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Spatial ecology and conservation of sea turtles in coastal foraging habitat

Thesis submitted by

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2	Shimada T, Jones R, Limpus C, Hamann M (2012) Improving data retention and home range estimates by data-driven screening. *Marine Ecology Progress Series* 457:171-180 doi:http://dx.doi.org/10.3354/meps09747	I designed the study. Limpus and I conducted field research at sea and I conducted terrestrial experiment. I analysed data and developed methods to screen GPS satellite telemetry data. I wrote the manuscript and all authors contributed to the editing.
3	Shimada T, Limpus C, Jones R, Hazel J, Groom R, Hamann M (2016) Sea turtles return home after intentional displacement from coastal foraging areas. *Marine Biology* 163:1-14 doi:http://dx.doi.org/10.1007/s00227-015-2771-0	Limpus, Hamann, Jones and I developed the concepts of the study. Limpus, Hamann, Groom and I conducted field research. I analysed data with advice provided by Jones. I wrote the manuscript and all authors contributed to the editing.
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Outputs Associated with This Thesis

Papers published or intended for publication

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Computer Programming

SDLfilter: an R package to screen satellite-derived data using the method described in Shimada et al. (2012) and Shimada et al. (2016). The latest package is available at an online code sharing and publishing service GitHub https://github.com/TakahiroShimada/SDLfilter.

Selected technical reports

Limpus C, Hamann M, Reed M, Bell I, Bowlett J, Mulville C, **Shimada T**, Smith A, Smith J (2015) Turtle telemetry project, Triangular Island, eastern Shoalwater Bay, June 2014 - March 2015. Brisbane: Department of Environment and Heritage Protection, Queensland Government.

Hamann M, Riggin J, **Shimada T**, Limpus (2014) Six month report on the interesting habitat use by flatback turtles off the Curtis Island coast: 2013 – 2014. Gladstone Ports Corporation.

Busilacchi S, Butler J, Skewes T, Posu J, **Shimada T**, Rochester W, Milton D (2014) Characterising fisheries of the Torres Strait Treaty Villages, Papua New Guinea. CSIRO.

Shimada T, Hamann M, Limpus C, Limpus D (2013) Turtle and dugong research and monitoring, western Shoalwater Bay, 25 June - 5 July 2012. B. Marine turtle satellite telemetry. A report made to the Great Barrier Reef Marine Park Authority.

Conference Presentations

Shimada T, Limpus C, Jones R, Groom R, Smith M, Hamann M (2014) Displaced Sea Turtles Return Home. Oral presentation at the Australian Marine Turtle 2nd Biennial Symposium, Perth, Australia.

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Shimada T (2013) Sea turtles; Master navigators. Three Minute Thesis, James Cook University, Townsville, Australia.

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Fuentes MMPB, Cleguer C, Liebsch N, Bedford G, Amber D, Hankin C, McCarthy P, **Shimada T**, Whap T, Marsh H (2013) Adapting dugong catching techniques to different cultural and environmental settings. *Marine Mammal Science,* 29**,** 159-166. doi:http://dx.doi.org/10.1111/j.1748-7692.2011.00531.x

Book Section

Shimada T (2013) Green turtles in the waters surrounding Hachijo Island. In: Kameda K (ed) Green Turtle of Japan. Sea Turtle Association of Japan, Okinawa, Japan, pp 93-98 (in Japanese and English).

Conference Presentations

Barrios-Garrido H, Espinoza-Rodriguez N, **Shimada T**, Wildermann N (2015) Body condition index in rescued Green turtles (*Chelonia mydas*) in the Gulf of Venezuela: a seven year assessment. Poster presentation at the 35th Annual Symposium on Sea Turtle Biology and Conservation, Muğla, Turkey.

Shimada T, Kameda K, Aoki S, Kamezaki N (2012) Diet habit of the green turtles *Chelonia mydas* in Japan as indicated by stable isotope analysis. Oral presentation at the Conference for the Northwest Pacific Green Turtle, Kobe, Japan.

Thesis Abstract

Spatial ecology investigates mechanisms in nature by examining spatial patterns. Developing our knowledge of spatial ecology will improve our approaches to the conservation of threatened species. Our understanding of spatial ecology is limited for marine species such as sea turtles, due to the complexity and methodological challenges involved in the investigation at-sea behaviour. Most sea turtle species are conservation-dependent due to historical and current anthropogenic threats, but a lack of ecological knowledge in the marine environment may hinder or prevent appropriate actions being taken by conservation practitioners.

Important knowledge gaps exist in our understanding of spatial and temporal movement of sea turtles in coastal foraging habitats where anthropogenic threats are high. These turtles may be relocated from their home habitats due to injury (e.g. from fisheries and boat strikes), following disasters (e.g. oil spills or extreme weather events), or following habitat loss (e.g. port expansion and dredging); thus, it is critical to understand the degree of fidelity and homing ability of turtles that have been displaced. For instance, if displaced turtles return to an oil spill area too soon after displacement, alternative conservation actions might be required. Additionally, if a turtle returns to its home habitat after displacement, as past studies have indicated, another question arises: how do the navigation mechanisms of sea turtles work? Current hypotheses theorise that sea turtles use geomagnetic cues for long-distance migration, but that they are likely to use non-geomagnetic cues during the last part of their migration. Details of their fine-scale navigation ability and potential cues are lacking.

Fidelity to foraging habitat has been indicated by previous studies but key questions remain; (a) What is the extent of sea turtle foraging habitats? (b) How long do they remain in such habitat? and (c) What factors affect their faithfulness to specific foraging habitat? Answering these questions will improve credibility of home range analysis and its applications to conservation planning or evaluation such as determining the effectiveness of Go Slow Zones in Moreton Bay. Moreton Bay is a significant foraging area for green and loggerhead turtles in eastern Australia but the risk of boat strikes is high because of extensive recreational and commercial vessel traffic. Management systems, such as Go Slow Zones, are in place in some shallow areas but vessel collisions still occur more frequently in Moreton Bay than elsewhere along the Queensland coast. Therefore there is a need for assessing whether current regulation is providing adequate protection to sea turtles against vessel collisions in Moreton Bay. My thesis addresses these knowledge gaps and aims to advance our knowledge of ecology and

conservation of sea turtles related to their spatial and temporal use of coastal foraging habitats, with particular focus on the Queensland region.

Fastloc GPS (FGPS) is a powerful tool for investigation of fine-scale animal spatio-temporal ecology. Satellite-linked FGPS tags provide researchers with almost unlimited temporal and spatial range to monitor animal movements, and give more accurate and larger quantities of locations than earlier methods (e.g. platform transmitter terminals). These large and detailed locational data make understanding certain aspects of turtle ecology possible, whilst also enabling delineation of accurate areas for protection. However, it remains important to identify and remove locations with high error because some location fixes are much less accurate than others. I use FGPS tags as my primary tool to track turtle movements, and therefore need to handle FGPS estimates with high error prior to any ecological and conservation-based analyses.

I began by investigating potential methods to screen FGPS data (Chapter 2). Increasing the number of source satellites required for a valid fix is a simple filter method but it comes at the cost of great data loss. Using data sets acquired from loggerhead turtles (*Caretta caretta*), I explored an alternative filtering approach, based on speed between successive locations, angles created by three consecutive locations, manufacturer's quality index, and number of satellites used for location calculation. The performance of the proposed filter method was evaluated by conducting terrestrial mobile tests. When my filter method was used, the linear error (mean ± SD) of Fastloc GPS data decreased from 2,645.5 ± 29,458.2 m (n = 1,328) to 47.1 ± 61.0 m (n = 1,246) while retaining more than 94% of data. My filter method also led to more accurate home range estimates than the simple filter method. This advance in processing satellite-derived data delivers an improved ability to analyse fine-scale animal movement. I went on to apply the filtering technique to my satellite telemetry data prior to subsequent analyses.

In chapter 3, I investigated whether highly mobile sea turtles can be expected to remain at a new location after they were displaced. I addressed this question for sea turtles at foraging grounds along the coast of north-eastern Australia. I analysed 113 tracks comprising four species (*Chelonia mydas*, *Caretta caretta, Lepidochelys olivacea, Eretmochelys imbricate*) fitted with satellite-linked devices. Turtles released at their original “home” areas all remained there (n = 54). Among displaced turtles (released away from their original area, n = 59), the large majority travelled back to their respective home areas (n = 52) or near home (n = 4). Homing turtles travelled faster and adopted straighter routes in cooler water, and travelled faster by day than by night. My results showed that displacement up to 117.4 km and captivity up to 514 days did not disrupt homing ability nor did it diminish fidelity to the home area. However, for homing turtles I infer energetic costs and heightened risk in unfamiliar coastal waters. Confirmed homing suggests that moving individuals away from danger might offer short-term benefit (e.g. rescue from an oil spill) but moving turtles to a new foraging area is unlikely to succeed as a long-term conservation strategy. Priority must rather be placed on protecting their original habitat.

As confirmed in Chapter 3 and previous studies, sea turtles have an exceptional ability to navigate accurately between known habitats as well as from unknown areas back to familiar habitat. In Chapter 4, I examined the turning and orientation behaviour of 29 displaced sea turtles of two species (*Chelonia mydas*, *Caretta caretta*), tracked *en route* back to their foraging habitats in eastern Australia. I found that sea turtles tended to alternate stationary and travelling phases during their trip home. Orientation corrections predominantly occurred immediately after a stationary phase and after sunrise. This is the first study to demonstrate time-restricted orientation by sea turtles and provided a new insight into their sophisticated navigational abilities.

My remaining data chapters (5, 6) focused on turtles' behaviour in their foraging habitats, and resultant applications for conservation planning. In Chapter 5, I tracked adult green and loggerhead turtles foraging in the coastal waters of eastern Australia, objectively quantified home range size and site fidelity, and then examined how their spatial selections were affected by ecologically meaningful variables such as season, extreme weather events (tropical cyclones and extreme rainfall), habitat location and sex. Many individual turtles were observed multiple times over extended periods using satellite telemetry (PTT, FGPS or both) and mark-recapture methods. Evidence from these multiple observations inferred that many turtles maintained high fidelity to their coastal foraging habitats for long periods - up to 20 years. Within these long-term foraging habitat areas defined by my analysis, turtles generally shifted their main foraging areas on a seasonal basis. These characteristics of sea turtles emphasise the importance of conserving areas according to their space use, with careful consideration given to identifying temporal trends in habitat selection. I also identified a geographical advantage of two sites in eastern Australia (eastern Moreton Bay and eastern Port Curtis) as foraging habitats for sea turtles with relation to extreme weather events such as tropical cyclones and extreme rainfall. These important foraging habitats would benefit from prioritised conservation planning and management actions. My findings have direct relevance to conservation managers for planning, or revision, of designated conservation habitat such as Marine Protected Areas or restricted area zones, to protect these threatened species from increasing human activities at their foraging habitats in Australia and other regions.

Finally, I investigated whether existing Go Slow Zones are providing adequate protection against boat strike for sea turtles foraging in Moreton Bay. To do so, I examined space use of green and loggerhead turtles in relation to the Go Slow Zones and water depth (Chapter 6). I found that most of the habitats used by my tracked turtles were in shallow water, and up to 55% of their habitats were included within the Go Slow Zones in eastern Moreton Bay. However, turtles are not protected from vessel collisions in the deeper zones (water depth ≥ 5 m), which lie adjacent to the Go Slow Zones, or in other shallow water zones in Moreton Bay. In particular, little or no protection is given to sea turtles in southern, western and northern Moreton Bay. By designating all shallow areas in Moreton Bay as Go Slow Zones, approximately 50% or more of the Bay's turtle habitats would become protected from vessel collisions. Additionally, my data indicate that shallow zones plus a 1.2 km, 2.4 km, or 3.6 km buffer would protect ≥80%, ≥90% or ≥95% respectively, of habitats used by both species because they cover the deeper zones adjacent to the shallow zones. The results of this study will be highly informative for conservation managers when revising the current Go Slow Zones for improved management of these threatened sea turtle populations.

The advanced technology and analytical tools I adopted in this thesis enabled me to overcome the difficulties associated with investigating sea turtle movements, and consequently to improve our understanding of their relationship with environmental variables. My approach has applications for investigating spatial ecology of other animals, including other populations of sea turtles. I concluded this study by discussing my key findings related to the behaviour of foraging sea turtles, highlighting conservation benefits that can be potentially derived from incorporating ecological knowledge into planning. I also suggest specific priorities for future research to enhance our knowledge of the spatial ecology of sea turtles, and consequently our ability to conserve these threatened marine reptiles which are necessary for healthy ecosystems.

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Chapter 1

General Introduction

"The world is unavoidably spatial, and each organism is a discrete entity that exists and interacts only within its immediate neighbourhood."

\- Tilman and Kareiva (1997)

Globally, the state of marine ecosystems has been affected by rapid growing human populations, especially in coastal areas (Jackson et al. 2001, Valiela et al. 2001, Millennium Ecosystem Assessment 2005, UNEP 2006, Halpern et al. 2008). One of the key components of coastal ecosystems is marine megafauna, such as marine mammals, seabirds and sea turtles. These marine wildlife groups often occur across large spatial areas and have significant roles for both marine ecosystems and human communities and cultures (Bjorndal and Jackson 2003, Campbell 2003). Conserving these species can be an effective approach for ocean conservation planning, because by conserving marine megafauna additional conservation benefits will be provided to other animals within their habitats, and in addition, marine megafauna often receive and generate significant public and political attention (Hooker and Gerber 2004, Frazier 2005).

Sea turtles are often referred to as charismatic marine wildlife. Each of the species show similar life history and reproductive patterns (Buskirk and Crowder 1994), and being long-lived late-maturing iteroparous animals, survivorship of large juveniles and adults greatly determines their reproductive fitness (Crouse et al. 1987, Heppell 1998). Many large juveniles and adult Cheloniidae (hard-shelled sea turtles) spend the majority of their life in coastal foraging habitat where anthropogenic threats are likely (Lutcavage et al. 1997). Yet, it is in the marine environment that we know the least about them. Therefore understanding the biology of, and conserving, foraging sea turtles, in particular large juveniles and adults, is vital for their conservation.

The process of conservation management requires comprehensive ecological knowledge (Kareiva et al. 2007, Barbier et al. 2008). Since spatial interactions between organisms and their neighbouring environments are the fundamental function of nature, it is critical to consider the potential influence of space use by animals, to fully understand mechanisms of nature (Tilman and Kareiva 1997). A key knowledge gap for highly mobile sea turtles is an understanding of the relationships between species, their habitats and their threats (Hamann et al. 2010). My thesis addresses the spatial aspect of in-water sea turtle ecology, with particular focus on large juveniles and adult Cheloniidae, and considers its applications for conservation planning.

1.1 Sea turtles under threat

Numerous anthropogenic activities are impacting sea turtles worldwide. Fisheries bycatch can cause death or severe injuries to sea turtles, or damage their habitats (Poiner and Harris 1996, Robins and Mayer 1998, Lewison et al. 2004, Peckham et al. 2007, Gilman et al. 2010). Coastal development such as dredging, coupled with the expansion or modification of coastal land may cause habitat loss (Eckert and Honebrink 1992). Collisions between turtles and vessels occur most often in coastal shallow waters which are heavily used by commercial and recreational vessels (Lutcavage et al. 1997, Hazel and Gyuris 2006, Limpus 2008). Oil spills (e.g. the Gulf of Mexico Deepwater Horizon accident) and other pollutants may greatly increase mortality of sea turtles (Swarthout et al. 2010, van de Merwe et al. 2010, Antonio et al. 2011, Komoroske et al. 2011, Stewart et al. 2011). These anthropogenic threats are serious issues for sea turtle conservation because many sea turtle populations are still recovering from past exploitation by humans such as harvest for their meat, eggs and carapace shells (Bjorndal and Jackson 2003, Campbell 2003).

One of used conservation approach is to enforce Marine Protected Areas (MPAs) to protect marine resources, including sea turtles, from known or potential anthropogenic threats (Hooker and Gerber 2004, Fernandes et al. 2005, Gaines et al. 2010). Levels of protection vary among MPAs. Some MPAs restrict human activities by setting limits for takes or boat operation while others provide more comprehensive protection with turtles protected from capture except for specifically permitted operations such as research and conservation activities (e.g. Queensland Government 1992, Pauly et al. 2002).

MPAs can provide the comprehensive protection required to conserve marine resources as long as the designated areas cover important habitats of targeted marine resources (Pressey et al. 2007, Agardy et al. 2011). However, knowledge of habitat coverage is not always available to conservation initiatives. In many cases, MPAs have been established without prior study of their conservation target, and consequently adequate protection could not be provided (e.g. Rojas-Bracho et al. 2006, Schofield et al. 2013b, Cleguer et al. 2015). Even for MPAs like the Great Barrier Reef Marine Park, the protection of larger mobile species is challenging (Dobbs et al. 2008, Dryden et al. 2008). MPA effectiveness could be improved with a more comprehensive understanding of the spatial ecology of key species and the spatial extent of their threats.

While MPAs form one component of protecting animals in situ, in cases when animals become debilitated (e.g. vessel collisions), or threats exist in their habitat (e.g. oil spills), animals must be removed from their original habitat to help them regain health or protect them from threats to their health. Rescued turtles are usually taken to rehabilitation centres which are often distant from their original habitat. For logistical and financial reasons, rescued turtles may not be released back into their original habitat. The consequences of such displacement has not been well investigated.

1.2 Challenges in studying foraging turtles and potential solutions

Sea turtles spend most of their life at-sea, in foraging habitats (Bolten 2003), where they are challenging to study because they are almost always under water, except for occasional surfacing for breathing (Lutcavage and Lutz 1997). In addition, foraging sea turtles can move long distances, particularly juveniles of some populations (Musick and Limpus 1997, Morreale and Standora 2005, Mansfield et al. 2009, Narazaki et al. 2015), and can also reside in areas with poor water clarity (Limpus et al. 2005). These behaviours have made it difficult for researchers to monitor the movements and habitat use of foraging sea turtles. Consequently, the foraging phase of sea turtles, in particular that of adults, has been less well-studied compared to other stages of their life cycle - such as the nesting and hatching stages (Hamann et al. 2010). Key knowledge gaps include habitat size, degree of site fidelity, navigational mechanisms, factors affecting sea turtle in-water behaviour, and application of ecological knowledge into conservation management (Hays 2008, Hamann et al. 2010).

Many of the key knowledge gaps related to foraging sea turtles can be addressed by investigating their fine-scale movement and their habitat use in relation to threats. Sea turtle researchers have traditionally adopted flipper-tags to study the movement of sea turtles, and have found evidence of long-distance migration and site fidelity, by both breeding and foraging sea turtles (e.g. Miller et al. 1998, van Dam and Diez 1998). However, only a snapshot of turtle movement can be obtained using the tagging technique because it can only provide the release and capture locations of each individual, and the time frames between tagging and recapture can span years, or even decades (Limpus et al. 1992, Godley et al. 2003). Since the 1960s, researchers have developed other techniques to track turtles, such as weather balloons to follow inter-nesting turtles (Carr 1967, Davis 2007), and more recently acoustic and radio telemetry to follow inter-nesting and/or foraging turtles (Kemmerer et al. 1983, Tucker et al. 1996, Whiting and Miller 1998, Seminoff et al. 2002, Avens et al. 2003, Makowski et al. 2006, Hazel et al. 2013). While these methods have potential advantages and have revealed turtle movements within small areas, their range of signal transmission is limited, which restricts the usefulness of these techniques in studying turtle movement because turtles can often move beyond their transmission range (Avens et al. 2003, Hazel et al. 2013).

Satellite telemetry has substantially improved animal tracking by providing full-time global coverage (Hazen et al. 2012). Since the early 1980s, platform terminal transmitters (PTTs) have allowed fairly crude tracking of animals, including sea turtles, using the Argos satellite system (Gillespie 2001, Godley et al. 2008). A PTT may be suitable to track long-distance movements of breeding and foraging turtles (e.g. Keinath and Musick 1993, Limpus and Limpus 2001, Hays et al. 2004, Shaver et al. 2005, Shaver and Rubio 2008, Bailey et al. 2012), but because the accuracy of the locations is low, it rarely allows fine-scale analysis of movements (Hays et al. 2001). However, the latter analysis is often required for studies on sea turtle populations that utilise coastal foraging habitat within a small area.

In the early 2000s, Fastloc GPS (FGPS) emerged as a system for obtaining detailed positional information using the GPS satellite system (Bryant 2007, Rutz and Hays 2009, Wildtrack Telemetry Systems Limited 2010). By linking a FGPS receiver with a PTT, detailed positional data can now be remotely relayed, allowing travel routes and space use to be accurately measured over extended spatial and temporal scales (Schofield et al. 2013b, Hays et al. 2014c).

Similarly, advances in analytical methods, and computer hardware/software to execute these analyses have allowed researchers to filter and process large datasets (e.g. Hoenner et al. 2012, Jonsen et al. 2013) and to undertake complex spatial and/or statistical analyses (e.g. Jonsen et al. 2005, Barraquand and Benhamou 2008, Bestley et al. 2014). By combining satellite telemetry data with contemporary analytical techniques, it is now possible to examine fine-scale animal movement and habitat use data to explore questions about the spatial ecology of foraging sea turtles.

However, a challenge remains. While most location estimates obtained by FGPS tags are highly accurate, FGPS data sets often contain location estimates with a high degree of error (Hazel 2009). Inaccurate estimates lead to unreliable results and inferences. So there is a need for objective methods for screening FGPS data, which I have identified as the first objective of my thesis. Once this issue is solved, fine-scale analysis can be achieved with high confidence.

1.3 Foraging sea turtles in Queensland, Australia

I will now provide a brief overview of foraging sea turtles with particular focus on the populations in Queensland waters. I consider this background information necessary for readers to follow the remainder of my thesis. I also highlight important knowledge gaps, which lead to the other objectives of my thesis.

1.3.1 Study species

Six of the seven species of marine turtle forage in Australian waters (Limpus 1995). In this thesis, I investigated the spatial ecology of green turtles (*Chelonia mydas*), loggerhead turtles (*Caretta caretta*), olive ridley turtles (*Lepidochelys olivacea*), and hawksbill turtle (*Eretmochelys imbricata*) in their coastal foraging habitat in Queensland, Australia (Figure 1.1).

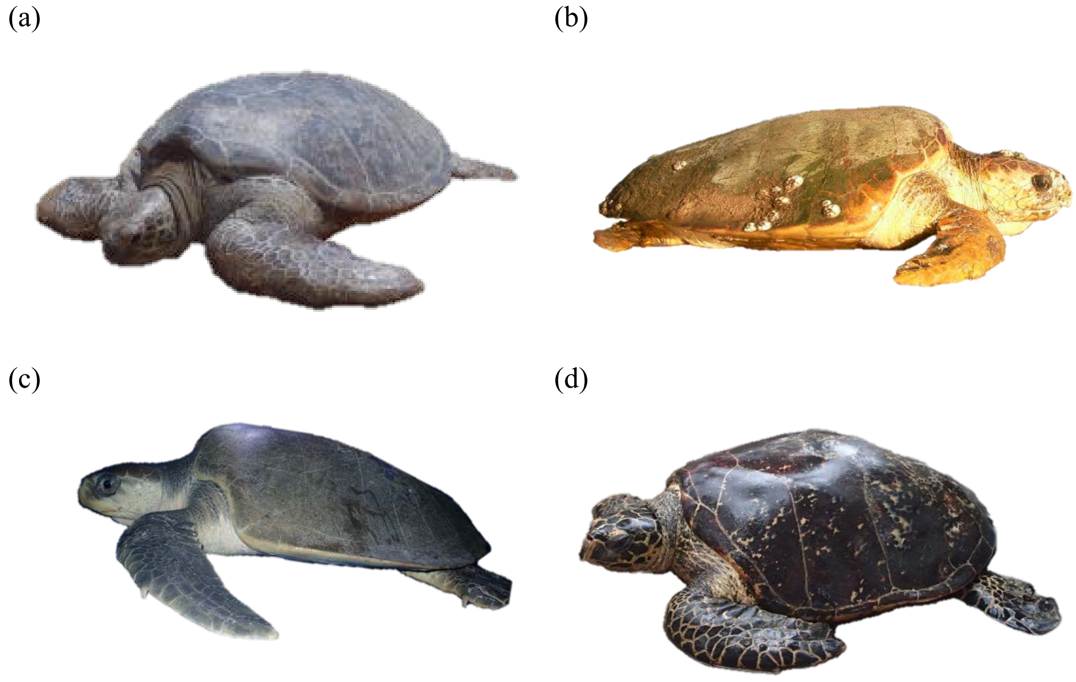

Figure 1.1 Pictures of study turtle species: (a) green turtle, (b) loggerhead turtle, (c) olive ridley turtle, (d) hawksbill turtle.

1.3.2 Distributions

Green and loggerhead turtles are the most common species of the shallow coastal waters found in the temperate to tropical eastern Australia (Limpus 2008). Olive ridley turtles have a similar latitudinal range to green and loggerhead turtles but they use deeper waters, and are not generally associated with inter-tidal habitats or shallow reef environments (Limpus 2008). Hawksbill turtles are typically found in tropical reef areas, but some appear to feed in shallow coastal seagrass habitats where green and loggerhead turtles also forage (Limpus and Miller 2008).

1.3.3 Diet

Green turtles residing in the coastal habitats of Queensland are predominantly herbivorous. Their main diet depends on the location of foraging habitat and the presence/absence of seagrass. In general, it appears that if seagrass is available it will form the major component of green turtle diet. In the absence of seagrass, macroalgae is the dominant diet component (Fuentes et al. 2006, Arthur et al. 2008b, Limpus 2008). Mangrove fruits and leaves can be consumed but are not believed to be common diet items in most regions, although this warrants further research attention (Limpus and Limpus 2000). Some green turtles may feed on gelatinous prey when opportunity arises (Arthur et al. 2007, Limpus 2008). Loggerhead turtles are carnivorous, mainly feeding on benthic invertebrates and less frequently on gelatinous prey (Limpus et al. 2001). Olive ridley turtles are also carnivorous, feeding on benthic invertebrates (Limpus 2008). Hawksbill turtles feed primarily on sponges and macroalgae, and also on seagrass in some regions (Meylan 1988, Whiting 2004, Bell 2013).

1.3.4 Foraging range

The size range of foraging areas for green turtles has not been well quantified in most foraging habitats in Queensland, with the exception of a limited numbers of turtles and areas in Moreton Bay, Shoalwater Bay, Low Isles and Torres Strait. These green turtles generally used habitat less than 17 km^2 but showed high individual variation, with some turtles using areas as large as 750 km^2 (Whiting and Miller 1998, Hazel 2009, Hazel et al. 2013, Gredzens et al. 2014). The size of foraging habitat has not been quantified for loggerhead turtles in Queensland waters. However, turtles foraging in the southern Great Barrier Reef (GBR) were shown to move at least 10 km using mark-recapture data (Limpus 1985), and turtles foraging in Moreton Bay were shown to move around 21 km using low resolution satellite telemetry (Limpus and Limpus

2001). The size range of foraging habitat has not been quantified for olive ridley and hawksbill turtles in Queensland waters and studies are rare Australia wide (Hoenner et al. 2015). Our knowledge of home range size for sea turtles is clearly incomplete along the Queensland coast, especially for turtles in the shallow coastal habitats where anthropogenic influences are high, requiring conservation measures with careful design, such as Moreton bay near Brisbane and Port Curtis in Gladstone.

1.3.5 Seasonal shifts in habitat

In Queensland, no studies on foraging sea turtles have shown changes in behaviour in response to water temperature or season. Moreton Bay is the southern-most foraging habitat for sea turtles in Queensland and sea surface temperature (SST) can drop below 15 °C. However, even at those temperatures turtles appear to continue foraging (Read et al. 1996). In contrast, sea turtles in the western North Atlantic, western North Pacific and Mediterranean appear to respond to cold water either by shifting their habitat to warmer waters in lower latitude or deeper offshore waters (Mendonca 1983, Morreale and Standora 2005, Mansfield et al. 2009, Narazaki et al. 2015), or becoming dormant (Carr et al. 1980, Hochscheid et al. 2005). Read et al. (1996) hypothesised that sea turtles in Queensland water may be more tolerant of cold water than other populations of sea turtles. This could also be reflected in the absence of cold-stunned sea turtles in eastern Australia compared to high numbers recorded off the East coast of the USA.

1.3.6 Developmental migration

Based on the size distribution of hawksbill turtles along the Queensland coast, Limpus (1992) hypothesised that hawksbill turtles may shift their foraging habitats from temperate or subtropical waters to warmer tropical waters as they grow. However, despite extensive mark-recapture research on tens of thousands of turtles, there is little evidence to suggest developmental shifts in habitat by any species of sea turtle foraging along the Queensland coast (Limpus and Limpus 2003a, Limpus 2008, Limpus and Miller 2008). Instead, the available data from Queensland suggests that turtles show long-term fidelity to particular sites.

This absence of seasonal and developmental migration is in strong contrast with that observed in sea turtles from several other regions. Ontogenetic shifts in habitat are common in green turtles in the western North Atlantic, as indicated by studies of size distribution (Mendonca and Ehrhart 1982, Bjorndal and Bolten 1988, Epperly et al. 1995, Meylan et al. 2011), mark-recapture (Bjorndal and Bolten 1995, Moncada et al. 2006) and genetic analysis (Lahanas et al.

1998, Bass and Witzell 2000). Green turtles in the western North Pacific are also inferred to shift their habitat as they grow based on stable isotope studies (Shimada et al. 2014) and genetic analysis (Hamabata et al. 2015).

1.3.7 Site fidelity

Our knowledge of site fidelity for foraging sea turtles in Queensland waters are mostly derived from mark-recapture studies. Many decades of mark-recapture studies at several sites in Queensland have suggested long-term site fidelity to foraging habitats by green turtles (Limpus et al. 1992, Limpus and Chaloupka 1997, Chaloupka and Limpus 2001), loggerhead turtles (Limpus et al. 1992, Chaloupka and Limpus 2001, Limpus and Limpus 2001) and hawksbill turtles (Chaloupka and Limpus 1997). There are no comparable studies of olive ridley turtles, so patterns of site fidelity remain unknown for this species in Queensland waters.

Satellite telemetry studies have also provided evidence of site fidelity to foraging habitat by female loggerhead turtles following breeding migration in Queensland (Limpus and Limpus 2001). In some cases, despite a suitable feeding habitat existing close to the nesting beach or migration routes, post-breeding turtles do not settle in these alternative feeding areas but return to their original foraging habitats (Limpus et al. 1992); demonstrating strong association with these habitats. Site fidelity to foraging habitat by breeding turtles was also observed elsewhere using satellite telemetry methods; for example, female green turtles, and female and male loggerhead turtles in the Mediterranean (Broderick et al. 2007, Schofield et al. 2010).

The site fidelity of foraging turtles has been challenged by researchers and conservation managers who displace turtles into unfamiliar habitats for reasons such as research (Yeomans 1995), rehabilitation (Molony et al. 2006), or management purposes (White et al. 2003, Chiarello et al. 2004, Yender and Mearns 2010). While experimental studies have found that some sea turtles returned to the area of capture after displacement (Limpus 1992, Avens et al. 2003), the behaviour of others remained unknown because the tracking methods used (mark-recapture, radio telemetry) failed to detect their post-displacement movements. The consequences of displacement for foraging sea turtles remain inconclusive and need to be assessed because we do not fully understand how human-induced displacement may affect sea turtle selection of foraging habitat.

