turtles transitioned from ARS to transit, compared to transit to ARS ($\chi2=20.84$, df=3, $P<0.001$). Turtles were more likely to transition from ARS to transit at sunrise or at night compared to during daylight (Figure 15, Appendix 6). There was no significant effect of tide phase ($\chi2=0.34$, df=3, P=0.95) though movement away from a resident area was somewhat more probable at low tide (Figure 15). Season, sex, age class and their interactions did not influence the probability of outward transit.

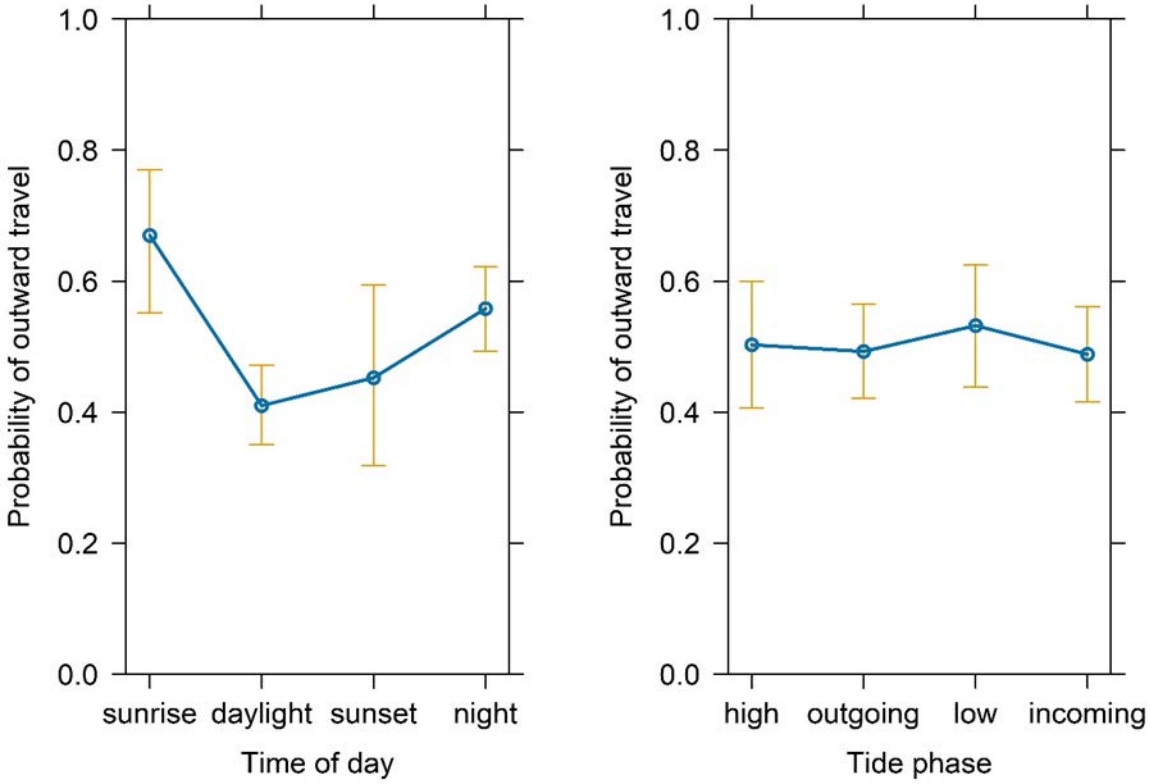


Figure 15 Fixed effects of generalised linear mixed model comparing probability of outward travel (±SE) across time-of-day periods and tide phases

### *4.4.4 Delineation of ARS vs transit habitats*

There was substantial overlap in the areas used for ARS and transit (Figure 16). However, the averaged ARS UD was considerably smaller in area (50%UD = 9.08 km$^2$, 95%UD=100.79 km$^2$) than that of transit (50%=174.28 km$^2$, 95%=192.36 km$^2$) (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.

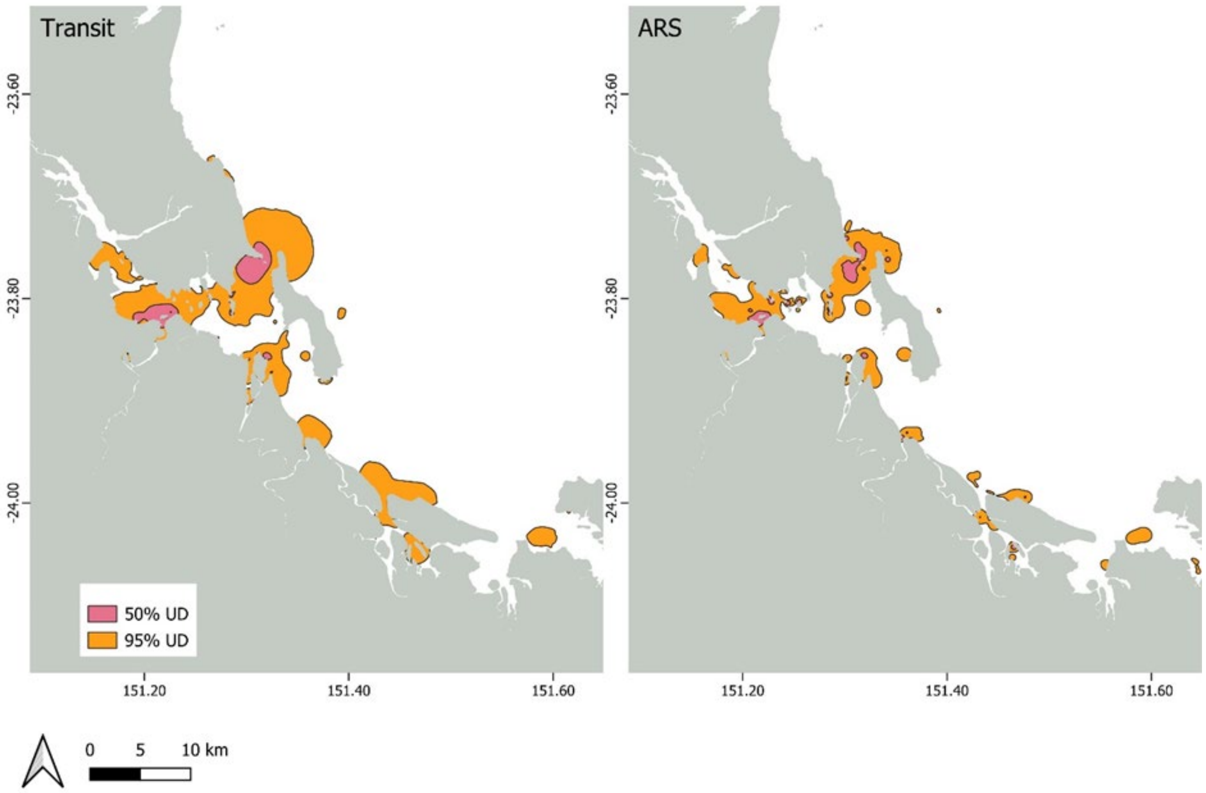


Figure 16 Map of probability density of occurrence from movement-based kernel density estimates from locations classified as transit (left panel) and ARS (right panel), averaged for all the tracked turtles, outlining the 50% and 95% utilisation distributions

## 4.5 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 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.

### *4.5.1 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 (100) and they stayed longer when there was an increase in the temperature that they experienced during the ARS segment.

### ***4.5.2 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 (201). 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 (267).

### ***4.5.3 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.

### ***4.5.4 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 (125,128). 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 (260), 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 (110,111). 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 (214).

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 (80,214,268). 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 microhabitats 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 (183). 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 (80,91,183). 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 (269). 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 (270). 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 (228). 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 (99,177)]. Nevertheless, foraging site fidelity is considered a favourable strategy under unpredictable environmental conditions (204). 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 (271). 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.

## 4.6 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.

## 4.7 Appendices

Appendix 3 Summary of selected (‘delta’, ‘minimum’ and ‘maximum’) Cox regression models (concordance=0.69, 0.79 and 0.84 respectively)

| | **coef** | **Exp(coef)** | **Se(coef)** | **Chisq** | **DF** | **P** |
|---|---|---|---|---|---|---|
| ‘delta’ | | | | | | |
| Delta temperature | -0.04 | 0.05 | 0.05 | 0.65 | 1 | 0.42 |
| Delta *Halophila* N | 0.11 | 0.06 | 0.06 | 4.11 | 1 | 0.04 |
| Delta temperature*delta *Halophila* N | 0.12 | 0.03 | 0.03 | 11.96 | 1 | <0.001 |
| Frailty(id) | | | | 22.17 | 15.4 | 0.12 |
| Minimum | | | | | | |
| Minimum Secchi depth | -0.40 | 0.09 | 0.08 | 19.95 | 1 | <0.001 |
| Minimum *Zostera* N | 0.27 | .008 | 0.07 | 12.56 | 1 | <0.001 |
| Minimum depth | -0.60 | 0.07 | 0.07 | 64.51 | 1 | <0.001 |
| Minimum significant wave height | 0.47 | 0.08 | 0.07 | 32.68 | 1 | <0.001 |
| Minimum tide height | 0.36 | 0.08 | 0.08 | 20.73 | 1 | <0.001 |
| Frailty(id) | | | | 63.23 | | <0.001 |
| Maximum | | | | | | |

| | coef | Exp(coef) | Se(coef) | Chisq | DF | P |
|---|---|---|---|---|---|---|
| Maximum Secchi depth | 0.48 | 0.08 | 0.07 | 33.60 | 1 | <0.001 |
| Maximum depth | 0.44 | 0.10 | 0.09 | 21.02 | 1 | <0.001 |
| Maximum significant wave height | -0.27 | 0.07 | 0.07 | 13.24 | 1 | <0.001 |
| Maximum tide height | -0.34 | 0.07 | 0.07 | 22.41 | 1 | <0.001 |
| Maximum depth*maximum tide height | 0.15 | 0.09 | 0.09 | 2.45 | 1 | 0.11 |
| Frailty(id) | | | | 63.04 | 28.5 | <0.001 |

Appendix 4 Results of mixed effects linear regression model to assess the influence of change in Secchi depth, change in depth and delta temperature on the probability of a turtle transitioning from ARS to transit compared to transit to ARS. Turtle id was included as a random effect

| | Estimate | SE | z | P |
|---|---|---|---|---|
| Intercept | -0.01 | 0.08 | -0.07 | 0.95 |
| Change in Secchi depth | 0.45 | 0.21 | 2.10 | 0.04 |
| Change in *Halophila* N | 0.19 | 0.21 | 0.92 | 0.36 |
| Change in depth | 0.52 | 0.19 | 2.84 | <0.01 |
| Delta temperature | -0.69 | 0.19 | -3.70 | <0.001 |

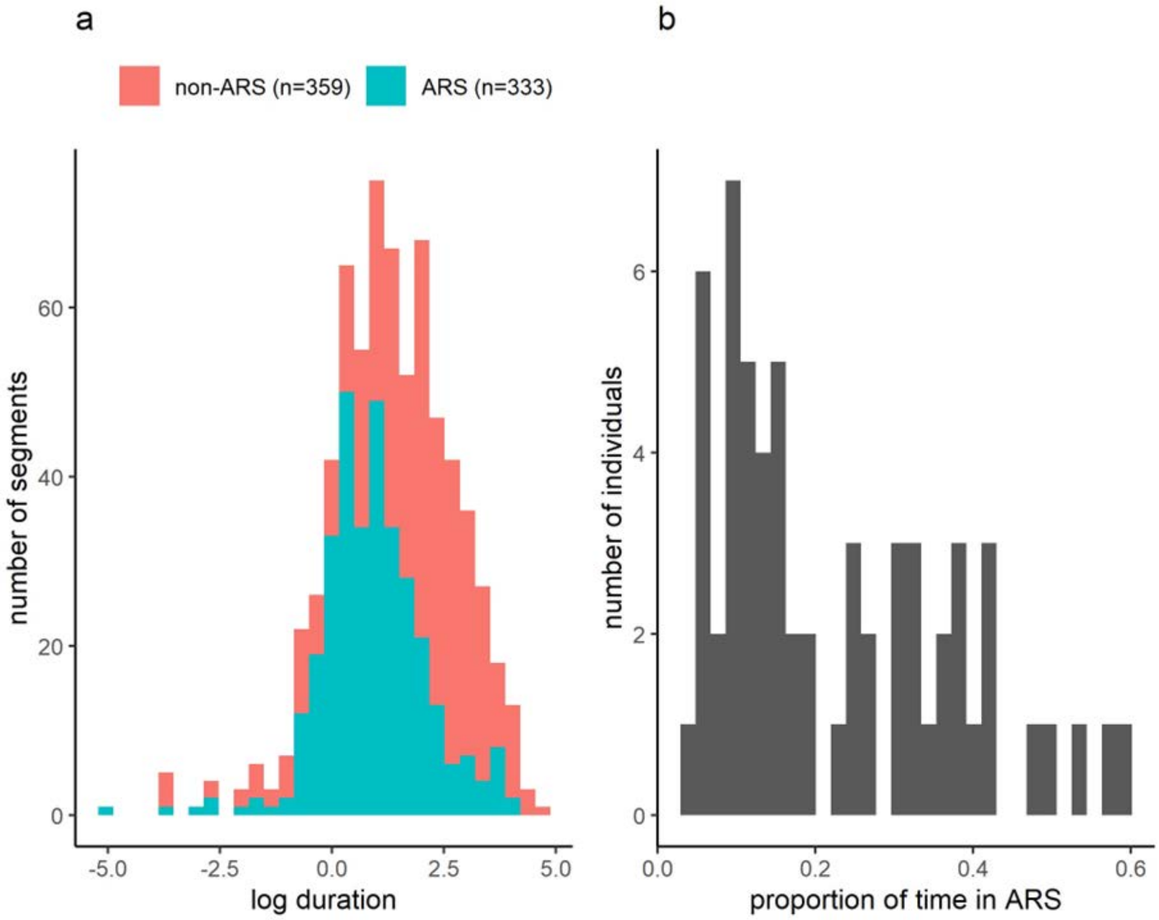
Appendix 5 results of F-tests performed separately on each covariate comparing the variance in that covariate at ARS to transit, and transit to ARS transition points. Random effects were ignored

| **Covariate** | **F** | **Df1, df2** | **p** |
|---|---|---|---|
| Change in temp | 0.77 | 290,291 | 0.03 |
| Change in Secchi depth | 0.55 | 290,291 | <0.0001 |
| Change in salinity | 0.48 | 290,291 | <0.0001 |
| Change in *Zostera* N | 0.42 | 290,291 | <0.0001 |
| Change in depth | 0.73 | 290,291 | <0.0001 |
| Change in wave height | 1.05 | 290,291 | 0.66 |
| Change in *Halophila* N | 0.52 | 290,291 | <0.0001 |
| Change in deep seagrass N | 0.55 | 290,281 | <0.0001 |
| Change in chla | 0.60 | 290,291 | <0.0001 |
| Delta temperature | 0.34 | 290,291 | <0.0001 |
| Delta Secchi depth | 0.44 | 290,291 | <0.0001 |
| Delta salinity | 0.31 | 290,291 | <0.0001 |
| Delta *Zostera* N | 0.25 | 290,291 | <0.0001 |
| Delta depth | 0.18 | 290,291 | <0.0001 |
| Delta wave height | 0.61 | 290,291 | <0.0001 |
| Delta *Halophila* N | 0.25 | 290,291 | <0.0001 |
| Delta deep seagrass N | 0.24 | 290,281 | <0.0001 |
| Delta chla | 0.72 | 290,291 | <0.01 |