1.3.8 Navigation

Migration for breeding is a well-documented behaviour of sea turtles and, as described above breeding sea turtles have shown high fidelity to both foraging and breeding habitats. To achieve migration between distant habitats, previous studies suggest sea turtles use geomagnetic cues for directional navigation (Lohmann et al. 2013, Brothers and Lohmann 2015). However, it has also been theorised that turtle they may use non-geomagnetic cues during the last part of the migration (Benhamou et al. 2011) when they have been observed making major corrections in their travel direction (Hays et al. 2014a). An example of a breeding migration travel path is provided in Figure 1.2. This female green turtle was tracked from her foraging habitat in Moreton Bay to her breeding habitat in the southern GBR. Once she departed Moreton Bay, she travelled north following the coast line. After reaching the northern coast of Fraser Island, she started travelling through open-ocean toward her breeding habitat. The latter migration path was relatively straight until she reached a point approximately 40 km away from her breeding habitat. At that point, the turtle made a sharp eastwards turn which significantly corrected the travelling direction toward her final destination. This fine-scale adjustment occurring near the travelling endpoint is clearly key to accurate directional navigation in sea turtles, but the underlying mechanism is not known. Nonetheless, these navigational abilities may also enable sea turtles to return to their foraging habitats after human-induced displacement into unfamiliar waters (Limpus 1992, Avens et al. 2003).

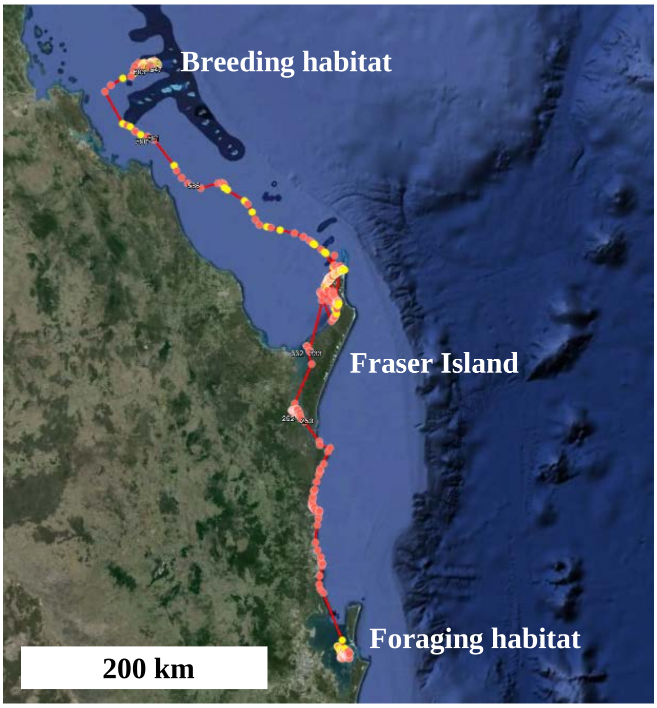

Figure 1.2 Migration route taken by a female green turtle from her foraging habitat in Moreton Bay to her nesting habitat in southern Great Barrier Reef (Limpus, unpublished data).

1.3.9 Threats and conservation

A significant number of green and hawksbill turtles were harvested in Australia for commercial purposes following European settlement (Daley 2005, Limpus 2008). Commercial harvest has been banned since the late 1960s but the population is still recovering from past exploitation (Chaloupka et al. 2008, Limpus 2008). Other species of sea turtles were not targeted for commercial consumption in Australia (Limpus 2008), but they remain susceptible to numerous other anthropogenic threats.

Current threats to foraging sea turtles in Queensland include vessel collisions (Hazel et al. 2007, Limpus 2008), habitat loss (Limpus 2008), incidental captures by fisheries and Shark Control programs (Robins 1995, Gribble et al. 1998, Robins and Mayer 1998). As a consequence of historical and current threats, all four study species are under threat regionally, as well as globally (Table 1.1).

Table 1.1 Current status of studied sea turtles species.

Species	Nature Conservation (Wildlife) Regulation 2006 [Queensland]	Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act) [Australia]	IUCN Red List ver. 3.1 [Global]
Chelonia mydas	Vulnerable	Vulnerable	Endangered
Caretta caretta	Endangered	Endangered	Endangered
Lepidochelys olivacea	Endangered	Endangered	Vulnerable
Eretmochelys imbricata	Vulnerable	Vulnerable	Critically Endangered

Vessel collision is a major threat to turtles in the shallow waters along the Queensland coast, particularly in areas such as Moreton Bay which are adjacent to large cities (Hazel and Gyuris 2006, Limpus 2008). The Queensland Government responded to this issue by regulating some shallow areas of Moreton Bay, Hervey Bay and Missionary Bay as Go Slow Zones. In Go Slow Zones, motorised water sports are prohibited and fishing or recreational boats must travel slowly so as to avoid collision with turtles and other air-breathing wildlife, e.g. dugongs (Queensland Government 2008). Despite the conservation initiatives, most boat strike incidences in Queensland still originate from Moreton Bay areas (Meager and Limpus 2012), indicating the current Moreton Bay Go Slow Zones may not be providing adequate spatial protection for turtles. Empirical data for sea turtles foraging in Moreton Bay are needed to assess whether the current Go Slow Zones are providing adequate protection for sea turtles in Moreton Bay.

1.4 Thesis objectives and structure

1.4.1 Primary research aim and objectives

I aimed to advance our knowledge of sea turtle ecology and assist conservation initiatives by investigating the spatial and temporal movement of sea turtles in coastal foraging habitats in Queensland waters, using FGPS tags as the primary tracking technique. More specifically, I propose the following objectives for the thesis:

1. To improve tracking data by developing an objective method to identify and remove FGPS fixes with high error.
2. To examine the effects of human-induced displacement on sea turtles' foraging habitat selection, and to investigate the underlying mechanism of their homing navigation using a detailed examination of their tracks.
3. To investigate home range and site fidelity of sea turtles in their coastal foraging habitat, and determine how existing Go Slow Zones relate to sea turtle habitat in Moreton Bay.

My research focuses on green turtles and loggerhead turtles in Queensland. They are the most common species in the shallow coastal waters where anthropogenic threats are high (Limpus 2008). Consequently most data were obtained from these two species but data from a small number of hawksbill and olive ridley turtles were also available. I explicitly state the species and locations of investigated turtles in the Methods and Materials section of each chapter.

1.4.2 Thesis structure

The thesis follows the order of the objectives listed above. In this way, I first provide solutions to deal with FGPS data with high error. The methods are fundamental to data preparation prior to any subsequent ecological and conservation-based analyses. I provide a schematic diagram of the thesis structure in Figure 1.3.

The thesis comprises seven chapters. At the final submission of this thesis, Chapters 2 and 3 have been published. Chapters 4, 5, 6 were also written with the intention of publication in peer-reviewed scientific journals. Therefore each chapter is presented as a stand-alone publication but some modifications have been made to ensure continuity of the thesis. Some important information is repeated in several different chapters so that each chapter can stand alone.

Chapter 1 provides a general introduction to the thesis. It provides the rationale for my research, which investigates the spatial ecology of sea turtles and its application to conservation planning. I then provide brief overviews of the current state of knowledge regarding the biology, threats and conservation of sea turtles, with particular focus on the populations foraging in Queensland waters. I also highlight key knowledge gaps and explain how they can be addressed by investigating sea turtle spatial ecology.

Chapter 2 aims to establish a method to improve accuracy of FGPS data set. I explore potential filtering methods to remove FGPS fixes with high error. The proposed method is developed using movement data obtained from loggerhead turtles but is designed to be applicable to tracking data from any other animal. I then evaluate how much the proposed method can improve the accuracy of FGPS datasets and home range estimates. The subsequent chapters use this filtering method to process FGPS data set prior to any analyses. I developed the R package SDLfilter to execute the proposed screening methods and made it publicly available (see https://github.com/TakahiroShimada/SDLfilter). This chapter has been published.

> Shimada T, Jones R, Limpus C, Hamann M (2012) Improving data retention and home range estimates by data-driven screening. *Marine Ecology Progress Series* 457:171-180 doi:http://dx.doi.org/10.3354/meps09747

Chapter 3 investigates how human-induced displacement affects sea turtles in their selection of foraging habitat. More specifically, I examine whether they settle in the areas of release, return to their original habitat or move to other habitats. Using displaced turtles which returned to their home habitats, I also examine what factors may have affected their homing behaviour. This chapter also describes a method to delineate tracks before and after resettlement following displacement. The following chapters use this method to prepare data to focus on particular subsets of data (e.g. behaviour during the homing journey, and behaviour within the home range). This chapter has been published.

Shimada T, Limpus C, Jones R, Hazel J, Groom R, Hamann M (2016) Sea turtles return home after intentional displacement from coastal foraging areas. *Marine Biology* 163:1-14 doi:http://dx.doi.org/10.1007/s00227-015-2771-0

Chapter 4 examines the mechanisms underlying fine-scale navigation in sea turtles. I use a subset of the data obtained from displaced turtles: that is, tracks between the release location and their arrival back at their original foraging habitat. I demonstrate a novel approach for analysis of sea turtle satellite telemetry data in relation to some plausible influencing environmental factors. I then infer potential navigational cues that sea turtles might use to make directional corrections.

Chapter 5 investigates the home range size and site fidelity of green and loggerhead turtles foraging in tropical and subtropical habitats along the Queensland coast. To enable statistical analysis of site fidelity, I demonstrate how site fidelity can be objectively quantified through time series analyses on utilisation distribution. Finally, I examine how ecologically meaningful factors may affect home range size and the degrees of site fidelity.

Chapter 6 evaluates habitat use by green and loggerhead turtles foraging in Moreton Bay, to quantify how much of their habitat is likely to be protected from vessel collisions by current legislation. I then provide guidance to improve protection of foraging turtles in Moreton Bay.

Finally, in **Chapter 7**, I summarise the findings from my five data chapters, and discuss how they can contribute to the ecology and conservation of sea turtles in Queensland, and elsewhere. I also discuss potential issues in my investigations and how they could be improved, leading to suggestions for future studies.

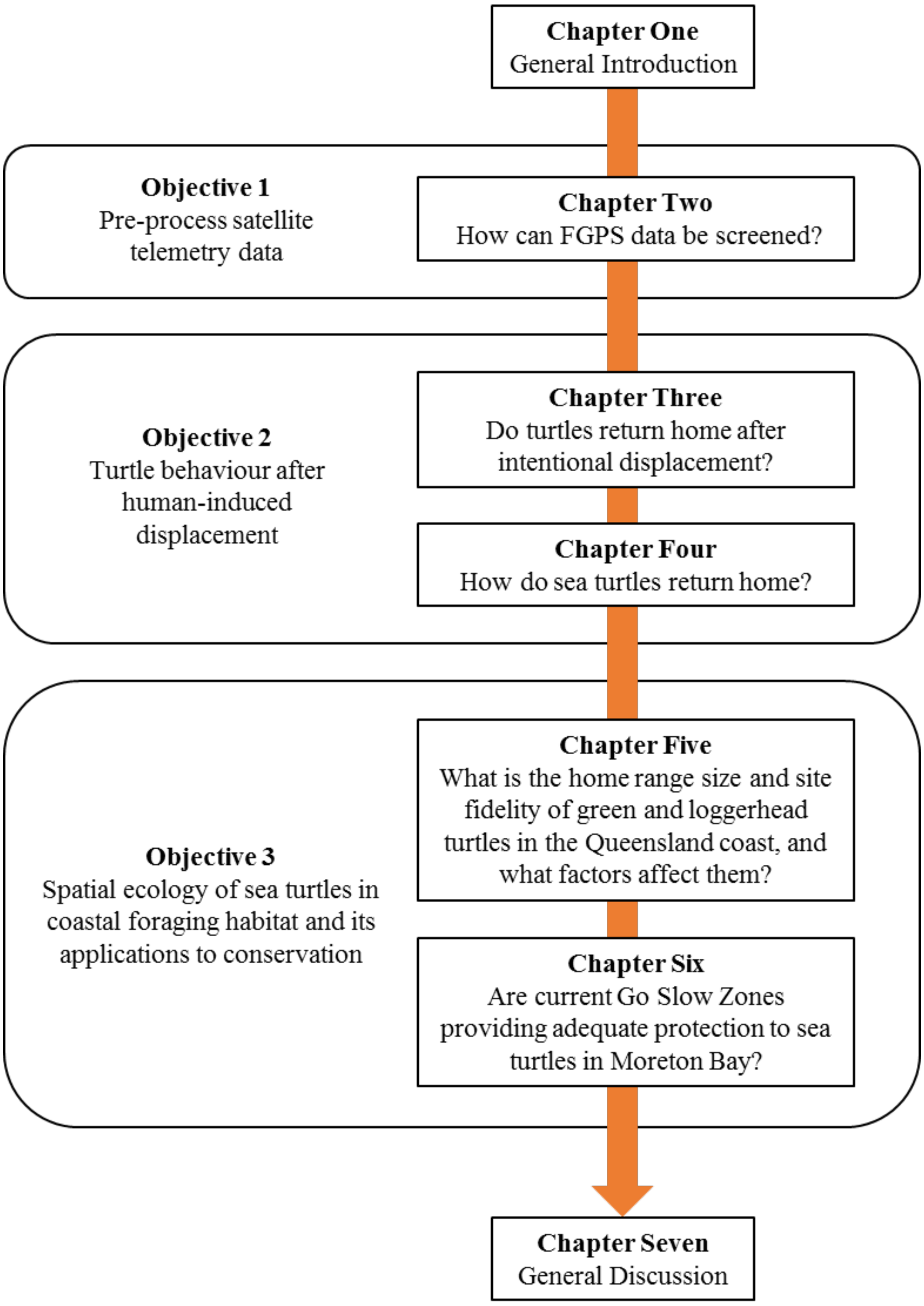

Figure 1.3 Schematic diagram of thesis structure.

Chapter 2

Improving data retention and home range estimates by data-driven screening

The knowledge gaps in spatial ecology of sea turtles identified in Chapter 1 can be answered by investigating the fine-scale movement of sea turtles. Satellite telemetry, in particular Fastloc GPS (FGPS), is best suited for this type of research but inaccurate FGPS fixes need to be screened prior to ecological and conservation-based analyses. In this chapter, I present an objective method to remove FGPS fixes with high error, and evaluate how it would improve the accuracy of FGPS data set and resulting home range estimates. The methodology developed in this chapter serves as a fundamental screening process necessary for FGPS data used in the subsequent chapters.

Published manuscript:

Shimada T, Jones R, Limpus C, Hamann M (2012) Improving data retention and home range estimates by data-driven screening. *Marine Ecology Progress Series* 457:171-180 doi:http://dx.doi.org/10.3354/meps09747

R package:

I developed the R package SDLfilter to execute the screening methods which are described in this chapter. The R package is made freely available in the online code sharing and publishing service GitHub (https://github.com/TakahiroShimada/SDLfilter).

2.1 Introduction

Home range analysis can provide fundamental insights into species ecology and has obvious implications for wildlife management (Peckham et al. 2007, Hays 2008, Hamann et al. 2010). Although home range investigations have been carried out for decades on a multitude of taxa, the quantification of home ranges remains challenging. Home range studies have difficulties everywhere, but are more advanced for terrestrial than for marine vertebrates because of the relative ease of animal capture and tracking especially via GPS tags. Marine studies have progressed more slowly; they tend to be more difficult to execute, and tagging hardware has the additional problem of either transmitting signals through water or relying on short exposure times as animals surface.

Since the 1980s satellite linked platform terminal transmitters (PTTs) have been used to study animal movement and their use in the marine environment has increased rapidly (Stoneburner 1982, Timko and Kolz 1982, Godley et al. 2008). However, the use of PTTs to understand habitat use in marine animals is often limited because signals can only be transmitted when the animal surfaces, and the surface time must be long enough for transmissions to be completed. As a result sample sizes for marine fauna tend to be lower than those for terrestrial fauna, moreover since the accuracy of an acquired location depends on the number of Argos satellites and the number of messages which reach them, accuracy may also be low (Goulet et al. 1999, Eckert and Stewart 2001, Godley et al. 2002). Hence, although Argos technology and methods for data analysis has improved over time (Jonsen et al. 2005, Patterson et al. 2010), PTTs are best applied to studies investigating larger scale habitat use such as long distance migration.

Standard GPS tags offer better accuracy but still require enough time on the surface to complete a fix, so relatively few attempts to acquire location are successful in the marine environment (Jay and Garner 2002). Some studies increased the frequency of successful location fixes by keeping the power of the tags on so that receivers acquire a GPS fix whenever they happen to surface, but battery life is then greatly reduced (Ryan et al. 2004, Elkaim et al. 2006). More recently the situation has been improved by the use of fast acquisition GPS technologies such as Fastloc GPS and quick fix pseudoranging (Tomkiewicz et al. 2010). Consequently, in recent years these alternative GPS tags have been, or have the potential to be, used on several marine species and age classes to investigate fine-scale habitat use (Sheppard et al. 2006, Sims et al. 2009, Kuhn et al. 2010), and their results are thus useful for marine spatial planning and habitat protection (Sheppard 2008).

The standard GPS technology is dependent on the number of source satellites for the accuracy of an initial fix but can increase the accuracy of location estimates by correcting the locations from successive GPS fixes. In stationary land-based tests, the accuracy of Fastloc GPS also improved as the number of source satellites increased (Bryant 2007, Hazel 2009). However, unlike standard GPS, Fastloc GPS records and uses only one set of raw data at each fixing attempt and thus there is no correction from successively obtained data. That is, while Fastloc GPS technology has achieved the ability to capture the necessary data in less than 0.1 seconds, its accuracy does not improve with successive location fixes (Rutz and Hays 2009, Sirtrack 2010). As the consequence of the trade-off, some Fastloc GPS locations are much less accurate than others if fewer satellites have been involved in fix acquisition. The occurrence of location fixes with high error leads to several data analysis challenges with Fastloc GPS data, especially with the analysis of tracking data and estimation of home ranges. Hence it is important to develop and use methods that can identify and account for locations with high error.

There are many published methods to screen location data when it is obtained with conventional PTT tags (McConnell et al. 1992, Tremblay et al. 2006, Freitas et al. 2008) but fewer exist for data acquired from Fastloc GPS tags, despite the increase in their use. The simplest screening method for Fastloc GPS data involves the use of residual errors. Residual error is a quality index that represents the level of accuracy of a location fix (Sirtrack 2010). This method alone may not remove all locations with high error but it can be supplemented by taking into account the number of satellites used for calculations – e.g. by rejecting locations involving fewer than a given number of satellites. However in some studies, this may result in a majority of the Fastloc GPS data being discarded (Lonergan et al. 2009). An approach which provides a more reliable filter while retaining more of the data is therefore highly desirable.

A screening method often used for Argos locations is the identification of behaviour that is biologically or ecologically unrealistic for the study species. This approach can also be used for Fastloc GPS data. Speed is the popular limiting factor and recent studies use the maximum speeds that were estimated from the conventional tracking methods such as acoustic or PTT telemetry to screen GPS data (Schofield et al. 2007, Preston et al. 2010, Witt et al. 2010). However because Fastloc GPS data are generally more abundant and more accurate than Argos data, maximum speeds estimated from Fastloc GPS data are likely to be more realistic than those obtained from Argos data. Further, the angle between three consecutive locations is also commonly used to filter location data, but the choice of angle is often arbitrary (Costa et al. 2010, Witt et al. 2010). Hence there is a need for an improved approach to define the limiting speeds and angles for Fastloc GPS data.

Once a data set has been obtained and appropriately filtered, estimation of home range has a choice of possible approaches. Some commonly used methods for home range estimation are minimum convex polygon, kernel density estimation, harmonic mean, linear home range, and grid cell count (Laver and Kelly 2008). Among those methods, kernel density estimator is currently the most frequently used and least biased home range estimator (Kernohan et al. 2001). Although the kernel method measures intensity of use by estimating the probability density along both x and y coordinates (Silverman 1986, Worton 1989), and therefore the influence of locations with high error or over-screening is presumed to be less, accuracy and precision of kernel estimates will be affected by the accuracy of location data and sample size.

Given the promising application of GPS satellite telemetry into wildlife studies, it is important to use appropriate filtering methods to increase data accuracy while minimising unnecessary data loss, and to allow accurate quantification of home range estimates. This chapter explores filtering approaches for Fastloc GPS data obtained from loggerhead turtles, and by conducting terrestrial tests, I evaluate the performance of the proposed filtering methods and determine which filter leads to the most accurate home range estimates.

2.2 Materials and Methods

2.2.1 Turtle tracking

In 2009 and 2010, four adult female loggerhead turtles (T93038, T81920, T54430, K22217) were captured while nesting at Mon Repos and four adult male loggerhead turtles (K24365, T53800, T74361, QA14215) were captured at the Moreton Bay foraging ground by a rodeo method (Limpus 1978). The sex and maturity of male turtles were identified either using laparoscopy or if the tail length from carapace was greater than 19.0 cm (Limpus and Limpus 2003a). A Fastloc GPS unit was mounted on the first through third vertebral scutes of carapace using Sika Anchor fix -3+ epoxy glue with fibreglass for extra strength. The tracking period ranged from 14 to 153 days and the data include the location fixes that were obtained during foraging, migrating and inter-nesting periods. T54430 was not tracked during foraging period due to device failure. The location data acquired during unit deployment, nesting and post-release activities were excluded from the data analysis.

2.2.2 Data retrieval and conversion

Data were transmitted via the Argos network (K24365, QA14215, T53800, T54430, T81920 and T93038) or via a USB link directly from device to computer (K22217, T74361 and terrestrial tests). I downloaded the data from each unit using manufacturer-supplied software (Sirtrack Fastloc software) and then decoded data into GPS locations. Finally the location data were converted to the Universal Transverse Mercator coordinate system.

2.2.3 Data screening

The first filtering method I used involved the use of the manufacturer's quality index (residual error) and the number of satellites used in each location calculation (hereafter referred to as the generic filter in this chapter). As per the manufacturer I excluded locations from the analysis when residual error values were greater than 30 or fewer than 4 satellites were used for location calculation (Sirtrack 2010). Data sets after additional filtering according to available satellite number will be referred to as generic># where # represents the number of source satellites (e.g. generic>4). Consequently generic>3 data set contains the maximum number of locations and generic>7 limits the data set to locations acquired with 8 satellites (the maximum possible with Fastloc GPS).

The second filtering method, a data-driven filter, extends the generic filter. The data-driven filter screens the data according to the speed between successive locations, and the angle created by three consecutive locations, as well as the number of satellites used for location calculation. Speed and turning angles may vary with turtle behaviour (e.g. foraging, migrating, escaping from predators) but currently there are few studies of behavioural effects on swimming speeds and turning patterns of loggerhead turtles. Therefore I derived the limiting speeds and angles as objectively as possible from the patterns of Fastloc GPS locations obtained from the turtles, informed by the accuracy associated with the number of source satellites. Because errors may increase substantially when the number of source satellites is limited to 4 (Bryant 2007, Hazel 2009), the data-driven filter is designed to remove erroneous locations derived from 4 satellites. The data group that has been screened by a data-driven filter will be referred to as data-driven>3.

To determine the limiting speed for the data-driven filter, and because high error may occur when only 4 satellites were used to estimate locations, I used data acquired from more than 4 satellites (i.e. generic>4) to estimate the maximum linear speed ($V_{\max}$) a loggerhead turtle was observed to swim between two consecutive locations. I then extracted the locations that were preceded and followed by unrealistically fast speeds (i.e. > $V_{\max}$) and labelled them over-speed error points (OSEPs). While this identified some erroneous locations (i.e. OSEPs), other obvious errors (e.g. locations on land) remained unscreened (e.g. Figure 2.1b). Therefore I developed additional limiting criteria to identify and screen additional locations with high error.

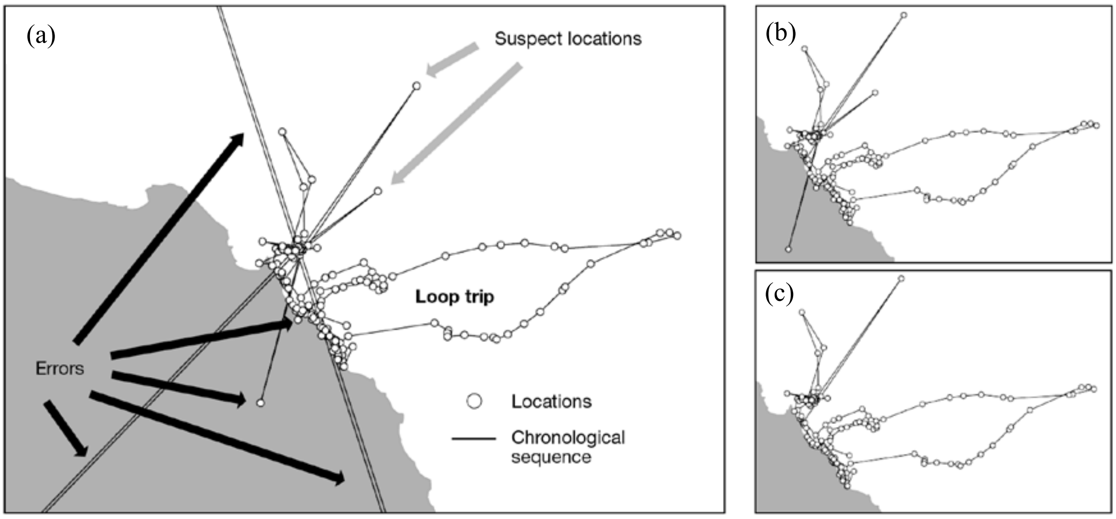

Figure 2.1 An example of errors, suspect locations and a loop trip in a data set (a) after screening using the generic>3 filter (i.e. requiring >3 source satellites), (b) after removing locations that were preceded and followed by unrealistically fast speeds, and (c) after screening using the data-driven>3 filter (see ‘2.2.3 Data screening’).

I calculated the angles between the bearings of lines joining successive location points. This represents 180° minus the animal's turning angle; I will call this the inner angle in this chapter. I then identified the inner angles that were associated with OSEPs for comparison with the angles associated with the remainder of the locations (non-OSEPs). Differences between the ranges of angles observed for OSEPs vs. non-OSEPs then guided selection of a limiting angle as described in the ”2.3.2 Data-driven filter” subsection of the Results section. The limiting angle was used to provide a preliminary identification of locations that may be erroneous (suspect locations).

Once suspect locations were extracted by the limiting angle, I calculated the linear speed for the turtle between the suspect location and both its previous location and its following location. The speeds were then compared to the speed of a loop trip for an additional check of the legitimacy of the suspect locations. Loop trip behaviour is represented by spatial departure and return with more than three consecutive locations (Figure 2.1a). Therefore a loop trip would have been considered as an outlier if there had been only one location obtained during the movement. In my study I considered continuous straight and fast movement to represent the departure to, and return from, a loop trip. Using generic>3 data set, I calculated the net (i.e. straight-line) distance between the departure and turning location as well as the turning and return location of the loop trip, and from that calculated the net speed in and out (V_{lp}). I considered the fastest V_{lp} observed in this study as the maximum inward or outward speed of loggerhead turtles during a loop trip. The suspect locations were removed when the speed between the suspect location and either its previous or subsequent location exceeded the maximum V_{lp}.

2.2.4 Kernel estimation

I used the kernel density estimator with Gaussian as the kernel function for home range estimation. I chose fixed over adaptive kernel estimators with least squares cross validation (LSCV) as an automated bandwidth selector, because adaptive kernel was not available in the software I used, and because the fixed kernel methods with LSCV to select smoothing parameters appear to produce more accurate and precise estimates of home range areas and are less sensitive to autocorrelation within data sets than adaptive kernel methods (Seaman and Powell 1996, Seaman et al. 1999). While several studies have demonstrated that LSCV can be highly variable (Park and Marron 1990, Gitzen and Millspaugh 2003) and fails to select appropriate bandwidth values when a sample size is too small (e.g. <30 locations; Seaman et al. 1999) or too large (e.g. >100 locations; Hemson et al. 2005), there have been attempts to improve the LSCV method by choosing more appropriate bandwidth values (Duong 2007, 2011). I used the improved LSCV bandwidth selector that is implemented in the R package ks (Duong 2011, R Development Core Team 2011). The ks package was also used to estimate continuous utilisation distribution. I used Geospatial Modelling Environment, an extension to ArcGIS, to generate volume contours from the utilisation distribution (R Development Core Team 2011, Beyer 2012). A resolution of 50 m was used for the kernel grid because the mean linear error for properly filtered Fastloc GPS data was consistently within 50 m in my terrestrial tests (see Table 2.1).

2.2.5 Terrestrial mobile test

I recorded walking and biking movements using both a hand held standard GPS receiver and a Fastloc GPS receiver in Townsville, Australia (terrestrial mobile test). The tests were conducted in open areas without overhead cover so as to mirror the environment of the turtles at sea. The tests were commenced after the standard GPS receiver (Garmin GPS60) gained the accuracy of <5 meters according to the indication integrated in the unit. Once the standard GPS receiver attains the location estimates with high accuracy, the expected error of the successive locations will remain less than 15 meters according to the manufacturer (Garmin Ltd. 2006). The Fastloc GPS unit was set to record a position every 4 minutes while the standard GPS receiver recorded a position every second. The clocks of the Fastloc GPS receiver and the standard GPS receiver were synchronised before the test began. Following the last test, the time difference between two units was recorded. Consequently using the following equation, the time of each Fastloc GPS fix was adjusted according to the clock difference with the standard GPS so the time of each standard GPS fix corresponds to the time of each Fastloc GPS fix:

$$\text{Adjusted } Ft_i = Ft_i \quad \frac{\Delta t\ (Ft_i - t_{sync})}{t_{end} - t_{sync}}$$

where Ft_i is the time when ith Fastloc GPS fix was acquired, Δt is the final clock difference between the two units, t_{sync} is the time at synchronisation and t_{end} is the time on the Garmin unit when Δt was recorded. The range of Δt was 1.6 to 4.6 seconds.

2.2.6 Evaluation of filter performance

I used the terrestrial data to evaluate how data screening improves the accuracy of Fastloc GPS data sets and to determine which screening method leads to the most accurate home range estimates. Because, unlike standard GPS, the accuracy of Fastloc GPS locations is not improved by successive fixes, the differences in the interval of location fixing between the turtle tracking and the terrestrial test will not affect the accuracy of Fastloc GPS fixes. Therefore the accuracy of Fastloc GPS locations in the terrestrial test should be comparable to their accuracy in the turtle data.

I screened the data acquired from the terrestrial mobile tests using both the generic and the data-driven filters following the same procedures taken for the turtle data (but with a variation of the loop criterion): the maximum V_{lp} of terrestrial mobile test was estimated by multiplying the terrestrial V_{max} by the ratio of maximum V_{lp} / V_{max} from the turtle data. I then calculated the linear distances between the standard GPS locations and simultaneous Fastloc derived GPS locations; I interpreted these values as the error distances of Fastloc GPS locations from true locations. After normalising the data by log-transformation, I compared the means of the linear errors between generic>3 and data-driven>3 data set using Welch's two sample *t*-test to assess the performance of the data-driven filter.

I subsampled the Fastloc GPS locations of the terrestrial data using each of the screening methods (i.e. generic>3, data-driven>3, generic>4, generic>5, generic>6 and generic>7). I then calculated the kernel estimates from each of the subsampled Fastloc GPS data and the standard

GPS data. I considered the kernel estimates derived from the standard GPS locations to represent the most accurate kernel home range estimates. To measure the differences in the kernel estimates derived from the standard GPS and each of the filtered Fastloc GPS data, I calculated the mean integrated squared error (MISE) as:

$$\text{MISE} = \frac{1}{n}\sum_{i=1}^{n} \left[f_{Fastloc}(x_i , y_i) - f_{Standard}(x_i , y_i) \right]^2$$

where n is the number of grid points, x and y are the grid coordinates, $f_{Fastloc}(x_i , y_i)$ is the estimated density derived from Fastloc GPS data at the ith grid point, and $f_{Standard}(x_i , y_i)$ is the accurate density derived from standard GPS data. MISE is widely used as a global measure of differences among different kernel estimates (Seaman and Powell 1996, Horne and Garton 2006, Fieberg 2007b). Because a smaller MISE indicates more similarity between estimates, I used MISE as an inverse index of accuracy for kernel estimates.