Appendix 6 Results of generalised linear mixed effects model to compare the probability of ARS-transit and transit-ARS across time of day and tidal phase. Results are shown in comparison to the reference categories ‘sunrise’ and ‘high tide’

| | **Estimate** | **SE** | **z** | **P** |
|---|---|---|---|---|
| Intercept | 0.67 | 0.32 | 2.05 | 0.04 |
| Daylight | -1.08 | 0.28 | -3.77 | <0.01 |
| Sunset | -0.87 | 0.39 | -2.24 | <0.03 |
| Night | -0.41 | 0.29 | -1.44 | 0.15 |
| Low tide | 0.13 | 0.28 | 0.47 | 0.64 |
| Outgoing tide | 0.02 | 0.25 | 0.09 | 0.92 |
| Incoming tide | -0.00 | 0.25 | -0.01 | 0.99 |

Appendix 7 a frequency distribution of durations of ARS and transit segments as determined by track partitioning, b frequency distribution of the proportion of the total track of individuals classified as ARS according to the track partitioning



# Chapter 5: A dynamic foraging habitat distribution estimate for green turtles in the Great Barrier Reef

## 5.1 Abstract

A detailed understanding of how protected species use their habitats can guide management interventions in areas of high human use. We develop telemetry-based habitat models with boosted regression trees to identify the environmental characteristics underpinning foraging habitat suitability for green turtles in the Great Barrier Reef region. We fit models to green turtle Fastloc GPS tracks from both modified and unmodified inshore foraging sites and using two types of pseudo-absences (background sampling and simulated correlated random walks). Different diet items and physical characteristics underpin turtle presence at modified compared to unmodified sites. We assess model performance by the ability to predict known foraging areas, true skill statistic, explanatory power (percent deviance explained) and predictive skill (AUC) of the models. We then predict potentially suitable foraging areas for green turtles in the Great Barrier Reef region using the model for unmodified habitats with correlated random walk pseudo-absences. Between 2010 and 2022, the total area of suitable foraging habitat declined, and nearshore habitat suitability retracted. In 2022, 50.0% of the predicted suitable habitat fell within habitat protection zones, and 19.4% in Marine National Park Zones of the Great Barrier Reef Marine Park. A detailed foraging distribution of the species is not established at this regional scale. Identifying which biophysical drivers are most important to infer possible foraging habitat in less data rich regions in Australia and overseas. Evaluating changes over time in habitat distribution provides insights into the degree to which broad-scale environmental changes and anthropogenic activities influence the condition of function of habitats, even within protected area boundaries.

## 5.2 Introduction

Detailed spatio-temporal information about how animals use their habitats both advances ecological knowledge and can be incorporated into systematic conservation planning to manage harmful human-wildlife interactions (153) and human activity that mediates habitat quality. For protected species, mitigating human-wildlife interactions in areas outside of marine park jurisdiction, such as within designated port areas, is considered to be a high priority (71). Human impacts on habitats, if not mediated, can affect populations of species at multiple life stages.

Habitat quality underpins population health for the green turtle *Chelonia mydas* (22,100), and is mediated by natural and anthropogenic disturbances. Foraging habitat for *C. mydas* includes subtidal and intertidal seagrass or algal flats, coral or rocky reefs, and estuarine areas. In eastern Australia, fewer female green turtles can acquire condition for breeding following flood years, because the influx of chemicals and sediment into coastal foraging grounds generally leads to reductions in the quantity/quality of their benthic food resources, most famously, seagrass (100).

The majority (97%) of eastern Queensland coastal waters lie within state or federal protected areas (79,80). Nevertheless, in eastern Queensland foraging areas, threats to green turtles include Indigenous harvest, boat strike, entanglement and ingestion of marine debris and habitat degradation (23,80,86,87), with the impacts of coastal degradation the most problematic to quantify and address. Much of coastal foraging habitat is coming under increasing pressure due to coastal developments, both urban and industrial such as habitat modification, chemical and terrestrial discharge, noise and light disturbance and vessel interactions (60,80,175). In shared marine spaces, aside from stranding records, there is generally a paucity of information on interactions between industry and marine turtles.

Green turtles occupy neritic foraging areas across age and sex cohorts and display high foraging site fidelity (92). There is evidence to suggest that they are not displaced by chronic and acute disturbances (89,228,230). Therefore, knowing where foraging habitats are distributed is important to manage new activities and existing human activities in and adjacent to these habitats appropriately to minimise risks to health and survivorship of turtles and maintain the health of their habitats e.g., go slow zones in shallow areas to reduce risk of boat strikes and protection measures to maintain seagrass presence and density.

Green turtles' tendency to remain in place, or continually return to a place, makes them vulnerable to habitat modifications. Safeguarding existing habitats is, therefore, crucial for the maintenance of turtle populations. Although green turtles may remain in altered habitats, attempts to understand how they do and do not respond to changes in their foraging habitat are relatively recent. For example, green turtle resource requirements, namely the relative contribution of animal prey to their diet (104), are not well understood.

Obtaining sufficiently detailed species location data for establishing knowledge about the distribution of habitats can be challenging. Delineating foraging areas is an important component of stock assessments and the definition of Key Biodiversity Areas (272) and Biologically Important Areas (273), however, the location of these habitats is largely unknown in areas that are difficult to access, or far away from human population centres. Aerial survey of the Great Barrier Reef region (219) captures a snapshot of adult marine turtle distribution, but does not distinguish between foraging, migrating and breeding life stages, and therefore cannot be used to make inferences about habitat use and resource requirements.

Satellite telemetry can provide observations of highly mobile species with high spatial and temporal accuracy, but it is expensive to collect, meaning sample sizes are generally small. Habitat information may be derived from remotely sensed data or modelled, but collating data collected for different purposes and by different methods can make it challenging to match the scale, resolution, and extent of datasets. Similarly, not all habitat variables are measurable and not all environmental data sources are publicly available. Nevertheless, integrating information from multiple biophysical and environmental datasets can improve estimates of spatio-temporal patterns of species distribution and enable habitat boundaries to be developed (274).

This study targets actions for the management of green turtles that were explicitly identified by the Queensland Marine Turtle Conservation Strategy in 2021 (71): “identify important inshore, shallow foraging grounds” (for the sGBR and nGBR genetic stocks); “assess the risk to those areas that are not currently protected and consider the most appropriate habitat mechanisms to ensure protection” (sGBR and nGBR), and “recording changes over time in foraging habitat”.

Based on these identified needs, this study aims to integrate green turtle satellite telemetry with publicly available spatial and spatio-temporal environmental datasets to develop telemetry-based habitat models that establish;

1. What characteristics make foraging habitat suitable for green turtles?
2. What is the distribution of suitable foraging habitat for green turtles in the Great Barrier Reef inshore region?
3. How has the extent and distribution of suitable foraging habitat in the region changed over time?
4. How much of these sites are protected?

To our knowledge, previous attempts to ascertain the distribution of foraging green turtles at a regional scale have relied on expert input rather than a quantitative approach (275). Opportunities for threat mitigation arise where habitat distributions highlight an overlap between habitat and expanding anthropogenic footprints. Therefore, this study serves as a baseline for assessing the risk of human-wildlife interactions based on modelled distribution of green turtle foraging habitat in space/time.

## 5.3 Methods

### *5.3.1 Study sites*

Turtles were tracked during foraging at Port Curtis, Shoalwater Bay and post-nesting from Raine Island (Figure 17). Port Curtis (Figure 17C) is a major multi-commodity port, in central Queensland, described in detail in (216). Shoalwater Bay (Figure 17B) in central Queensland is a heritage-listed, shallow estuarine area receiving numerous freshwater inputs. As a military training area, Shoalwater Bay experiences minimal disturbance from human activities. The bay is bordered by mangroves, contains fringing reefs, rocky shores and supports extensive seagrass meadows.

Raine Island (Figure 17A), 120 km from the mainland in the northern Great Barrier Reef is the largest green turtle rookery in the world. Green turtles nesting at Raine Island largely pertain to the northern Great Barrier Reef genetic stock and migrate to Raine Island from foraging grounds along the shallow coast of eastern Australia or coral reefs. For this study, we considered Port Curtis to be highly modified and Shoalwater Bay and Raine Island to be unmodified.

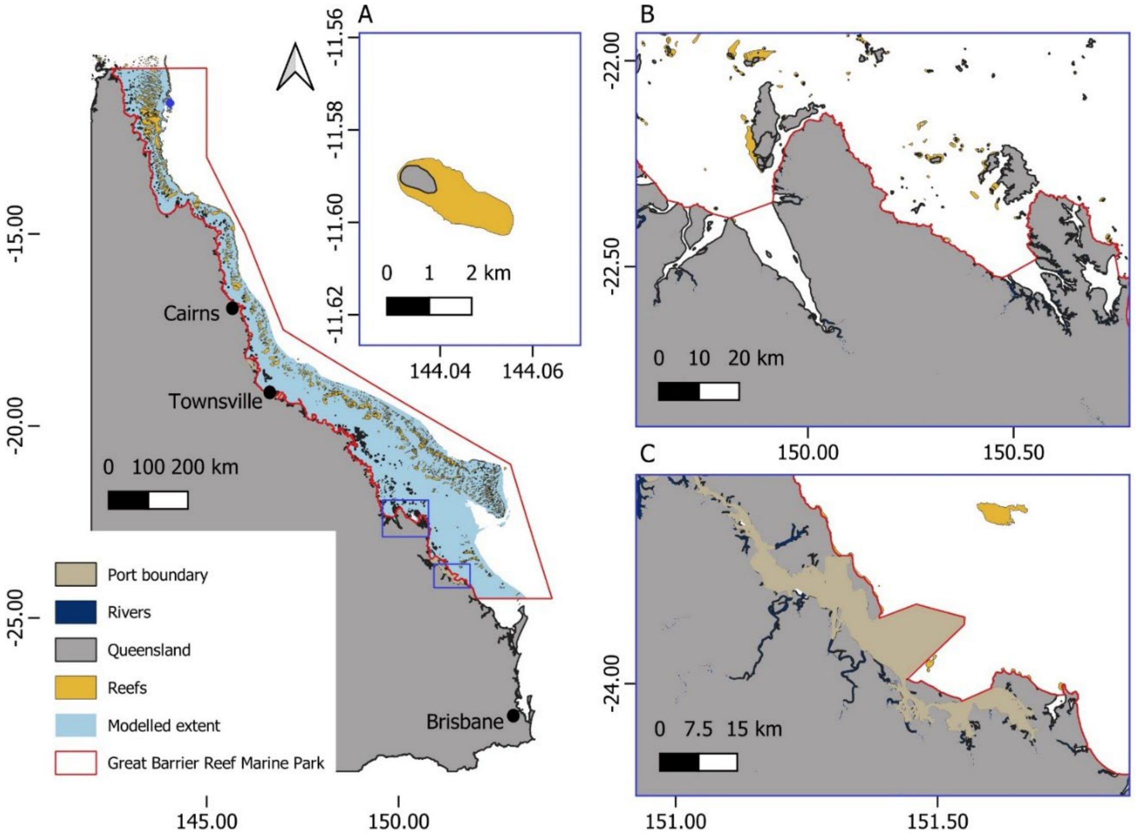


Figure 17 Map of Queensland with blue overlays indicating three study sites where green turtles were deployed, A. Raine Island, B. Shoalwater Bay and C. Port Curtis

### *5.3.2 Satellite tracker deployment*

Green turtles were captured as detailed in (2,216). Turtles were tracked with Fastloc GPS (mean error 40m) and/or ARGOS tags (mean error ranging <1km to >10km) opportunistically between 2010 and 2021, resulting in a mixed sample of sex and maturity cohorts across the three study sites (Appendix 8, Figure 17). This study included 85 foraging turtles from Port Curtis, 4 from

Shoalwater Bay, and 5 females tagged while nesting at Raine Island who were tracked post-nesting to foraging sites within the Great Barrier Reef World Heritage Area. Sex, maturity and curved carapace length (CCL) were recorded for each tracked individual. Capture of turtles, transmitter attachment and data collection for this study were approved by either the JCU Animal Ethics Committee or the Department of Agriculture and Fisheries Ethics Committee and conducted within an approved Queensland Government project.

### *5.3.3 Tracking data filtering*

We discarded the first 24 hours of the tracks from Port Curtis and Shoalwater Bay. We removed duplicates and empty rows, spurious locations determined from unrealistic travel speeds and turning angles, and locations falling above the high tide line using the SDLfilter R package (147). We treated tracks as independent when a single track contained gaps of more than 72 hours between successive locations, and only retained independent tracks consisting of more than 20 locations. We used both Fast-loc GPS and ARGOS locations where available, but only retained ARGOS points with location classes 1, 2 and 3. We removed nesting and post-nesting tracks of Raine Island turtles by visually identifying the end of directed travel from Raine Island. We also removed possible breeding migrations of Port Curtis turtles identified as a long-distance (greater than 150 km) departure from their release site to known breeding sites for the species during summer months.

The tracking dataset post-filtering included 85 turtles at Port Curtis (mean±SD CCL= 84.78±21.66 cm), 4 at Shoalwater Bay (mean±SD CCL= 92.93±2.33 cm) and 5 from Raine Island (mean±SD CCL= 102.89±2.72 cm). The Port Curtis turtles comprised of 35 females, 36 males and 14 unidentified sex, and the Shoalwater Bay were 1 female and 3 males. The Raine Island turtles were all post-nesting adult females. We note that 18 juveniles and 24 subadult turtles were tracked at Port Curtis (49% of turtles in modified habitats were immature), while only 1 juvenile was tracked at Shoalwater Bay (11% of turtles in unmodified habitats were immature).

### *5.3.4 Telemetry-based habitat models*

To identify the environmental characteristics that make foraging habitat suitable for green turtles we developed telemetry-based habitat models. These models combine species presences and pseudo-absences generated from telemetry data with environmental data to identify environmental predictors underpinning species presence and can be used to predict distributions in space and time. We adopted the approach of (276). Though similar to species distribution modelling, telemetry-based habitat modelling does not use abundance or true presence data to simulate a realized distribution of a species. Instead, presences derived from tracking are non-random and therefore spatially biased, and pseudo-absences are simulated to control for these biases. The model output reflects the habitat conditions that best explain turtle presence.

#### 5.3.4.1 Presences and pseudo-absences

We derived presences from the tracking data by selecting regular locations in time, and accounting for telemetry error, with time-varying move persistence models in the aniMotum R package (277). We have attempted to reduce autocorrelation and imperfect detection biases with state space models (movement persistence models), which interpolated the irregularly sampled data points to produce an estimated location at at least 12-hour intervals (277,278). We assumed the data had symmetric spatial error, using aniMotum's default error margins for ARGOS locations, and estimated error from (216) for Fast-loc GPS. For each independent track, we examined state-space models with diagnostic visualisations of 1) a time-series, b) qq-plots and c) autocorrelation functions.By visually examination of candidate state-space model outputs we determined the most appropriate timestep, 12 hours where possible, or lower resolution models for tracks with sparser data (24 or 48 hours). Sparse data resulted in non-convergence or unrealistic patterns (straight lines or perfect loops), which were discarded.