2.2.7 Home ranges of turtles

I subsampled each turtle data set using each of the alternative screening methods (i.e. generic>3, data-driven>3, generic>4, generic>5, generic>6 and generic>7) and computed home range estimates from the subsampled data sets. I aimed to examine the impact of data screening on the estimates of home range areas of the loggerhead turtles. Since the true home ranges of these animals are not known, the accuracy of the estimates could not be evaluated for the turtle data.

2.3 Results

2.3.1 Filter performance in terrestrial tests

The duration of the terrestrial mobile tests ranged from 44 to 136 minutes and a total of 1,583 Fastloc GPS locations were recorded. However I excluded 255 of them from analysis because the corresponding standard GPS locations were not acquired. The $V_{\max}$ derived from the terrestrial mobile test was 11.9 km h^{-1} (n = 1,017). The maximum V_{lp} of the terrestrial data was then calculated as 2.4 km h^{-1} following the ratio of maximum V_{lp} and $V_{\max}$ of the turtle data that are described in the following subsection (1.8 km h^{-1} : 8.9 km h^{-1}). The linear distance between standard GPS and Fastloc GPS locations (Δ_{loc}) decreased as the number of source satellites increased or the data-driven filter was applied (Table 2.1). In particular, when locations derived from >3 satellites (i.e. generic>3) were used, the linear error (mean ± SD, max) was decreased from 2,645.5 ± 29,458.2, 484,640.1 m (n = 1,328) to 47.1 ± 61.0, 699.5 m (n = 1,246) by using the data-driven filter ($t_{(2)\,2239.6} = 2.43$, $p < 0.05$). Increasing the number of source satellites required for a valid fix offered further reductions in the linear error but it came at the cost of much greater data loss (Table 2.1).

Table 2.1 Linear differences in meters (mean ± SD, max) between standard GPS locations and screened Fastloc GPS locations (Δ_{loc}). The numbers in the brackets are the percentage of each sample size (i.e. number of locations) when compared to that of generic>3 data set.

# satellites	Filter	Mean Δ_{loc}	SD	Max Δ_{loc}	N (%)
>3	generic	2,645.5	2,9458.2	484,640.1	1,328 (100)
>3	data-driven	47.1	61.0	699.5	1,246 (94)
>4	generic	33.1	35.4	328.7	866 (65)
>5	generic	24.8	22.5	319.5	491 (37)
>6	generic	19.6	10.8	64.5	228 (17)
>7	generic	18.8	9.2	40.1	79 (6)

I also investigated how data screening influences the accuracy of the home range estimates in the terrestrial test. The kernel estimates derived from data-driven>3 data had the lowest MISE, followed by those derived from generic>4. The remaining generic filters led to higher MISE in the ascending order of generic>5, generic>6, generic>7, and the kernel estimates derived from generic>3 had the highest MISE (Figure 2.2).

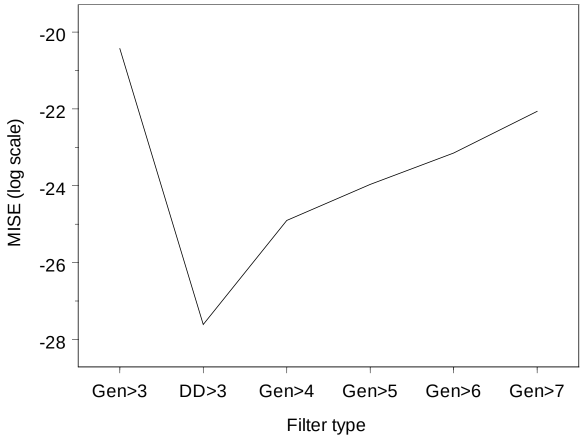

Figure 2.2 Mean integrated squared error (MISE) of kernel estimates derived from the Fastloc GPS locations in the terrestrial mobile test. The Fastloc GPS data were screened by the data-driven filter (DD>3) and the generic filters that limited the use of locations by requiring the number of source satellites to be more than 3 (Gen>3), 4 (Gen>4), 5 (Gen>5), 6 (Gen>6), and 7 (Gen>7).

2.3.2 Data-driven filter

I estimated the V_{max} of the loggerhead turtles as 8.9 km h^{-1} using the location data derived from >4 satellites (n = 3,921 fixes). A total of 23 over-speed error points (OSEPs) was then identified in the data from eight turtles (n = 6,154 fixes) because the speed both from a previous and to a subsequent location exceeded 8.9 km h^{-1}. I found that all the inner angles at OSEPs were less than 59 degrees while the inner angles at non-OSEPs were generally higher, ranging up to 180 degrees. The proportion of inner angles less than or equal to 59 degrees was significantly different between OSEPs and non-OSEPs (Binomial test, $p < 0.0001$). However using 59 degrees as a limiting angle may be too conservative as a filter since OSEPs are the locations with the most extreme error. Moreover a previous study using Argos satellite telemetry found that most errors were associated with acute inner angles (i.e. less than 90 degrees) (Keating 1994). Therefore I used acute inner angles to make a preliminary identification of suspect locations. I then compared the linear speed immediately prior to and following the suspect location, to the maximum V_{lp} to check the legitimacy of each suspect location. The maximum V_{lp} was calculated as 1.8 km h^{-1} from 57 loop trips; each loop trip has two V_{lp} (mean ± SD: 0.4 ± 0.3, n = 114). This resulted in a final filtering rule as follows: locations were removed if

- the speed both from a previous and to a subsequent location exceeded 8.9 km h^{-1},

or if ALL the following criteria applied:

- the number of source satellites was limited to 4,
- the inner angle was acute and,
- the speed either from a previous or to a subsequent location exceeded 1.8 km h^{-1}.

2.3.3 Effect of screening on turtle data

The data-driven filter successfully removed all obvious locations with high error when applied to the generic>3 data sets (e.g. Figures 2.1c & 2.3) while keeping more than 95% of the locations (Table 2.2). All the locations with high error identified by the data-driven filter were also removed when the generic filters limited the use of locations to those made using >4 satellites (i.e. generic>4) because the obvious errors were all derived from 4 satellites. However, moving from generic>3 to generic>4 (i.e. requiring at least 5 satellites for a valid fix) removed more than a quarter of the location data (Table 2.2).

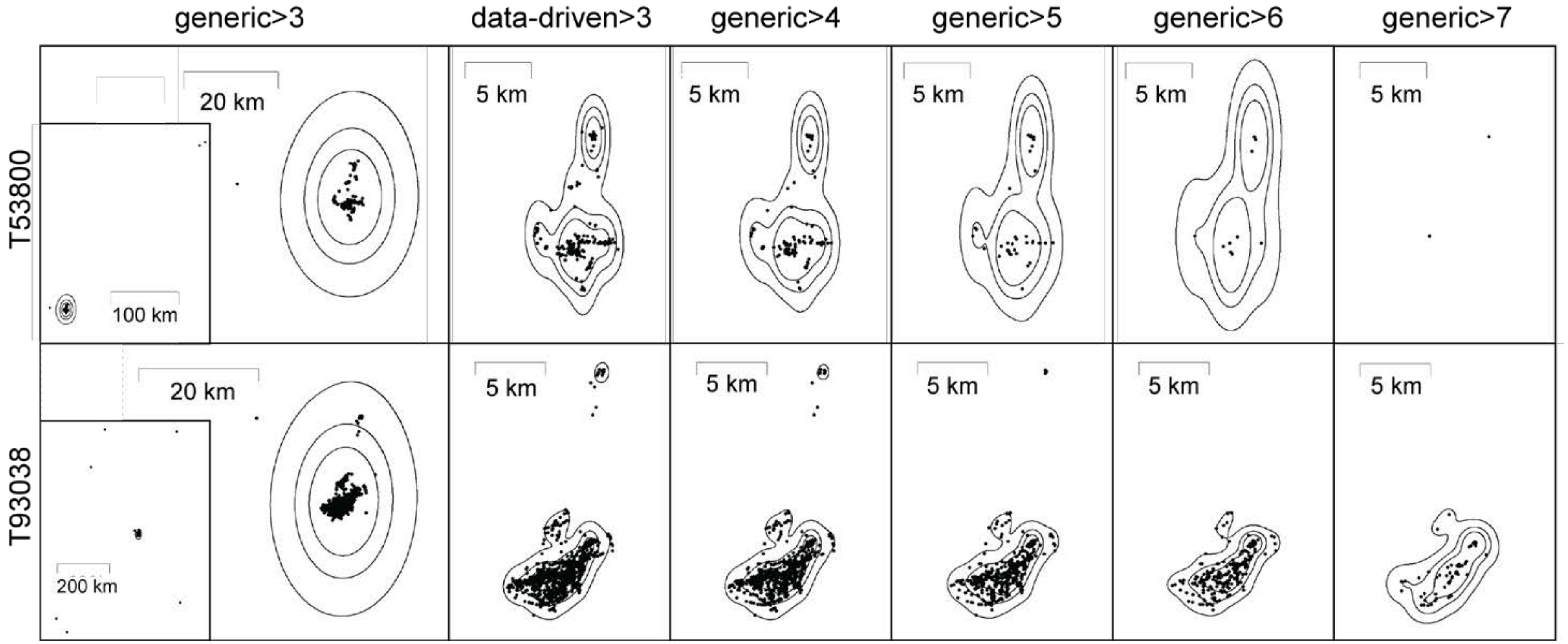

Figure 2.3 Density contours of home range estimates for T53800 and T93038 during foraging period. Data were screened by the data-driven filter (data-driven>3) and the generic filters that limited the use of locations by requiring the number of source satellites to be more than 3 (generic>3), 4 (generic>4), 5 (generic>5), 6 (generic>6), and 7 (generic>7). Lines represent 95, 75, 50% volume contours of the home range estimate. Dots are Fastloc GPS locations.

Table 2.2 The remaining number of Fastloc GPS locations after each filter was applied. Only the data acquired during foraging period is shown in this table. The numbers in the brackets are the percentage of each sample size (i.e. number of locations) when compared to that of generic>3 data set from the same turtle.

No. satellites	Filter	Number of locations (percentage against generic>3)						
		K22217	K24365	QA14215	T53800	T74361	T81920	T93038
>3	generic	475 (100)	504 (100)	226 (100)	219 (100)	964 (100)	1,058 (100)	1,174 (100)
>3	data-driven	469 (99)	500 (99)	223 (99)	215 (98)	951 (99)	1,009 (96)	1,123 (96)
>4	generic	334 (70)	309 (62)	106 (47)	119 (54)	705 (73)	565 (53)	823 (70)
>5	generic	242 (51)	167 (33)	40 (18)	45 (21)	459 (48)	299 (28)	490 (42)
>6	generic	127 (27)	73 (15)	16(7)	11 (5)	250 (26)	121 (11)	261 (22)
>7	generic	46 (10)	16 (3)	3 (1)	2 (1)	92 (10)	38 (4)	64 (6)

The shape and sizes of the home range areas of each turtle varied subject to varying proportions of high-error locations and sample size resulting from the use of different filters (e.g. Figure 2.3). The home range boundaries estimated from the generic>3 data were expanded greatly due to the presence of outlying fixes. The data of T53800 did not retain enough locations for home range estimation when it was screened by the generic>7 filter.

2.4 Discussion

Results of my terrestrial test and turtle tracking showed that only a small proportion of Fastloc GPS data was highly erroneous but they led to inaccurate quantification of home range estimates (Figures 2.2 & 2.3). I found that a screening method for Fastloc GPS data can be developed by identifying and checking suspect locations characterised by unlikely turning angles and speeds, informed by the location accuracy associated with the number of source GPS satellites.

The maximum linear speed for the loggerhead turtles ($V_{\max}$), the preliminary limiting factor used by the data-driven filter, is estimated as 8.9 km h^{-1} in my study. This is similar to the near sprint linear speed of the same species measured by boat chases (Heithaus et al. 2002) but it is faster than the commonly used limiting speed of 5 km h^{-1} which was estimated using Argos data obtained from post-nesting green turtles *Chelonia mydas* (Luschi et al. 1998). The swimming ability assessed by my study using Fastloc GPS confirms that the linear speed of the loggerhead turtles is likely to be variable.

The variation in swimming speed is less critical in the filtering process for Argos data because the long interval between consecutive locations would have made short periods at high speed less obvious. Now that more accurate and shorter intervals between locations can be expected using Fastloc GPS, short periods of rapid movement may be mistakenly removed if conventional limiting speeds are used. Through using the faster limiting speed quantified in this study ($V_{\max}$: 8.9 km h^{-1}), I found that the risk of over-screening is minimised but many locations with high error will not be identified because so few data fell into this category. The locations identified by $V_{\max}$ (i.e. OSEPs) can be regarded as the most extreme errors, and additional screening is still needed. The combination of acute inner angles and a lower value for limiting speed (i.e. maximum V_{lp}) provided that additional screen.

My turtle tracking data indicate that OSEPs were associated with inner angles less than 59 degrees, suggesting that the 20 degrees used by Witt et al. (2010) as a limiting angle may be too conservative when used as a filter for Fastloc GPS data, at least for loggerhead turtles. While I used 90 degrees as the limiting angle, it resulted in removing as much as 34% of the original location data in my data set if it was used as a standalone filter. Removing this proportion of data can lead to over-screening: 95% of Fastloc GPS locations had errors ≤219 m in the terrestrial mobile test (this study) or ≤101 m in a stationary test (Hazel 2009) which will be acceptable for many wildlife studies. I overcame the issue of over-screening by supplementing the use of the angle criterion with a maximum loop speed estimate and consequently managed to retain more than 95% of turtle tracking data. Note that the data driven filter still has the potential to screen real but short sprinting out-and-back movements because animals are capable of short bursts of very fast speed which cannot be maintained for the long periods between most telemetry locations. Although I did not encounter this with my study, researchers should be aware of this possibility when using the data-driven approach.

The generic filters have an advantage in their simplicity and my terrestrial study found a positive relationship between the number of source satellites and the accuracy of locations for mobile transmitters (Table 2.1), as found in stationary land-based tests (Bryant 2007, Hazel 2009). Therefore using only the location data derived from larger numbers of source satellites can be a straight forward screening method. However I found that there is a risk of excluding smaller scale but important habitats by the generic filters, even when original sample size is large. For example, the sample size obtained from T93038 was the largest of eight turtles but when the use of locations were limited by requiring the number of source satellites to be more than 6 (i.e. generic>6, generic>7), the northern-most aggregation disappeared because the patch consisted of locations derived from 4, 5 and 6 satellites (Figure 2.3). Although the proportion of locations that generated the northern-most patch is small (1.5%), the habitat may be important to the animal during particular times of the year or with variation in availability of food or environmental preferences. In this case, if the use of locations had been limited to those derived from >6 satellites by the generic filters, the habitat distribution would have been underestimated and may not have picked up patches of peripheral habitat that are important to the animal. Moreover, in smaller data sets (e.g. T53800) over-screening may not retain enough locations for a home range analysis (Figure 2.3).

For very large data sets (e.g. T93038), requiring locations to be derived from >4 satellites (i.e. generic>4) may be an adequate filtering method because locations with high error were associated with 4 satellites in my data set and expected errors (mean ± SD) for generic>4 data sets were low 33.1 ± 35.4 m (Table 2.1). The drawback of the generic>4 filter is nonetheless to screen locations more than necessary: moving from generic>3 to generic>4 removed up to 53% of locations in my turtle data set (Table 2.2). Large reduction of sample size will result in decrease in precision of kernel estimates (Fieberg 2007a), loss of valuable ecological information such as detailed animal movements (Mills et al. 2006, Arimoto 2012), and reduction in the power of statistical comparison (Whitlock and Schluter 2009).

For constructing home range boundaries, removing large proportion of data by the generic>4 filter may not be so critical since the home range areas derived from data-driven>3 and generic>4 data sets are very similar (e.g. Figure 2.3). Based on the result of my terrestrial tests, I considered kernel estimates derived from data-driven>3 data sets to represent better home range models than those derived from generic filtered data. The similarity in the home range areas derived from data-driven>3 and generic>4 data sets indicates that the fixed kernel estimator with the improved LSCV as a bandwidth selector is robust against reduction in sample size as long as high-error locations are properly screened, at least in the volume contours of home ranges.

Although unnecessary data loss by the generic>4 filter did not appear to have large influence on the construction of home range boundaries, there is few reason to use the generic>4 filter over the data-driven filter when the latter method is available because the data-driven filter (1) will lead to more accurate home range estimates than the generic filters, and (2) will satisfactorily remove locations with high error while retaining more data than the generic filters as shown in my terrestrial test. Unlike the generic filters, the criteria used in the data-driven filter would need to be determined for each species, and may need to be evaluated separately for different habitats or populations. When the filtering criteria used for data-driven filter cannot be determined, the generic>4 filter may be an useful alternative screening method.

2.5 Chapter Summary

- Fast acquisition GPS technologies such as Fastloc GPS have been commonly used in recent years to study fine-scale spatio-temporal ecology of marine vertebrates.
- While Fastloc GPS gives more accurate locations than earlier methods, it remains important to identify and remove locations with high error because some location fixes are much less accurate than others. Increasing the number of source satellites required for a valid fix is a simple filter method but it comes at the cost of great data loss.
- Using data sets acquired from loggerhead turtles, I explored an alternative filtering approach, based on speed between successive locations, angles created by 3 consecutive locations, manufacturer's quality index, and number of satellites used for location calculation. The performance of the proposed filter method was evaluated by conducting terrestrial mobile tests.
- When my filter method was used, the linear error (mean ± SD) of Fastloc GPS data decreased from 2,645.5 ± 29,458.2 m (n = 1,328) to 47.1 ± 61.0 m (n = 1,246), while retaining more than 94% of data. My filter method also led to more accurate home range estimates than the simple filter method.
- Improvements in data retention and home range estimates will give more reliable information for marine spatial planning and habitat protection.

Chapter 3

Sea turtles return home after intentional displacement from coastal foraging areas

In Chapter 1, I identified potential influences on turtles' selection of foraging habitat by human-induced displacement. This is a concerning issue because these anthropogenic actions may affect foraging behaviour of sea turtles and if so, the habitat and its ecosystem are likely to be affected. Thus primary question of this chapter is whether displaced sea turtles settle in the areas of release, return to their original habitat or move to other habitats. Homing behaviour of displaced turtles is also examined.

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R package:

I included the additional screening methods described in this chapter (e.g. using water depth, removing duplicated estimates) in the R package SDLfilter written for Chapter 2. The latest package can be downloaded from the GitHub (https://github.com/TakahiroShimada/SDLfilter).

3.1 Introduction

In diverse situations, wild animals may be removed from their normal habitat and subsequently released at a new location with expectation of a beneficial outcome. The objective may be to establish threatened species in a new area, reintroduce them in an area of local extinction, or augment a locally diminished population (for examples see Griffith et al. 1989, Fischer and Lindenmayer 2000). In addition, a localised environmental catastrophe, such as oil spills, may prompt the removal of vulnerable animals to a safer location (e.g. Barham et al. 2006). Furthermore, animals that have been temporarily held in captivity, e.g. for research or rehabilitation, may be released at locations distant from their area of origin for logistical feasibility or in expectation of more favourable conditions for the animals.

Biological background knowledge is essential in assessing the feasibility of moving vulnerable wild species (Stamps and Swaisgood 2007, IUCN/SSC 2013). A fundamental question must be considered for a highly mobile species (Stamps and Swaisgood 2007) namely: can the displaced animals be expected to remain at the new location? Clearly a positive answer is necessary to meet most conservation goals, yet a negative answer must be assumed if animals are expected to return home after displacement for research or rehabilitation. For many species, no clear answer is available.

For hard-shelled sea turtles (Cheloniidae), there is evidence of long-term fidelity to foraging sites, long-term fidelity to breeding sites, and the capacity for migration between these sites at irregular intervals (Miller 1997, Plotkin 2003, Broderick et al. 2007, Schofield et al. 2010). However, these common patterns can be subject to variation. For example, while Schofield et al. (2010) found fidelity to primary foraging grounds by sea turtles, the authors also showed that turtles may use up to 5 distinct foraging sites. Additionally, seasonal and ontogenetic shifts in foraging habitat have been reported for some species at some locations (e.g. Musick and Limpus 1997, Morreale and Standora 2005, Shimada et al. 2014). Consequently, inference from natural behaviour offers uncertain guidance about potential responses of sea turtles to unnatural displacement.

Direct studies of displaced turtles have predominantly investigated the ocean navigation ability of adult female turtles after experimental displacement from breeding sites (Luschi et al. 1996, Luschi et al. 2001, Hays et al. 2003a, e.g. Lohmann et al. 2008). Information about turtles displaced from coastal foraging areas tends to be sparse and site-specific (e.g. Limpus 1992, Avens et al. 2003) and largely reliant on recapture of marked animals. Although some displaced turtles in the Avens study (Avens et al. 2003) were radio-tracked briefly, that technology was unsuitable for continuous tracking over long duration and distance.

With satellite-linked devices, wild animals can be very effectively tracked over extended time periods and almost unlimited geographic range (Godley et al. 2008, Hazen et al. 2012). Platform transmitter terminals (PTTs) allow long duration tracking with remote delivery of estimated positions but location accuracy is relatively low (Hays et al. 2001, Hazel 2009). More accurate and more frequent locations can be obtained from Fastloc GPS (FGPS) receivers (Hazel 2009) although these must be linked with the Argos PTT system to allow remote data delivery. Despite the technical capacity of satellite-linked systems, research is typically limited by logistical and funding constraints. For the present study, these two factors, as well as ethical considerations, precluded a large scale displacement experiment. Instead, I sought insight from tracking data that had been gathered for diverse purposes at diverse times during prior work and my PhD research for other purposes (Chapters 2, 5, 6) with Cheloniidae in coastal foraging areas of Queensland, Australia.

The primary objective for this chapter was to investigate whether or not free-living sea turtles tend to remain at a new location after displacement from their foraging areas. Based on evidence of strong site fidelity at Australian coastal foraging sites (Limpus 2008), I hypothesised that the majority of my study turtles would not remain at their new locations and would attempt to make their way back to their original areas. However, I suspected that distance of displacement or duration in captivity might reduce a turtle's motivation or ability to return to its original area. I therefore wanted to investigate environmental variables that could influence speed of travel and whether direct or indirect routes were adopted. In combination, speed and straightness of track would determine the overall duration of successful return journeys.

I accepted that an opportunistic study sample would not be comprehensive for all species or balanced for all variables of interest. However, the present study encompassed multiple species and a wide range of displacement situations that had occurred during prior work and my PhD research. By drawing on existing tracking data I aimed to gain new insights while avoiding new deployment costs and additional intervention in the lives of turtles.

3.2 Materials and Methods

3.2.1 Study turtles

I assembled 113 tracks of turtles that had been captured in shallow water (<10 m) in various tropical and subtropical foraging habitats of north-eastern Australia between 1996 and 2014 (Figure 3.1, Appendix - Table A1). My complete data set comprised 79 green turtles *Chelonia mydas*, 30 loggerhead turtles *Caretta caretta* (one of them tracked twice), two olive ridley turtles *Lepidochelys olivacea* and one hawksbill turtle *Eretmochelys imbricata*. Turtles were captured for research by the rodeo method (Limpus 1978) (n = 105) and captured incidentally on a baited drum-line set by the Queensland Shark Control Program (n = 1). Other turtles were taken into care after being found debilitated on or near the shore (n = 6), hereafter termed rescued turtles. The study turtles included adult and immature individuals of both sexes as identified by laparoscopic examination of the gonads, by curved carapace length (CCL), or by combination of CCL and tail length (Limpus and Reed 1985, Limpus and Limpus 2003a, Limpus 2008). Turtle sizes ranged from 38.1 to 121.2 cm CCL, median 98.0 cm (interquartile range = 91.1 to 106.1 cm). Research turtles were released within 5 days of original capture. Rescued turtles were released after 69 to 514 days in rehabilitation centres (Appendix - Table A1).

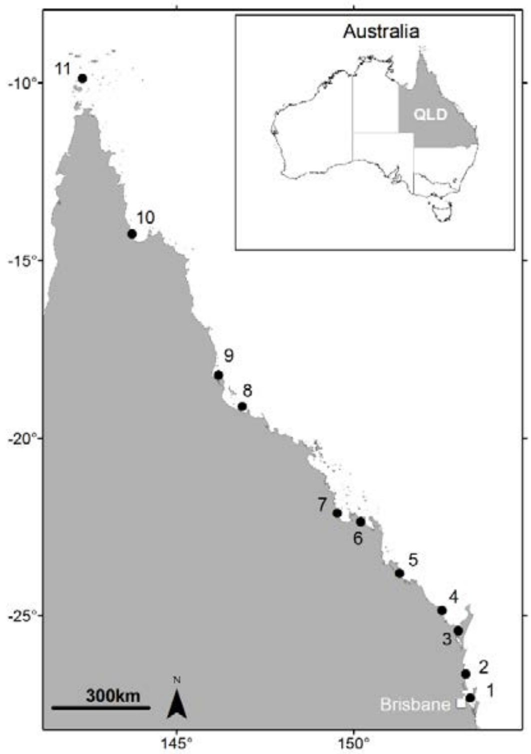

Figure 3.1 Release sites of study turtles were dispersed widely along the coast of Queensland, Australia.

Before release each turtle was fitted with a tracking device attached to the carapace with epoxy glue and fibreglass (Chapter 2). Some turtles received a PTT (*n* = 27), while the majority (*n* = 86) received an Argos-linked FGPS device that provided PTT locations in addition to FGPS data. Turtles were released at <0.1 to 431.2 km from their capture locations. Tracking periods ranged from 5 to 915 days (Appendix - Table A1).

3.2.2 Data preparation

Preliminary screening was applied to all tracks (i.e. both FGPS and PTT data), using the R package SDLfilter (available from https://github.com/TakahiroShimada/SDLfilter), to remove temporal and spatial duplicates and retain only a single fix (latitude/longitude pair) per time and location. For concurrent FGPS fixes, the fix derived from the highest number of satellites was retained (Hazel 2009, Chapter 2). For concurrent PTT fixes, the fix with highest Location Class (LC) was retained (CLS 2011). When concurrent fixes had the same quality index, the fix with the shortest summed distances to the previous and subsequent fix was retained. I excluded any locations acquired during breeding migrations. I also excluded any locations on land (above high tide line) because in eastern Australia foraging sea turtles rarely ascend beaches above the high tide line, although some individuals may rest on intertidal substrate where they become exposed at low tide (Limpus et al. 2005). All analyses were conducted using R software (R Core Team 2015).

3.2.3 Classification of displaced and non-displaced turtles

To determine (a) whether a turtle had been displaced from its original area and (b) whether displaced turtles returned to their original areas, I used PTT locations because these were available for all tracks (*n* = 113) and in some instances the PTT data provided a longer tracking duration than the corresponding FGPS data (in a device that used both tracking systems, the PTT component could remain functional after FGPS operation was halted by diminishing battery power or by epibiont growth on the GPS receiver).

To improve the relatively low accuracy of raw PTT locations I fitted hierarchical Bayesian state-space models (hSSM) following Jonsen et al. (2006). This technique provides more accurate location estimates by accounting for observation error and heterogeneity using tracking data from multiple animals. Because the process involves highly intensive computation, I balanced processing time against the benefits gained from multiple tracks as follows: my PTT data set was divided into 12 smaller portions with each subset containing 9,836 to 12,903 observations acquired from 9 to 13 turtles. The model was fit to each subset of PTT data via two

Markov Chain Monte Carlo (MCMC) chains using the R package bsam, provided by Jonsen et al. (2013). Each MCMC chain was run for 300,000 iterations, excluding the first 200,000 samples as a burn-in. Every 100th of the last 100,000 samples was retained to reduce autocorrelation. Convergence and autocorrelation for hSSM were examined using diagnostic plots generated by the bsam package. The hSSM locations were estimated at six hourly intervals (mean interval of the raw Argos fixes). I dropped hSSM locations that fell on land and locations for periods when raw Argos fixes were absent for more than 5 days, the latter because error of hSSM locations appeared to inflate if 20 or more consecutive positions were missing (Bailey et al. 2008). Finally the high-quality PTT locations (LC 3, 2, 1) were merged with the hSSM data. These locations, with an expected mean error of 2.2 km (Hoenner et al. 2012), are hereafter referred to as post-processed hSSM data.

I used the post-processed hSSM data to calculate the utilisation distribution (UD) for each turtle. To avoid problems of autocorrelation I applied the movement-based kernel density method of Benhamou (2011) as implemented in the R package adehabitatHR (Calenge 2006, 2015a) using fixed parameters (see Appendix - Table A2). To define the resettlement area of each turtle I used the 95% contour of the UD, with a buffer of width 2.2 km (expected mean error of my post-processed hSSM data). A turtle was deemed to have settled in the buffered 95% UD provided the turtle did not move outside the 95% UD for longer than 1 day. In cases where the 95% UD comprised two or more disjunct polygons, an earlier polygon was excluded if the turtle had moved out of it and did not return to it.

A turtle was classified as displaced if its release location was outside its resettlement area, and classified as non-displaced if its release location was within its resettlement area (Figure 3.2). Provided the capture location was contained within the resettlement area, the resettlement area was deemed to represent the original area of that turtle. Thus a displaced turtle that subsequently returned to its original area was regarded as returning home (Figure 3.2b). If a turtle did not return to its original area, the distance between capture and resettlement was measured to the periphery of the resettlement area. In the special case where transmission ceased while a turtle was still travelling (n = 2), the resettlement area could not be estimated. In this situation I classified the turtle as non-displaced if the distance between its capture and release locations was shorter than 95th percentile diameters of circularised resettlement areas of all other turtles (16.8 km, n = 111). If the distance was greater than this, the turtle was classified as displaced.

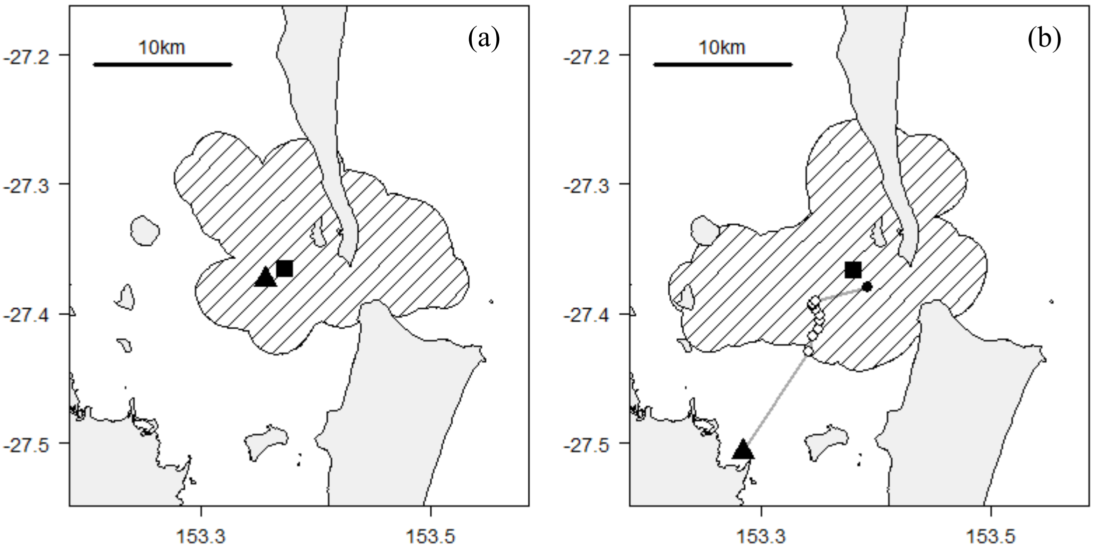

Figure 3.2 At site 1 (see Figure 3.1) a loggerhead turtle *T53800* was tracked twice. (a) On the first occasion in 1998 the turtle was not displaced. After release it remained in its original foraging area. (b) On the second occasion in 2010 the turtle was displaced by 18.3 km from its capture location. It travelled back to its original area, thus was regarded as a homing turtle. Square = capture location, triangle = release location, cross-hatched polygon = resettlement area. Grey line is the travelling path after displacement. Empty circle = location of relatively low residency, filled circle = location of relatively high residency.