We generated pseudo-absences via both background sampling (i.e., within a bounding box that encompasses all tracked locations, randomly generating 100 points around each location, and assigning these points the same time stamp and step number as the tracked location. This is done to capture the full range of conditions where animals could be present) and correlated random walks (CRW, i.e., where the animal could have gone based on track simulations defined by step lengths and turning angles from the interpolated tracking data, Appendix 9) as per (276). We used two pseudo-absence types to enable us to make inferences about habitat use on broad and fine scales respectively. Background models were used to infer drivers of turtle presences on large scales, and CRW on local scales. Our approach assumes presences and pseudo-absences are independent, despite tracking data being inherently autocorrelated in space and time. Turtles tracked for longer are more represented in the presence/pseudo-absences, as are turtles tracked in Port Curtis compared to other sites (Appendix 9).

#### 5.3.4.2 Environmental predictors

To investigate the relationship between probability of turtle presence and environmental conditions, we developed a set of environmental predictor layers from which to ascertain the conditions at each tracked location in space and time. We catalogued freely available environmental datasets with spatial coverage of the coastal Great Barrier Reef region, and selected variables with known relevance to green turtle foraging ecology based on current literature, with at least 4 km spatial resolution, and appropriate temporal coverage of the tracking period (static datasets developed since 2010 or time-varying spatial data covering late 2010 to late 2019). Selected datasets are summarized in Table 6.

Table 6 Selected datasets from which environmental predictors were derived for telemetry-based habitat modelling

| Data source | Variables selected | Resolution | Temporal resolution | Temporal range | Scale | Append method OR Transformations applied | Rationale for inclusion |
|---|---|---|---|---|---|---|---|
| eReefs hydrodynamic model (257,279) | Temperature,<br>Salinity,<br>Mean seawater velocity,<br>Mean wind speed | 4 km | daily | Sep 2010 to present | GBR | Extracted values at corresponding pixels (in space and time) | Thermoregulation (236,237)<br>Tolerance of a range of temperatures (129).<br>Juveniles have fidelity to feeding sites where temperature is stable (129,239).<br>Small temperature range at Port Curtis (92,118).<br>Chronically high values would affect primary producers (82,209).<br>Green turtle tolerance of a range of values (23).<br>Tides provide intermittent access to intertidal habitat. Currents aid passive transport (244).<br>In Port Curtis currents are primarily tidal.<br>Possible windborne navigational cues (280,281).<br>Wind direction affects water movement – currents and wave action. |
| eReefs biogeochemical model (258,282) | Secchi depth,<br>Ecology fine inorganics (EFI i.e., sum of fine sediment and mud concentrations, derived as total suspended solids/1000),<br>Large zooplankton nitrogen | 4 km | daily | Dec 2010 to Apr 2019 | GBR | Extracted values at corresponding pixels (in space and time) | Chronically high values affect primary producers (82,209).<br>Sediment and chemical influx and resuspension affect primary producers and are associated with toxicity and pathogens in turtles (178).<br>Food source (104,283) |

| Data source | Variables selected | Resolution | Temporal resolution | Temporal range | Scale | Append method OR Transformations applied | Rationale for inclusion |
|---|---|---|---|---|---|---|---|
| Digital Earth Australia (284) | Mangrove canopy cover (Landsat): "Distance to mangroves" | 30 m | annual | 1987-2022 | National | Distance to pixels of at least 20% canopy cover in corresponding year | Food source (110) |
| Geoscience Australia Intertidal Model Relative Extents (285) | Tidal exposure | 25 m | static | 1987-2015 | National | Extracted values at corresponding pixels (in space only) | Intermittent access to intertidal habitat (244). |
| Carter (NESP TWQ Project 5.4, TropWATER, JCU) (286) | Seagrass probability | 30 m | Static | 1984-2023 | Coastal GBR | Extracted values at corresponding pixels (in space only) | Food source (101,114) |
| Carter (NESP TWQ Project 5.4, TropWATER, JCU) (286) | Seagrass community type | categorical | static | 1984-2023 | Coastal GBR | Overlap with polygon feature | Food source (101,114) |
| (287) | Geomorphology | categorical | static | 2008 | National | Overlap with polygon feature | Structural features for foraging, resting and predator avoidance (91,201) |
| Queensland transport and main roads (288) | Recreational boating facilities: "Distance to boat ramps" | Categorical | Static | 2021 | Queensland | Distance to pixels containing features | Modified structural features for foraging, resting and predator avoidance (91,201). |
| Geoscience Australia Intertidal Model Relative Extents (285) | Distance to coast | 25 m | Static | | Queensland | Distance to nearest pixel exposed at highest 80-100% of the observed tidal range (land) | Documented as influential in prior studies |
| GBRMPA GBR features (289) | Distance to reefs | Categorical | Static | 2003 | Queensland | Distance to nearest 'reef' pixel | Food source (106,112). Structural features for foraging, resting and predator avoidance (201) |
| Geoscience Australia Surface Hydrology Polygons (290) | Distance to rivers | Categorical | Static | 2015 | Queensland | Distance to nearest 'river' pixel | Diseases in coastal populations are associated with chemical and sediment runoff from river outflows (70,89,178). Brackish food resources (mangroves, crustaceans, ctenophores) (31,110). Shelter for resting and predator avoidance (201,235). |
| Geoscience Australia (291) | Geomorphic habitats of Australia: "Geohabitat" | 30 m | Static | 2005 | Coastal national | Overlap with polygon feature | Structural features for foraging, resting and predator |

| Data source | Variables selected | Resolution | Temporal resolution | Temporal range | Scale | Append method OR Transformations applied | Rationale for inclusion |
|---|---|---|---|---|---|---|---|
| | | | | | | | avoidance (201,235) |
| Marine monitoring program (TropWATER) (292) | Long-term frequency of water types 1 and 2: "Acute flood frequency" | 250 – 1000 m (MODIS and Sentinel) | Static | 2002-2022/23 summer | GBR | Extracted values at corresponding pixels (in space only) | Sediment and chemical influx and resuspension affect primary producers (82) and are associated with toxicity and pathogens (70,89,178). Acute events. |
| Marine monitoring program (TropWATER) (292) | Long-term exposure to above guideline value concentrations of land-sourced pollutants: "Chronic floodwater exposure" | 250 – 1000 m (MODIS and Sentinel) | Static | 2002-2022/23 summer | GBR | Extracted values at corresponding pixels (in space only) | Sediment and chemical influx and resuspension affect primary producers (82) and are associated with toxicity and pathogens (70,89,178). Chronic conditions |
| Beaman 2017 (256) | Bathymetry,<br>Rugosity,<br>Slope | 100 m | Static | 2018 | GBR | Extracted values at corresponding pixels (in space only). Ruggedness was calculated with QGIS "Terrain Ruggedness Index" and Slope with QGIS Raster analysis "Slope" tool. | Green turtles in foraging grounds throughout coastal Queensland and the GBR most frequently occupy depths 0-30m and rarely below 60 m (80). Rugosity and slope may be indicative of geomorphic habitat type, physical structures and benthic communities. |

We sampled values of each environmental predictor for each presence and pseudo-absence point corresponding to their timestamp and location. For static datasets (a single, non-time-varying layer) (Table 6) we used terra::extract() for grid data, and sp::over() for shapefile (categorical) data. We extracted values of eReefs variables via a custom R script to query the AIMS THREDDS server. We downloaded annual mangrove maps (284) from the Digital Earth Australia data cube using Dask and used these to generate annual maps of Euclidean distance to pixels of at least 20% canopy cover [i.e., minimum class where mangroves were present in the mangrove dataset (284)] in QGIS. Additionally, we generated 30m (to match the high resolution of bathymetry data) grids of distance to recreational boating facilities, distance to coast, distance to reefs, and distance to rivers in QGIS (details in Table 6). Prior to modelling, we evaluated the temporal coverage of the variables derived from the eReefs biogeochemical model, with data hosted on the THREDDS server ceasing in April

2019. We therefore removed presences and pseudo-absences corresponding with timestamps after April 2019.

#### 5.3.4.3 Modeling approach

We used boosted regression trees to develop the telemetry-based habitat models for 1) the entire dataset (hereby 'global' model), 2) modified and 3) unmodified sites separately, with the gbm.fixed() function of the dismo R package (293). For each model formulation, we adapted the approach outlined in (294), creating separate models with background sampling (3 models) and CRW pseudoabsences (3 models). This approach assumes that presences are not autocorrelated (276,294).

We randomly sampled 75% of the combined presences and pseudo-absences data for training and retained the remaining 25% for testing. We used a tree complexity of 5, learning rate of 0.005, 2000 trees, and a bag fraction of 0.75. Hyper-parameters were chosen to match those used in (276), and informed by (294). We plotted the relationship of each predictor in the input data with the response, to inform our specification of the var.monotone argument of gbm.fixed(). We evaluated pruning parameters with out of bag cross-validation and increased the number of trees to 9000 for the CRW model, the number of iterations at which mean change in predictive deviance reached a minimum. We evaluated each model's predictive skill with area under the curve (AUC) and true skill statistic (TSS), and its explanatory power with percent deviance explained.

To investigate environmental predictors in relation to foraging habitat for green turtles, we obtained a ranking of the most influential environmental predictors. Variable importance is assessed as the total contribution by each variable to a reduction in the loss function. We visually examined the shape of the relationship with the response for each predictor with variable importance greater than 100/number of predictors in the model, with partial deviance plots. Influential two-way interactions were identified with gbm.interactions().

To estimate the distribution of suitable foraging habitat for green turtles in the Great Barrier Reef inshore region, we first created grids of each environmental predictor, with matching projection (EPSG: 3577), origin, resolution (500 m pixels), and extent (clipped to the extent of the (286) seagrass dataset).

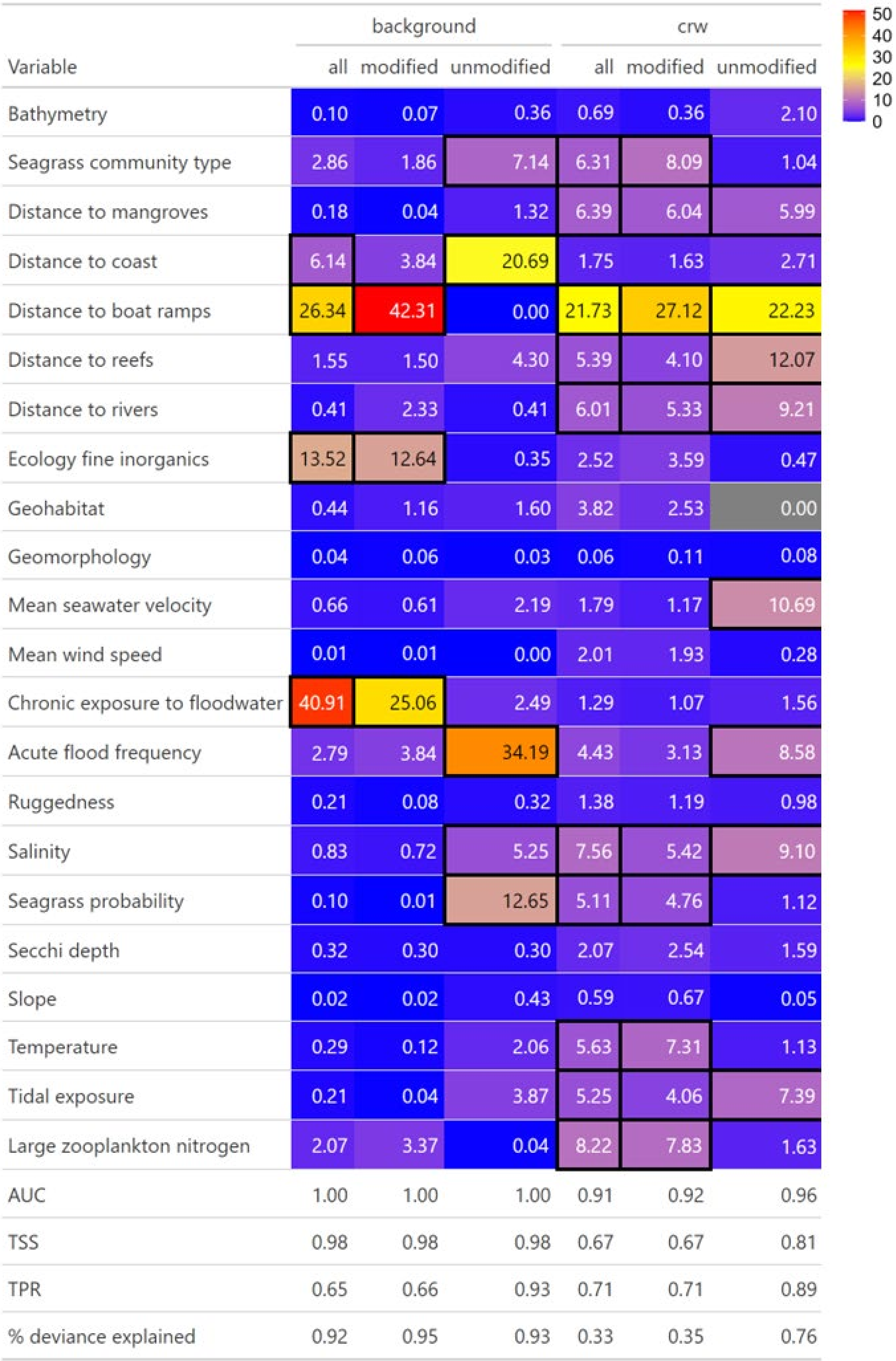
To evaluate how the extent and distribution of suitable foraging habitat in the region changed over time, we compared the area and spatial distribution of predictions of probability of foraging turtle presence for two time periods, December 2010 and December 2022, from the CRW unmodified model because 1) we are trying to generalize habitat conditions for all turtles across the modelled range and 2) CRW more than background sampling, reflects the range of conditions available to turtles on the scale of their foraging movement decisions.. We evaluated these differences by varying influential time-varying (not static) predictors underpinning the model. Variables from the eReefs biogeochemical model in 2022 were available at daily, rather than monthly aggregations.

Finally, to quantify the amount these sites are within or outside of protected areas, we calculated the proportion of the predicted suitable foraging habitat, from the CRW unmodified model, that was located within the Great Barrier Reef Marine Park boundary, specific marine park zones and designated port areas. The scripted R workflow for this study is available in a public Github repository as per Appendix 10.

## 5.4 Results

Turtle presences were concentrated close to the coast (<50 km), largely in shallow bays and inlets. Presence of some individuals fell upstream of river mouths (n=15 turtles) and on coral reefs (n=12 turtles). The sampling of presences and pseudo-absences in this study was skewed to turtles foraging in Port Curtis (n=85) over the other capture sites. Background sampling yielded pseudo-absences that spanned the entire extent of the modelled area while pseudo-absences from CRW more closely resembled the distribution of the presences, though less tightly concentrated than the presences and extending to > 70 km from the coastline. Environmental separation was, in general, larger for the background compared to the CRW models (Table 7).

All background models and the CRW unmodified model had AUC >0.95. Predictive skill was high with TSS ≥0.8 for all except the global and modified models with CRW pseudo-absences. Deviance explained was >0.9 for the background models and >0.75 for the CRW unmodified model (Figure 18). Deviance explained was <0.5 for the global and modified CRW models.



| | background | | | crw | | |
|---|---|---|---|---|---|---|
| Variable | all | modified | unmodified | all | modified | unmodified |
| Bathymetry | 0.10 | 0.07 | 0.36 | 0.69 | 0.36 | 2.10 |
| Seagrass community type | 2.86 | 1.86 | 7.14 | 6.31 | 8.09 | 1.04 |
| Distance to mangroves | 0.18 | 0.04 | 1.32 | 6.39 | 6.04 | 5.99 |
| Distance to coast | 6.14 | 3.84 | 20.69 | 1.75 | 1.63 | 2.71 |
| Distance to boat ramps | 26.34 | 42.31 | 0.00 | 21.73 | 27.12 | 22.23 |
| Distance to reefs | 1.55 | 1.50 | 4.30 | 5.39 | 4.10 | 12.07 |
| Distance to rivers | 0.41 | 2.33 | 0.41 | 6.01 | 5.33 | 9.21 |
| Ecology fine inorganics | 13.52 | 12.64 | 0.35 | 2.52 | 3.59 | 0.47 |
| Geohabitat | 0.44 | 1.16 | 1.60 | 3.82 | 2.53 | 0.00 |
| Geomorphology | 0.04 | 0.06 | 0.03 | 0.06 | 0.11 | 0.08 |
| Mean seawater velocity | 0.66 | 0.61 | 2.19 | 1.79 | 1.17 | 10.69 |
| Mean wind speed | 0.01 | 0.01 | 0.00 | 2.01 | 1.93 | 0.28 |
| Chronic exposure to floodwater | 40.91 | 25.06 | 2.49 | 1.29 | 1.07 | 1.56 |
| Acute flood frequency | 2.79 | 3.84 | 34.19 | 4.43 | 3.13 | 8.58 |
| Ruggedness | 0.21 | 0.08 | 0.32 | 1.38 | 1.19 | 0.98 |
| Salinity | 0.83 | 0.72 | 5.25 | 7.56 | 5.42 | 9.10 |
| Seagrass probability | 0.10 | 0.01 | 12.65 | 5.11 | 4.76 | 1.12 |
| Secchi depth | 0.32 | 0.30 | 0.30 | 2.07 | 2.54 | 1.59 |
| Slope | 0.02 | 0.02 | 0.43 | 0.59 | 0.67 | 0.05 |
| Temperature | 0.29 | 0.12 | 2.06 | 5.63 | 7.31 | 1.13 |
| Tidal exposure | 0.21 | 0.04 | 3.87 | 5.25 | 4.06 | 7.39 |
| Large zooplankton nitrogen | 2.07 | 3.37 | 0.04 | 8.22 | 7.83 | 1.63 |
| AUC | 1.00 | 1.00 | 1.00 | 0.91 | 0.92 | 0.96 |
| TSS | 0.98 | 0.98 | 0.98 | 0.67 | 0.67 | 0.81 |
| TPR | 0.65 | 0.66 | 0.93 | 0.71 | 0.71 | 0.89 |
| % deviance explained | 0.92 | 0.95 | 0.93 | 0.33 | 0.35 | 0.76 |

Figure 18 Relative importance of environmental predictor variables in telemetry-based habitat models using pseudo-absences from correlated random walks or background sampling. Colour is indicative of relative importance. Variables with greater than null explanatory power (relative importance > 100/number of variables in the model) are outlined in black. Evaluation metrics of each model are provided (AUC= area under the curve, TSS= true skill statistic, TPR= true positive rate, % deviance explained= (null deviance – residual deviance) / null deviance)

### *5.4.1 What characteristics make foraging habitat suitable for green turtles?*

In the background models, the variables with highest ranked importance for predicting turtle presence differed between the modified and unmodified habitats. Chronic floodwater exposure, distance to boat ramps and fine inorganics (EFI) explained the presence in modified habitats (Figure 18). Acute flood frequency, distance to coast, seagrass community type, seagrass probability and salinity were influential variables in the unmodified, but not the modified habitats. In the CRW models, large zooplankton nitrogen, distance to boat ramps, distance to mangroves, seagrass community type, seagrass probability, distance to rivers, salinity and temperature were influential variables in modified habitats. In unmodified habitats, distance to rivers, distance to mangroves, distance to boat ramps and salinity were also among the influential variables, as well as distance to reefs, mean seawater velocity, acute flood frequency and tidal exposure. The predictor values appended to presences and pseudo-absences that were all at least 70% correlated with each other were distance to coast, distance to rivers and distance to mangroves. Ruggedness and slope were correlated, as were chronic floodwater exposure and frequency of primary and secondary waters [water types are characterized by salinity, colour and water quality (295)]. For CRW data, chronic floodwater exposure and acute flood frequency were also correlated with bathymetry, distance to coast, distance to mangroves, and Secchi depth.

The shape of the relationships between influential variables and the probability of turtle presence for each model is depicted in Appendix 11. Influential variables that also appeared amongst the five highest ranking two-way interactions for that model are listed in Appendix 12. The seagrass communities (286) predictive of turtle presence from each model are summarized in Appendix 13.

Table 7 Bhattacharyya's coefficient for the four most influential variables identified in each habitat model, indicating environmental separation between presences and pseudo-absences

| | Background | | CRW | |
|---|---|---|---|---|
| Variable rank importance | modified | unmodified | modified | unmodified |
| 1 | Distance to boat ramps<br>0.12 | Acute flood frequency<br><0.01 | Distance to boat ramps<br>0.77 | Distance to boat ramps<br>0.77 |
| 2 | Chronic floodwater exposure<br><0.01 | Distance to coast<br>0.02 | Seagrass community type<br>0.90 | Distance to reefs<br>0.97 |
| 3 | Ecology fine inorganics<br><0.01 | Seagrass probability<br>0.44 | Large zooplankton nitrogen<br>0.99 | Mean seawater velocity<br>0.70 |
| 4 | | Seagrass community type<br>0.70 | Temperature<br>0.99 | Distance to rivers<br>0.85 |

### *5.4.2 Where is suitable foraging habitat for green turtles in the Great Barrier Reef inshore region?*

The CRW unmodified model is the most appropriate for generalising the environmental characteristics underpinning habitat suitability across the modelled extent prior to human modification and has pseudo-absences that represent environmental separation at the scale at which turtles are making movement decisions in foraging grounds. This predicted suitable habitat from this model excluded deep areas between the coast and mid and offshore reefs. In contrast, the other models failed to capture reef habitats and locations upstream of river mouths which are known foraging areas for green turtles. This includes the Capricorn Bunker group of islands, which are identified as important foraging areas for the southern Great Barrier Reef stock by the Queensland Marine Turtle Conservation Strategy (71).

The CRW unmodified model predicted 2.4% of the modelled area as being suitable habitat for foraging green turtles (5,281 km$^2$ had more than 50% predicted probability of turtle presence). In comparison, the CRW modified model predicted 0.2%, and the background modified and unmodified models respectively predicted 1.2% and 2.2% of the modelled area as being suitable.

### *5.4.3 Has the extent and distribution of suitable foraging habitat in the region changed over time?*

Our CRW unmodified model suggested that the total area where predicted probability of turtle presence was >0.5 decreased from 8986.5 km$^2$ in 2010 to 5281.75 km$^2$ in 2022 (Figure 19). 50.9% and 75.7% of the predicted suitable habitat area was within 50 km of the coast in 2010 and 2022 respectively. In 2010, suitable habitat was distributed more broadly both near mid-shelf reefs, and close to the coast than in 2022, based on predictions from the CRW unmodified model. In 2022 there was substantially less suitable habitat between Hydrographer's Passage and the Swains Reefs than in 2010. The time-varying influential predictors in this model (having variable importance score greater than 100/number of predictors) were distance to mangroves, mean seawater velocity and salinity. Temporal differences could also be the result of the cumulative effect of several lower-ranked time-varying covariates- namely Secchi depth and large zooplankton nitrogen (Figure 20). Notably, values of Secchi depth and large zooplankton nitrogen for the 2022 predictions were derived from daily rather than monthly aggregations of the eReefs biogeochemical model due to availability of near-realtime data. Therefore the 2022 data for these variables could be capturing day-to-day variability, rather than representing broader temporal patterns.

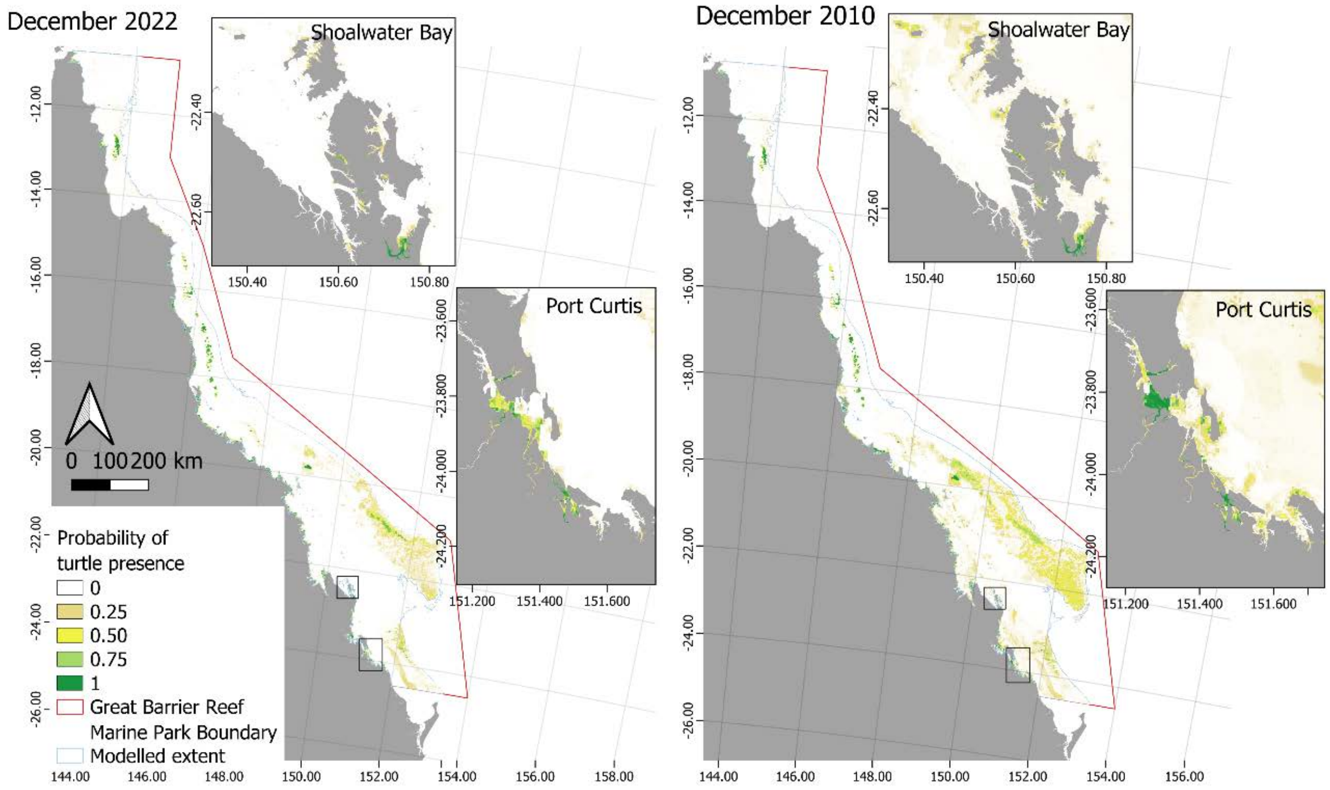


Figure 19 Distribution of suitable foraging habitat for green turtles in December 2022 and December 2010 marine park boundary, predicted from telemetry-based habitat models with pseudoabsences generated from correlated random walks in unmodified habitats.

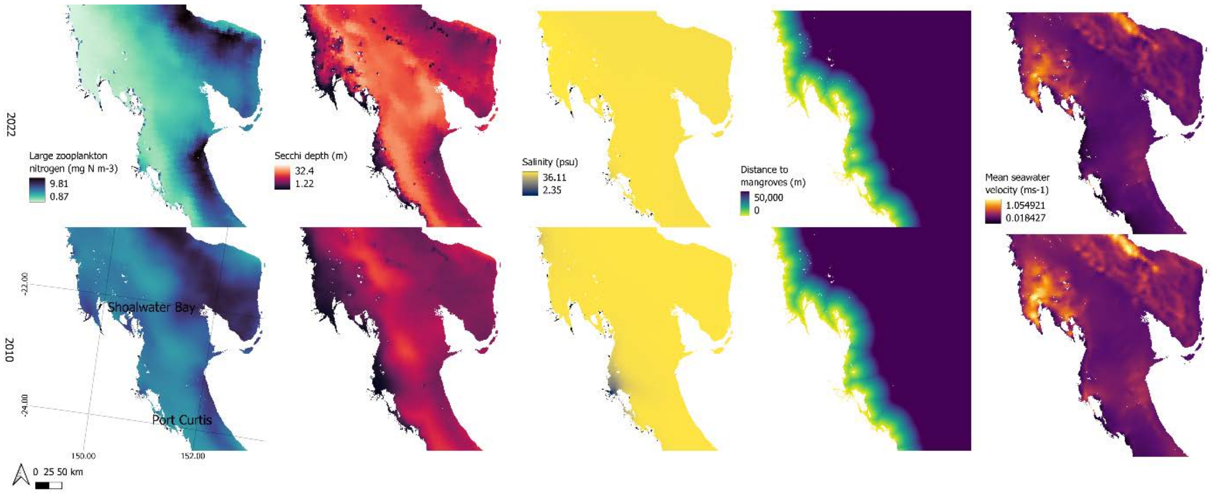


Figure 20 Time-varying covariates large zooplankton nitrogen (mg N m$^{-3}$), Secchi depth (m), salinity (psu), distance to mangroves (m) and mean seawater velocity (ms$^{-1}$) in December 2010 and December 2022

### *5.4.4 How much of suitable foraging habitat is protected?*

Of the total suitable habitat in the modelled area, 50.0% fell within habitat protection zones, 19.4% in marine National Park, 10.4% in conservation park, 9.1% in general use zones, and 2.8% in the remaining Great Barrier Reef Marine Park zones, based on the prediction from the 2022 CRW unmodified model. Of total suitable foraging habitat, 4.4% fell within designated port areas. Noting that our modelled extent was clipped to match the extent of the input environmental data (286), 8.3% of identified suitable habitat fell inland of the Great Barrier Reef Marine Park boundary (i.e., within port areas and areas landward of the low water mark including rivers and estuaries).

## 5.5 Discussion

We created a dynamic regional distribution model of suitable foraging habitats for green turtles in eastern Queensland. This fills a substantial gap in the existing knowledge for the species, where foraging distribution was previously defined by the locations of index sites, post-nesting tracks of breeding females, and opportunistic capture close to human populations (206). We expected green turtles to be distributed all along the coast of Queensland, with the highest density in mid reefs, and lower density in the outer reefs. The predicted habitat distribution sensibly captured known shallow coastal areas used by foraging green turtles within the modelled region, including Port Curtis, Shoalwater Bay, mid-shelf reefs including the Capricorn Bunker group of islands, [Cleveland Bay, river mouths (23,71)], while excluding improbable areas (deep areas between the coast and the mid-shelf reefs). We ascertained that the total area of potentially suitable habitat has decreased between 2010 and 2022, and the distribution of suitable habitats shifted from the nearshore, to the mid-shelf placing emphasis on the safeguarding of existing habitats. Given the established relationship between weather events and habitat quality for marine turtles in coastal foraging grounds (82,100,118,209,219) we would expect changes in foraging habitat to align with weather events in confined coastal areas. However, away from coasts and across broad areas, particularly reefs, habitat change will likely occur with the speed of climate change.