3.2.4 Detailed analyses for homing turtles

Displaced turtles that returned to their original areas were classified as homing turtles. For these turtles I merged FGPS locations with high-quality PTT locations (LC 3, 2, 1) and then used the R package SDLfilter to apply additional filtering as follows. In order to remove locations above the high tide line, the water depth at track locations was estimated using bathymetry models and tidal data. Horizontal resolution of the bathymetry models was 110 m for one release site (site 11, see Figure 3.1) (Daniell 2008) and 100 m for the other release sites (Beaman 2010). Tidal data were obtained from the Australian Bureau of Meteorology and Queensland Department of Transport and Main Roads. Filtering according to water depth was applied to the high-quality PTT locations and to the FGPS fixes derived from four satellites. Filtering by water depth was deemed unnecessary for FGPS fixes derived from >4 satellites because these fixes had estimated accuracy <64 m at site 1 and <33.1 m at site 8 (Hazel 2009, Chapter 2), thus higher accuracy than the bathymetry models. After filtering by water depth I applied a data-driven filter following the method of Chapter 2. Location fixes were removed if the speed both from a preceding location and to a subsequent location exceeded the maximum realistic swimming speed (V_{max}) or if all of the following applied: (a) fixes were derived from only four GPS satellites or from the PTT system, the inner angle (180° minus the animal's turning angle) was <90°, and the speed either from a preceding location or to a subsequent location exceeded a maximum "loop trip" speed (V_{lp}) estimated for each species (Table 3.1). Estimated error (mean ± SD) for high-quality data filtered by this method was 47.1 ± 61.0 m (Chapter 2).

Table 3.1 Data preparation for detailed analyses of homing turtle behaviour: Threshold speed (km h^{-1}) used in the data driven filter. V_{max} = maximum swimming speed, Max. $V_{\text{l}p}$ = maximum "loop trip" speed, as defined in Chapter 2.

Species	V_{max}	Max. V_{lp}	Data source
Chelonia mydas (*n* = 12)	9.9 (10,189 fixes)	2.0 (716 loop trips)	This study
Caretta caretta (*n* = 8)	8.9 (39,21 fixes)	1.8 (57 loop trips)	Chapter 2

To investigate homing behaviour in detail, my analyses focused on the homing segment of the track, that is, from point of release to the first location of relatively high residency within the resettlement area (Figure 3.2b). I used the residence time method (Barraquand and Benhamou 2008), implemented in R package adehabitatLT (Calenge 2006, 2015b) to distinguish locations of relatively high and low residency. I excluded from my detailed analysis any homing tracks that included locations <100 m from land, other than during the first 3 h after release. This was necessary because very close proximity to land would restrict direction of travel and introduce a confounding effect on straightness of the track. I calculated straightness index (Batschelet 1981) equal to straight-line distance from first to last location (beeline distance) divided by summed track length. Summed track length was simply the sum of distances between successive locations along the track. Thus a turtle swimming in a straight line all the way would have straightness index = 1 and a turtle swimming along a more circuitous path would have a straightness index <1.

I used generalised linear models (GLMs) to model travelling speed and straightness index during the overall homing trip as functions of displacement distance, sea surface temperature (SST) at release, season, latitude, and species. I also checked correlations between travelling speed and straightness. I obtained SST as daily estimates derived from satellite data at a resolution of 0.1°(NASA Earth Observations 2014). The Australian seasons were defined as: *spring* September–November, *summer* December–February, *autumn* March–May, and *winter* June–August (Bureau of Meteorology 2015). Potential effects of bathymetry were not considered because estimated water depths were consistently shallow (mean ± SD = 7.3 ± 4.0

m, $n = 1{,}046$) and the bathymetry models (resolution 100 – 110 m) would not identify small features in the complex substrate at my study sites.

I also evaluated travelling speed and straightness index during diurnal and nocturnal periods, using track segments between the first and last fixes of each day and night. To differentiate day and night periods I estimated time of sunrise and sunset at each location using the R package StreamMetabolism (Sefick 2015). I again examined factors affecting travelling speed and straightness index in generalised linear mixed effects models (GLMMs) and included day/night as a fixed effect, together with other significant effects identified in the preceding analyses. Individual turtles were treated as random effects because some turtles required multiple day/night periods for their journey.

I chose distributions for response variables in the GLMs and GLMMs as follows: Travelling speed (continuous, positive, and skewed to right) was fitted with the gamma distribution and straightness index (proportion) was fitted with the beta distribution. I used the R package stats to fit gamma GLMs (R Core Team 2015), package betareg to fit beta GLMs (Cribari-Neto and Zeileis 2010), and package glmmADMB to fit both gamma and beta GLMMs (Fournier et al. 2011, Skaug et al. 2015). For each model, I computed the variance inflation factors (VIF) among the covariates using the R package car (Fox and Weisberg 2011). I considered collinearity was not an issue if the values were <3 (Zuur et al. 2010). Homogeneity of variance was assessed by plotting residuals versus fitted values. Transformations were applied to data when necessary to meet assumptions of the models. Response variables were centred to have a mean of zero for analyses with GLMs and GLMMs (Becker et al. 1988). I used the R package MuMIn (Barton 2015) to rank all possible models by second-order Akaike Information Criterion (AICc). I selected a set of models within two AICc units of the best-ranked model to identify models with similar explanatory power (Burnham and Anderson 2002). AICc model weights (ω_i) were computed as the weights of evidence in favour of each model *i* within the "best subset". I compared each model in the "best subset" to a null model by likelihood ratio test using the R package lmtest (Zeileis and Hothorn 2002).

I originally wanted to examine the relationship with speed and straightness of travel for all variables of interest (species, displacement distance, season, SST, latitude, and day/night period). However, it emerged that the relevant portion of my data set (i.e. displaced turtles that returned home and had tracks not restricted by very close proximity to land) suffered from collinearity and was highly unbalanced with respect with season, species and latitude; for example, none of these turtles were released during the summer months; season was highly correlated with SST (VIF > 3); green turtle tracks began at six different sites spread over a wide latitudinal range but all loggerhead tracks began at one site. I was therefore obliged to analyse different combinations of variables for separate subsets of the homing turtles. See "3.3.3 Homing behaviour of displaced turtles" section for details of turtle subsets and the variables addressed for each subset.

3.3 Results

3.3.1 Outcomes for displaced turtles

Fifty-nine turtles were classified as displaced. They comprised 44 green turtles (including two rescued), 13 loggerhead turtles (one rescued), and two olive ridley turtles (both rescued). These displaced turtles had been retained for <1 to 514 days (median = 1 day, interquartile range = 0.9 to 1.5 days) and they had been displaced from their capture locations by 6.6 to 432.1 km (median = 17.5 km, interquartile range = 13.3 to 21.3 km) (Appendix - Table A1).

Most displaced turtles (*n* = 52 or 88%), including two rescued turtles, returned home and resettled in their original areas (e.g. Figure 3.2b, 3.3ab). Another four displaced turtles moved towards their respective capture areas and settled within 1.8 to 14.1 km of their capture location but their resettlement areas (95% UD) did not include the capture location: these comprised two green turtles (one research, one rescued), an olive ridley turtle (rescued), and a loggerhead turtle (rescued) (e.g. Figure 3.3c).

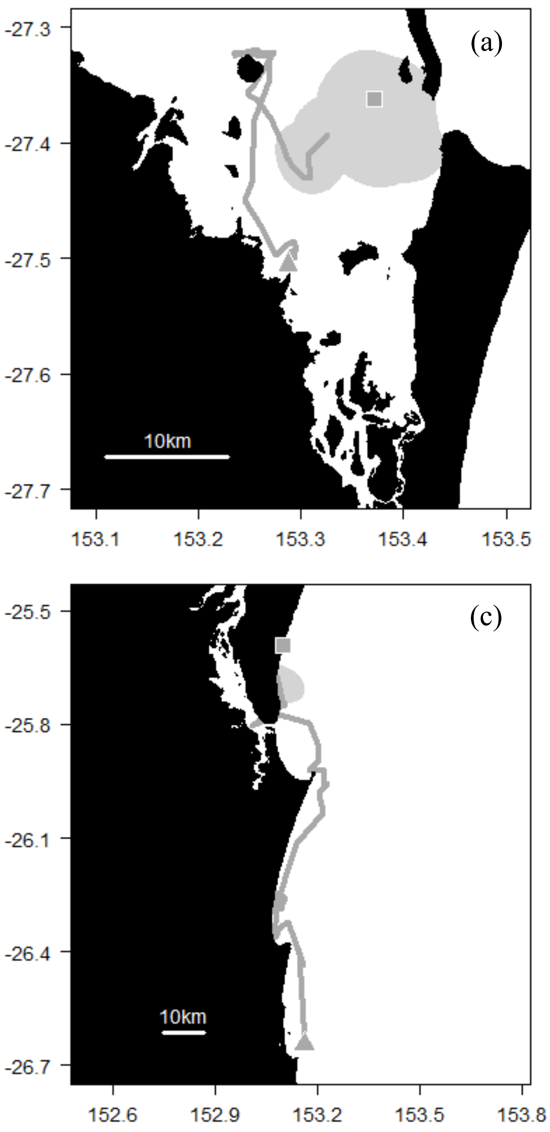

Figure 3.3 Representative tracks of turtles after displacement: square = capture location, triangle = release location, grey line = travelling path, grey filled polygon = resettlement area. (a, b) At Site 1 these green turtles were displaced and returned to their areas of capture. (c) At Site 2 this olive ridley turtle was found debilitated and displaced after rehabilitation. The turtle moved toward its capture area but its resettlement area did not include the capture location. (c) At Site 5 this green turtle was displaced and resettled away from its capture location.

Two displaced turtles (research) travelled towards their capture locations but satellite transmission ceased before these turtles reached their area of capture. For one individual (K89296 green turtle, displaced by 19.2 km, Appendix - Figure A1 j *red*) the transmissions abruptly ceased on the 31st day, at which time the turtle had reached a point 10.7 km from the capture location. The other individual (QA12903 loggerhead turtle, displaced by 432.1 km, Appendix - Figure A1 h) had moved 53.6 km towards its capture location when transmission ceased on the 54th day. Detail of this turtle's track showed that during the first 20 days after release it moved 44.5 km towards its capture location. For the next 5 days, its movements were localised along the coast. For the last 29 days most locations indicated a nearby beach. There was a notable change in the PTT data quality: during the first 20 days of travel only 9% of the data were high-quality fixes (LC 3, 2, 1) whereas during the last 34 days 86% of the data were high-quality fixes.

Only one displaced turtle (research) did not move towards its capture location during its tracking period of 120 days. Instead this turtle (QA45689 green turtle, displaced by 7.8 km) settled in an area 35.1 km from its capture location (Figure 3.3d).

3.3.2 Outcomes for non-displaced turtles

Fifty-four turtles were classified as non-displaced. They comprised 35 green turtles, 18 loggerhead turtles and one hawksbill turtle (one rescued green turtle, all others research). The non-displaced turtles had been held for <1 to 170 days (median = 1 day, interquartile range = 0.9 to 1.9 days) and released at locations <0.1 to 8.9 km (median = 4.2 km, interquartile range = 1.9 to 6.1 km) away from their capture locations. After release all non-displaced turtles remained in their original areas (95% UD) (e.g. Figure 3.2a).

3.3.3 Homing behaviour of displaced turtles

Of the displaced turtles that returned home, 29 qualified for detailed analyses because they were tracked with Argos-linked FGPS devices and their homing tracks were unrestricted by very close proximity to land (e.g. Figure 3.2b, 3.3b). Some of these turtles took a very direct route while others swam along a relatively circuitous path. Table 3.2 contains summary statistics for variables of interest associated with the homing track of each turtle. The effects of these variables were addressed separately for different subsets of the homing turtles (see "3.2.4 Detailed analyses for homing turtles" section). The effects of latitude were examined only for green turtles (homing turtle subset 1). The effects of species were examined only for turtles associated with site 1 (homing turtle subset 2). Relocation distance, SST, and travelling speed/straightness index were included as possible explanatory variables in both cases. I omitted season as an explanatory variable in all models because of its strong correlation with SST. This means that SST may act as a surrogate variable for other environmental attributes which change seasonally.

Table 3.2 Summary statistics for 29 turtles that were included in detailed analyses of homing behaviour. Data values shown as: median (minimum to maximum). For homing segments, sample size (*n*) is the number of homing tracks. For day/night segments, sample size (*n*) is the number of daytime and night-time track segments analysed for each species i.e. 22 green turtles and 7 loggerhead turtles.

Variables	*Chelonia mydas*	*Caretta caretta*
Homing segments	$n = 22$	$n = 7$
No. locations per track	22 (6 to 149)	46 (9 to 90)
Displacement distance: km	17.99 (7.96 to 28.10)	18.38 (13.65 to 26.91)
Homing time: d	1.95 (0.36 to 21.15)	3.03 (1.06 to 4.35)
Beeline distance: km	15.55 (7.69 to 55.09)	17.72 (10.89 to 26.51)
Summed track length: km	26.23 (11.25 to 191.81)	29.23 (19.69 to 38.93)
Latitude at release: S°	27.48 (9.96 to 27.52)	27.51 (27.50 to 27.51)
SST at release: °C	22.8 (17.8 to 28.9)	23.9 (18.2 to 26.3)
No. seasons (spring, summer, autumn, winter)	12, 0, 4, 6	0, 0, 5, 2
Travelling speed: km h^{-1}	0.66 (0.34 to 1.72)	0.54 (0.26 to 0.78)
Straightness index	0.60 (0.12 to 0.94)	0.53 (0.37 to 0.93)
Day/night segments	Day $n = 58$, Night $n = 45$	Day $n = 20$, Night $n = 15$
No. locations per day/night track segment		
Day	6 (2 to 13)	8 (2 to 13)
Night	4 (2 to 14)	8 (3 to 16)
Time between first and last fixes: h		
Day	8.09 (1.63 to 12.53)	9.29 (2.33 to 11.30)
Night	8.21 (1.58 to 11.60)	10.89 (4.63 to 12.24)
Beeline distance: km		
Day	3.55 (0.04 to 12.87)	1.86 (0.23 to 6.55)
Night	1.14 (0.02 to 9.09)	1.74 (0.16 to 6.07)
Summed track length: km		
Day	5.78 (0.20 to 19.41)	4.40 (0.61 to 9.56)
Night	2.51 (0.05 to 14.61)	3.36 (0.31 to 9.21)
Travelling speed: km h^{-1}		
Day	0.90 (0.05 to 2.53)	0.58 (0.05 to 1.29)
Night	0.37 (0.01 to 1.61)	0.40 (0.03 to 0.84)
Straightness index		
Day	0.66 (0.08 to 0.99)	0.51 (0.12 to 0.90)
Night	0.58 (0.08 to 0.98)	0.59 (0.16 to 0.90)

The first homing turtle subset comprised 22 green turtles, for which I tested the effects of latitude and other relevant variables using the following two global models.

1. Global model:

Travelling speed ~ Displacement distance + SST + Straightness index + Latitude

Latitude did not appear in the best-ranked model and the model selection process resulted in only one model being included in the "best subset". This model had SST as its only predictor (Table 3.3). Neither latitude, displacement distance, nor straightness index provided any improvement in prediction of travelling speed.

Table 3.3 Detailed analyses for homing turtle tracks: overall movements. Overall travelling speed (TS) and straightness index (SI) modelled with gamma and beta GLMs respectively. Explanatory variables are displacement distance (DD), sea surface temperature (SST), latitude (Lat), species (Sp) as well as TS or SI. *p* values, AICc, ΔAICc, and AICc model weights (ω_i) are provided for each best-ranked model. *Cm* = *Chelonia mydas*, *Cc* = *Caretta caretta.*

Homing turtle subset	Global model	Best-ranked models	*p*	AICc	ΔAICc	ω_i
Subset 1 (*Cm n* = 22)	TS ~ DD + SST + SI + Lat	TS ~ SST	<0.001	1.8	0.00	1
	SI ~ DD + SST + TS + Lat	SI ~ Lat	0.069	-1.1	0.00	0.347
		SI ~ (Null)	NA	-0.5	0.61	0.256
		SI ~ TS	0.135	0.0	1.07	0.203
		SI ~ SST	0.142	0.1	1.16	0.195
Subset 2 (*Cm n* = 12, *Cc n* = 7)	TS ~ DD + SST + SI + Sp	TS ~ SST + Sp	0.002	3.4	0.00	0.514
		TS ~ SST	0.002	3.5	0.11	0.486
	SI ~ DD + SST + TS + Sp	SI ~ SST	0.007	-7.3	0.00	1
Subset 1+2 (*Cm n* = 22, *Cc n* = 7)	TS ~ DD + SST + SI + Sp	TS ~ SST + Sp	<0.001	-3.7	0.00	0.555
		TS ~ SST	<0.001	-3.2	0.44	0.445
	SI ~ DD + SST + TS + Sp	SI ~ SST	0.013	-6.9	0.00	1

2. Global model:

Straightness index ~ Displacement distance + SST + Travelling speed + Latitude

Four models were included in the "best subset" of models but the "best subset" included the null model, that is, a simple estimate of the mean straightness index with no explanatory variable as predictor (Table 3.3). This result, together with likelihood ratio tests, indicates that none of the variables including latitude had any perceptible influence on the straightness index.

The second homing turtle subset comprised green turtles (*n* = 12) and loggerhead turtles (*n* = 7) that were released in the same area (site 1). For this subset I tested the effects of species and other relevant variables as expressed in the following third and fourth global models.

3. Global model:

Travelling speed ~ Displacement distance + SST + Straightness index + Species

Two models were included in the "best subset" of models (Table 3.3). The best-ranked model used both SST and species as predictors of travelling speed, and the second-best model included only SST. Neither displacement distance nor the straightness index appeared to affect travelling speed (Table 3.3).

4. Global model*:*

Straightness index ~ Displacement distance + SST + Travelling speed + Species

Only one model was included in the "best subset": the model included SST as a solo predictor (Table 3.3). Neither species, displacement distance nor travelling speed appeared to influence the straightness index (Table 3.3).

5. I re-analysed the data using all qualified homing turtles (subset 1 + subset 2, *n* = 29), omitting latitude as a covariate because my results for the first homing data subset indicated latitude had no effect on travelling speed or straightness. I used the same global models (3 and 4 above) that I had applied to my second homing data subset. The inclusion of additional green turtles from different sites did not change the results of the model selection with the second homing subset (Table 3.3). That is, cooler SST values were in general associated with faster travelling speed (Figure 3.4a) and with straighter (less circuitous) routes (Figure 3.4b). The result also indicated that green turtles tended to travel faster than loggerhead turtles (Figure 3.4a).

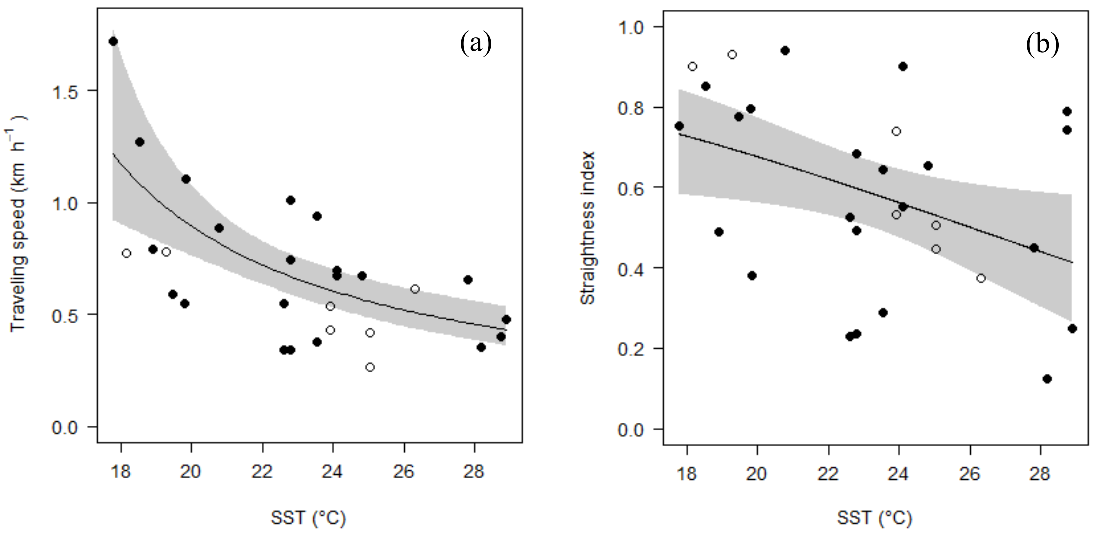

Figure 3.4 (a) Travelling speed and (b) straightness index for tracks of homing turtles that were released at various sea surface temperatures (SST): green turtles = filled circle, loggerhead turtles = empty circle. The solid line is model fit, grey band denotes 95% confidence interval.

3.3.4 Day/night movements

Among the 29 homing turtles analysed in detail, there were large variations in travelling speed and straightness index by day and by night (Table 3.2). Day/night effects on homing behaviour were tested with SST and species as explanatory variables. My selection of these two variables was determined by results of preceding analyses of overall movements. I used data for all qualified homing turtles (subset 1 + subset 2, *n* = 29) in the following two global models.

6. Global model:

Day/night travelling speed ~ SST + Day/night + Species

Two models were selected in the “best subset” (Table 3.4). Day/night was an important variable since it occurred in both models. Turtles tended to travel faster during the day than the night (Figure 3.5). SST also occurred in both models as expected. Species was retained in the best model which had considerable support relative to the other model: the AICc model weights were more than double when species was included (Table 3.4). Day/night travelling speed decreased approximately 0.06 km h^{-1} per 1 °C increase, and in general, green turtles travelled faster (fit = 0.85 km h^{-1}) than loggerhead turtles (fit = 0.60 km h^{-1}).

Table 3.4 Detailed analyses for homing turtle tracks: day/night movements. Diel travelling speed (DTS) and straightness index (DSI) modelled with gamma and beta GLMMs respectively. Explanatory variables are sea surface temperature (SST), day or night (DN), and species (Sp). *p* values, AICc, ΔAICc, AICc model weights (ω_i) are provided for each best-ranked model. *Cm* = *Chelonia mydas*, *Cc* = *Caretta caretta*.

Homing turtle subset	Global model	Best-ranked models	*p*	AICc	ΔAICc	ω_i
Subset 1+2 (*Cm n* = 12, *Cc n* = 7)	DTS ~ SST + DN + Sp	DTS ~ SST + DN + Sp	<0.001	147.5	0.00	0.677
		DTS ~ SST + DN	<0.001	149.0	1.48	0.323
	DSI ~ SST + DN + Sp	DSI ~ (Null)	NA	-23.8	0.00	0.458
		DSI ~ Sp	0.191	-23.3	0.41	0.373
		DSI ~ DN	0.716	-21.8	1.99	0.169

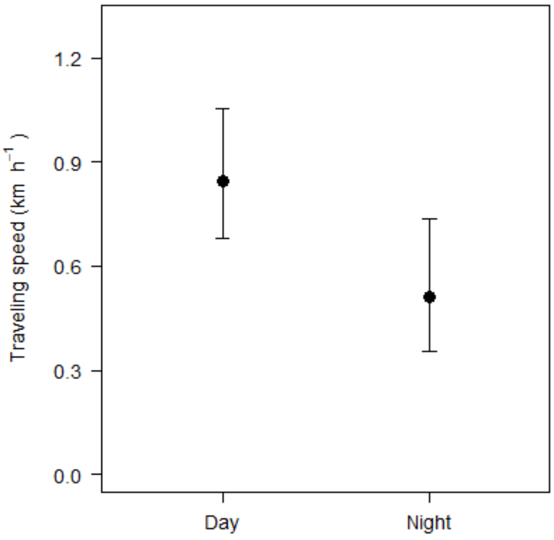

Figure 3.5 Estimated travelling speed of homing turtles by day and by night. Filled circle is model fit, error bars denote 95% confidence interval.

7. Global model:

Day/night straightness index ~ SST + Day/night + Species

None of the variables was associated with straightness of day/night segments of homing tracks: the best-ranked model was the null model (Table 3.4).

3.4 Discussion

This study presented substantial evidence that highly mobile marine species like Cheloniidae cannot be expected to remain at new human-selected locations after the animals have been intentionally displaced from their original coastal foraging grounds.

3.4.1 Confirmation of homing behaviour

The results provided strong support for my initial hypothesis: most displaced turtles attempted to return home and furthermore, most of them succeeded. For my study turtles, homing ability was not limited by distance of displacement (up to 117.4 km) or by captivity duration (up to 514 days). The successful homing animals included green turtle adults and juveniles of both sexes and loggerhead turtle adults of both sexes. In addition, one olive ridley turtle returned home and the other resettled near its capture area. The single hawksbill turtle was not displaced.

A few turtles did not return home according to strict study criteria, but did not conclusively fail to return. Most of the non-returned turtles travelled to areas near their respective capture areas. The single displaced turtle that adopted a resettlement area far (35.1 km) from its capture location appears to indicate a rare instance of failure to return home. However, I noted that this turtle was tracked for 120 days, a period shorter than the median tracking duration (157 days) and there remains a highly speculative possibility that the turtle could have completed a homing journey after the cessation of tracking.

My results showed no evidence of impaired homing capacity for rescued turtles that had spent 69-514 days in rehabilitation centres. One apparent failure to home was not a rescued turtle. Of the five rescued turtles that were displaced, two returned home and the other three resettled near home. It was plausible that the near-home rescued turtles had actually returned to their true original areas. A rescued turtle may have drifted beyond its home area while it was in a debilitated state, in which case its capture location (where it was found and rescued) would have been outside its true original area.

3.4.2 Potential fitness benefits and costs

Almost all the displaced turtles showed a strong homing tendency and all non-displaced turtles remained in their original areas after release. This finding was consistent with long-term site fidelity, a widely reported phenomenon in groups as diverse as Chiropterans (Lewis 1995) and

Elasmobranchs (Knip et al. 2012) albeit with intra-taxon variation. The development and persistence of site fidelity would imply this behaviour is associated with a fitness benefit in terms of evolutionary adaptation (Parker and Smith 1990).

Details of the potential fitness benefit accruing to Cheloniidae through their fidelity to foraging areas have not been determined experimentally. The benefit might be explained in broad terms by site familiarity. This intuitively relevant concept has seldom been included in habitat selection models and remains difficult to measure (Piper 2011). I surmise that, through long familiarity with a particular area, sea turtles would discover where to find food efficiently, where to find shelter for resting, where predators typically occur, and where they can best be evaded. Such site familiarity could enable individuals to adjust their foraging behaviour to balance food acquisition and predation risk, as has been observed in sea turtles in Western Australia (Heithaus et al. 2008). Thus I infer that each turtle derives a fitness benefit by remaining faithful to its home foraging area and conversely, I infer fitness costs will accrue for a displaced turtle. It must necessarily expend energy in travelling back to its home area after unnatural displacement, and it may face greater risk and forage less efficiently while it is in unfamiliar habitat.

3.4.3 Factors influencing homing travel

Sea surface temperature (SST) was the key factor identified as influencing homing behaviour: in cooler water, the study turtles travelled faster and followed straighter routes. Greater speed in cooler water was an unexpected finding for Cheloniidae. They are ectothermic animals that are affected by ambient water temperature (Spotila et al. 1997). Cooler water has been found to slow the metabolic rate of green turtles (Southwood et al. 2003, Southwood et al. 2006) and reduce their activity. For example, green turtles within the southern part of my study area were found to make notably longer resting dives at cooler temperatures than at warmer temperatures (Hazel et al. 2009). Similarly, slower travel could be expected at cooler temperatures yet my results indicated the converse. In the scientific literature I could find no plausible explanatory principle. Insight regarding this surprising finding might be gained through future research involving systematic displacement experiments.

Although the straightness of complete homing tracks was strongly associated with SST, the same association was not evident when I evaluated day/night effects. This may reflect imprecise estimates of straightness index for my day/night track segments. These segments were short and thus each segment contained relatively few locations (median 4 to 8 locations used for straightness index of a day/night segment, Table 3.2).

Inter-specific differences in travelling speed of the homing turtles probably reflect differences in swimming ability. Green turtles generally swim faster than loggerhead turtles (Heithaus et al. 2002), and my results are consistent with that observation. In contrast to travelling speed, straightness indices were similar for green turtles and loggerhead turtles. The similarity in straightness of tracks could suggest both species have similar way-finding ability in coastal waters.

3.4.4 Way-finding ability of homing turtles

The present study was not designed to investigate navigational capacity *per se*, but my results clearly confirmed the ability of displaced turtles to find the way back to their original areas. For sea turtles, the underlying mechanisms for open ocean navigation are understood to involve predominantly geomagnetic cues at greater distances from the destination, potentially progressing to a hierarchy of other cues at closer range, details of which remain to be elucidated (Åkesson et al. 2003, Avens and Lohmann 2003, Hays et al. 2003a, Benhamou et al. 2011, Lohmann et al. 2013). It seems plausible that a similar hierarchy of cues guided my study turtles, although they did not undertake oceanic travel and generally travelled within a few kilometres of the mainland shore.

My finding that displaced turtles travelled faster during the day might imply greater availability of way-finding cues during daylight and hence might suggest that visual information could be important for way-finding. This difference is not necessarily related to way-finding; for example, turtles that are not travelling also appear to be more active during the day, as reported for foraging turtles within my study area (Hazel et al. 2009). Furthermore, the findings of Åkesson et al. (2003) suggest that sea turtles do not use celestial cues for orientation. Nevertheless, additional insight might be gained if future studies were to include day/night information when analysing way-finding and navigational behaviour of sea turtles.

3.4.5 Premature disruption of tracking

Transmission from a tracking device may cease for diverse reasons (Hays et al. 2007), and I speculated about the cause of two transmission failures during homing travel. For turtle QA12903, the sudden and concurrent changes in movement pattern and in quality of PTT fixes suggested the turtle became debilitated or died in the area where movement became localised. I suspect this turtle probably became stranded on the shore, given the unusually large proportion of high-quality fixes acquired around the intertidal area during the last period of transmission.

The tracking period was relatively short for this turtle (54 days) and there was no apparent sign of degradation in device performance prior to cessation. I was unable to confirm turtle death or investigate possible causes because the site of suspected stranding was inaccessible.

For turtle K89296, signals stopped abruptly after only 31 days, while the turtle was travelling slowly close to shore. There was no evidence of a change in turtle behaviour. Detachment of the tracking device seemed more likely than an early technical failure. Perhaps the adhesive bond had been gradually weakened by the turtle rubbing its carapace on rocky outcrops that were potentially available *en route*. A similar explanation might apply for the two non-displaced turtles that had similarly short tracking durations (≤31 days) and no apparent change in behaviour. Rare events like boat strike or attack by a very large predator could disrupt tracking, but I remain cautious about over-interpreting the cessation of tracking. In my study the tracking data offered persuasive evidence for morbidity or mortality in only one case, turtle QA12903 described above. The wide temporal and geographic range of my study precluded using this single case to derive a quantitative estimate of mortality, as has been done in different circumstances (Hays et al. 2003b).

3.4.6 Conservation implications

My findings suggest that displacement and periods in captivity do not disrupt a turtle’s ability to find its way back to its original foraging area nor diminish its fidelity to that area. However, there must be an energetic cost for homing turtles and there might be heightened risk of harm in unfamiliar coastal waters. The potential fitness costs of displacement should not be ignored, despite my strong evidence that the majority of displaced turtles can be expected to return home.