We identified important variables that characterise suitable foraging habitats for green turtles. Among these variables, we identified the distribution of food resources (i.e., seagrass communities and mangroves) and physical characteristics of those habitats (e.g., chronic floodwater exposure and frequency of acute floods, tidal exposure, salinity) as having the strongest influence on the probability of turtle presence. Our results are consistent with the existing understanding of green turtle diets. In Queensland, green turtles consume a variety of seagrasses (*Halophila ovalis, Halodule uninervis, Zostera capricorni, Halophila spinulosa, Halodule pinifolia, Cymodocea serrulate, Thalassia temprichii, Enhalus acoroides*) and a range of red, brown and green algae (77,101,102,106–109). At some sites, green turtles consume mangrove roots, fruits and cotelydons (*Rhizophera* and *Avicenia* sp.), though these usually contribute to relatively small proportions of the diet (110,296,297). Macroplankton (*ctenophora*, fish and crustaceans) are occasionally consumed but can contribute substantially to an individual diet sample (102). Diet items may be supported by specific physical characteristics, but those physical characteristics may not dictate turtle habitat distribution directly. For example, seagrass variables were not influential in the CRW unmodified model. Seagrasses may dominate diets at seagrass meadows, and macroalgae at algal pastures and rocky reefs such as Heron/Wistari Reefs (112), and parts of Port Curtis (111) and Moreton Bay (31). Algal distribution was not included in our model, despite being likely to dominate diets of foraging turtles occupying reef habitats. Though the seagrass (286) dataset leverages the benthic light variable from eReefs, the Secchi depth did not appear influential in any model.

The influential physical characteristics we identified align with previously described requirements for the region; Green turtles in foraging grounds throughout coastal Queensland and the Great Barrier Reef most frequently occupy depths 0-30m and rarely below 60 m, reflecting the spatial distribution of predicted habitat presented here (80). Distance to boat ramps and distance to the coast were highly correlated to each other but rarely both appeared as highly influential predictors in a single model. This may be an artefact of the decision tree approach whereby if a split related to one of correlated variables explains a large amount of deviance, subsequent splits related to the other variable will have low explanatory power. Regardless, turtle presence was predicted by both nearshore and mid-shelf habitats in our chosen model. Water quality (i.e., flood plume frequency and exposure, salinity) was highly influential to our models. However, in Queensland, the leading cause of green turtle stranding in coastal populations is disease, presumably associated with chemical and sediment runoff from river outflows and seasonal fluctuations in temperature and rainfall (69,70). Artificial structures can provide a foraging habitat for green turtles by supporting epifauna, infauna and macroalgal growth and or providing structures for resting (240,298). The degree to which turtles use man-made structures is likely linked to their risk of anthropogenic interaction, including boat strike and incidental capture, and would be a useful avenue for future projects.

The higher relative importance of seagrasses in modified compared to unmodified habitats according to the CRW models may reflect the availability of alternative foraging resources to seagrasses, including algae, at sites other than Port Curtis, particularly at coral and rocky reefs (e.g., 210). It may also reflect the low explanatory power of the global and modified CRW models, e.g., though at some sites green turtles consume substantially larger proportions of seagrass in their adult diet compared to during immature stages (31,283), the turtles tracked at unmodified sites included fewer juveniles than in modified sites. On broad scales (background models) distance to boat ramps and exposure to flood plumes were relatively more influential in modified compared to unmodified habitats, a possible artifact of sampling at the modified site, close to populated areas (294,299,300). Hazen et al. 2021 (276) found that models with the greatest environmental separation (i.e., background models) had the best performance metrics, but these were not always biologically realistic predictions relative to known distributions.

Our modelling approach could be further improved my incorporating dynamic rather than static environmental data as it becomes available (e.g., built infrastructure has changed throughout the study period). We have included predictors with non-causal relationships to our response and potentially redundant predictors (301). We note that we were only able to make predictions of suitable habitat where and when there was sufficient environmental data. In marine environments, more data exist for areas close to coasts and in shallow water (302) e.g., the modelled (286) seagrass data was lacking for estuaries, and beyond the mid-shelf. Matching scale, resolution, and extent across the environmental predictor datasets highlighted the mismatch between the fine spatial resolution achievable with tracking technology and the achievable resolution of spatial data at large scales. This will likely be better matched in future as spatial data collection and modelling methods improve. For model improvement we suggest inclusion of variables like waves, sediment, predator distributions, and connectivity. Our turtle locations were biased towards tracked animals in Port Curtis. The inclusion of additional tracking data from unmodified foraging sites, or capture data from foraging site monitoring programs, would likely improve reliability of our output. This work is intended as a baseline upon which it would be possible to overlay anthropogenic threats layers to quantitatively assess susceptibility of turtle foraging habitat to these threats, similar to (14,303,304). It provides a prediction in space and time of likelihood of occurrence of the species during foraging; it does not represent turtle density. Future attempts to quantify density could incorporate detectability measures or abundance estimates from in-water capture into our approach (300,305).

Less than 20% of predicted suitable foraging habitat for green turtles fell within no-take zones and 8.3% fell outside of the Marine Park boundary (i.e., in designated port areas or inland of mean high water). Our results suggest that the area and distribution of suitable habitat has changed from 2010 to 2022. Even within protected areas, turtle habitats are susceptible to indirect effects of climate change, which can be exacerbated by human activities (e.g., runoff), as well as direct impact human-wildlife interactions (e.g., boat strike). In designated port areas and upstream of rivers, anthropogenic use can be intensive, and there are competing needs for space between human uses and marine habitats. Thus, there is a need to evaluate the threat landscape in these areas. Designation of protected areas may not be appropriate or feasible due to conflicting environmental, economic, social, and cultural interests in these areas. Therefore appropriate, effective, and enduring conservation initiatives must consider and balance environmental objectives with information on human-use. The predicted range of suitable foraging habitat we present does not equal the realised foraging range for this species, because anthropogenic activities are not encompassed in the input data.

Green turtles may reside in a single foraging area between breeding migrations (109) and across decades (92,94). For green turtles, home ranges in foraging grounds are closely linked to foraging resource distribution (197,306). The quality of available forage affects growth rates, age to maturity and reproductive output of the species (103). Fidelity to foraging and nesting habitat may limit sea turtles' capacity to displace from depleted sites or recolonise recovered sites (307). Protection of a few targeted key sites is therefore likely to confer considerable conservation benefit (171,173,308). However, MPAs might not be appropriate in low-density foraging grounds, and concentrating conservation efforts on small discrete areas may exacerbate the risk of unexpected impacts. Our results suggest that some foraging areas are more affected by changes over time in weather and temperature than others. While some major foraging habitats are very affected, others which are less impacted might be more suited to protection on broader timescales. In addition, preventative interventions can help to target general habitat health rather than conservation of specific, high-density areas e.g., targeting sources of land-based runoff through land restoration programs to manage the impact of rainfall events on nearshore benthic habitats.

Considering this, dynamic management strategies may be appropriate in large areas where sea turtle aggregations are sparse. Dynamic management may involve implementation of temporally or spatially variable restrictions on take, recreational use (e.g., go-slow zones) or urban and industrial development in order to mitigate direct anthropogenic impacts to sea turtles and their habitats. Dynamic management with regular re-evaluation is also pertinent considering long-term changes to coastal and marine environments. However, realistic timeframes for 'flexible' interventions or protections are yet to be established e.g., yearly management changes would be very challenging to implement. Despite local and regional conservation successes, mitigating impacts of habitat loss and deterioration over time on marine turtles is an ongoing global challenge (149).

## 5.6 Appendices

Appendix 8 Inventory of tracked green turtles with identifiers Primary tag (flipper tag), platform terminal transmitter (PTT) and tracker type. Maturity is coded as Adult (A), Subadult (SA) and Juvenile (J), and sex as male (M), female (F) or not determined (I)

| Primary tag | PTT | Deploy site | Tracker Type | Sex | Maturity | CCL (cm) | Year deployed | Independent track segments (n) | Track duration (days) |
|---|---|---|---|---|---|---|---|---|---|
| QA86025 | 40934 | Port Curtis | SPLASH10-BF-297B | M | SA | 96 | 2018 | 1 | 92 |

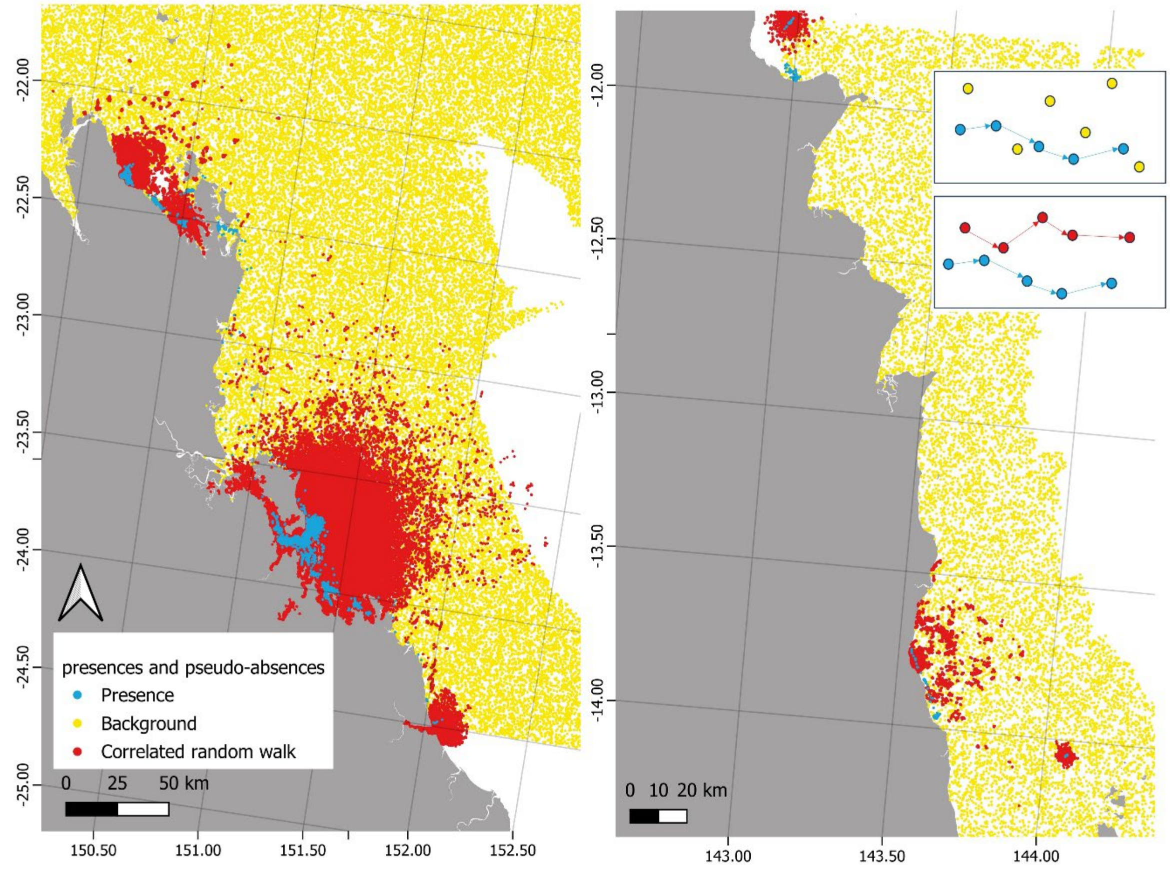
| Primary tag | PTT | Deploy site | Tracker Type | Sex | Maturity | CCL (cm) | Year deployed | Independent track segments (n) | Track duration (days) |
|---|---|---|---|---|---|---|---|---|---|
| QA81288 | 45769 | Raine Island | SPLASH10-F-334C | F | A | 102.4 | 2017 | 1 | 62 |
| QA81295 | 45778 | Raine Island | SPLASH10-F-334C | F | A | 102.7 | 2017 | 1 | 112 |
| QA15580 | 45787 | Raine Island | SPLASH10-F-334C | F | A | 106.2 | 2017 | 1 | 37 |
| QA80430 | 45791 | Raine Island | SPLASH10-F-334C | F | A | 102.6 | 2017 | 1 | 68 |
| QA36853 | 48862 | Shoalwater Bay | Sirtrack | F | J | 95.2 | 2014 | 1 | 100 |
| QA86189 | 61689 | Port Curtis | SPLASH10-BF-344E | M | A | 98 | 2018 | 1 | 74 |
| QA86190 | 61690 | Port Curtis | SPLASH10-BF-344E | M | SA | 70.3 | 2018 | 3 | 129 |
| QA86302 | 61691 | Port Curtis | SPLASH10-BF-344E | M | A | 91.3 | 2018 | 1 | 114 |
| QA86247 | 61692 | Port Curtis | SPLASH10-BF-344E | M | SA | 71.5 | 2018 | 1 | 112 |
| QA87017 | 64747 | Port Curtis | SPLASH10-F-334D | I | SA | 67.2 | 2018 | 3 | 108 |
| QA87018 | 64748 | Port Curtis | SPLASH10-F-334D | I | SA | 67.4 | 2018 | 3 | 77 |
| K93085 | 72448 | Port Curtis | Sirtrack Fastloc | I | J | 51.3 | 2010 | 3 | 212 |
| QA36851 | 96776 | Shoalwater Bay | Sirtrack | M | A | 91.8 | 2014 | 1 | 87 |
| K93087 * | 96777 | Port Curtis | Sirtrack Fastloc | M | A | 104.3 | 2010 | 7 | 81 |
|  | 96777 | Raine Island | Sirtrack | F | A | 96.1 | 2012 | 3 | 11 |
| QA46109 | 96777 | Shoalwater Bay | Sirtrack | M | A | 94.5 | 2014 | 3 | 150 |
| K93088 | 96778 | Port Curtis | Sirtrack Fastloc | M | A | 92.2 | 2010 | 6 | 220 |
| T83097 | 96780 | Port Curtis | Sirtrack Fastloc | F | A | 104.4 | 2010 | 2 | 118 |
| K55740 | 96780 | Shoalwater Bay | Sirtrack | F | A | 97.3 | 2012 | 1 | 780 |
| K93086 | 96781 | Port Curtis | Sirtrack Fastloc | M | A | 85.6 | 2010 | 2 | 167 |
| QA28798 | 120640 | Shoalwater Bay | WC | F | SP | 102.1 | 2012 | 3 | 194 |
| QA27532 | 120641 | Shoalwater Bay | WC | F | A | 95.5 | 2012 | 2 | 143 |
|  | 126272 | Port Curtis | SPLASH10-F | F | A | 106.2 | 2013 | 5 | 203 |
|  | 126273 | Port Curtis | SPLASH10-F | F | SA | 101.6 | 2013 | 4 | 22 |
|  | 126274 | Port Curtis | SPLASH10-F | F | A | 113.8 | 2013 | 4 | 156 |
|  | 126275 | Port Curtis | SPLASH10-F | M | J | 58.8 | 2013 | 7 | 249 |
|  | 126276 | Port Curtis | SPLASH10-F | M | J | 54.6 | 2013 | 5 | 132 |
|  | 131862 | Port Curtis | SPLASH10-F | I | J | 52.1 | 2013 | 1 | 65 |
|  | 131868 | Port Curtis | SPLASH10-F | M | A | 97.7 | 2013 | 4 | 114 |
|  | 131869 | Port Curtis | SPLASH10-F | F | A | 96.2 | 2013 | 2 | 79 |
|  | 131872 | Port Curtis | SPLASH10-F | I | J | 52.7 | 2013 | 2 | 152 |
| QA33394 | 133758 | Port Curtis | SPLASH10-F-297A | I | J | 43.6 | 2013 | 3 | 36 |
| QA64318 | 133758 | Port Curtis | SPLASH10-F-297A | F | A | 94.6 | 2017 | 1 | 66 |
| QA33349 | 133759 | Port Curtis | SPLASH10-F-297A | I | J | 42.6 | 2013 | 1 | 145 |

| Primary tag | PTT | Deploy site | Tracker Type | Sex | Maturity | CCL (cm) | Year deployed | Independent track segments (n) | Track duration (days) |
|---|---|---|---|---|---|---|---|---|---|
| QA33368 | 133760 | Port Curtis | SPLASH10-F-297A | I | J | 46 | 2013 | 1 | 64 |
| QA34529 | 133761 | Port Curtis | SPLASH10-F-297A | I | J | 47.9 | 2013 | 1 | 64 |
| QA32523 | 133762 | Port Curtis | SPLASH10-F-297A | I | J | 49.1 | 2013 |  | 36 |
| QA33350 | 133763 | Port Curtis | SPLASH10-F-297A | I | J | 42.1 | 2013 | 1 | 46 |
| K74859 | 133763 | Raine Island | WC10BF334A | F | A | 105.5 | 2016 |  |  |
| QA33342 | 133764 | Port Curtis | SPLASH-10-F-296A | F | A | 111 | 2013 | 1 | 87 |
| QA33327 | 133765 | Port Curtis | SPLASH-10-F-296A | M | A | 96.5 | 2013 | 1 | 67 |
| QA43066 | 133766 | Port Curtis | SPLASH-10-F-296A | F | A | 105.7 | 2013 | 1 | 44 |
| K70229 | 133767 | Port Curtis | SPLASH-10-F-296A | F | A | 105.7 | 2013 | 4 | 73 |
| QA43063 | 133768 | Port Curtis | SPLASH-10-F-296A | M | A | 93.5 | 2013 | 1 | 70 |
| QA33348 | 133769 | Port Curtis | SPLASH-10-F-296A | F | A | 107.3 | 2013 | 1 | 56 |
| QA43023 | 133770 | Port Curtis | SPLASH-10-F-296A | F | A | 102.7 | 2013 | 1 | 68 |
| QA36875 | 134178 | Port Curtis | SPLASH-10-F-296A | M | A | 97.6 | 2014 | 2 | 147 |
| QA33335 | 134180 | Port Curtis | SPLASH-10-F-296A | F | A | 89 | 2014 | 2 | 33 |
| QA45627 | 134181 | Port Curtis | SPLASH-10-F-296A | I | J | 63.1 | 2014 | 3 | 199 |
| QA13938 | 134182 | Port Curtis | SPLASH-10-F-296A | M | A | 95.4 | 2014 | 3 | 187 |
| QA45524 | 134183 | Port Curtis | SPLASH-10-F-296A | F | A | 101.7 | 2014 | 2 | 73 |
| QA45554 | 134184 | Port Curtis | SPLASH-10-F-296A | F | A | 116.6 | 2014 | 1 | 194 |
| QA45601 | 134185 | Port Curtis | SPLASH-10-F-296A | I | SA | 79 | 2014 | 5 | 183 |
| QA45654 | 134186 | Port Curtis | SPLASH-10-F-296A | I | J | 50.2 | 2014 | 1 | 24 |
| QA45689 | 134187 | Port Curtis | SPLASH-10-F-296A | M | A | 102.5 | 2014 | 4 | 107 |
| QA45566 | 134188 | Port Curtis | SPLASH-10-F-296A | F | A | 110.9 | 2014 | 3 | 77 |
| K283 | 143704 | Port Curtis | SPLASH-10-F-296A | F | A | 98.1 | 2014 | 2 | 97 |
| QA58221 | 149080 | Port Curtis | SPLASH10-F-297A | F | A | 95.1 | 2015 | 5 | 170 |
| QA58209 | 149081 | Port Curtis | SPLASH10-F-297A | M | A | 89.1 | 2015 | 2 | 92 |
| K28651 | 149082 | Port Curtis | SPLASH10-F-297A | M | A | 98.9 | 2015 | 5 | 175 |
| QA58239 | 149083 | Port Curtis | SPLASH10-F-297A | M | SA | 77.8 | 2015 | 2 | 96 |
| QA58284 | 149084 | Port Curtis | SPLASH10-F-297A | M | A | 92.2 | 2015 | 1 | 111 |
| QA58211 | 149085 | Port Curtis | SPLASH10-F-297A | F | SA | 99.7 | 2015 | 2 | 91 |
| QA58210 | 149086 | Port Curtis | SPLASH10-F-297A | M | SA | 80.1 | 2015 | 1 | 68 |
| QA43123 | 149087 | Port Curtis | SPLASH10-F-297A | F | A | 108.2 | 2015 | 7 | 203 |
| QA58206 | 149088 | Port Curtis | SPLASH10-F-297A | F | SA | 81.5 | 2015 | 3 | 115 |
| QA58295 | 149089 | Port Curtis | SPLASH10-F-297A | F | SA | 83.8 | 2015 | 1 | 95 |
| QA58291 | 149090 | Port Curtis | SPLASH10-F-297A | M | A | 94.1 | 2015 | 1 | 11 |

| Primary tag | PTT | Deploy site | Tracker Type | Sex | Maturity | CCL (cm) | Year deployed | Independent track segments (n) | Track duration (days) |
|---|---|---|---|---|---|---|---|---|---|
| QA64830 | 157925 | Port Curtis | SPLASH10-F-297A | M | A | 94.7 | 2016 | 3 | 120 |
| QA64930 | 157926 | Port Curtis | SPLASH10-F-297A | F | A | 108.7 | 2016 | 4 | 140 |
| QA64931 | 157927 | Port Curtis | SPLASH10-F-297A | F | A | 96.8 | 2016 | 1 | 85 |
| QA64933 | 157928 | Port Curtis | SPLASH10-F-297A | M | SA | 85.3 | 2016 | 2 | 165 |
| QA64932 | 157929 | Port Curtis | SPLASH10-F-297A | F | A | 103.5 | 2016 | 1 | 60 |
| QA65177 | 157930 | Port Curtis | SPLASH10-F-297A | F | A | 114.6 | 2016 | 1 | 76 |
| QA65088 | 157931 | Port Curtis | SPLASH10-F-297A | M | A | 101.7 | 2016 | 2 | 110 |
| T88971 | 157932 | Port Curtis | SPLASH10-F-297A | F | A | 98.6 | 2016 | 1 | 152 |
| QA65085 | 157933 | Port Curtis | SPLASH10-F-297A | M | A | 96.4 | 2016 | 3 | 101 |
| QA66466 | 157934 | Port Curtis | SPLASH10-F-297A | M | A | 92.9 | 2016 | 4 | 105 |
| QA66526 | 157935 | Port Curtis | SPLASH10-F-297A | F | A | 97.3 | 2016 | 1 | 69 |
| QA86202 | 176006 | Port Curtis | SPLASH10-BF-297B | M | SA | 77.2 | 2018 | 3 | 180 |
| QA91605 | 181366 | Port Curtis | SPLASH10-F-385 | F | SA | 71.5 | 2019 | 1 | 132 |
| QA84342 | 181367 | Port Curtis | SPLASH10-F-385 | M | J | 45.1 | 2019 | 1 | 143 |
| QA87129 | 181368 | Port Curtis | SPLASH10-F-385 | M | SA | 76.6 | 2019 | 2 | 197 |
| QA91173 | 181369 | Port Curtis | SPLASH10-F-385 | M | J | 47.1 | 2019 | 2 | 184 |
| QA91603 | 181370 | Port Curtis | SPLASH10-F-385 | F | J | 60.4 | 2019 | 3 | 136 |
| QA91766 | 194460 | Port Curtis | SPLASH10-F-385 | F | SA | 99 | 2019 | 1 | 72 |
| QA91767 | 194461 | Port Curtis | SPLASH10-F-385 | M | J | 49.2 | 2019 | 1 | 94 |
| QA91768 | 194462 | Port Curtis | SPLASH10-F-385 | F | J | 45.1 | 2019 | 1 | 55 |
| QA91791 | 194463 | Port Curtis | SPLASH10-F-385 | F | SA | 83.4 | 2019 | 1 | 94 |
| QA91639 | 194464 | Port Curtis | SPLASH10-F-385 | F | J | 64.1 | 2019 | 3 | 105 |
| QA98165 | 201295 | Port Curtis | SPLASH10-F-387 | F | J | 53.8 | 2021 | 1 | 115 |
| QA91842 | 201297 | Port Curtis | SPLASH10-F-389 | F | J | 44.7 | 2021 | 2 | 171 |
| QA91840 | 201298 | Port Curtis | SPLASH10-F-390 | F | J | 50.8 | 2021 | 1 | 23 |
| QA91843 | 201299 | Port Curtis | SPLASH10-F-386 | F | J | 48.5 | 2021 | 2 | 86 |
| QB9172 | 201300 | Port Curtis | SPLASH10-F-385 | M | A | 76.8 | 2021 | 1 | 48 |
| QB14428 | 201301 | Port Curtis | SPLASH10-F-385 | M | SA | 85.6 | 2021 | 1 | 99 |
| QB8899 | 201302 | Port Curtis | SPLASH10-F-385 | M | SA | 111.2 | 2021 | 1 | 84 |
| QB8898 | 201303 | Port Curtis | SPLASH10-F-385 | F | SA | 97.3 | 2021 | 1 | 42 |
| QA87126 | 201304 | Port Curtis | SPLASH10-F-385 | M | SA | 82.2 | 2021 | 1 | 100 |

## Appendix 9 Locations of green turtles’ presences from movement persistence modelling and pseudo-absences from background sampling and simulated correlated random walks, used as inputs in

telemetry-based habitat models, calculation of pseudo-absences types is depicted conceptually in the right hand panels, adapted from (22)

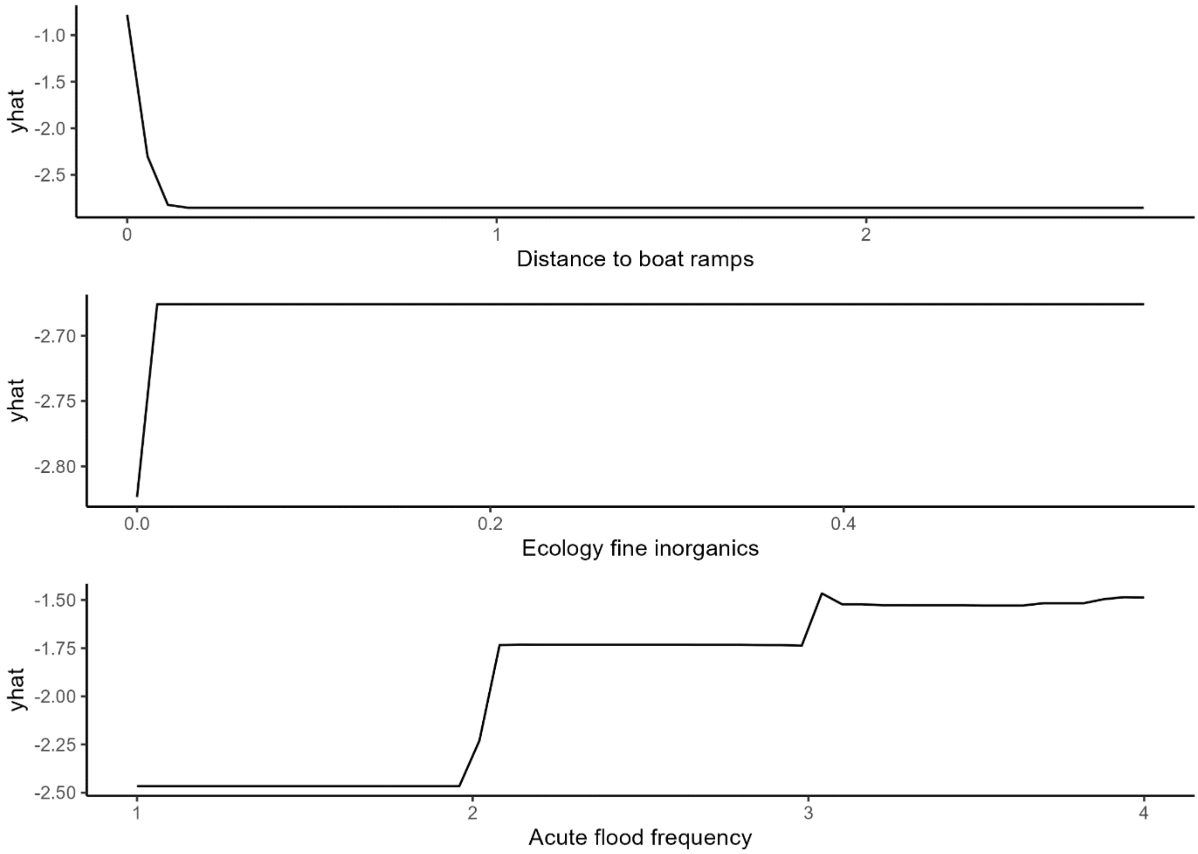


Appendix 10 Availability of scripted R workflow

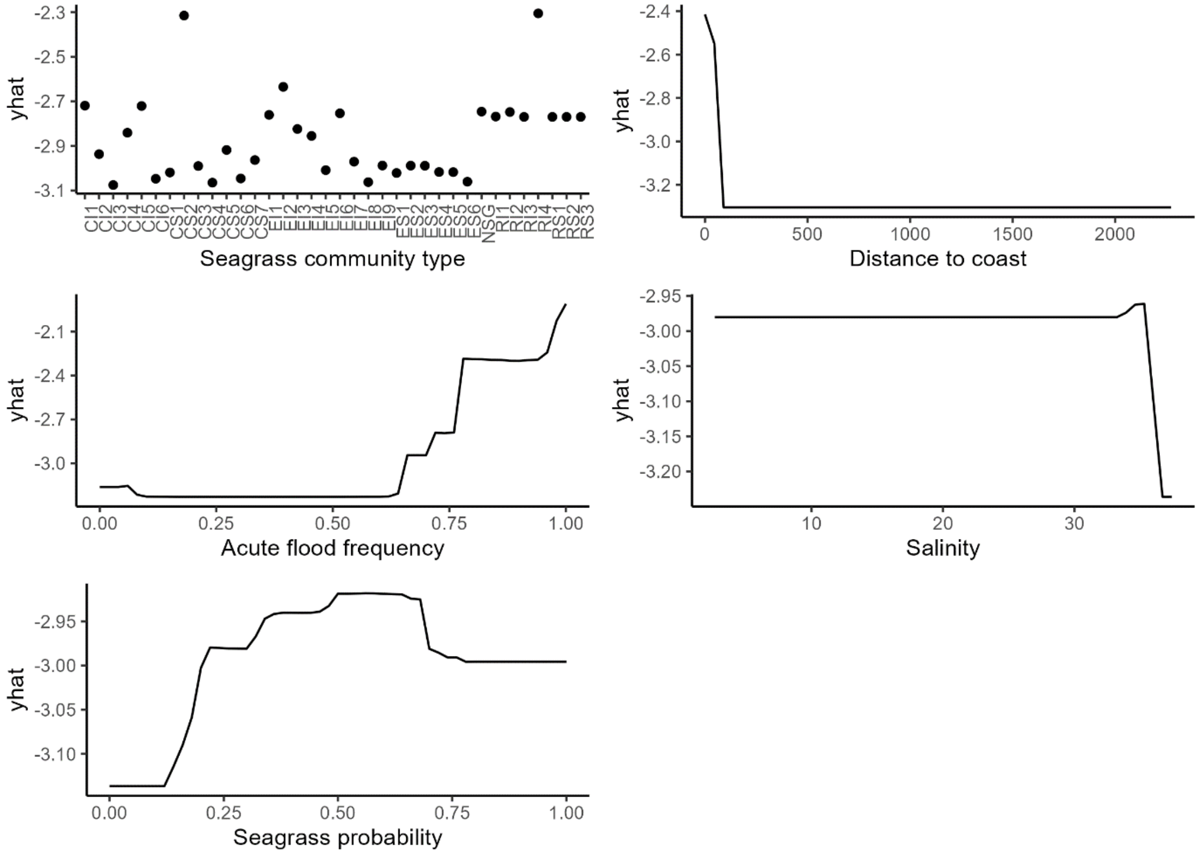
The scripted workflow for the analysis presented in this study is available at https://github.com/egwebster/SSM-SDM-public