Confirmed homing ability suggests that moving individual turtles away from danger could be effective only as a short-term conservation measure, e.g. rescue from temporary threats such as oil spills. The relocation of turtles from their established coastal foraging ground to a new area cannot be expected to succeed as a long-term conservation strategy. Priority must rather be placed on protecting their original habitat.

3.5 Chapter Summary

- Vulnerable species may be removed from their normal habitat and released at a new location for conservation reasons (e.g. re-establish or augment a local population) or due to difficulty or danger in returning individuals to original sites (e.g. after captivity for research or rehabilitation). Achieving the intended conservation benefits will depend, in part, on whether or not the released animals remain at the new human-selected location.
- The present study tested the hypothesis that hard-shelled sea turtles along the coast of north-eastern Australia (9-28°S, 142-153°E) would not remain at new locations and would attempt to return to their original areas.
- I used satellite-tracking data gathered previously for different purposes over several years (1996 to 2014). Some turtles had been released at their capture sites, inferred to be home areas, while other turtles had been displaced (released away from their inferred home areas) for various reasons.
- All non-displaced turtles (n = 54) remained at their home areas for the duration of tracking. Among displaced turtles (n = 59) the large majority travelled back to their respective home areas (n = 52) or near home (n = 4). Homing turtles travelled faster and adopted straighter routes in cooler water, and travelled faster by day than by night.
- My results showed that displacement up to 117.4 km and captivity up to 514 days did not disrupt homing ability nor diminish fidelity to the home area. However, for homing turtles I infer energetic costs and heightened risk in unfamiliar coastal waters.
- Confirmed homing suggests that moving individuals away from danger might offer short-term benefit (e.g. rescue from an oil spill) but moving turtles to a new foraging area is unlikely to succeed as a long-term conservation strategy. Priority must rather be placed on protecting their original habitat.

Chapter 4

Stop and go: Sea turtles halt to reassess direction and use sunrise related cues for fine-scale navigation

Chapter 3 confirmed that displaced turtles returned to the area of capture following release. The behaviour demonstrate that sea turtles have an ability to find correct direction toward their home foraging habitat from the waters for which they have no prior knowledge. In this chapter, I analysed tracks of displaced turtles in detail to look into their navigational mechanisms.

Manuscript in preparation:

Shimada T, Jones R, Limpus C, Hamann M (in prep.) Stop and go: Sea turtles halt to reassess direction and use sunrise related cues for fine-scale navigation. Target journal: *Journal of Experimental Marine Biology and Ecology*.

4.1 Introduction

Navigation is a critical component of the life history of many animals, ranging from plankton to large vertebrates (Bauer et al. 2013). An accurate directional sense enables the animals to travel between distant habitats to meet their needs, such as food acquisition and reproduction. Sea turtles are well known for their exceptional navigational ability and high fidelity to their foraging and breeding habitats following long-distance migration (Limpus and Limpus 2001, Schofield et al. 2010). Displacement experiments have also shown that turtles are capable of navigating though unknown waters and consistently return to the area of capture following displacement (Luschi et al. 2003, Chapter 3).

A variety of cues are used by wild animals for navigation (Bauer et al. 2013). In sea turtles, the ability to migrate long-distances appears to depend upon geomagnetic cues (Lohmann et al. 2013). For example, an experimental study using a coil system exposed juvenile green turtles (*Chelonia mydas*) to a magnetic field 340 km south or north of the test sites, and demonstrated that each turtle swam toward the general area of the magnetic field to which they were exposed (Lohmann et al. 2004). Yet, magnetic compass may not guide turtles to a specific end point but merely to the general area due to its relatively low accuracy as a directional cue (Papi 1992). An example is that navigation of green turtles was adversely affected by magnets mounted on their heads when they were 50 to a few kilometres away from their home habitat, but was not affected by the magnets during the last part of their migration (Benhamou et al. 2011).

The last fine-scale navigation appears to be a critical element of the migration process because that is when breeding loggerhead turtles (*Caretta caretta*) tracked by satellite telemetry were observed to make major corrections in their travelling direction in relation to their observed end point (Hays et al. 2014a). Chemical cues carried by wind or currents have been suggested as navigational aids for sea turtles over short distances but these can only provide useful directional information in situations where a turtle swims against the current or wind thereby allowing detection of cues from the target destination (Hays et al. 2003a, Lohmann et al. 2013). Alternative hypotheses suggest that sea turtles may obtain navigational cues during the day (Avens and Lohmann 2003, Mott and Salmon 2011, Chapter 3); however, details of fine-scale at-sea navigational behaviour, particularly in relation to daylight, are lacking for sea turtles.

Most displaced turtles tracked in Chapter 3 were relocated relatively short distances from their capture site and so their travels back to their home habitat are in the category of short distance navigation. In this case, since I know the target the turtles were aiming for, the tracks of these displaced turtles provide an opportunity to examine possible hypotheses about how short-range navigation might work. Here I demonstrate a novel approach to look in details at the actual tracks taken by turtles during the final phase of their homing journey and its relation to the sun to see if they offer any insights into potential mechanism.

4.2 Materials and Methods

4.2.1 Homing tracks

I used tracks from 22 green and 7 loggerhead turtles which were used in the detailed analysis in Chapter 3. These 29 turtles were displaced by up to 28.1 km (Table 3.2), returned home, and had tracks not restricted by very close proximity to land. I analysed turtle location data starting at the point of release and ending when they had returned to their ‘home’ habitat (Chapter 3). The data contained 1,013 FGPS fixes and 33 high-quality Argos fixes from the 29 tracks. All analyses were executed with R software (R Core Team 2015).

4.2.2 General patterns in tracks

I first provide a description of general spatial and temporal patterns (i.e. direction, duration, distance, turning, timing) seen in the tracks as a whole, with a particular focus on sequences of consistent behaviour ("travelling" versus "stationary" states) and the transitions between them. I used the residence time method (Barraquand and Benhamou 2008) and a partitioning method (Lavielle 2005) to divide each track into travelling or stationary periods (Figure 4.1). The residence time method estimates the amount of time spent by an animal within a circle of a given radius centred at each observed location. The Lavielle’s partitioning method, which identifies the point of change in residence time based on a penalised contrast, was then used to delineate successive locations of relatively high residency (i.e. a stationary period) from those of relatively low residency (i.e. a travelling period). I used the R package adehabitatLT (Calenge 2006, 2015b) to execute residence time calculation and track partitioning (see Appendix - Table A3 for the parameters used).

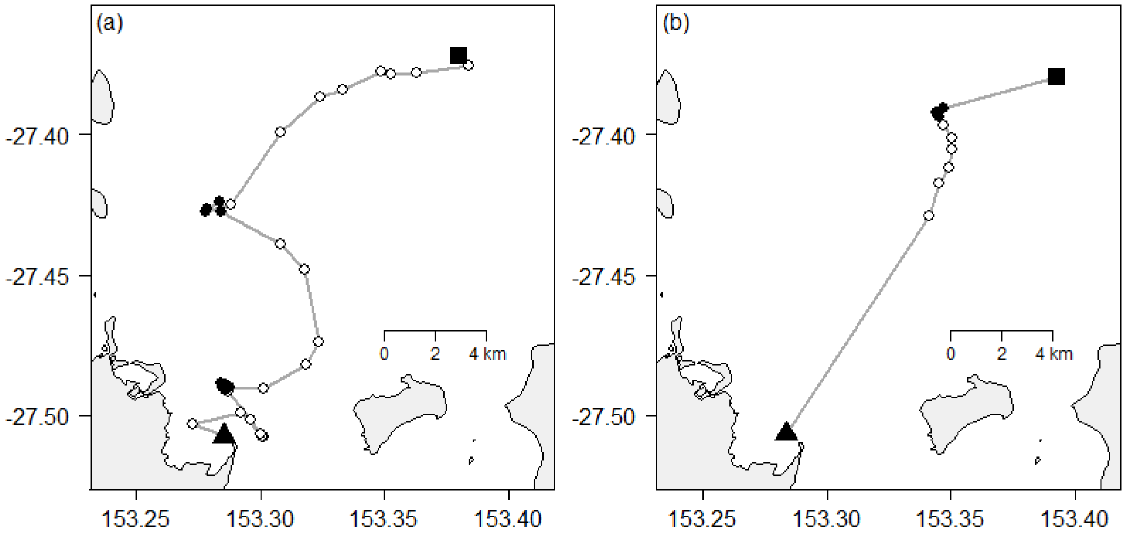

Figure 4.1 Homing tracks of (a) green turtle K92598 and (b) loggerhead turtle T53800 following displacement: triangle = release point, empty circle = travelling state, filled circle = stationary state, square = end point. Successive locations are connected by grey lines.

Distances moved during each travelling or stationary period were quantified in two different ways: beeline distance and track distance. For each period, beeline distance is the straight-line distance from the first and last locations, and track distance is the sum of distances between consecutive fix locations. Beeline distance represents how far each turtle relocated, and track distance represents minimum actual distance moved during each travelling and stationary period.

The absolute turning angle was estimated at each fix within travelling periods. For stationary periods, the absolute turning angle was estimated at each interpolated location which was the intersection of the moving directions from the last fix in each travelling period to the first fix in the following stationary period, and from the last fix in each stationary period to the first fix in the following travelling period (Figure 4.2a). The absolute turning angle ($\theta_{turn}°$) was calculated as;

$$\theta_{turn} = 180 - \theta_{inner}$$

where θ_{inner} is the absolute inner angle of three consecutive points (Figure 4.2a). Absolute inner angle was calculated using the R package trip (Sumner 2014).

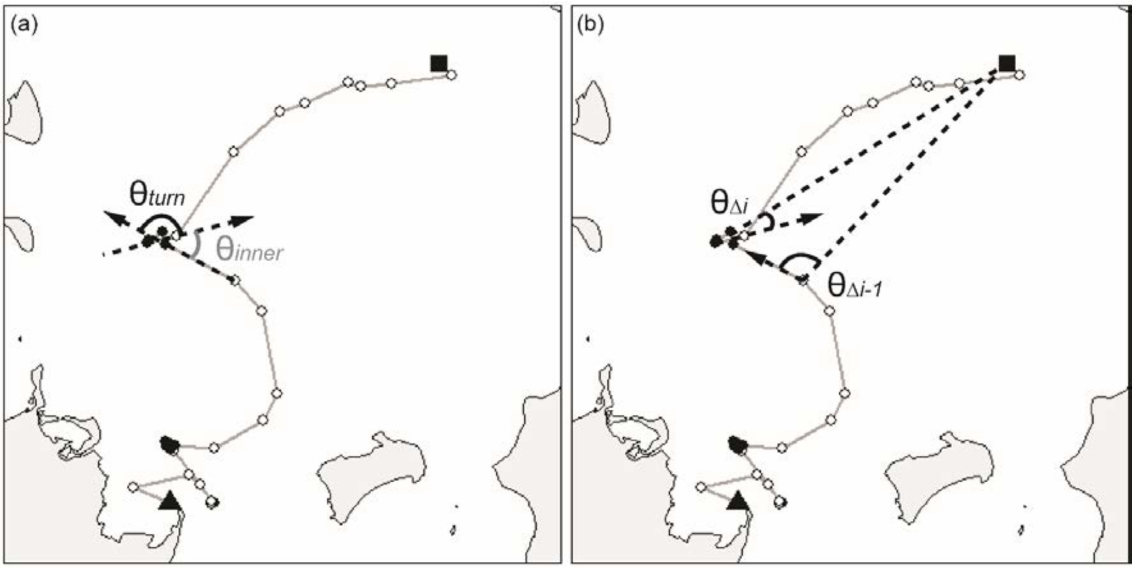

Figure 4.2 Schematic diagrams for (a) absolute turning angle θ_{turn} at a transition between stationary and travelling states and (b) deviation from end point following two examining points, $\theta_{\Delta_i}$and θ_{i+1}. Triangle = release point, empty circle = travelling state, filled circle = stationary state, square = end point. Successive locations are connected by grey lines. Dashed arrow = actual heading between two successive points, dashed line = direct path to the end point.

Diurnal patterns in turtle movement were examined using frequency distributions across a day. I segmented time of day according to the diurnal patterns and time of sunrise and sunset. Sunrise and sunset time at each location was estimated using the R package StreamMetabolism (Sefick 2015).

4.2.3 Directional correction

The movement appear to be characterised by a series of stationary and travelling periods, and turns following a stationary period appeared pronounced compared to turns within a travelling period (e.g. Figure 4.1). I therefore looked for evidence of directional correction at the transitions between stationary and travelling states by testing whether following a transition to the travelling state, there is an adjustment in direction which better orients the direction of travel toward the target.

For any movement between two fixes, the heading was estimated as bearing from one point to the next using the R package geosphere (Hijman 2014). I then estimated deviation from the end point as the absolute difference between the actual heading and the bearing to the end point (Figure 4.2b). Absolute deviation following *i*th point (θ_{Δ_i}°) was calculated as;

$$\theta_{\Delta_i} = |\theta_{end} - \theta_{i+1}|$$

where $\theta_{\Delta_i} \in (0, 180)$, θ_{end} is the bearing to the end point and θ_{i+1} is the bearing to a successive location. A correction following *i*th point (θ_{cor_i}°) was then defined as;

$$\theta_{cor_i} = \theta_{\Delta_{i-1}} - \theta_{\Delta_i}$$

where $\theta_{\Delta_{i-1}}$ and θ_{Δ_i} are the deviations following two examining points (Figure 4.2b). For travelling period, corrections were estimated following each fix. Corrections at transition between stationary and travelling periods were estimated as the difference in deviation following the last fix in travelling period and the last fix in the subsequent stationary period (Figure 4.2b). Positive correction values indicate that turtles corrected their direction towards the end point following *i*th point. Zero values indicate no correction; and negative values indicate turtles headed away from the end point.

4.2.4 Temporal patterns in directional corrections

Finally, I look at whether the timing of directional corrections can suggest what navigational cues the turtles might be using. I also considered stationary duration, distant to the end point and cloud cover as covariates to account for the potential effects on turtles' behaviour. Stationary duration was calculated as the time from the first and last locations during each stationary period. Weather data were from the Australian Bureau of Meteorology.

4.2.5 Statistical methods

To compare non-circular data between two groups, I used the two-sample t-test if data were normally distributed (either in their original form or when transformed), and Wilcoxon rank-sum test if data were not normally distributed. Mean values and standard deviation (± SD) were reported for normally distributed data; median and interquartile range (IQR) were reported otherwise. The binomial test was used to compare samples of binary data.

The Watson's two-sample U^2 test was used to test for differences between two circular distributions (Watson 1961). The p-value for the Watson's test was estimated by generating 9999 randomised samples (Pewsey et al. 2013). Analysis of circular data were conducted using the R package circular (Agostinelli and Lund 2013).

I modelled directional correction using analysis of covariance (ANCOVA) as functions of time of day and other ecologically meaningful covariates. Bathymetry was not included as a covariate in the model because water depths at the turtle locations were mostly shallower than 10 m (Chapter 3) and higher resolution of bathymetry models would be required to represent the complex benthic structure at my study sites. Collinearity was not detected among the covariates based on the variance inflation factors to be less than 3 (Zuur et al. 2010). Homogeneity of variance was assessed by plotting residuals versus fitted values. Normality was examined by Q-Q normal plot. Where appropriate, transformations were used to achieve homogeneity of variance and normality. Response variables were centred to have a mean of zero for the analysis (Becker et al. 1988). I used the R package MuMIn (Barton 2015) to rank all possible models by second-order Akaike Information Criterion (AICc). I selected models within 2 AICc units of best-ranked model to identify models with similar explanatory power (Burnham and Anderson 2002). Model results are presented with the estimated values (fit) and 95% confidence intervals (CI).

4.3 Results

4.3.1 General spatial patterns in tracks

Most initial headings were approximately directed to their end point of their return journey (Figure 4.3). Although the absolute deviation of initial headings from bearings to end points could be as much as 164° for green turtles and 180° for loggerhead turtles, most were much smaller: 81° ± 47 for greens (n = 22) and 69° ± 58 for loggerheads (n = 7). The differences between species were not significant ($t_{(2)\,27}$ = -0.54, p = 0.60).

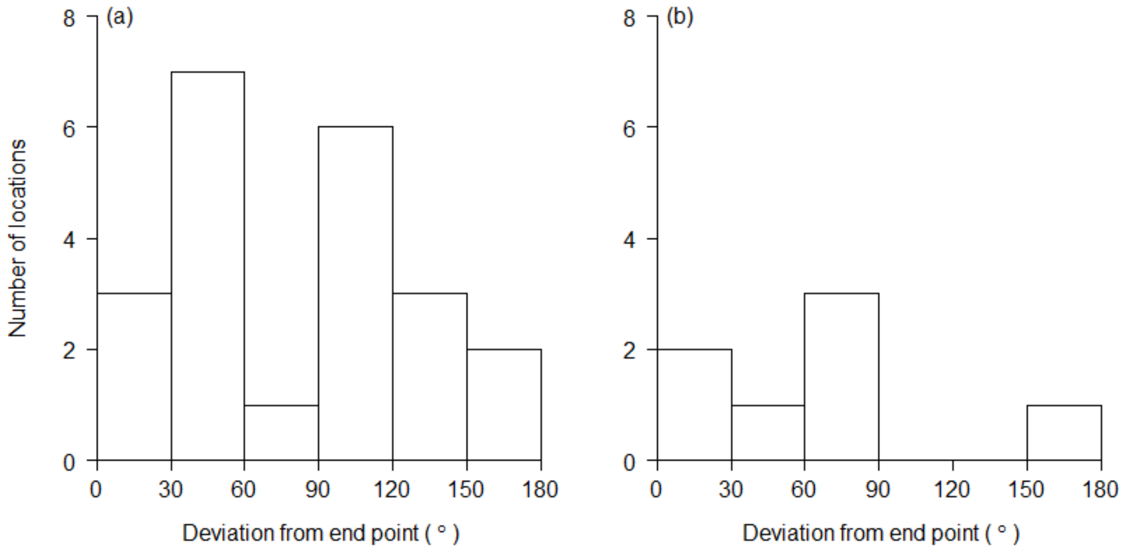

Figure 4.3 Absolute deviation between initial headings and bearings to end points for the displaced (a) green turtles and (b) loggerhead turtles. Initial heading is the bearing from the release location to the first satellite fix.

The most striking attribute of the tracks is the alternation of travelling and stationary periods (Figure 4.1). During travelling periods, turtles moved considerable distances relative to stationary periods (Table 4.1). In the travelling period, the median distance between successive fixes was 0.93 km for greens (*n* = 470) and 0.54 km for loggerheads (*n* = 202); in the stationary state it was 0.32 km for greens (*n* = 297) and 0.09 km for loggerheads (*n* = 105), not much greater than the margin of error for the fix (0.05 km ± 0.06; Chapter 2). It is important to note that the turtles were still in water during the stationary phase, and subject to passive movement by currents as well as any voluntary movement. Although the duration of a travelling period could be as long as 170.6 h for greens and 41.8 h for loggerheads, most travelling durations were much shorter: the median was 8.0 h for green turtles and 13.7 h for loggerhead turtles (Table 4.1). Similarly, although a stationary period could be as long as 158.8 h for green turtles and 50.3 h for loggerhead turtles, the median was 8.8 h for green turtles and 9.0 h for loggerhead turtles (Table 4.1).

Table 4.1 Duration and distance moved during each movement period. Data are presented in median with data range in brackets. Beeline distance is a straight-line distance from the first and last locations and distance moved is the sum of distance between consecutive locations during each period. Duration was calculated as the time from the first and last locations during each movement state. N is the number of each period observed.

Movement period	Beeline distance: km	Track distance: km	Duration: h	N
Chelonia mydas				
Travelling	5.7 (0.1 - 43.3)	8.7 (0.1 - 70.6)	8.0 (0.1 - 170.6)	46
Stationary	0.7 (<0.1 - 31.7)	1.7 (0.2 - 50.0)	8.8 (1.6 - 158.8)	37
Caretta Caretta				
Travelling	4.2 (0.1 - 19.5)	8.8 (1.0 - 23.2)	13.7 (1.3 - 41.8)	15
Stationary	0.5 (<0.1 - 1.8)	1.6 (0.1 - 12.5)	9.0 (2.7 - 50.3)	7

Within a single travelling period, there was a tendency for absolute turning angles between fixes to be small for green turtles (median = 39°, IQR = 15° to 81°, $n = 470$) and loggerheads (median = 31°, IQR = 16° to 72°, $n = 202$), and also to be predominantly to the left or predominantly to the right, producing a smoothly curved track (e.g. Figure 4.1). Probability of turning to the same direction as the previous turn (i.e. left or right) is significantly higher than 0.5 for green turtles ($p < 0.05$, $n = 434$); for loggerheads, the bias did not achieve significance ($p = 0.19$, $n = 189$). The existence of a left or right turning bias during a travelling period meant that a turtle progressively changed direction over time, so that even if it had started oriented toward the target, the degree of divergence was likely to increase.

Within a stationary period, not only was the distance between successive fixes much smaller than those in travelling periods, but the absolute turning angles were greater for green turtles with a median at 117° ($W = 7861$, $p < 0.05$) but not for loggerheads with a median at 28° ($W = 624$, $p = 0.33$), and less consistent for greens (IQR = 33° to 139°, $n = 25$) but not for loggerheads (IQR = 13° to 39°, $n = 8$). In general, for green turtles, major changes in the direction of the track occurred after a stationary period but there were large variations in turning angles (Figure 4.4). I therefore hypothesised that these changes in direction after a stationary period were when any directional corrections were occurring.

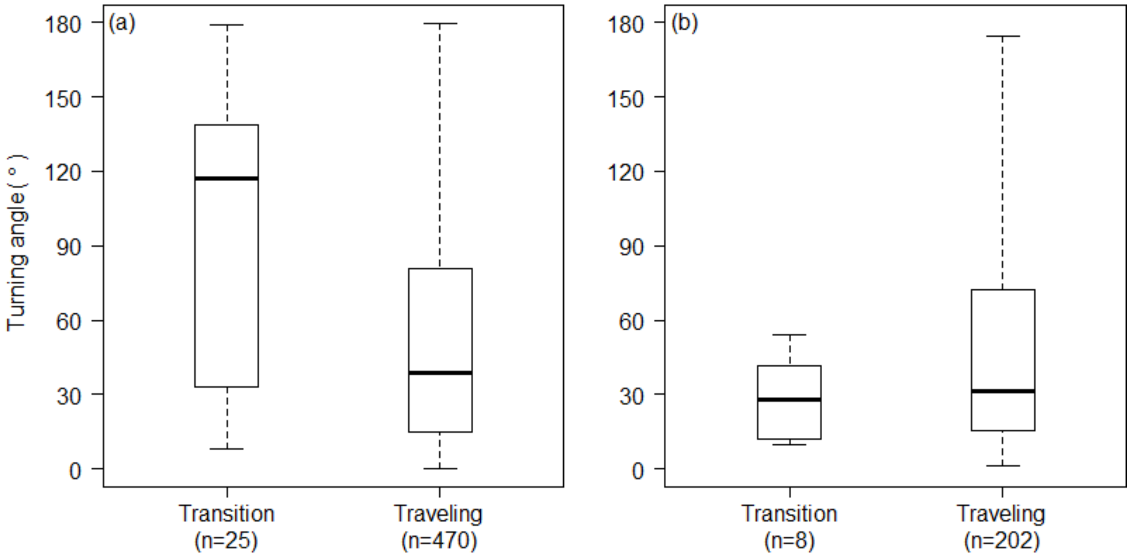

Figure 4.4 Absolute turning angles at the transitions between stationary and travelling periods (transition) and during travelling period (travelling): (a) green turtles and (b) loggerhead turtles. The whiskers extend to the most extreme data point.

4.3.2 Directional correction at the movement transitions

Directional corrections tended to occur at the transition between stationary and travelling states for both green and loggerhead turtles (Figure 4.5). At the transitions, corrections were 38° ± 56 ($n = 25$) for green turtles and 23° ± 15 ($n = 8$) for loggerhead turtles; mean corrections were significantly greater than zero for green turtles ($t_{(2)\,24} = 3.41$, $p < 0.05$) and loggerhead turtles ($t_{(2)\,7} = 4.33$, $p < 0.05$). Contrarily, during travelling period, corrections were -1° ± 50 ($n = 388$) for green turtles and 0° ± 48 ($n = 175$) for loggerhead turtles; mean corrections were not different from zero for green turtles ($t_{(2)\,387} = -0.30$, $p = 0.77$) nor loggerhead turtles ($t_{(2)\,174} = 0.02$, $p = 0.98$). However it was also clear that not all transitions resulted in a correction (Figure 4.5b). I therefore examined whether the existence of directional corrections was associated with time of day.

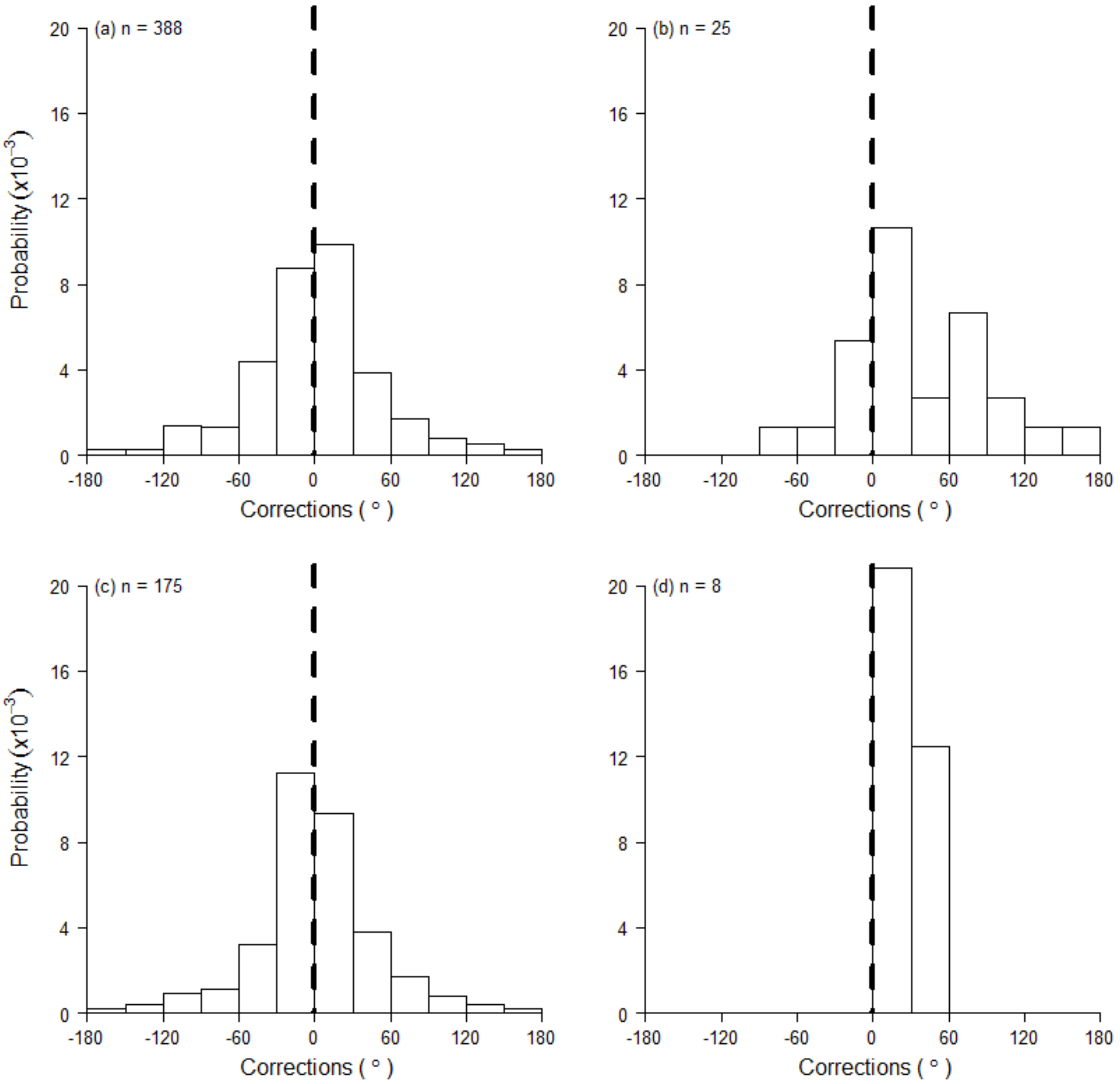

Figure 4.5 Probability distribution of corrections (a, c) during travelling periods, and (b, d) at the transition between stationary and travelling states. Dashed line = no correction. (a, b) green turtles, (c, d) loggerhead turtles.

4.3.3 General temporal patterns in tracks

There was evidence of diurnal patterns in travelling vs stationary phases. The travelling state appeared to occur more frequently during the day than at night for both green and loggerhead turtles (Figure 4.6ac); the distributions were not different between species ($U^2 = 0.113$, $p = 0.21$). Stationary state appeared to occur less frequently around early morning for green turtles or in the early afternoon for loggerhead turtles (Figure 4.6bd); but the differences between species were not significant ($U^2 = 0.394$, $p = 0.08$).

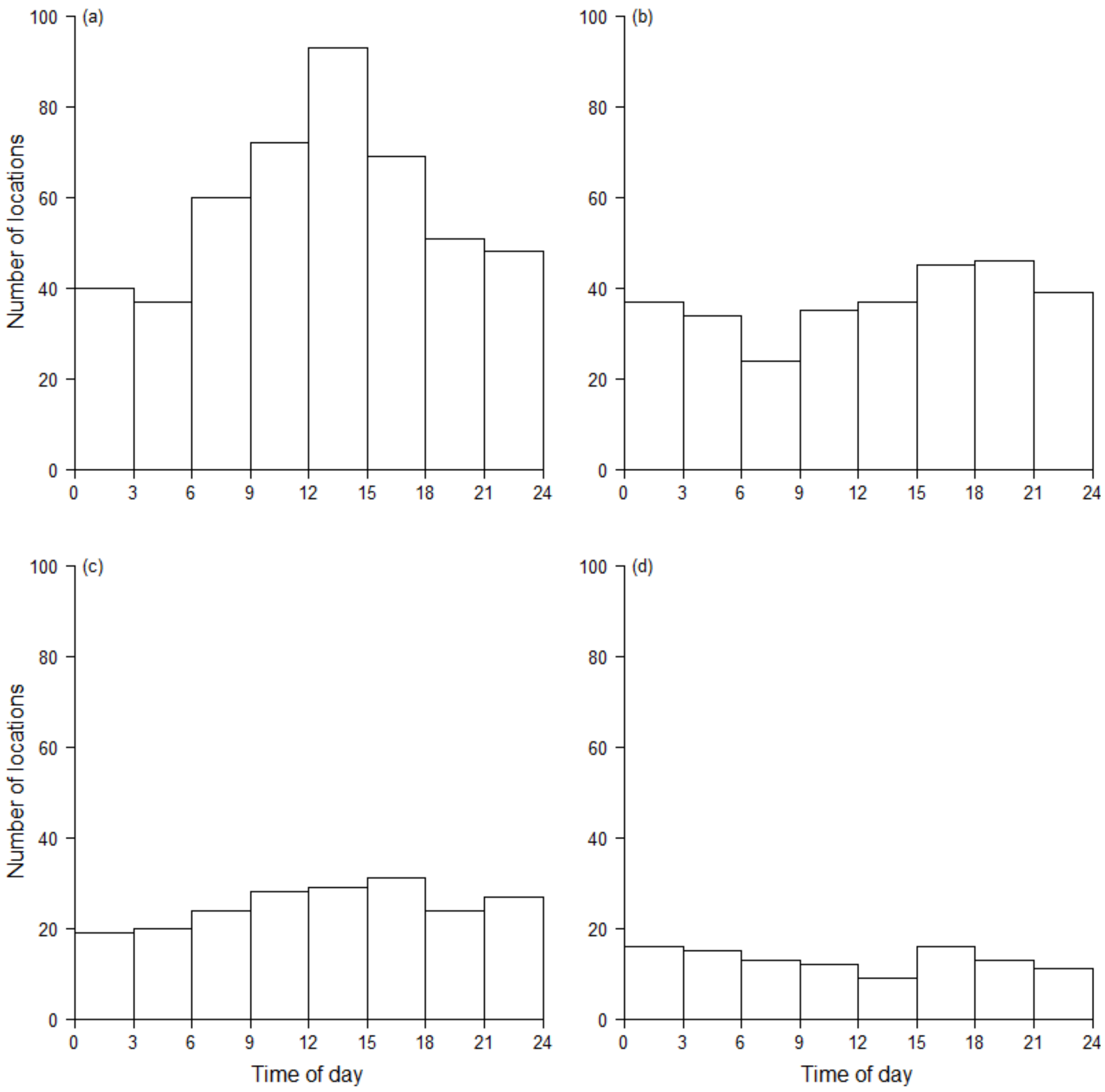

Figure 4.6 Frequency distributions of locations identified as (a, c) travelling state or (b, d) stationary state across a day. (a, b) green turtles, (c, d) loggerhead turtles.

There was also evidence of a diurnal pattern in the transitions between movement states. In particular, for green turtles, transition from a stationary state to a travelling state (the last locations during stationary periods) had a substantial peak in the early morning (Figure 4.7a). In contrast, transition from travelling state to stationary state (the first locations during stationary period) had bimodal distribution with peaks in the late afternoon and late evening (Figure 4.7b). Sample size for loggerhead turtles were too small to detect diurnal patterns (Figure 4.7cd); however the differences between two species in diurnal distributions were not significant for transitions from stationary to travelling state ($U^2 = 0.527, p = 0.07$) nor transitions from travelling to stationary state ($U^2 = 0.582, p = 0.06$).

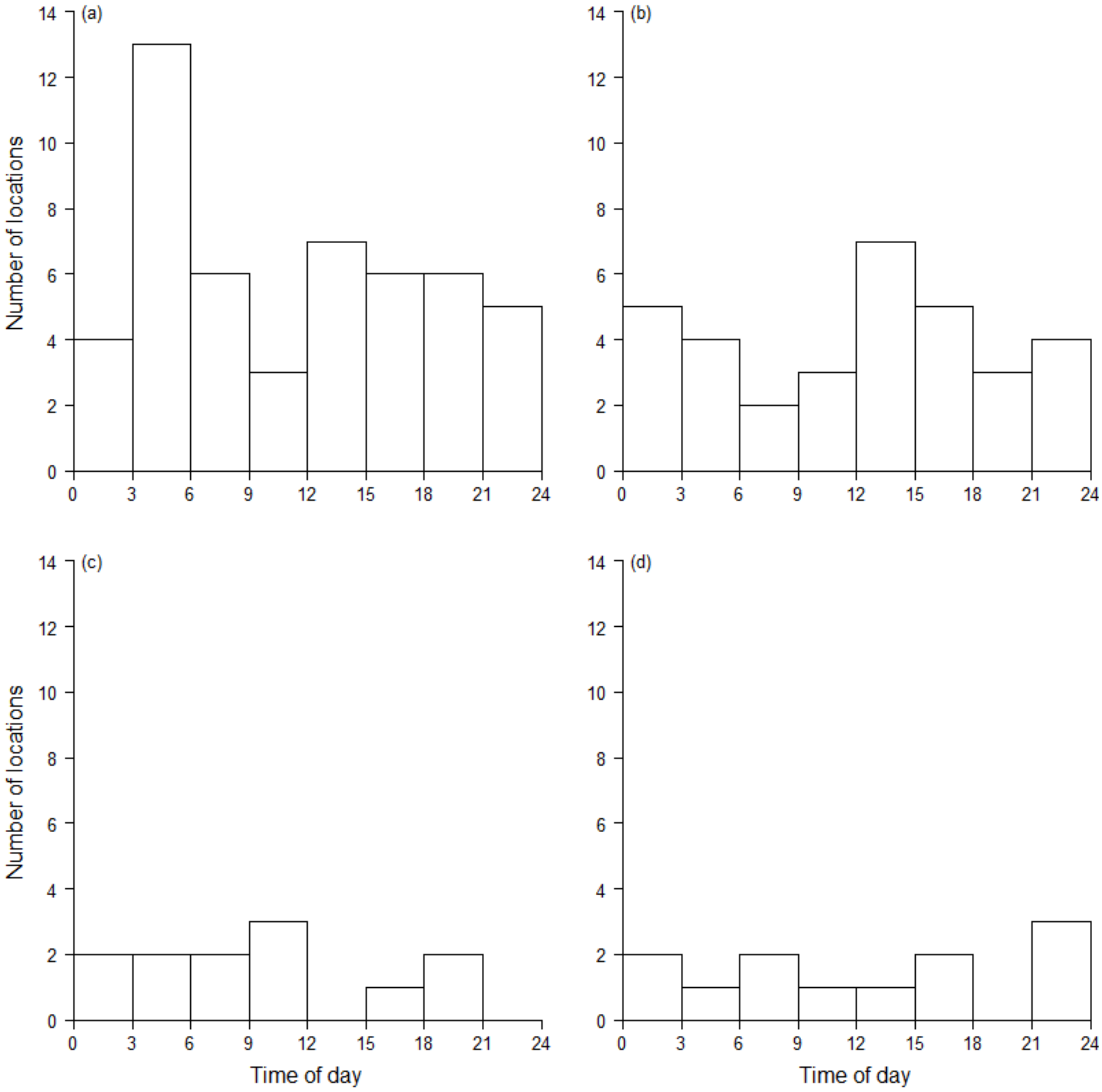

Figure 4.7 Frequency distributions of (a, c) the last and (b, d) the first locations during stationary period through a day. The former represents turtles' transition timing from travelling state to stationary state, and the latter represents the transition timing from stationary state to travelling state. (a, b) green turtles, (c, d) loggerhead turtles.

To assess the effect of time of day on directional correction, I segmented time of day into three categories following the distribution of transition timing from stationary to travelling states (Figure 4.7a): early morning as time of sunrise ± 2 hours, daytime as the time after early morning and at sunset, and night-time as the time after sunset and before early morning.

4.3.4 Temporal patterns in directional corrections at the movement transitions

I examined factors affecting directional corrections made by green turtles. The global model is:

Directional corrections ~ time of day + stationary duration + distance to the end point

The model selection process resulted in only one model being selected as a best-ranked model. This model had time of day as a solo predictor. In particular, only transitions occurring in the early morning were strongly associated with directional correction (fit = 60°, CI = 33 - 88°, *n* = 14): the mean correction was not significantly different from zero when transitions occurred later in the day or at night (Figure 4.8a). Neither stationary duration nor distance to the end point had any perceptible influence on directional correction of green turtles. The effect of weather was tested in a separate model using 63% of data for which weather data was acquired. This model added cloud cover to the existing model as a covariate but the results of the model selection stayed the same.

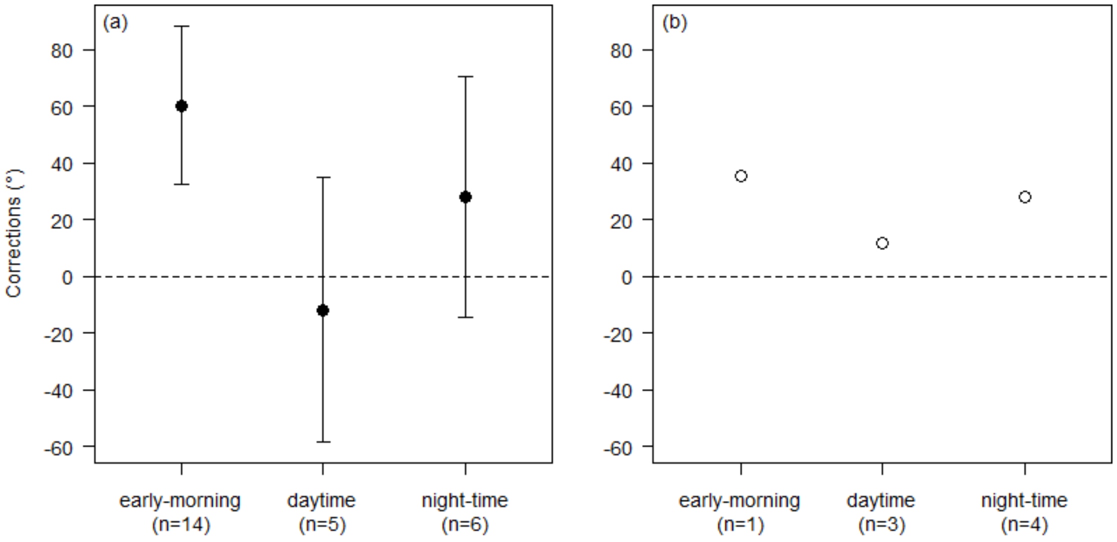

Figure 4.8 Estimated corrections made by (a) green and (b) loggerhead turtles at the transitions between stationary and travelling periods during different time of day; early morning (sunrise ± 2hrs), daytime (after early morning, before sunset) and night-time (after sunset, before early morning). Filled circle = model fit, empty circle = mean, error bars = 95% confidence interval, *n* =number of locations, dashed line = no correction.

The ANCOVA analysis was not conducted for data of loggerhead turtles due to the insufficient sample size (Figure 4.8b). However, temporal patterns in directional corrections at the transitions between stationary and travelling period are similar to those of green turtles across a day: the correction occurring in the early morning were high relative to the mean corrections occurring during daytime and night-time (Figure 4.8).

4.4 Discussion

I demonstrate that fine-scale navigation in sea turtles is often characterised by a series of stationary periods where turtles appear to reassess their heading direction. The turtles I examined also appeared to obtain critical cues for directing short distance movement in the hours around sunrise, with significant corrections only observed to occur at this time of day. Despite these significant corrections made around time of sunrise, the subsequent travel direction would often curve away from the most direct path to the end point. The turtles then may have needed to wait for the next sunrise to calibrate their “internal compass”, and thus keep their navigation ‘on track’.

The influence of sunrise on a turtle’s ability to navigate may simply be an obvious eastwards marker. Alternatively, sea turtles may use polarised light cues when the sun is near the horizon as seen in birds (Muheim et al. 2006), to recalibrate their internal compass at sunrise. Sound is another possible cue given vocalising activities observed with marine and freshwater turtles (Giles et al. 2009, Ferrara et al. 2014). Sea turtles may recognize distinctive noise from their habitat (e.g. fish, shrimp, water break, etc), in particular low frequency sounds that are in the range that turtles can hear and travel well in water. The noise may be more audible in the early morning when the sea is typically flatter and calmer. Celestial-related cues present later in the day and at night may carry less information for sea turtles across short distances because turtles were not observed to make significant corrections at these times.

Green turtles appeared to deviate from direct path to the end point during travelling period relative to loggerhead turtles. The difference in deviation is potentially due to the effects of cross-flowing current (Hays et al. 2014a). Given that two species were released on different time and site (except site 1), green turtles may have experienced stronger cross-flowing current than loggerhead turtles which resulted in greater deviation during each travelling period. It is also possible that slower loggerhead turtles (Chapter 3) may correct their direction as they swim and therefore may need smaller corrections at each transition. Concurrent tracking of both species together with fine-scale current data may allow these alternative mechanisms to be tested.

Turns at movement transitions were related to route corrections by both species but more pronounced turns were made by green turtles than loggerhead turtles. This difference corresponds to the inter-specific differences in divergence of tracks during travelling period; green turtles tended to make successive turns in the same direction as the previous turn while loggerhead turtles did not. The pronounced turns at transition by green turtles were probably to compensate divergence during travelling periods but loggerhead turtles were less in need of pronounced turns. The differences in turning angles between species may also due to the small sample size in loggerhead turtles, particularly in the early morning during which significant corrections occurred in green turtles. Most turnings at the transition observed in green turtles occurred in the early morning (14 out of 25 turns) and therefore resulted in more pronounced turns overall. In contrast, for loggerhead turtles, only one turn was observed at the transition during early morning and thus turning angles at the transition may not be as great as green turtles as a whole.

This study demonstrates that sea turtles tend to halt and reassess before making course corrections, with corrections predominantly occurring at sunrise. My findings indicate that further investigation into the importance of stationary periods and sunrise during fine-scale travel may be a valuable area of future research to further our understanding of the sophisticated navigational abilities of sea turtles.

4.5 Chapter Summary

- Sea turtles have an exceptional ability to navigate accurately between known habitats as well as from unknown areas back to familiar habitat.
- Current evidence suggests their ability to migrate long-distances depends upon geomagnetic cues, but they appear to rely on other undetermined cues during the finer-scale navigation required when they are close to their destination. At this stage turtles have been observed to make major corrections in their travelling direction.
- It has been suggested that they may use visual cues as a compass during daylight hours, but detailed analysis of their small-scale movements when travelling at-sea close to their destination are lacking.
- I examined the turning and orientation behaviour of 29 displaced sea turtles of two species, tracked *en route* back to their foraging habitats in eastern Australia.
- I found that sea turtles tended to alternate stationary and travelling phases during their trip home. Orientation corrections predominantly occurred immediately after a stationary phase and after sunrise.
- This is the first study to demonstrate time-restricted orientation by sea turtles and provided a new insight into their sophisticated navigational abilities.

Chapter 5

Home range and site fidelity of sea turtles in coastal foraging habitat: incorporating temporal effects for a robust conservation planning

Chapter 3 identified sea turtles return to their home habitat after being displaced. Those results indicate that each turtle derives a fitness benefit by remaining faithful to its ‘home’ foraging area. The remaining questions are (1) What is the extent of foraging habitats they stay in? (2) How long do they remain in the habitat? and (3) What factors affect their faithfulness to foraging habitat. In this chapter, I objectively quantify home range size and degree of site fidelity, and then examined the potential effects of environmental and biological factors on home range size and site fidelity. The knowledge gained in this chapter will improve credibility of home range analysis. Improved home range estimates will then provide more reliable information for marine conservation planning.

Manuscript in review:

Shimada T, Jones R, Limpus C, Groom R, Hamann M (in review) Home range and site fidelity of green and loggerhead turtles in Queensland, Australia: Incorporating temporal effects for a robust conservation planning. *Marine Ecology Progress Series*.

5.1 Introduction

Conservation goals for species and their habitats can be achieved through spatial management such as activity exclusion/restriction zones and marine protected areas (Hooker and Gerber 2004, Pressey et al. 2007, Gaines et al. 2010, McCay and Jones 2011). These types of protection have been applied at both large ecological scales (e.g. the Great Barrier Reef - Fernandes et al. 2005) and at smaller scales to manage threats to particular habitat zones (e.g. Macquarie Island - Environment Australia 2001) or species of conservation concern (e.g. dugong and sea turtles - McCook et al. 2010). It has become increasingly clear that the scale of the management intervention such as a protected area and the spatial scale of species habitat use requiring conservation initiatives should match for effective species protection (Dryden et al. 2008, Whittock et al. 2014, Cleguer et al. 2015), because designation of protected areas without consideration of the animals' space use may not achieve conservation goals of the protected areas (e.g. Rojas-Bracho et al. 2006, Schofield et al. 2013b).

Home range analysis is a powerful tool to identify priority areas for conservation, or 'hotspots' (e.g. Maxwell et al. 2011, Peckham et al. 2011). Burt (1943) defined home range as the area where an animal normally travels in search of food during a given period of its life. That is, home range is not exclusively the entire area used during the life of the animal but more broadly refers to the areas used during particular time of its life: I adopted his concept of home range in this study.

Reliable estimation of home ranges requires accurate location data, appropriate analytical methods and monitoring animals for prolonged periods. Since the establishment of the home range concept (Burt 1943), there has been tremendous advancement in the tools used to collect accurate location data (Ropert-Coudert and Wilson 2005, Rutz and Hays 2009) and to objectively quantify home range of animals (Benhamou 2011, Cumming and Cornélis 2012). Despite these advances, estimating home range is still challenging for many species. Highly mobile species may use different habitats at different times of day, year or during different life stages, so temporally-biased location data may only partially represent their habitat use. Clearly understanding temporal variation in animals' movement is essential for defining reliable home ranges (Fieberg and Börger 2012, Powell and Mitchell 2012).

Green turtles (*Chelonia mydas*) and loggerhead turtles (*Caretta caretta*) are highly mobile and conservation dependent species (IUCN 2014), making them priority targets for research and protection. Important knowledge gaps exist for their movements across space and time in foraging habitat, where they spend most of their lives (Musick and Limpus 1997, Bolten 2003, Godley et al. 2008). Some turtles undertake seasonal movements of over tens to thousands of kilometres between distant foraging habitats, but such long-distance foraging movements are typically seen in temperate waters (Morreale and Standora 2005, Mansfield et al. 2009, González Carman et al. 2012, Narazaki et al. 2015). Past research has found that seasonal migrations are not common in subtropical and tropical coastal habitats, where turtles generally show fidelity to small geographic areas (Musick and Limpus 1997, Hart and Fujisaki 2010). Yet the site fidelity observed in those studies does not preclude potential finer-scale seasonal movements by turtles in warmer subtropical and tropical waters because detection of such movements was generally beyond the technical limitation of the previous tracking methods (i.e. mark-recapture, radio/sonic telemetry, Argos satellite telemetry). In particular it is clear that some turtles in tropical and subtropical habitats display long-term site fidelity across decades within localised foraging areas but it is unclear how the temporal and spatial scale of site fidelity behaviour might change across phases of a turtle life history. Addressing this knowledge gap requires long-term, high-resolution tracking data. The newer Fastloc GPS (FGPS) tags, introduced in 2002 (Wildtrack Telemetry System Limited, Leed, UK), are capable of obtaining high-quality location data from marine animals with full-time global coverage (Hazel 2009, Dujon et al. 2014, Chapter 2) spanning seasons out to a few years (e.g. Chapter 3)

The primary objective of this study was to investigate the temporal variation in the home range of green turtles and loggerhead turtles that forage along shallow coastal waters in Queensland, Australia. Both species are listed as threatened under Australian legislation (Environment Protection and Biodiversity Conservation Act 1999) due to past and current anthropogenic threats, and require comprehensive conservation efforts. I examined the temporal variation in home range size and site fidelity at longer (>1 year) and shorter (<1 year) scales for both species in order to find for evidence for long-term site fidelity and also to investigate possible seasonal effects on habitat use.

Additionally, I wanted to explore the effects of extreme weather events on home range size and site fidelity. During late 2010 to early 2011, the strongest La Niña events in 40 years occurred in the South Pacific Ocean, and resulted in heavy rainfall and tropical cyclones Tasha, Anthony and Yasi hitting the north-eastern Australian coast. These events caused major flooding (Bureau of Meteorology 2012) and significant destruction of seagrass meadows (Devlin et al. 2012, McKenzie et al. 2012). In the months following the series of extreme weather events, sea turtle strandings along the Queensland coast were around five times greater than annual totals collected since 2000 (Meager and Limpus 2012). I hypothesised that sea turtles would respond to the weather events by extending their home ranges in search of food, and would consequently show lowered site fidelity compared to times without extreme weather events. I tested this hypothesis by comparing the estimated home range size and site fidelity between months with and without influence of the extreme weather events.

5.2 Materials and Methods

5.2.1 Field work

Data were collected from 52 green turtles and 20 loggerhead turtles in various tropical and subtropical sites along north-eastern Australia (Figure 5.1, Table 5.1). Turtles were captured at their foraging habitats using a rodeo method (Limpus 1978) during research trips (*n* = 66), except for six loggerhead turtles, which were captured at Mon Repos beach following their successful nesting activities (Figure 5.1). Study turtles were female and male adults as identified by gonad examination using laparoscopy, curved carapace length (CCL), or combination of CCL and the tail length from carapace (Limpus and Reed 1985, Limpus and Limpus 2003a). The body size (CCL) ranged from 85.6 to 121.2 cm (median = 105.7 cm) for green turtles and 85.5 to 100.7 cm (median = 94.9 cm) for loggerhead turtles (Table 5.1).

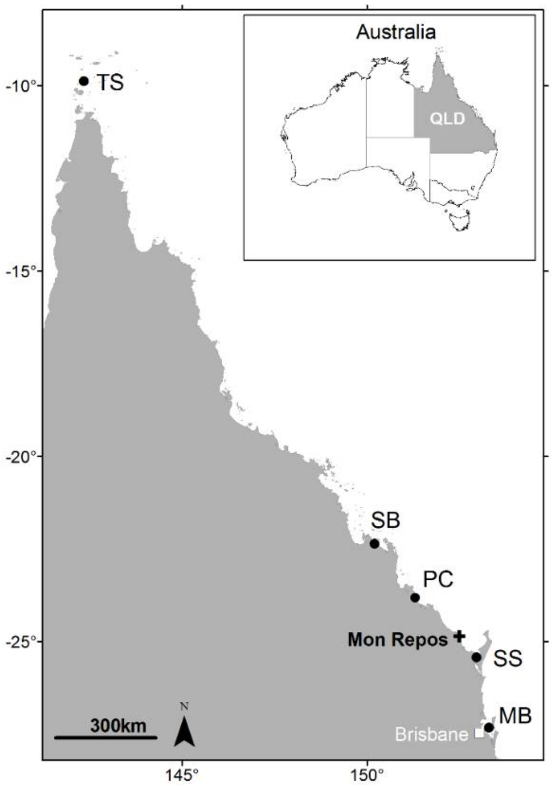

Figure 5.1 Study locations in Queensland, Australia. MB = Moreton Bay, SS = Sandy Strait, PC = Port Curtis, SB = Shoalwater Bay, TS = Torres Strait.

Table 5.1 Summary of satellite telemetry on green turtles (*Cm*) and loggerhead turtles (*Cc*) in north-eastern Australia. F = female, M = male. N is number of tracked turtles. Data are presented in median with minimum and maximum values in parentheses.

Site	Sex	N	CCL: cm	Tracking days	N. fixes	95% UD: km^2
Cm						
MB	F	16	110.5 (101.6 to 119.9)	156 (22 to 350)	977 (112 to 2131)	42.5 (5.6 to 80.4)
	M	2	95.1 (94.0 to 96.1)	119 (107 to 132)	1294 (849 to 1740)	82.5 (70.3 to 94.8)
SS	F	6	108.3 (106.1 to 121.2)	301 (179 to 564)	1466 (712 to 2678)	61.8 (7.7 to 126.5)
	M	0	-	-	-	-
PC	F	10	105.7 (89.0 to 116.6)	98 (55 to 241)	324 (130 to 723)	24.9 (3.6 to 121.7)
	M	8	96.0 (85.6 to 104.3)	165 (66 to 240)	647 (417 to 1378)	17.9 (9.5 to 61.8)
SB	F	6	98.9 (95.5 to 104.5)	334 (140 to 778)	1049 (225 to 14295)	7.2 (2.8 to 25.1)
	M	0	-	-	-	-
TS	F	4	103.8 (98.0 to 118.0)	114 (45 to 202)	604 (239 to 854)	46.7 (5.1 to 166.3)
	M	0	-	-	-	-
Cc						
MB	F	11	95.2 (85.5 to 100.1)	230 (56 to 999)	802 (362 to 1751)	23.9 (10.3 to 47.2)
	M	9	94.4 (87.9 to 100.7)	196 (59 to 906)	747 (246 to 1004)	24.0 (15.0 to 350.6)

All but three of the loggerhead turtles were tracked once with highly accurate Argos-linked FGPS tags between 2008 and 2014. Three were tracked twice: a male loggerhead turtle (T53800) that was first tracked in 1998-1999 with a platform terminal transmitter (PTT) and a second time in 2010-2012 with a FGPS tag; a female loggerhead turtle (T14914) that was first tracked in 1996-1997 with a PTT and a second time in 2011-2012 with a FGPS tag; and a female loggerhead turtle (T93038) that was first tracked in 2010 and second time in 2012 with FGPS tags on both occasions. Each turtle was tracked after release until transmission ceased.

5.2.2 Data acquisition & preparation

Argos-linked FGPS devices provided Argos fixes in addition to FGPS fixes, and PTT provided Argos fixes only. For tracks obtained with Argos-linked FGPS device (*n* = 72) I merged FGPS fixes with high-quality Argos fixes (Location Classes 3, 2, 1), and for tracks obtained with PTT (*n* = 3) I used only high-quality Argos fixes.

Prior to analysis, satellite telemetry data were thoroughly screened by water depth, spatial and temporal duplicates, and a data driven filter as described in Chapter 2 and Chapter 3 using the R package SDLfilter (Shimada 2015). The data driven filter improves accuracy of satellite-derived data by removing fixes with high error; estimated mean error for filtered FGPS fixes is less than 50 m (Chapter 2).

The turtles captured in their foraging habitats were relocated at locations between 0.2 to 28.1 km away from the capture point and subsequently tracked back to the area of capture (Chapter 3). The nesting loggerhead turtles were released on the same beach where they were captured and tracked to their foraging habitats. I excluded fixes acquired prior to turtles' arrival at their foraging habitats (see Chapter 3). My tracking data did not include any nesting activities adjacent to the described foraging habitats (i.e. no consecutive FGPS fixes were acquired on a beach during nesting season), confirming that the tracks used in the subsequent analyses represent only their foraging behaviour.

5.2.3 Definition of home range and site fidelity

For each turtle I estimated utilisation distributions (UDs) in three ways. Overall UD was estimated using the entire sequence of fixes available; yearly UDs were estimated using subset of fixes grouped by a duration of 12 months since the initial fix; and monthly UDs were estimated using subset of fixes grouped by each calendar month.

Home range was defined as the areas containing 95% of a UD. That is, for each turtle, I estimated home range at three different time scale; overall home range using overall UD, yearly home range using yearly UDs, and monthly home range using monthly UDs. I used overall home range only to provide numerical estimates of area size used by each turtle during the entire tracking period. Yearly home range was only used to visually inspect space use of turtles by a block of 12 months. Monthly home range was used to estimate home range size of each turtle in each calendar month, and also to examine temporal effects on home range size.

As an index for site fidelity, I calculated mean integrated squared error (MISE) between pairs of monthly UDs for each turtle. MISE measures the difference between two UDs as:

$$\text{MISE} = \frac{1}{n} \sum_{i=1}^{n} \left[f_1(x_i, y_i) - f_2(x_i, y_i) \right]^2 \tag{5.1}$$

where n is the number of grid points, x and y are the longitude and latitude at each grid point, f_1 (x_i, y_i) and f_2 (x_i, y_i) are the estimated density at the ith grid point of two UDs estimated from different months. A smaller MISE indicates more similarity between UDs.

I estimated UDs using movement-based kernel density estimators based on a biased random bridge (Benhamou 2011). Only fixes acquired with FGPS tags were used to estimate UDs. High tide lines were treated as a boundary for UD estimation because foraging sea turtles rarely ascend beaches above high tide lines within my study sites. As expressed in equation 5.1, MISE values are dependent on area size and number of grid points. Therefore size of the areas analysed and grid resolution must be kept consistent throughout any UD estimation so that MISE values are comparable. I estimated each UD with a grid resolution of 50 m over a fixed area of 13,000 km^2, which was large enough to enclose fixes of every turtle at each study site. The R package adehabitatHR (Calenge 2006, 2015a) was used to estimate the UDs and to obtain home range size for each turtle (see Appendix - Table A2 for the parameters used). UDs estimated from less than 30 fixes were excluded in the subsequent analyses to avoid bias in kernel-based estimates resulting from small sample sizes (e.g. Seaman et al. 1999, Blundell et al. 2001).

5.2.4 Variables potentially affecting home range size and site fidelity

I examined effects of seasons and the extreme weather events on monthly home range size and site fidelity indices. I also included location and sex as covariates to account for their potential effects. Since water temperature is dependent mainly on season, I used sea surface temperature (SST) as a surrogate variable for seasons. Daily SST was extracted from the NOAA High Resolution SST (0.25 degree resolution) database provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their website (http://www.esrl.noaa.gov/psd/). To test the effects of SST on monthly home range size, I obtained monthly SST by averaging daily SST values.

To test the effects of the extreme weather events on monthly home range size, I associated each monthly home range to the timing of the extreme weather events. The months when the extreme weather events occurred (October 2010 to January 2011) and the following 12 months were regarded as “affected months” (Figure 5.2). I considered this time frame to be the period during which turtles may have been affected by degradation of food sources, because seagrass meadows were observed to start recovering within 12 months following the extreme weather events (Rasheed et al. 2014), and similar rates of recovery were also observed in many species of seagrass under experimental environment (Rasheed 2004). The months before and after the “affected months” (before October 2010 and after January 2012) were regarded as “normal months” (Figure 5.2).

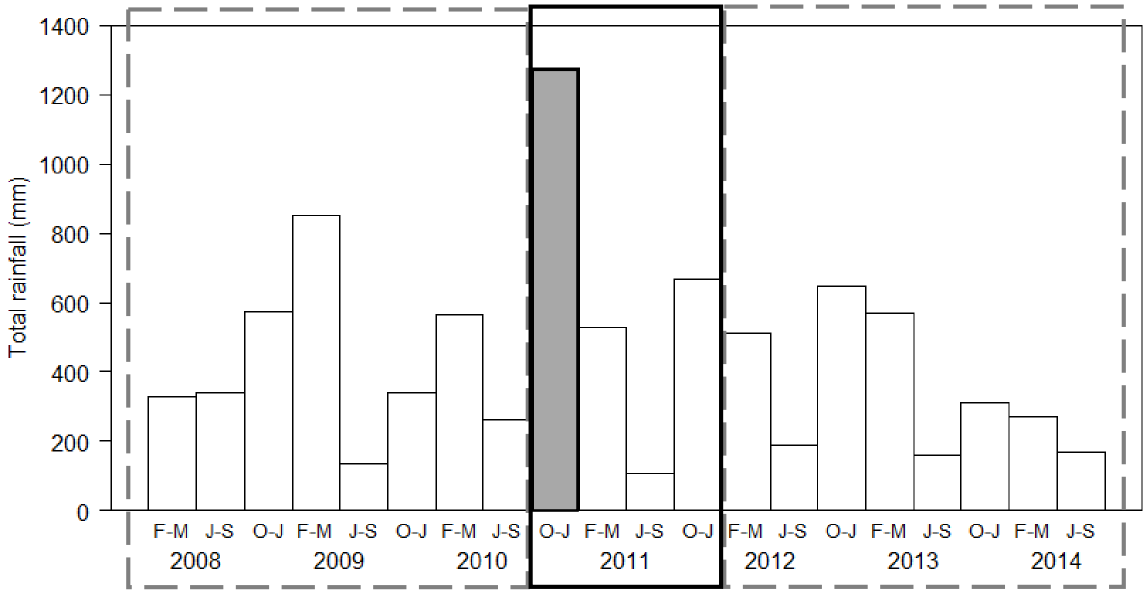

Figure 5.2 Schematic diagram of time frame in relation to the series of extreme weather events occurred in Moreton Bay (shaded in grey). Solid line encloses the "affected months" when the extreme weather events occurred and the following 12 months. Dotted lines enclose the "normal months" before and after the "affected months".

To test the effect of SST on site fidelity, I calculated absolute differences in monthly SST (ΔSST) between any pairs of months for which MISE values were estimated. To test the effect of weather on site fidelity, the MISE values were again grouped into two categories. The first group comprised MISE values between two "normal months". The second group contained MISE values measured either between a "normal month" and an "affected month" or between two "affected months" (Figure 5.2). The first group represents the range of shifts in habitat by turtles which occurred during the "normal months", and the second group represent the degrees of shifts in habitat during the "affected months" or between "normal months" and "affected months".