Appendix 11 Partial plots depicting the relationship of environmental variables with greater than null explanatory power (relative importance > 100/number of variables in model) to probability of green turtle presence for habitat models generated with pseudo-absences from background sampling in A modified, B unmodified habitats, and with correlated random walks in C modified, and D unmodified habitats. *yhat* is the log-odds of the probability of turtle presence being 1. NSG stands for “non-seagrass habitat”, (E=estuary, C=coastal, R=reef, I=intertidal, S=subtidal)

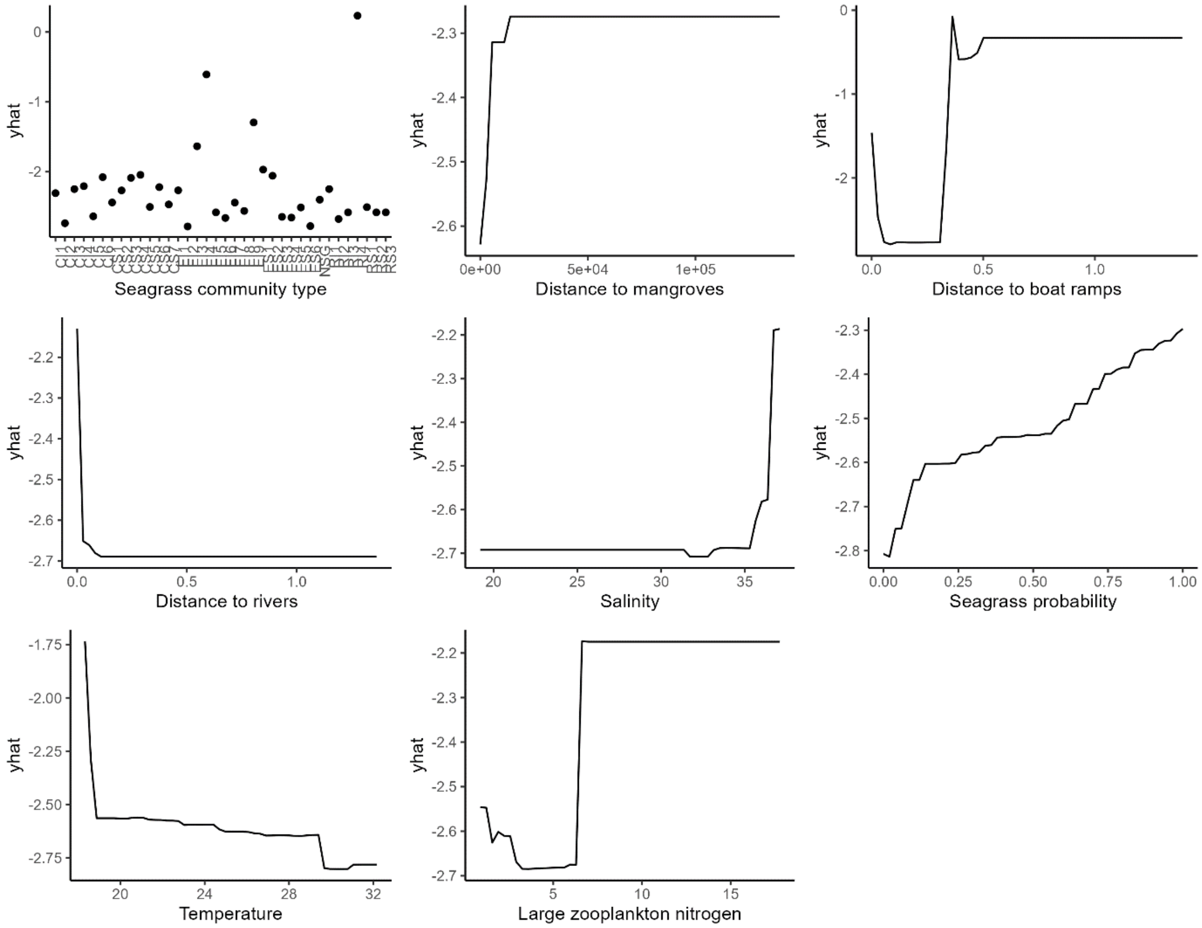
A- Background, modified



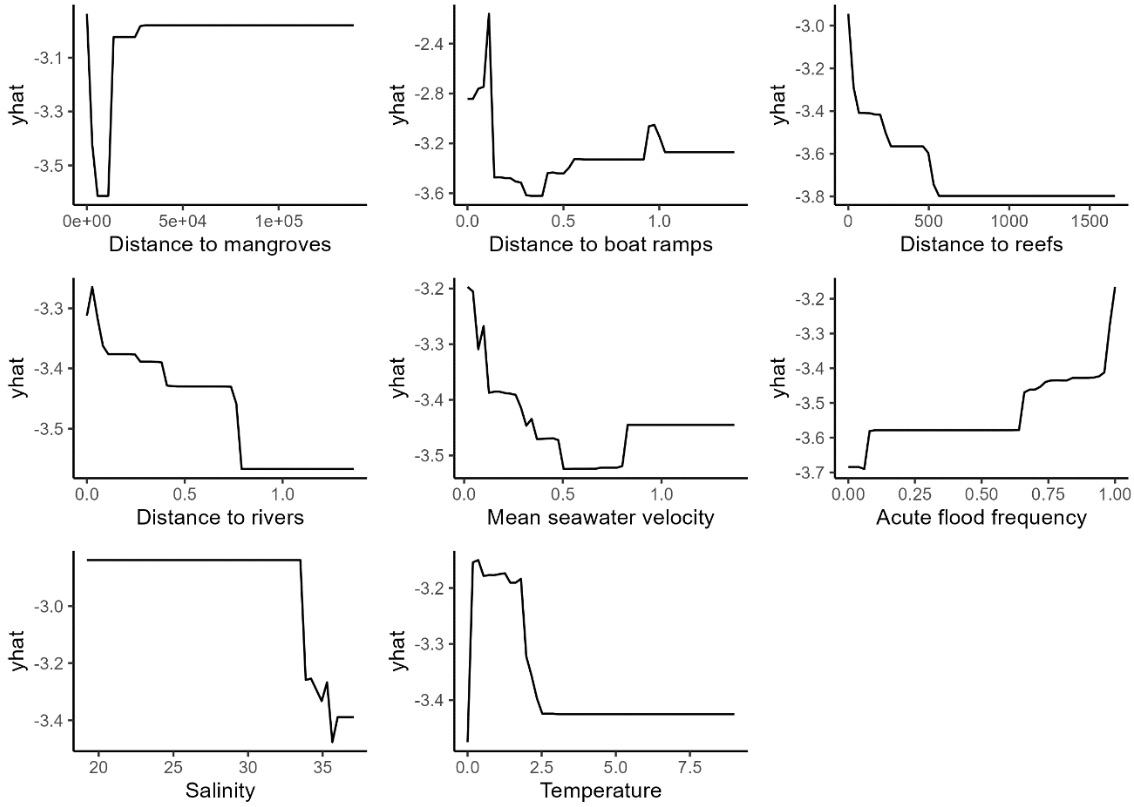
B- Background, unmodified



C- CRW, modified



D- CRW, unmodified



Appendix 12 Two-way interactions involving any influential predictors, ranked in top five

| Background | | CRW | |
|---|---|---|---|
| modified | unmodified | modified | unmodified |
| Chronic floodwater exposure X Geohabitat | Seagrass community type X Acute flood frequency | Temperature X Distance to boat ramps | Distance to reefs X Distance to rivers |
| Distance to boat ramps X Seagrass community type | Acute flood frequency X Distance to coast | Distance to boat ramps X Geohabitat | Seagrass community type X Distance to reefs |
| Distance to boat ramps X Salinity | Distance to coast X Distance to reefs | Distance to boat ramps X Seagrass community type | Seagrass community type X Mean seawater velocity |
| Chronic floodwater exposure X Distance to reefs | Distance to coast X Temperature | Temperature X Salinity | Mean seawater velocity X Distance to boat ramps |
| Chronic floodwater exposure X Large zooplankton nitrogen | Acute flood frequency X Seagrass probability | Seagrass community type X Geohabitat | |

Appendix 13 Ranked list of top 10 seagrass community types (27) predictive of green turtle presence as identified in each habitat model (E=estuary, C=coastal, R=reef, I=intertidal, S=subtidal). Seagrass community type was not identified as an influential predictor in the Background-modified and CRW-unmodified models

| | Background | | CRW | |
|---|---|---|---|---|
| Rank of most predictive | modified | unmodified | modified | unmodified |
| 1 | | RI4 | RI4 | |
| 2 | | CS2 | EI4 | |
| 3 | | EI2 | EI9 | |
| 4 | | CI1 | EI3 | |
| 5 | | CI5 | ES1 | |
| 6 | | Non-seagrass habitat | CS4 | |
| 7 | | RI2 | ES2 | |
| 8 | | EI6 | CI6 | |
| 9 | | EI1 | CS3 | |
| 10 | | RI1 | CI4 | |

# Chapter 6: General Discussion

Green turtles are often the subject of broader conservation planning (e.g., 275) because they are considered to have social, cultural, economic, and ecological importance. Few empirical studies demonstrate what their ecological role is. They are often perceived as large herbivorous grazers (e.g., 312,313), despite their documented omnivory (23,31,104), and in large numbers they have been noted to inhibit the growth of seagrasses (311,312). To me, a key factor spurring the importance of green turtles is that they coincide with benthic habitats that support diverse organisms (2), including seagrass, mangrove, intertidal and coral reef systems. A goal to protect iconic and charismatic marine turtles gives weight to initiatives to safeguard their habitats. Refining the spatial and temporal boundaries of green turtles' occupation of their habitats underpins protective interventions. Additionally, understanding the foraging life stages of green turtles can provide insight into their likely responses to environmental changes, their susceptibility to specific threats, and potential factors influencing broader population trends.

Green turtles can make their foraging homes in several different habitat types and conditions (313) because they have diverse, and regionally specific diets (283,314). As a result, foraging habitat use is geographically varied (2,118). However, in many regions of the world, the distribution and use of foraging habitats, resource requirements, and potential consequences to foraging green turtles in a changing climate (315), and with expanding human activities, are unknown. In addition, the threats foraging turtles are exposed to, and their response to and ability to tolerate these threats varies across their geographic range. Therefore, developing large scale knowledge about the spatial ecology of the species is complex.

Nonetheless, global knowledge of marine turtle spatial ecology is growing. Early attempts to disentangle the spatial ecology of green turtles consisted of flipper tag-recapture studies (316). As females marked on nesting beaches were increasingly found around the world, connectivity, breeding site fidelity and dispersal to faraway foraging grounds after breeding began to become apparent (128,317,318). However, while these early studies identified the endpoints of the migration, migration pathways remained a mystery until satellite tracking technology was invented (144,319–321). Since the 1990s, more attention has been drawn to the in-water life stages of green turtles, with the study of dispersal, development and foraging facilitated by tracking. Dispersal and development are difficult to decipher because of the challenge of attaching trackers to very small, growing turtles (322,323).

My thesis focused on spatial ecology during the relatively understudied foraging life stage of green turtles. I have contributed to addressing several established knowledge gaps: defining representative foraging distributions, identifying environmental drivers of fine-scale movement, characterising favourable foraging habitat, investigating intraspecific variability of behavior in a foraging aggregation, and study of immature and male turtles. Below, I highlight how my thesis contributes to the state of knowledge of green turtle foraging and use my findings to make recommendations for management initiatives and future work.

## 6.1 Outcomes for informing management

### *6.1.1 Obtaining representative sample sizes*

The large number of turtle tracks (n=72 individuals) in Chapter 2 enabled me to quantify minimum samples for estimating representative foraging ranges (n=21 across all monitored sites). The foraging ranges I established in Chapter 2 were spatially confined (median 9.4 km$^2$), consistent with other estimates in this region (118). Representative distributions were established at two monitored sites of the Queensland Turtle Conservation Program, the Pelican Banks (achieved with n=12 individuals), and Wiggins Island (with n=5 individuals) in Port Curtis. Notably, representation was not achieved for five sites or in every study year. Therefore, an important consideration for tracking studies, particularly across large spatial and temporal scales, is that deploying tracking devices haphazardly, because animals have been caught or because funding is available to purchase a few trackers, may not provide a sufficient basis to answer large scale questions about the ecology of a population. Establishing clear project aims with explicit planning of which areas and periods are of interest is necessary to ensure that any tracking study is fit-for purpose. For projects aiming to identify population-scale distribution patterns, some knowledge of the site fidelity, intraspecific variability in behaviour and distribution, behavioural responses to environmental change, resource requirements e.g., diet, is useful. For example, individuals may be sparsely distributed, mobile or highly variable in their behaviour, in which case many tracks may be required, while for less mobile or resident animals with highly overlapping home ranges, fewer are required.

### *6.1.2 Safeguarding established habitats*

Green turtles are exemplar of the popular knowledge that marine turtles return to their natal areas for nesting (33,34). More recently, their faithfulness to their foraging grounds has also been demonstrated (92,118,128). In 50 years of tag recaptures recorded in the Queensland Turtle Conservation Program, no *Chelonia mydas* individuals marked at breeding and later resighted in foraging grounds have been sighted at more than one foraging site (92). Chapter 2 supports the growing body of evidence of high foraging site fidelity in green turtles with 78% of the tracked animals in this study displaying range residency behaviour. There was a mean 83% overlap in 95% utilisation distributions over successive calendar seasons amongst the tracked animals. Nonetheless, in Chapter 3, I found five of 80 individuals (6.25%) tracked in Port Curtis performed long-range movements >80km from the place where they were captured. Long-range movements of foraging turtles, though rare, have been recorded at other coastal sites in Queensland, most notably in the Sandy Strait which receives freshwater input from the Mary River. The influence of flooding on foraging habitat condition in Port Curtis and Sandy Strait may increase the likelihood of turtles utilizing multiple foraging locations, while at sites without major river outlets (Cardwell, Moreton Bay, and Shoalwater Bay) fewer turtles are recorded foraging over expanded areas. This suggests that foraging site fidelity is conditional on stable conditions, and some individuals might be motivated to forage across a larger area, or multiple discrete areas if their primary diet items are depleted. However, multiple lines of evidence point to foraging site fidelity as the most common strategy, even if individual turtles must temporarily withstand suboptimal conditions to enact it (204). Due to the long-term fidelity of most turtles to their foraging areas, alterations in these habitats from climate change and anthropogenic stressors are likely to significantly impact health, survival, and breeding of resident individuals. Thus, it is crucial to protect established foraging habitats, particularly where there are medium to high density foraging aggregations.

### *6.1.3 Human-wildlife interactions*

Detailed foraging ranges can inform the implementation of conservation measures, such as go-slow zones for boating activity. Including dynamic information in distribution estimates, for example behavioral responses to change, may aid with the development of dynamic and adaptive interventions, such as the implementation of temporary go-slow zones. In Chapter 4 I identified that turtles were more likely to transit following a drop in temperature and when turbidity becomes very high, and that the areas used for transit were more expansive than for residency. Thus, temporary go-slow zones could be implemented following major floods or during planned dredging to reduce the likelihood of vessels interacting with mobile turtles. During fieldwork for this study, we observed anecdotally that green turtles seldom occupy the deep dredged shipping channels of Port Curtis and consider the risk of commercial vessel strike to be relatively low at this site. We also observed turtles using the artificial structures of sea walls for resting and/or refuge, suggesting the existence of human modifications does not inherently imply an impediment to foraging turtles.

### *6.1.4 Marine protected areas*

The majority of known foraging habitat for green turtles in the Great Barrier Reef region and globally are protected within MPAs (171). Green turtle foraging habitats were explicitly considered in the design of the Great Barrier Reef Marine Park zoning in 2004 (275). Identified high priority foraging sites for the nGBR and sGBR stocks (n=6) included Hedge Reef to Howick group, Hinchinbrook to Cape Bowling Green group, Hydrographers Passage to Swains group, Shoalwater Bay to Cosio Bay group and Capricorn Bunker group. All these high priority sites were identified in my prediction of suitable foraging habitat for 2022 (Chapter 5), but generally, our predictions did not encompass the entirety of these areas. Notably, the output from Chapter 5 represents foraging habitat suitability, not the realised distribution or density of the turtles.

Though substantal protections are offered to turtles by the Great Barrier Reef Marine Park zones, with 19% of potential suitable habitat for green turtles in 2022 within no-take areas, 50% was within Habitat Protection Zones, which until 2027 allow large mesh gill netting. The Australian and Queensland governments have commited to phasing out gill netting in the Great Barrier Reef World Heritage area by 2027 (324). Only 10.4% of predicted habitat was within Conservation Park Zones, which allow limited fishing and collecting.

For improvement of the model presented in Chapter 5, more representation of turtles who forage on reefal habitat could contribute to robust predictions of suitable reefal habitats. Similarly, tracking requires a minimum sized animal (i.e., tags cannot weigh more than 5% of the animal's body weight) to avoid impediment to the movement and behaviour of the animal (151). The outputs throughout this thesis are therefore not likely to represent habitat-use and movement for young turtles with a curved carapace length smaller than 42.1 cm, the smallest tracked for this thesis.

I predicted an expansive area of suitable foraging habitat for green turtles covering the entire latitudinal gradient of the Great Barrier Reef region. Because of the faithfulness of marine turtles to their foraging grounds, MPAs will likely be effective in protecting the individuals that are resident within them (93,174), and may be an excellent tool in high-density foraging grounds. However, MPAs may not be an appropriate tool for use in protecting turtles residing in low-density foraging grounds.

### *6.1.5 Functional habitats*

Ecological processes and human systems operate irrespective of the boundaries of MPAs. For safeguarding habitats, a functional approach to promoting ecosystem health may be beneficial to turtles and other sympatric organisms (325). In Chapter 2, I discovered that range size varies across the monitored sites at Port Curtis, suggesting that distribution hinges upon the variety and availability of food sources in different microhabitats. Different diet items influenced the likelihood of turtles being present at modified compared to unmodified sites in Chapter 5 (seagrass community type, seagrass probability, large zooplankton and distance to mangroves in modified habitats, and distance to mangroves only in unmodified habitats). Salinity, mean seawater velocity and frequency of acute floods were influential phyiscal predictors in unmodified habitats. In Chapter 2 foraging range size varied significantly in different years, suggesting that periods of high rainfall prompted turtles to expand their range to obtain sufficient forage or use alternative food resources. In Chapter 3 I suggested that long-distance movements of some foraging individuals could be due to declines in habitat conditions caused by frequent natural disturbances from severe rainfall events, in combination with adjacent human activity, including land use, leading to runoff. In Chapter 4, acute changes in local conditions led to behavioural change, with turtles initiating outward transit when moving through water that was too clear or too turbid, too deep or too shallow, and staying in place when temperature increased. Therefore, a suite of dynamic factors in the habitat influence turtle space-use, activity and diet.

To support resilient and functional habitats, human activities that exacerbate the detrimental impacts of environmental disturbances could be targeted. For example, throughout this thesis I have discussed that coastal flooding can limit food availability for foraging turtles and facilitate the spread of disease. In Chapters 3 and 4 I determined that deviation from range residency may occur following floods as a few turtles venture further to aquire sufficient food. Across a catchment, land restoration and site stewardship by landholders can benefit coastal ecosystems by mediating the composition and quantity of sediment loads delivered following rain (Reef2050 Water Quality Improvement Plan 2017-2022, Queensland Reef Water Quality Program). Adhering to dredging best practices contributes to improved water quality at the site and at the time of dredging operations (326), but also at adjacent sites and afterwards (327) when resuspension can occur.

Effective and enduring habitat management needs to consider social, cultural, economical, and ecological contexts (328). For example, joint management (or co-management) is an avenue for achieving enhanced outcomes for conservation, cultural preservtion, economic and social benefits (including capacity building and employment), and improved governance in managed marine areas. However, there may at times be tension between intended biodiversity outcomes and cultural or social ones (329). The limitations of joint management include stakeholder participation, resourcing, capacity, tools, and recognition of the need (330). Measuring the effectiveness of joint management poses a challenge (331,332), particularly in a changing climate, where conservation outcomes and traditional knowledge are likely to evolve (333).

### *6.1.6 Green turtles as an indicator species*

Green turtles are widely regarded as large herbivores, vulnerable to human impact, and as a result, are considered sentinels and mediators of ecosystem change (309,334). However, my thesis suggests that green turtles are not a good indicator species. They persist in murky environments (Chapter 4), when there’s no seagrass (Chapters 2 and 3), in areas of high human use (Chapter 5), sometimes to the detriment of their body condition and survival (89). Furthermore, they persist in these areas, often for decades. Age at maturity and growth rates of green turtles are mediated by the environmental conditions at the foraging ground. Age at maturity is between 20-50 years (103).

Therefore, changes to immature populations of turtles arising from changing environmental conditions at foraging grounds (e.g., persistent lack of foraging resources could result in slow growth and fewer adults coming into breeding) may take decades to be measurable at index nesting sites. Similarly, most nesting aggregations are made up of turtles from multiple, often distant, foraging areas (87,90,94). Local monitoring at foraging grounds (health, growth, rather than abundance) can give timely insight into conditions occuring there, while larger population trends (numbers of nesting females at distant nesting sites) may mask the signal.

### *6.1.7 Biologically Important Areas*

The Australian federal government protocol for designating important areas for breeding, migration and foraging of marine turtles (Biologically Important Areas, or BIAs) is currently under review (273). This includes reassessing the thresholds that need to be met for an area to be considered ‘important’, and attempting to incorporate foraging areas (not included prior to 2024). The new protocol weights information from direct observation above modelled outputs and satellite telemetry data because the latter cannot ascertain the behaviour of the turtles with certainty. Inclusion only of direct observations would bias the BIA to regions close to human populations. However, in Chapter 5, I determined that large areas of suitable habitat for green turtles exist across the entire latitudinal gradient of the Great Barrier Reef, including the mid-shelf. In addition, the foraging, migrating and breeding periods of marine turtles can be easily distinguished from tracking data. Remotely sensed and modelled data can be used to designate BIAs with the approval of independent expert review (273). I would argue that these approaches are invaluable to the designation of BIAs, particularly away from coasts and urban centers. In Chapter 5 I established a dynamic estimate of foraging habitat distribution for green turtles across the Great Barrier Reef. I intend to provide the outputs of Chapter 5 for consideration in green turtle BIAs for foraging.

### *6.1.8 Conservation challenges*

The increasing frequency of large flood events, increasing needs for human infrastructure near coasts, and continued loss and degradation of foraging habitat (seagrasses and coral reefs) have come to light throughout this thesis as future problems for the species. Though the sGBR stock is recovering (71), the nGBR stock is considered as having a very poor outlook, with low hatching success, low recruitment and feminization at Raine Island posing major issues.

Satellite tracking at foraging grounds provides information on green turtle males and immature turtles, where previously there has been strong bias towards female adults in the literature (17,18,144). The Queensland Marine Turtle Conservation Strategy (71) emphasises the importance of studying males to evaluate population viability for nGBR, and sub-adults as early indicators of population trends to measure the success of the Raine Island recovery project.

Methods from this thesis can be adapted to target the management of the species elsewhere. For example, the approach to the calculation of representative foraging ranges as in Chapter 2 can be adapted to support the expansion of GoSlow zones at high-density foraging sites throughout the Great Barrier Reef (64). The habitat modelling in Chapter 5 can be used as an initial indication of unknown foraging areas. With the addition of detectability data, these models could generate estimates of abundance and density (294,300), indicating the locations of high-density foraging sites. Habitat distributions can also serve as a baseline against which to assess risk to foraging areas that are not currently protected through vulnerability analysis (14,304,335).

### *6.1.9 Data challenges*

My thesis incorporates an unusually large amount of tracking data for a single site and some of the most advanced and detailed spatio-temporal models and simulations in the world [eReefs, DeepReefs, Digital Earth Australia and TropWATER products; (256,286,336,337)]. However, in each of my chapters data availability presented limitations. I faced temporal and spatial gaps in the tracking data, barriers to accessing privately owned datasets, missing data for variables of interest, and the challenge of matching the resolution, scale, and extent of behavioral and environmental data. For example, in Chapter 3, sufficient tracking data was not available at a pertinent period following flood events to enable a detailed assessment of fine-scale movements following flooding. In Chapters 4 and 5, the spatial resolution of the environmental data and simulation results was substantially coarser than that of the tracking data. For example, the eReefs dataset had a spatial resolution of 4 km (279,282), which, when compared to the median 95% UD area of 9.7 km$^2$ established in Chapter 2, is too coarse to identify fine-scale habitat features which may be influencing turtle movement and distribution. Given the challenges I faced to obtain sufficiently detailed data to elucidate ecological patterns for marine turtles, which have been studied over decades in the Great Barrier Reef (71), elucidating patterns for other organisms and systems is likely fraught with challenges. My thesis therefore showed that, despite great advances in the availability and utility of environmental datasets needed to understand ecological systems at large scale in this region (e.g., 286,292,336), there is much work to be done. Specific improvements include a) making data openly accessible with unrestrictive licenses, b) easier access via APIs and well-structured metadata, now enabled by emerging protocols such as STACSPEC (339), and c) higher resolution data products enabled by burgeoning earth observation data archives, which continue to reduce the spatial resolution of sensors for environmental data collection.

In general, monitoring systems for the environment could be improved by developing methods for monitoring over time that do not require long-range deployment of field teams. This might include remotely sensed data, or local engagement and capacity building for monitoring by local organisations and citizen scientists. Guidelines for consistent data collection, formatting and naming can facilitate compilation of multiple datasets e.g., Movebank and CCAMLR Ecosystem Monitoring Program standard methods (340,341). Leveraging open data and multiple data types may facilitate the generation of more environmental data in more regions. The expense of data collection, both technology and fieldwork, access to remote and deep sites, having unified goals across investigators and management agencies, and technical limitations (e.g., data storage, shareability, useability, metadata standards, computing power) are ongoing challenges.

## 6.2 Future research directions

Across Australia large gaps exist in our knowledge of the population dynamics and ecology of particular marine turtle stocks, such as in the Coral Sea and northern Australia (71). Leveraging traditional ecological knowledge is one means by which researchers could establish population baselines (342), identify unknown and important sites for foraging and nesting (343), and to enhance harvest management for marine turtles (344). Additionally, co-design of research, monitoring and management initiatives, particulary in remote locations, has the potential to achieve both social and ecological outcomes (345). However the social benefits of participating in research/monitoring, or arising from its outputs are not well studied. Understanding how people use and value coastal ecosystems and marine turtles, and the value they receive from programs is going to be key to enduring engagement and success of conservation (346). To fill some of the knowledge gaps for marine turtles, the approach I used in Chapter 5 could be expanded, modelling habitat distribution to establish where turtles are, their resource requirements and their vulnerability to climate change and anthropogenic threats in these understudied areas. Climate vulnerability analysis is commencing for nesting turtles in Australia (347), but not yet in foraging grounds. Additionally, there are increasing opportunities to incorporate ecological studies with social science (e.g., CSIRO’s SELTMP).

It can be challenging to adequately collect, analyse and interpret ecological data that considers both spatial and temporal dimensions. However, ecosystem processes are not static, and baselines are shifting at unprecedented rates. Conservation planning must consider change (348) especially under changed climate scenarios. Ecosystem function is generated and maintained by natural processes and mediated by changing human activities. Thus, considering dynamic ecological processes and their threats is necessary to develop interventions that can adequately ensure ecosystem persistence. For green turtles, if sea temperatures warm, the distribution and temporal stability of algae and possibly seagrass are likely to change, impacting turtle distribution at both small and large scales. While uncertainty can sometimes hinder decision making, it is also key that realistic estimates of uncertainty are incorporated into study approaches so that decision-makers can take it into account. Many studies do not address error and biases in data collection, assumptions in modelling or statistical analyses, the unpredictability of ecological processes and the combination of these. There are opportunities to improve how we estimate uncertainty in ecological studies e.g., Bayesian statistics. Frameworks that integrate uncertainty into decision-making processes are also essential, for example evaluating management strategies based on the likelihood of several outcomes and their associated risks.

Intraspecific variability in marine turtle populations remains poorly understood (349). This thesis demonstrates multiple examples of intraspecific variability in movement and space-use. In Chapter 2 deviations from range residency were displayed by 22% of tracked individuals. Chapter 3 demonstrated the long-range movement of 5 out of 80 individuals. In Chapter 4, individuals had significantly different responses to cues to move, and all the tracked turtles displayed behavioural changes and could not be grouped into “stayers” or “goers”. It is, therefore, unlikely that a tendency to stay in place is an inherent trait of individuals, but rather mediated by when and where they were tracked, and the conditions experienced there. The next step to untangling intraspecific behavioural differences could be to investigate the consequences or advantages of different behavioural strategies on growth rates, survival, breeding rates and emigration rates, however I was unable to do so with the present dataset. Doing so would require longitudinal studies to track the same individuals at several timepoints, and collect biometric measurements (weight, length, breeding status) over time. Behavioural strategies of individuals are unlikely to be fixed, particularly as the individual ages and experiences changing environmental conditions.

## 6.3 Concluding remarks

Marine turtles are considered umbrella species, and have cultural, social, and economic value. They are charismatic and can serve as a tool for engagement and education about the broader issues of climate change and habitat loss. Protecting turtles is enshrined in our state and national legislation and can sway future environmental commitments.

This thesis supports previous research in identifying foraging site fidelity as a predominant strategy for green turtles, suggesting that safeguarding existing habitats is vital, particularly in high density foraging grounds. Nonetheless, in coastal environments, severe weather contributes to changes in turbidity and temperature, depleting foraging resources and prompting some individuals to mobilise on large and fine scales. Doing so may increase their likelihood of interacting with threats. Lastly, it highlights that while marine protected area boundaries include some suitable habitat for foraging turtles, these habitats are susceptible to climate and human-mediated changes. Therefore, managing spaces that are shared by humans and wildlife is not necessarily about completely avoiding direct interactions with wildlife, but adopting practices that minimize impact to ecosystem health and function across a broader spatial plan (350).

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