However the dataset was unbalanced in terms of weather, species, sex and locations. Only female green turtles in Moreton Bay, male green turtles in Port Curtis, and loggerhead turtles of both sex in Moreton Bay were tracked during the "affected months". Female green turtles were tracked at five locations but male green turtles were tracked only at Moreton Bay and Port Curtis. Both female and male loggerhead turtles were tracked only in Moreton Bay (Table 5.1).

I therefore used five different data subsets to investigate different questions about monthly home range size and site fidelity. The effects of weather were examined for female green turtles in Moreton Bay (Subset 1) and male green turtles in Port Curtis (Subset 2). The effect of locations was only examined for female green turtles, which were tracked in five different locations (Subset 3). I also examined the effects of sex for green turtles tracked in Moreton Bay and Port Curtis (Subset 4). Finally the last data subset only used loggerhead turtles in Moreton Bay to examine the effects of sex and weather (Subset 5). The effect of SST was tested in all data subsets.

5.2.5 Statistical methods

I used generalised additive mixed models (GAMMs) to model monthly home range sizes and site fidelity indices (i.e. MISE) as functions of the environmental and biological variables. Together with the variables specified in each data subset, either monthly SST or ΔSST were included in all models as explanatory variables. When data included turtles from multiple locations, I tested interaction effects of location and monthly SST or ΔSST. Since multiple home ranges were estimated for each turtle (i.e. monthly home ranges), I treated each turtle as a random effect to allow for within-turtle correlations. I verified that there was no issue with collinearity among covariates: variance inflation factors were all less than 3 (Zuur et al. 2010). Wald tests were performed to examine the effect of each explanatory variable tested in the GAMMs. I used the R package mgcv to fit GAMMs and to perform the Wald tests (Wood 2015). All analyses were executed using R software (R Core Team 2015).

5.3 Results

5.3.1 General properties of tracking data, home range and site fidelity

Tracking durations with Argos-linked FGPS tags ranged from 22 to 778 days (median = 158 days) for 52 green turtles and 56 to 999 days (median = 221 days) for 20 loggerhead turtles (Table 5.1). The estimated overall home range size of green turtles was highly variable, ranging from 2.8 to 166.3 km^2 (median = 31.3 km^2). The variation in overall home range size was also large in loggerhead turtles, ranging from 10.3 to 350.6 km^2 (median = 24.0 km^2) (Table 5.1).

Tracking duration in months, measured between the first and last months for which monthly home range was estimated, ranged from 1 to 26 months (median = 5 months) for green turtles and 2 to 34 months (median = 8 months) for loggerhead turtles. Note monthly home range was not always estimated for each month during each tracking period due to lack of location fixes (i.e. $n < 30$) in some months. Consequently monthly home range was estimated for up to 26 different months (median = 5 months) for each green turtle and up to 10 different months (median = 5 months) for each loggerhead turtle. Monthly home range size ranged from 0.7 to 174.3 km^2 (median = 12.3 km^2) for green turtles, and from 1.2 to 424.7 km^2 (median = 15.1 km^2) for loggerhead turtles (Table 5.2). Variation in monthly home range size within each individual ranged from <0.1 to 152.7 km^2 (median = 5.1 km^2) for green turtles and from <0.1 to 400.2 km^2 (median = 9.0 km^2) for loggerhead turtles.

Table 5.2 Monthly statistics on green turtles (*Cm*) and loggerhead turtles (*Cc*) tracked in north-eastern Australia. See Figure 5.1 for study locations. F = female, M = male. Data are presented in median with minimum and maximum values in parentheses.

Location	Sex	N. fixes per month	95% UD: km^2 per month	SST: °C per month	ΔSST: °C between months
Cm					
MB	F	140 (32 to 471)	21.3 (1.8 to 97.7)	23.6 (19.2 to 27.1)	2.5 (0.2 to 6.9)
	M	283 (43 to 462)	38.1 (5.4 to 98.8)	21.1 (19.7 to 22.6)	1.4 (0.6 to 2.9)
SS	F	146 (32 to 333)	20.0 (0.7 to 127.2)	22.4 (18.2 to 27.3)	3.3 (0.0 to 9.2)
	M	-	-	-	-
PC	F	84 (30 to 294)	10.3 (1.9 to 131.0)	23.4 (19.6 to 27.0)	1.3 (0.0 to 3.8)
	M	114 (33 to 412)	12.8 (3.5 to 50.3)	22.3 (19.6 to 27.6)	2.1 (0.1 to 7.2)
SB	F	250 (33 to 700)	4.8 (1.0 to 27.6)	23.1 (19.9 to 28.0)	2.9 (0.0 to 8.2)
	M	-	-	-	-
TS	F	148 (31 to 289)	5.5 (0.8 to 174.3)	28.2 (25.6 to 30.4)	1.3 (0.1 to 4.5)
	M	-	-	-	-
Cc					
MB	F	148 (30 to 490)	12.1 (1.7 to 45.8)	24.5 (19.2 to 27.3)	2.1 (0.1 to 6.8)
	M	119 (31 to 428)	21.6 (1.2 to 424.7)	21.8 (20.2 to 27.1)	2.4 (0.0 to 6.9)

Monthly SST ranged from 18.2 to 30.4 °C (median = 23.3 °C) when green turtles were tracked at five different locations, and from 19.2 to 27.3 °C (median = 23.0 °C) when loggerhead turtles were tracked in Moreton Bay (Table 5.2). There was large variation in ΔSST during my tracking periods in different locations (Table 5.2). Analysis of variance (ANOVA) indicated significant association between locations and ΔSST ($F_{4,\,1199} = 16.99$, $p < 0.0001$): ΔSST was significantly smaller in Port Curtis and Torres Strait than in other locations (Figure 5.3).

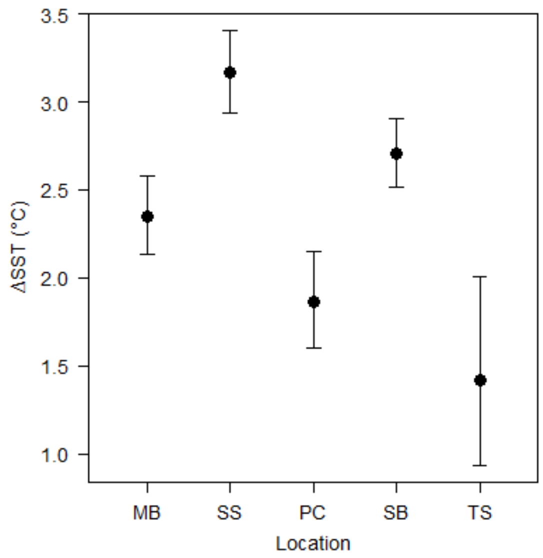

Figure 5.3 Absolute difference in SST (ΔSST) between any pairs of UDs estimated in different habitat locations. See Figure 5.1 for study locations. Dots are ANOVA model fits with error bars denoting 95% confidence intervals.

A total of 11 turtles were tracked for more than one year: female green turtles (*n* = 5), female loggerhead turtles (*n* = 5) and a male loggerhead turtle (*n* = 1). In particular, over two years of tracking was achieved using single tracking units on three turtles: a female green turtle in Shoalwater Bay for 2.5 years (Figure 5.4a), a female loggerhead turtle in Moreton Bay for 2.7 years (Figure 5.4e) and a male loggerhead turtle in Moreton Bay for 2.1 years (Figure 5.4i). Each 11 turtle used overlapping habitat repeatedly over multiple years: there were substantial overlaps between home ranges estimated in consecutive years for each turtle or, between home ranges and Argos fixes acquired for the same turtle up to 16.3 years apart (Figure 5.4). Yearly home ranges of 9 turtles are presented in Figure 5.4 because second year home ranges could not be estimated for two other female green turtles due to an insufficient number of location fixes (i.e. less than five fixes) during the second year of tracking.

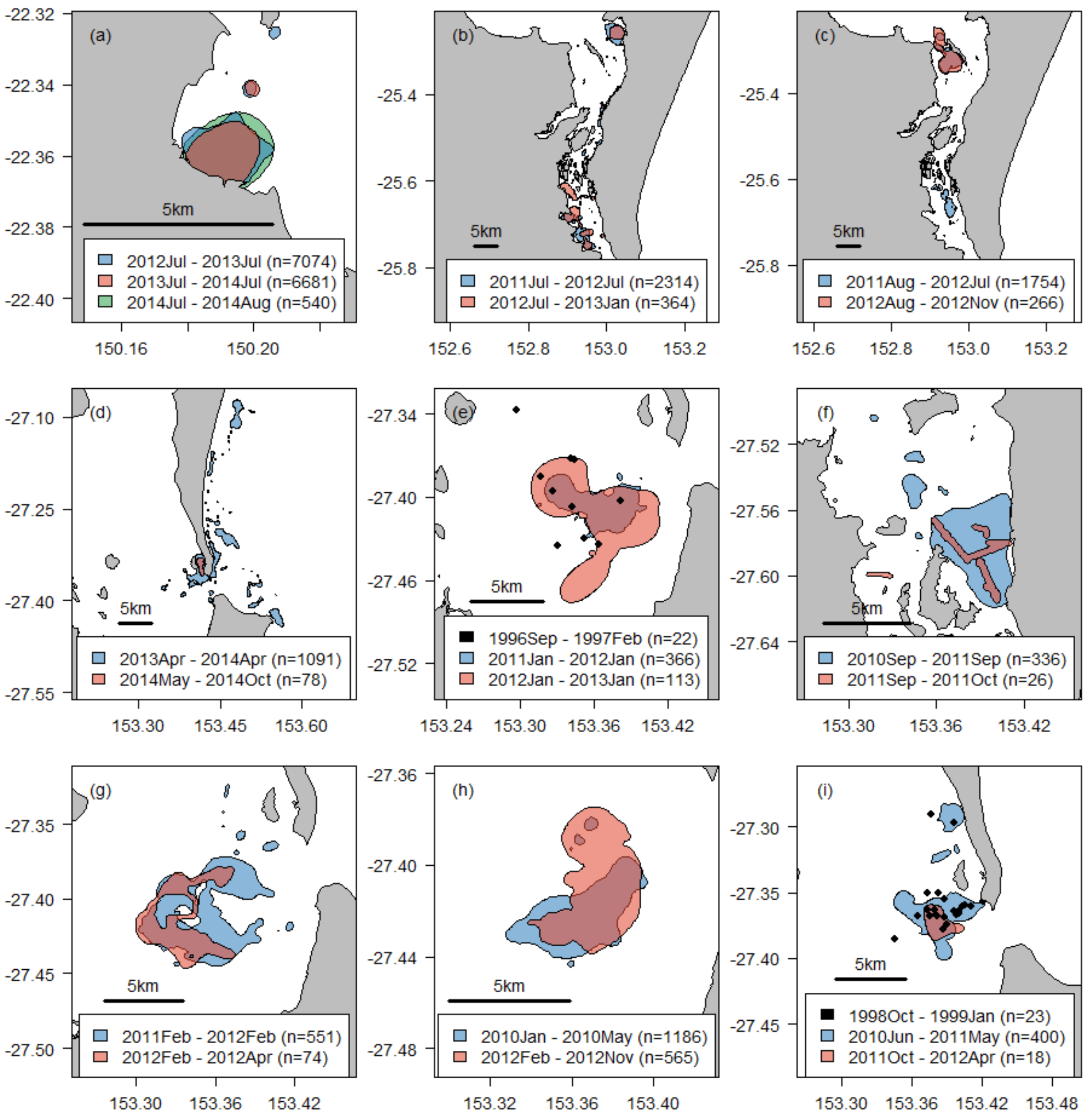

Figure 5.4 Yearly home ranges of sea turtles which were tracked for more than one year. Coloured polygons are home ranges in different years of each turtle and black dots are high-quality Argos fixes (LC 3, 2, 1). Home ranges were estimated using the location fixes acquired during the periods shown in the legend with the number of fixes presented in brackets. (a) female green turtle *K55740* in Shoalwater Bay, (b) female green turtle *QA23117* in Sandy Strait, (c) female green turtle *QA23188* in Sandy Strait, (d) female loggerhead turtle *QA34297* in Moreton Bay, (e) female loggerhead turtle *T14914* in Moreton Bay, (f) female loggerhead turtle *T23158* in Moreton Bay, (g) female loggerhead turtle *T29282* in Moreton Bay, (h) female loggerhead turtle *T93038* in Moreton Bay, (i) male loggerhead turtle *T53800* in Moreton Bay.

5.3.2 Monthly home range size

I asked four different questions related to monthly home range size using subsets of the tracking data.

(1) I tested the effect of the extreme weather events on monthly home range size of female green turtles in Moreton Bay (Subset 1) and male green turtles in Port Curtis (Subset 2) in separate models. The model is:

$$\text{Monthly home range size} \sim \text{Weather} + f(\text{SST})$$

Neither weather nor SST was associated with variation in the monthly home range size (Table 5.3 - Subset 1, 2). Based on these results, subsequent analyses used data regardless of association with the extreme weather events.

Table 5.3 Effects of environmental and biological variables on monthly home range size (mHR) of green turtles (*Cm*) and loggerhead turtles (*Cc*). See Figure 5.1 for study locations. F = female, M = male. All data subsets include fixes acquired during “affected months” and “normal months” (weather). *f*(SST) indicates SST was allowed to have a nonlinear effect.

Data subsets			Response	Random effects	Fixed effects	df	*F*	*p*
Species	Location	Sex						
Subset 1								
Cm	MB	F	mHR	Individual	Weather	1	0.17	0.682
					f(SST)	1.57	0.67	0.316
Subset 2								
Cm	PC	M	mHR	Individual	Weather	1	0.27	0.608
					f(SST)	1	0.48	0.493
Subset 3								
Cm	All	F	mHR	Individual	Location	4	6.47	<0.001
					f(SST): MB	1	0.59	0.442
					f(SST): SS	2.84	11.55	<0.001
					f(SST): PC	1	1.11	0.294
					f(SST): SB	1	0.11	0.745
					f(SST): TS	1	0.00	0.998
Subset 4								
Cm	MB, PC	F, M	mHR	Individual	Sex	1	1.18	0.279
					Location	1	9.18	0.003
					f(SST): MB	1	1.40	0.238
					f(SST): PC	1	0.06	0.811
Subset 5								
Cm	MB	F, M	mHR	Individual	Weather	1	0.91	0.344
					Sex	1	1.24	0.268
					f(SST)	1	0.24	0.629

(2) I examined the geographical effects on monthly home range size of female green turtles tracked at five different locations (Subset 3). The model is:

Monthly home range size ~ Location + *f*(SST):Location

Location had a significant effects on the monthly home range size (Table 5.3 - Subset 3). Female green turtles in Shoalwater Bay had significantly smaller monthly home ranges than those in other locations (Figure 5.5). SST was only associated with the monthly home range size of turtles in Sandy Strait (Table 5.3 - Subset 3). Home range size of green turtles in other locations was consistent through the range of SST recorded during my tracking study (Figure 5.6acde). Green turtles in Sandy Strait used larger areas in warmer water, indicating a seasonal change in home range size (Figure 5.6b). Thus I modelled monthly home range sizes of turtles in Sandy Strait as a function of month using GAMM. Month of year had a significant effect on the monthly home range size of the turtles in Sandy Strait ($F = 7.46$, $df = 3.52$, $p < 0.001$); smaller during winter and larger during summer (Figure 5.7).

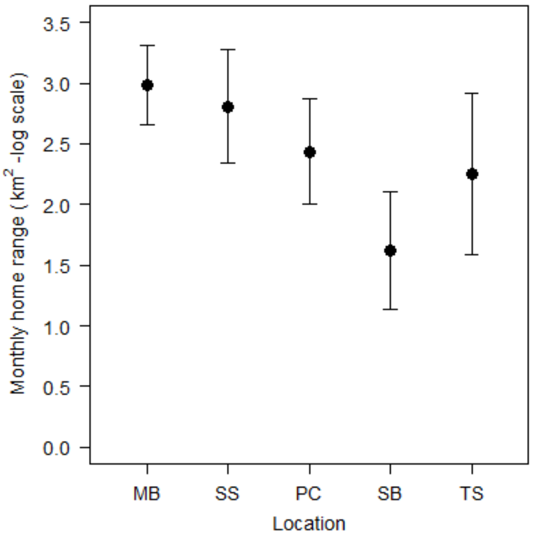

Figure 5.5 Geographical differences in home range size of adult female green turtles in north-eastern Australia. See Figure 5.1 for study locations. Dots are GAMM model fits with error bars denoting 95% confidence intervals.

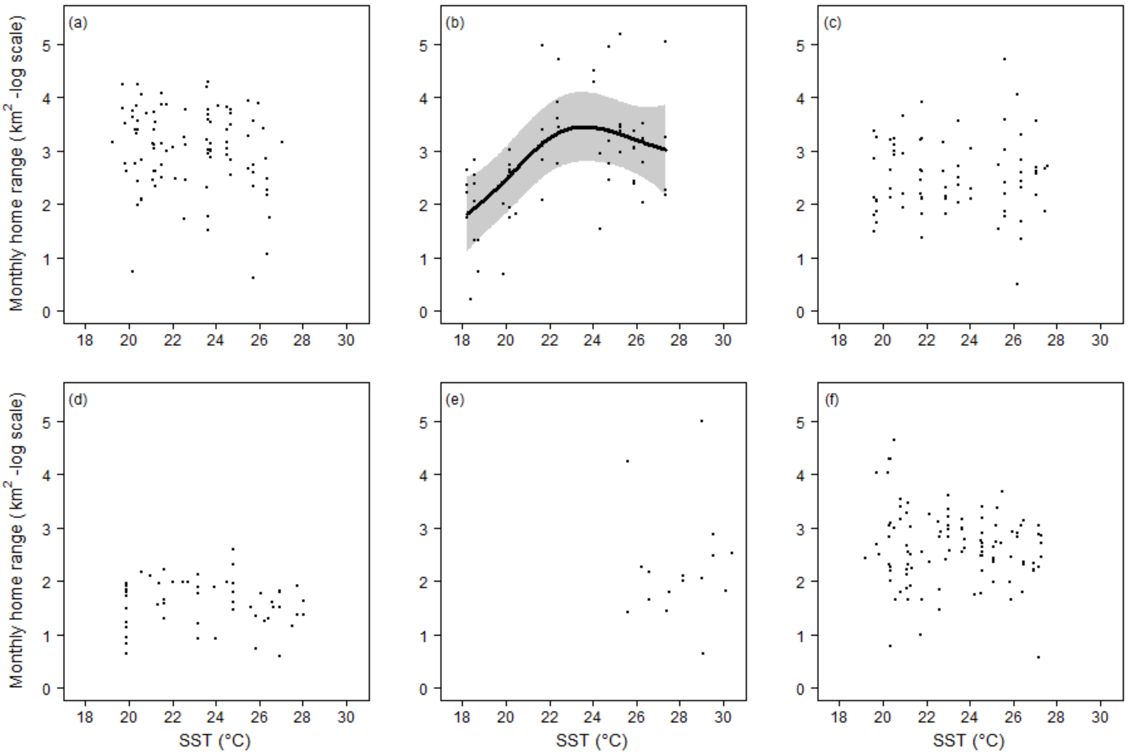

Figure 5.6 Estimated effects of SST on monthly home range size of (a) adult female and male green turtles in Moreton Bay, (b) adult female green turtles in Sandy Strait, (c) adult female and male green turtles in Port Curtis, (d) adult female green turtles in Shoalwater Bay, (e) adult female green turtles in Torres Strait, and (f) adult female and male loggerhead turtles in Moreton Bay. Dots are predicted values for each observation. For significant relationship as shown in Table 5.2, GAMM model fit (solid line) is also presented with 95% confidence interval (grey band).

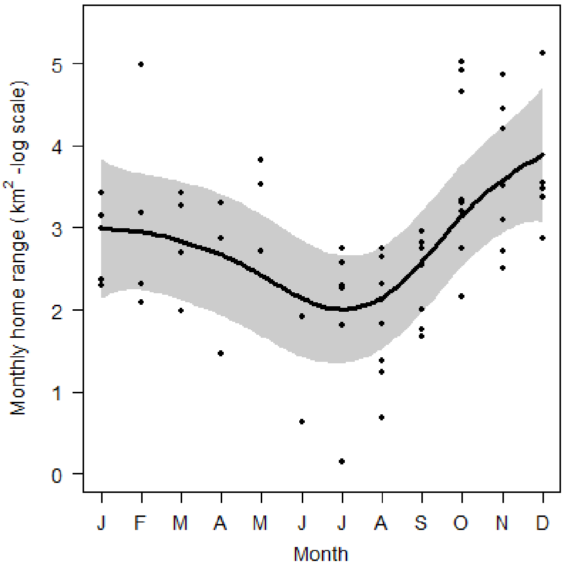

Figure 5.7 Estimated home range size of adult female green turtles in Sandy Strait in each month of year. Solid line is GAMM model fit with grey band denoting 95% confidence interval. Dots are predicted values for each observation.

(3) The sexual differences in monthly home range size of green turtles were tested for turtles in Moreton Bay and Port Curtis (Subset 4). The model is:

$$\text{Monthly home range size} \sim \text{Sex} + \text{Location} + f(\text{SST}):\text{Location}$$

Sex did not have an effect on the monthly home range size (Table 5.3 - Subset 4). Location had a significant effect but SST was not associated with the monthly home ranges of turtles in Moreton Bay and Port Curtis.

(4) Finally I tested the effects of the extreme weather events, sex, and SST on monthly home range size of loggerhead turtles in Moreton Bay (Subset 5). The model is:

$$\text{Monthly home range size} \sim \text{Weather} + \text{Sex} + f(\text{SST})$$

Neither weather, sex nor SST had significant effects on monthly home range size (Table 5.3 - Subset 5). The effect of location could not be tested for loggerhead turtles because they were tracked only in Moreton Bay.

5.3.3 Site fidelity

I also investigated four different questions related to site fidelity using subsets of tracking data.

(5) I first examined the effect of the extreme weather events on site fidelity for female green turtles in Moreton Bay (Subset 1) and male green turtles in Port Curtis (Subset 2). The model is:

$$\text{MISE} \sim \text{Weather} + f(\Delta\text{SST})$$

Weather did not have an effect in either Moreton Bay or Port Curtis (Table 5.4 - Subsets 1, 2). ΔSST was only associated with site fidelity for female green turtles in Moreton Bay (Table 5.4 - Subset 1) but not for male green turtles in Port Curtis (Table 5.4 - Subset 2). Based on the results, the following analyses used data regardless of the association with extreme weather events.

Table 5.4 Effects of environmental and biological variables on site fidelity (MISE) of green turtles (*Cm*) and loggerhead turtles (*Cc*). See Figure 5.1 for study locations. F = female, M = male. All data subsets include fixes acquired during “affected months” and “normal months” (weather). $f(\Delta\mathrm{SST})$ indicates ΔSST was allowed to have a nonlinear effect.

Data subsets			Response	Random effects	Fixed effects	df	*F*	*p*
Species	Location	Sex						
Subset 1								
Cm	MB	F	MISE	Individual	Weather	1	1.77	0.185
					$f(\Delta\mathrm{SST})$	1	4.33	0.038
Subset 2								
Cm	PC	M	MISE	Individual	Weather	1	0.89	0.349
					$f(\Delta\mathrm{SST})$	1	0.36	0.550
Subset 3								
Cm	All	F	MISE	Individual	Location	4	0.42	0.797
					$f(\Delta\mathrm{SST})$: MB	1	6.46	0.011
					$f(\Delta\mathrm{SST})$: SS	1	37.04	<0.001
					$f(\Delta\mathrm{SST})$: PC	1	0.08	0.780
					$f(\Delta\mathrm{SST})$: SB	1	111.50	<0.001
					$f(\Delta\mathrm{SST})$: TS	1	1.00	0.318
Subset 4								
Cm	MB, PC	F, M	MISE	Individual	Sex	1	0.26	0.610
					Location	1	0.02	0.904
					$f(\Delta\mathrm{SST})$: MB	1	5.83	0.016
					$f(\Delta\mathrm{SST})$: PC	1	0.89	0.346
Subset 5								
Cc	MB	F, M	MISE	Individual	Weather	1	1.05	0.306
					Sex	1	0.92	0.337
					$f(\Delta\mathrm{SST})$	1	24.45	<0.001

(6) I tested the effect of location on site fidelity for female green turtles (Subset 3). The model is:

$$\mathrm{MISE} \sim \mathrm{Location} + f(\Delta\mathrm{SST})\mathrm{:Location}$$

Location had no effects on site fidelity but ΔSST had significant effects on site fidelity for female green turtles in Moreton Bay, Sandy Strait and Shoalwater Bay; the effects were not significant in Port Curtis and Torres Strait (Table 5.4 - Subset 3).

(7) I tested for sex-based differences in site fidelity for green turtles using turtles tracked in Moreton Bay and Port Curtis (Subset 4). The model is:

$$\mathrm{MISE} \sim \mathrm{Sex} + \mathrm{Location} + f(\Delta\mathrm{SST})\mathrm{:Location}$$

Neither sex nor location had an effect on site fidelity (Table 5.4 - Subset 4). ΔSST was significantly related to site fidelity in green turtles in Moreton Bay but the effect was not significant in Port Curtis (Table 5.4 - Subset 4).

(8) Finally I examined the effects of the extreme weather events, sex, and ΔSST on site fidelity of loggerhead turtles in Moreton Bay (Subset 5). The model is:

$$\text{MISE} \sim \text{Weather} + \text{Sex} + f(\text{SST})$$

As seen in green turtles, ΔSST had a significant effect but neither weather nor sex was associated with site fidelity for loggerhead turtles (Table 5.4 - Subset 5).

There were linear relationships between ΔSST and MISE (log scale) for turtles in Moreton Bay, Sandy Strait and Shoalwater Bay (Figure 5.8). There were linear relationships between ΔSST and MISE (log scale) for turtles in Moreton Bay, Sandy Strait and Shoalwater Bay (Fig. 8), suggesting turtles changed habitat according to SST. Since SST is strongly affected by seasons, this result suggests turtles shifted their habitat in a seasonal base. Therefore I examined how the shifts in habitat were related to seasons. To do so, I extracted data subset for which the first month of paired monthly UDs was in summer (i.e. December to February) so that shifts in habitats could be examined for a particular season. For example, if a pair of monthly UDs was estimated first in December (summer) 2010 and second in June (winter) 2011, the MISE value of the pair represents the difference in habitat between summer and winter. I chose this data subset because, for both green and loggerhead turtles, temporal range (i.e. number of months apart between paired monthly UDs) were widest in this category than the other data subsets for which the first month of paired monthly UDs was fall, winter or spring. I used GAMMs to model MISE as a function of the number of months since summer. This analysis did not include data for green turtles in Port Curtis and Torres Strait due to their lack of relationship between MISE and ΔSST (Table 5.4 - Subset 3).

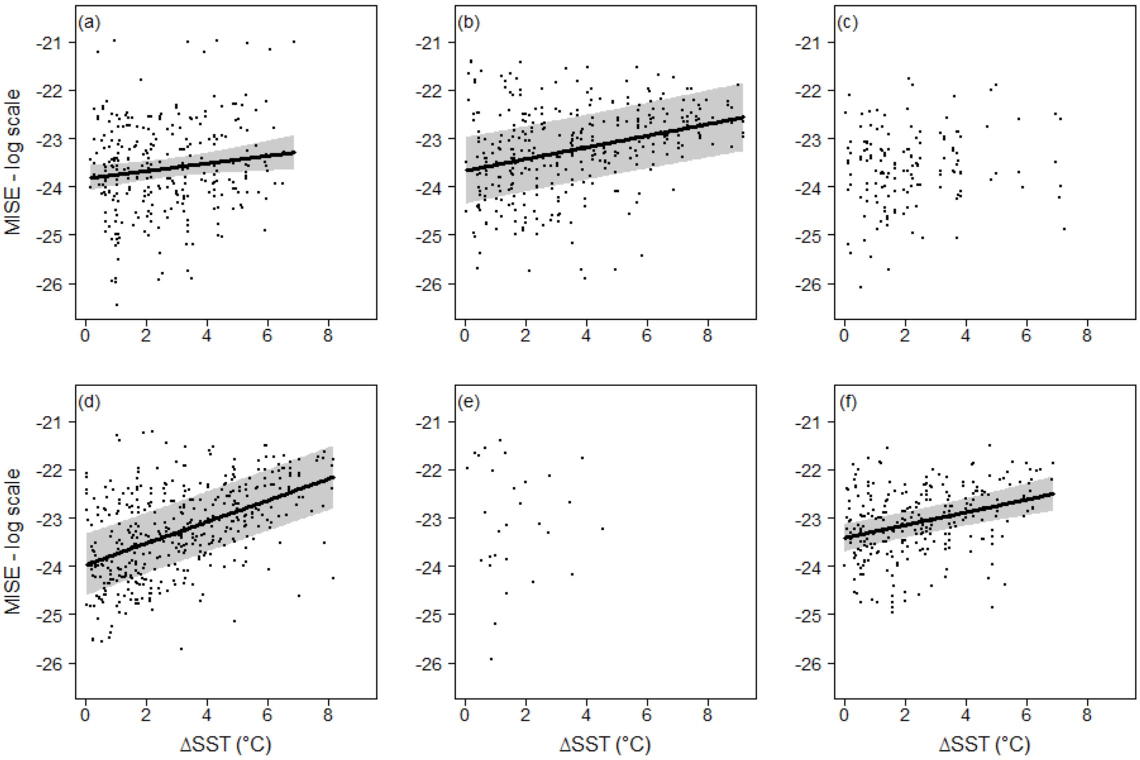

Figure 5.8 Estimated effects of SST on site fidelity by (a) adult female and male green turtles in Moreton Bay, (b) adult female green turtles in Sandy Strait, (c) adult female and male green turtles in Port Curtis, (d) adult female green turtles in Shoalwater Bay, (e) adult female green turtles in Torres Strait, and (f) adult female and male loggerhead turtles in Moreton Bay. MISE is the differences between each combination of UDs (a smaller MISE value indicate similar home ranges). ΔSST is the absolute difference in SST between each combination of UDs. Dots are predicted values for each observation. For significant relationship as shown in Table 5.4, GAMM model fits (solid line) are also presented with 95% confidence intervals (grey band).

A total of 186 pairs of monthly UDs were in the category of "shifts since summer months" for green turtles. The maximum time difference between each pair of monthly UDs was 20 months. Green turtles shifted their habitats between the summer months and the following winter months during the first year of tracking, but towards the summer months in the second year of tracking, they shifted back to the habitats where they used during the previous summer months (Figure 5.9a, Figure 5.10abc). As the time moved away from the summer months in the second year, the turtles again shifted away from the summer habitat (Figure 5.9a).

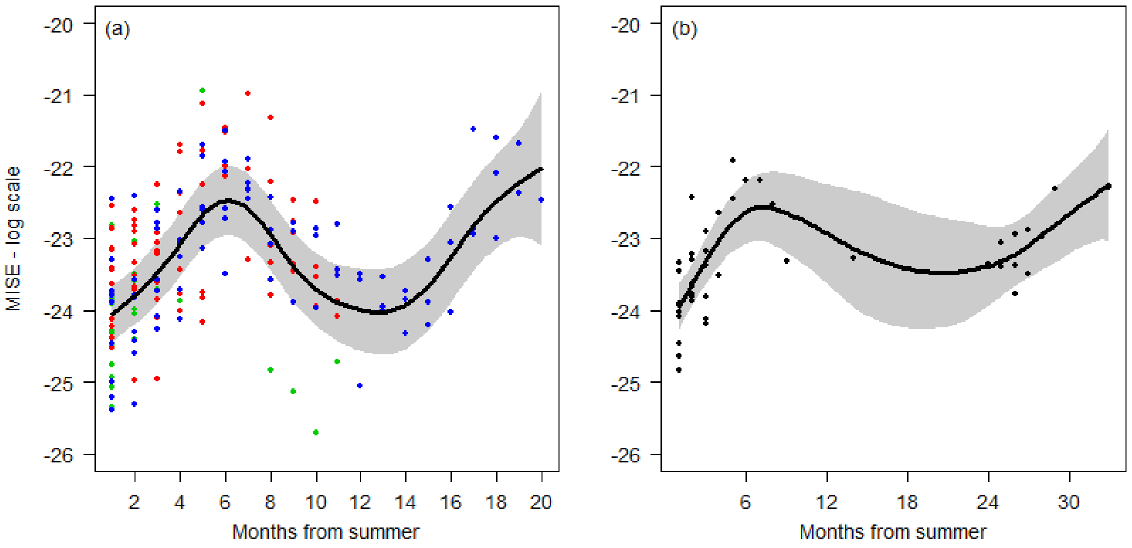

Figure 5.9 Chronological shift in habitat from summer months (a) by adult green turtles in Moreton Bay *green*, Sandy Strait *red*, Shoalwater Bay *blue* and (b) by adult loggerhead turtles in Moreton Bay. MISE is the differences between each combination of UDs (a smaller MISE value indicate similar home ranges). Solid lines are GAMM model fits with grey bands denoting 95% confidence intervals. Dots are predicted values for each observation.

For loggerhead turtles, a total of 48 pairs of monthly UDs were in the category of “shifts since summer months”. The maximum time difference between each pair of monthly UDs was 33 months. Like green turtles, loggerhead turtles showed seasonal shift in habitat between the summer months and the following winter months in the first year of tracking (Figure 5.9b, Figure 5.10d).

Both species remained in shallow coastal habitats throughout the year and there was no apparent movement that resembles migration to warmer water (Figure 5.10). Particularly during winter, turtles did not migrate to waters in lower latitude or to deeper off-shore where temperature would be higher.

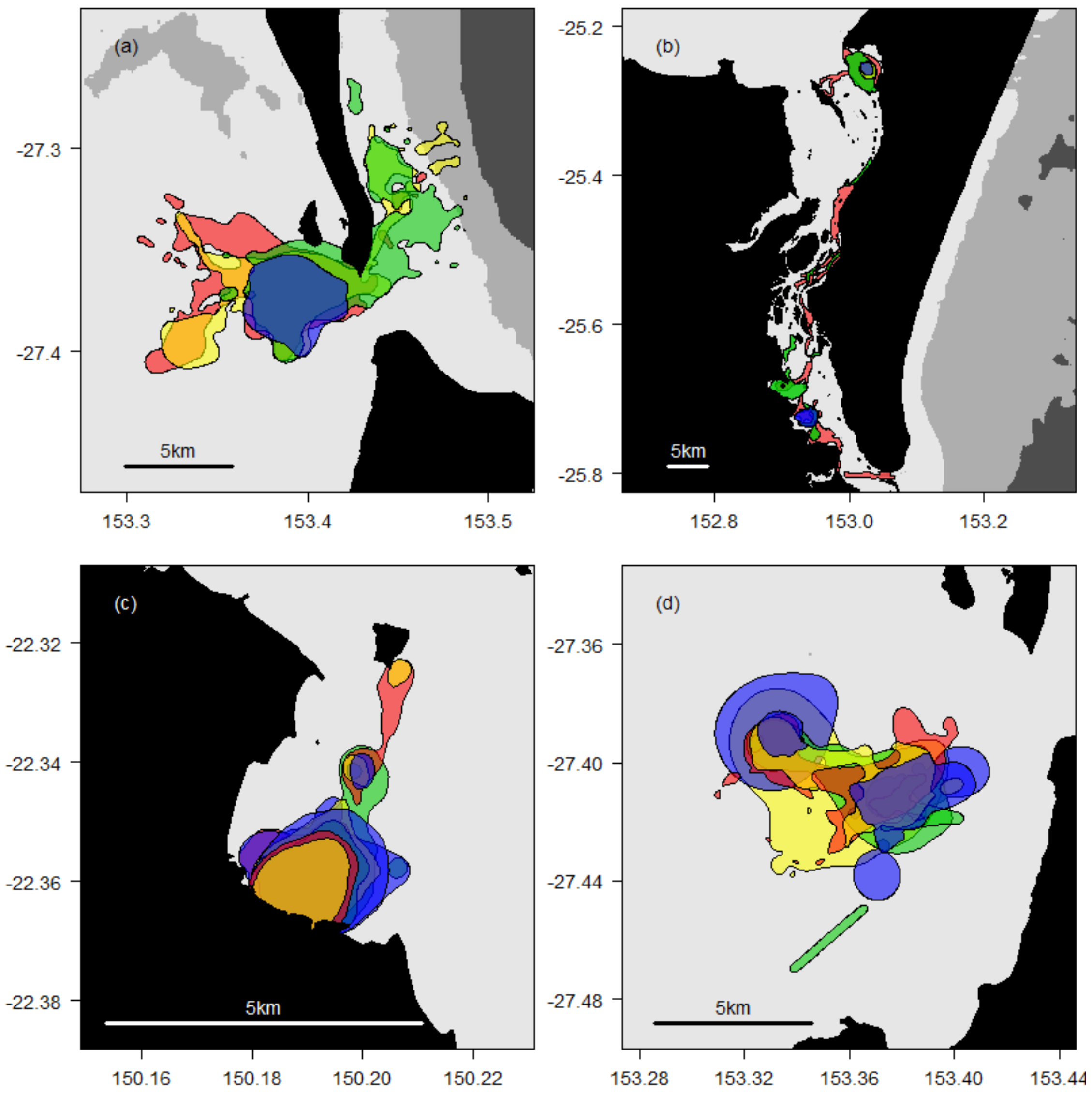

Figure 5.10 Seasonal home range of (a) a female green turtle *T5561* in Moreton Bay, (b) a female green turtle *QA23117* in Sandy Strait, (c) a female green turtle *K55740* in Shoalwater Bay, and (d) female loggerhead turtle *T14914* in Moreton Bay. Coloured polygons represent summer (red), autumn (yellow), winter (blue), and spring (green) from each year. Water depth zones at mean sea level are shown by grey gradient: >0 - 25 m (light grey), >25 - 50 m (grey) and >50 m (dark grey).

5.4 Discussion

I demonstrated that spatio-temporal home range analysis can reveal important movement patterns of threatened sea turtles. My results represent the first evidence of seasonal variation in habitat use by adult green and loggerhead turtles in subtropical coastal foraging habitat in the southern hemisphere. I also provide further evidence of long-term fidelity to foraging habitats and geographical variation in home range size for those populations.

Site fidelity for more than one year was clearly demonstrated by green and loggerhead turtles at various foraging areas along the Queensland coast. In particular, a female (T14914: 17 yr) and a male (T53800: 20 yr) loggerhead turtle appeared to use the same areas over a decade. Both used overlapping areas while being tracked by satellite telemetry, and they had been also caught multiple times within the habitats during annual sea turtle monitoring exercises conducted before and between the tracking occasions (Limpus, unpublished data). These are among the longest periods of fidelity to particular foraging habitats reported in foraging marine turtles. Limpus and Limpus (2003a) recorded loggerhead females maintaining foraging residency on a single small coral reef for up to 23 yr, following their recruitment from oceanic pelagic dispersal to benthic foraging on these reef and continuing across multiple foraging periods between successive adult breeding migrations. Having long-term site fidelity may increase sea turtles' biological and reproductive fitness by ensuring reliable access to good foraging and resting areas and possibly reducing the impacts of predation by knowing where predators are most likely found and where they can be evaded.

Within each long-term habitat, the study turtles were observed to seasonally shift their main habitat in Moreton Bay, Sandy Strait, and Shoalwater Bay. The seasonal shifts made by green turtles in Sandy Strait were due to habitat expansion during summer months and contraction during the winter. Yet, for turtles in Moreton Bay and Shoalwater Bay, the shifts in habitat were not necessarily related to changes in home range size; rather, these shifts indicated changes in fidelity resulting from shifts to overlapping habitat of similar area during different seasons (Figure 5.6, Figure 5.8).

The seasonal shifts in habitat and variations in home range size may be driven by spatial shifts of the turtles' food sources. As shown by previous studies in my study locations, seagrass is the main diet for green turtles while loggerhead turtles mostly feed on benthic invertebrates (Garnett et al. 1985, Limpus et al. 2001, Limpus et al. 2005, Arthur et al. 2008b). Green turtles may have simply followed any shifts in the spatial distribution and abundance of seagrass, which is known to be affected by various environmental and geographical factors (Rasheed and Unsworth 2011). Loggerhead turtles in Moreton Bay forage on benthic invertebrates, which are often found in seagrass meadows (Limpus et al. 2001). It may be expected that the home range of loggerhead turtles changed in concert with seasonal distributions of seagrass and associated invertebrate prey species. Temporal blooms of gelatinous plankton at my study locations (Arthur et al. 2008a) may also have contributed to the observed shifts in habitat, as some loggerhead and green turtles are also known to consume planktonic invertebrates at my study sites (Limpus et al. 2001, Arthur et al. 2007).

Previous studies have identified access to food resources and thermoregulation as possible factors driving habitat shifts in sea turtles and some marine mammals. For example, juvenile loggerhead and kemp's ridley turtles (*Lepidochelys kempii)* in the western North Atlantic and juvenile loggerhead turtles in the western North Pacific move away from their resource-rich summer foraging habitat to warmer waters in lower latitudes or deeper waters as water temperatures drop (Morreale and Standora 2005, Mansfield et al. 2009, Narazaki et al. 2015). Dugongs (*Dugong dugon*) in the western Pacific and the West Indian manatees (*Trichechus manatus*) also showed behaviour appearing to search out warmer waters during winter (Deutsch et al. 2003, Sheppard et al. 2006). The movements recorded by the turtles in my study did not resemble this summer-winter behaviour seen in these other studies (i.e. moving long distance to deeper off-shore or lower latitude in response to cold water in winter). However the small-scale movements I found could be related to variation of microclimates and do not preclude potential thermoregulatory effects. In particular, habitat contraction in the winter seen in Sandy Strait green turtles may reflect reduced foraging behaviour as response to cooler water temperature. Testing this hypothesis requires concurrent data of turtle movements and water temperature at high resolution (e.g. hourly SST at 50 m grid resolution to match the expected resolution of FGPS data).

A seasonal shift in habitat was not detected in turtles from Port Curtis although the climate in Port Curtis is similar to Moreton Bay, Sandy Strait and Shoalwater Bay. That is likely because turtles in Port Curtis were not tracked across periods with major seasonal changes (e.g. summer to winter), and consequently changes in SST across the tracking periods were significantly smaller in Port Curtis than in the other subtropical habitats (Figure 5.3). The same explanation may apply for failure to detect seasonal shifts in habitat by turtles from the Torres Strait. However the Torres Strait being nearer to the equator (approximately 9-10°S), it is also likely that seasonal effects were trivial in Torres Strait. These hypotheses could be verified through additional satellite telemetry data across periods including both summer and winter.

I did not find any evidence that the extreme weather events affected home range size or site fidelity of sea turtles at my study locations in the eastern Moreton Bay and eastern Port Curtis despite an increase of stranded turtles along the Queensland coast during 2011 (Meager and Limpus 2012). Similarly, the extreme weather events did not appear to affect the space use of herbivorous dugongs in Moreton Bay (Sobtzick et al. 2012). The flood plumes generally do not spread on to the seagrass meadows of my study area in eastern Moreton Bay, largely because eastern Moreton Bay is relatively distant from the major river (e.g. approximately >15 km from the mouth of Brisbane river) and part of the strong Eastern Australian Current streams into the Bay. Unlike the eastern Moreton Bay, the flood plumes reached my turtle tracking site in Port Curtis. However I speculate much flood plume may have been carried away quickly by the currents through the adjacent passage linking to the outside of the Bay. Testing this hypothesis requires high-resolution current data and satellite imagery. Nonetheless these potential geographical advantages underline the high conservation value of the eastern Moreton Bay and eastern Port Curtis as foraging habitats for many wildlife species including sea turtles and dugongs.

Geographical variations in home range size were evident in this study and others (Hart and Fujisaki 2010, Gredzens et al. 2014). Home range size may be determined by distribution and abundance of food sources, and therefore is highly dependent on the unique environmental and biological factors present at each location. While climate may be another determinant for home range size, I did not find any evidence that latitude affected the home range size in the subtropical and tropical habitats (Figure 5.5). Nonetheless, this is potentially an important indication for research and management to be examined at local scales.

My findings suggest that comparison of home range (for areas or fidelity) can be challenging when data from varying tracking durations and seasons are used. This is because tracking duration is likely to influence home range size or site fidelity indices (e.g. MISE) if animals undertake seasonal shifts in habitat. The issue with tracking duration when estimating home range size has been also documented in other studies that used different species or simulations (Swihart and Slade 1997, Börger et al. 2006). Therefore I emphasize that tracking duration and season should always be accounted for when comparing multiple home ranges or data across studies to avoid misleading statistical inferences. This precaution would be highly relevant to most studies using satellite telemetry because transmission can unexpectedly cease for many reasons (Hays et al. 2007), resulting in shortened tracking duration.

Long-term fidelity to foraging habitat is a strong behavioural feature of multiple sea turtle species (e.g. *Chelonia mydas* - Chaloupka et al., 2004, Shimada et al., 2014, this chapter; *Caretta caretta* - Limpus and Limpus, 2001, 2003, Thomson et al., 2012, this chapter; *Eretmochelys imbricate* - Limpus, 1992), which possibly persists for decades even after human-induced displacement (Chapter 3). Ideally, the home range of sea turtles should be estimated using year-round tracking data, as shown by the seasonal circulation within foraging habitats observed during my study. These characteristics of sea turtle behaviour warrant careful consideration by conservation managers when planning or revising designated conservation areas such as Marine Protected Areas or restricted area zones (e.g. “Go Slow Zones”) to protect threatened species or their habitat from increasing human activities at their foraging habitats. Given that food sources and other environmental variables are expected to vary among seasons, this guidance could be applicable to research and conservation of a wide variety of other animals in marine and terrestrial habitats globally.

5.5 Chapter Summary

- Home range analysis is a powerful tool to identify priority areas for conservation but estimating home range is still challenging for many species.
- To undertake home range analysis on threatened sea turtles, I used satellite-linked tags to track adult green and loggerhead turtles foraging in the coastal waters of eastern Australia, objectively quantified home range size and site fidelity, and examined how their spatial selections were affected by ecologically meaningful variables such as seasons, extreme weather events (tropical cyclones and extreme rainfall), locations and sex.
- Evidence from multiple observations using satellite telemetry and mark-recapture methods inferred that many turtles maintained high fidelity to their coastal foraging habitats for long periods - up to 20 years.
- Within the long-term foraging habitat area defined by my analysis, turtles generally shifted their foraging areas on a seasonal basis.
- These characteristics of sea turtles emphasise the importance of protecting habitat areas according to the turtles' space use, with careful consideration given to identifying temporal trends in habitat selection.
- I also identified two sites in eastern Australia (eastern Moreton Bay and eastern Port Curtis) which provided stable foraging habitats for sea turtles despite extreme weather events such as tropical cyclones and extreme rainfall. These important foraging habitats would benefit from prioritised conservation planning and management actions.
- My findings have direct relevance to conservation managers for planning or revision of designated conservation habitat such as Marine Protected Areas or restricted area zones to protect these threatened species from risks associated with increasing human activities at their foraging habitats in Australia and other regions.

Chapter 6

Marine protected areas as sea turtle habitats in Moreton Bay, Australia

Moreton Bay is one of the significant foraging habitats for green and loggerhead turtles in Australia. Boat operation is regulated in some part of Moreton Bay to protect sea turtles from vessel collisions but vessel collisions are still major threats to sea turtles in Moreton Bay. In this chapter, I estimated the extent of turtle habitat in Moreton Bay using satellite telemetry data, and then quantified how much of their habitat is likely to be protected by the current regulations. I then provide guidance for improving protection of foraging turtles in Moreton Bay.

Manuscript in preparation:

Shimada T, Limpus C, Jones R, Hamann M (in prep.) Marine protected areas as sea turtle habitats in Moreton Bay, Australia. Target journal: *Ocean & Coastal Management*.

6.1 Introduction

Vessel collision is a major threat to air breathing marine fauna (Lutcavage et al. 1997, Marsh et al. 2011). This is especially the case for species residing in shallow coastal waters that are used regularly by commercial and recreational vessels, such as waters adjacent to cities with large human population (Lutcavage et al. 1997, Marsh et al. 2011). Marine turtles are particularly vulnerable to vessel interaction because not only must they surface to breathe, but many live in shallow environments and lack agile responses that may prevent their escape from potential collisions (Hazel et al. 2007).

Protection from vessel collision can be provided through spatially based management such as Marine Protected Areas. For effective management, the spatial planning initiatives require ecological data for targeted species (Hooker and Gerber 2004, Cleguer et al. 2015). The evidence-based management is particularly relevant in coastal waters where human population is on the rise so an optimal balance can be obtained between conservation of marine resources and quality of human life that relies on the marine environment (Chua et al. 2006, Barbier et al. 2008).

There are high levels of human activity in Moreton Bay, situated on the coast of Queensland, Australia (Figure 6.1), which is also an ecologically important area for a variety of marine fauna. Being adjacent to the capital city of Queensland, Moreton Bay is extensively used for commercial and recreational boating and is thus a hotspot of vessel traffic along the Queensland coast (Blackman 2011). Moreton Bay is also an important foraging habitat for some of the largest green turtle (*Chelonia mydas*) populations in the world (Chaloupka et al. 2008, Limpus 2008), and for depleted loggerhead turtle (*Caretta caretta*) populations (Limpus and Limpus 2003b). Within the bay turtles regularly use both the intertidal and subtidal seagrass areas for foraging. Large numbers of foraging turtles combined with high use for boating have led to the bay being a high risk area for vessel-turtle collisions (Hazel et al. 2007, Limpus 2008).

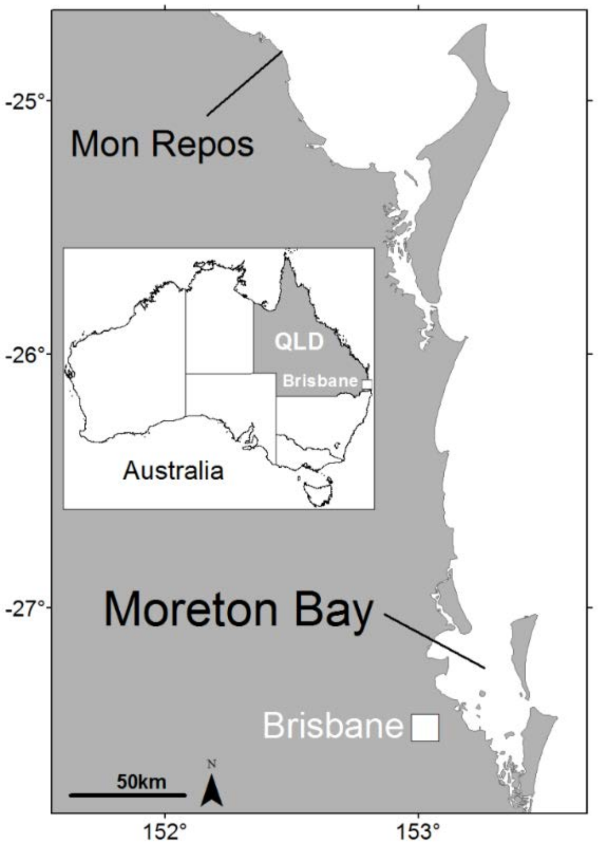

Figure 6.1 Release locations of green turtles (Moreton Bay) and loggerhead turtles (Moreton Bay and Mon Repos). All tracked turtles settled in Moreton Bay.

As a mitigation strategy, the Queensland state government designated “Go Slow Zones” within the Moreton Bay Marine Park Zoning Plan to protect marine wildlife including sea turtles in some of the shallow water areas of eastern and southern Moreton Bay (Figure 6.2). Because reduced vessel speed significantly decreases the risk of collisions between vessels and sea turtles (Hazel et al. 2007), Go Slow Zones were established to regulate activity by eliminating motorised water sports and setting maximum travel speeds for vessels to avoid collision with turtles. Implementation of the Go Slow Zones resulted in reduction of vessel-related accidents on sea turtles in some areas of Moreton Bay (Limpus 2008). However according to Queensland Marine Fauna strandings data, most boat strike incidents in Queensland still come from the Moreton Bay area (Meager and Limpus 2012). These reports indicate that the current Go Slow Zones may not be providing adequate spatial protection to sea turtles in Moreton Bay.

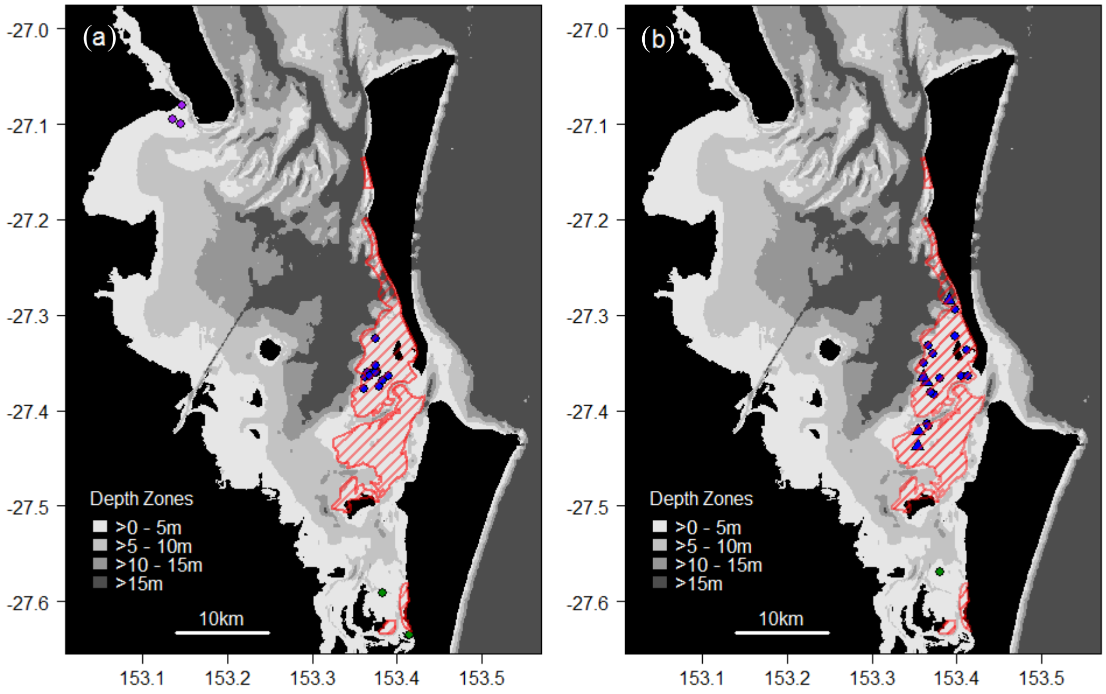

Figure 6.2 Capture locations of (a) green turtles and (b) loggerhead turtles in Moreton Bay. Most turtles (*n* = 32) were captured in northern (purple circle), eastern (blue circle) and southern (green circle) Moreton Bay during this study. Other female loggerhead turtles (*n* = 6) were captured and release at their nesting habitat in Mon Repos during this study but five were previously captured at their foraging habitat in eastern Moreton Bay (blue triangle) prior to this study. Red hatched polygons denote the Go Slow Zones for turtles and dugongs.

Since exact locations of vessel-related incidents are not known, currently most Go Slow Zones are placed in eastern Moreton Bay where high densities of green and loggerhead turtles are known to occur and where turtles with vessel-related injuries were frequently recorded (Haines and Limpus 2001, Meager and Limpus 2012). Water depths ≤5 m at mean sea level, shallow zones hereafter, are considered high risk depths for turtles (submerged vessel depth + turtle height + tide) and were used as a boundary to delineate the Go Slow Zones from the adjacent deeper zones (Queensland Government 2008). This is based on the assumption that turtles in shallow waters are more prone to vessel collisions than those in deeper zones. While the assumption for vertical relevance may stand, given that turtles must surface to breathe, the horizontal coverage may not be sufficient if the current Go Slow Zones and actual turtle habitats do not overlap as much as expected. Additionally many other areas in Moreton Bay including shallow zones are not designated as Go Slow Zones, so turtles residing outside Go Slow Zones may be exposed to elevated risk of vessel collisions.

To be effective as a conservation tool, Go Slow Zones may need to be designed based on turtles' habitat use rather than being based on physical features. In particular the boundaries should recognize that sea turtles in Moreton Bay are strongly associated with their foraging habitats for many years, and within the long-term habitats they tend to make small-scale seasonal shifts in habitat (Chapter 5). The fidelity to specific foraging areas persists across breeding migrations (Limpus et al. 1992, Limpus and Limpus 2001) and human-induced displacement (Chapters 3, 5).

Since sea turtles tend to use small areas in Moreton Bay (Limpus and Limpus 2001, Hazel 2009, Chapter 5), a tool is required to quantify habitat use at a high resolution for assessing conservation initiatives such as Go Slow Zones. However at the time the legislation was initiated suitable tools were not available to researchers. The technical issues are now much less constrained with the new Fastloc GPS (FGPS) technology (Rutz and Hays 2009) which enabled marine animals to be tracked in detail with full-time global coverage (Hazel 2009, Chapter 2).

In this study, I used Argos-linked FGPS tags to investigate space use of green and loggerhead turtles in Moreton Bay in relation to the Go Slow Zones and water depth. Based on my findings, I identify potential issues in the current regulation, and provide guidance on how it can be revised to provide more comprehensive protection to these threatened marine reptiles.

6.2 Materials and Methods

6.2.1 Study turtles

I investigated space use of 18 green turtles and 20 loggerhead turtles foraging in subtropical Moreton Bay, eastern Australia (Figure 6.1). The behaviour of each turtle was tracked with a highly accurate satellite-linked FGPS tag attached on the carapace (Chapter 2). FGPS tags were set to acquire a GPS location at intervals ranging from 15 minutes to one hour.

Thirteen, three and two green turtles were captured while in the foraging habitats of eastern, northern and southern Moreton Bay respectively (Figure 6.2a). Loggerhead turtles were captured at their foraging habitats in eastern (*n* = 13) and southern (*n* = 1) Moreton Bay or at the Mon Repos beach (*n* = 6) following their successful nesting activities (Figure 6.1 & 6.2b). Five of the nesting loggerhead turtles were previously captured in eastern Moreton Bay (Figure 6.2b) so their destinations were predicted to be eastern Moreton Bay at the time of satellite tag attachment (Limpus et al. 1992, Limpus and Limpus 2001). One nesting loggerhead turtle had no previous capture records and her foraging destination was not known at the time of tag attachment.

The turtles captured in Moreton Bay (*n* = 32) were relocated 0.2 to 28.1 km away from the capture location for tag attachment, released and then tracked back to the area of initial capture (Chapter 3). The nesting loggerhead turtles (*n* = 6) were released on Mon Repos beach and tracked as they migrated back to their foraging habitats in Moreton Bay; five of them settled in eastern Moreton Bay adjacent to their previous capture locations, and the sixth, which had no prior capture records, settled in western Moreton Bay.

Turtles tracked in eastern Moreton Bay (*n* = 31) had been captured at least once inside the Go Slow Zones during present or previous research (Figure 6.2). The turtles tracked in northern and southern Moreton Bay (*n* = 6) were captured outside the Go Slow Zones: the straight distances between capture locations and the nearest Go Slow Zones ranged from 0.4 to 22.5 km (Figure 6.2).

The 38 turtles comprised female and male adults as identified by nesting activity, gonad examination via laparoscopy, curved carapace length (CCL), or combination of CCL and the tail length from carapace (Limpus and Reed 1985, Limpus and Limpus 2003a, Limpus et al. 2005). The body size (CCL) ranged from 94.0 to 119.9 cm (median = 110.0 cm) for green turtles and 85.5 to 100.7 cm (median = 94.9 cm) for loggerhead turtles.

6.2.2 Data acquisition and pre-processing

Argos-linked FGPS tags provided both FGPS and Argos fixes. I merged FGPS fixes and high-quality Argos fixes (LC 3, 2, 1), and applied filtering according to quality indices, water depth, spatial and temporal duplicates, and a data driven filter as described in Chapter 2 and Chapter 3 using the R package SDLfilter (Shimada 2015). The water depth at each turtle location was estimated using a bathymetry model with a 100 m grid resolution (Beaman 2010) and tidal data provided by the Australian Bureau of Meteorology and Queensland Department of Transport and Main Roads. I also excluded locations acquired prior to turtles' arrival at their foraging habitats (see Chapter 3).

6.2.3 Spatial analysis

Turtles' space use was represented by the utilisation distributions (UDs). To minimise the effects of varied tracking duration and seasons among turtles on UD estimation (Swihart and Slade 1997, Börger et al. 2006, Chapter 5), I first estimated a UD per season for each turtle and then averaged the individual UDs of the same season to obtain multi-individual UDs per season. I followed the standard definitions of seasons in Australia; *spring* Sep-Nov, *summer* Dec-Feb, *autumn* Mar-May, *winter* Jun-Aug (Bureau of Meteorology 2015). I then averaged the seasonal UDs to derive a multi-individual/multi-seasonal UD, overall UD hereafter. Overall UDs were produced per site using subsets of turtles tracked in northern, eastern, southern and western Moreton Bay (Figure 6.2).

Each UD was estimated using movement-based kernel density estimators based on a biased random bridge (Benhamou 2011). High tide lines were treated as a boundary for UD estimation because foraging sea turtles rarely ascend beaches above high tide lines in eastern Australia. I defined the area containing 95% of the overall UD as the turtles' habitat. The R package adehabitatHR (Calenge 2006, 2015a) was used to estimate UDs and to calculate the size of turtles' habitat (see Appendix - Table A3 for the parameters used). I also estimated the water depth of each grid cell of turtles' habitat using the bathymetry model at a resolution of 100 m (Beaman 2010). All analyses were conducted using R software (R Core Team 2015).

6.3 Results

Green turtles were tracked throughout four seasons in eastern and northern Moreton Bay and across three seasons in southern Moreton Bay (Table 6.1). Loggerhead turtles were also tracked throughout four seasons in eastern Moreton Bay and across three seasons in southern Moreton Bay and two seasons in western Moreton Bay (Table 6.1).

Table 6.1 Seasonal habitat areas of green turtles (*Cm*) and loggerhead turtles (*Cc*) in eastern, southern, northern and western Moreton Bay. N is the number of turtles used to estimate the habitat areas.

Sites	Season	N	Habitat (km^2)
Cm			
East	Summer	4	61.2
	Fall	5	79.6
	Winter	7	103.3
	Spring	11	161.6
South	Summer	3	19.1
	Fall	0	NA
	Winter	1	10.9
	Spring	3	14.7
North	Summer	3	68.5
	Fall	1	58.4
	Winter	3	126.2
	Spring	3	80.0
Cc			
East	Summer	8	96.4
	Fall	15	97.2
	Winter	13	269.6
	Spring	12	99.7
South	Summer	1	12.4
	Fall	1	16.1
	Winter	0	NA
	Spring	1	46.8
West	Summer	1	8.0
	Fall	1	21.3
	Winter	0	NA
	Spring	0	NA

The habitat area occupied by green turtles were 128.8 km^2 in eastern Moreton Bay, 23.7 km^2 in southern Moreton Bay and 121.8 km^2 in northern Moreton Bay. Their proportion of the habitat located within the Go Slow Zones was relatively low in eastern Moreton Bay (39%), less in southern Moreton Bay (3%) and zero in northern Moreton Bay (Figure 6.3a).

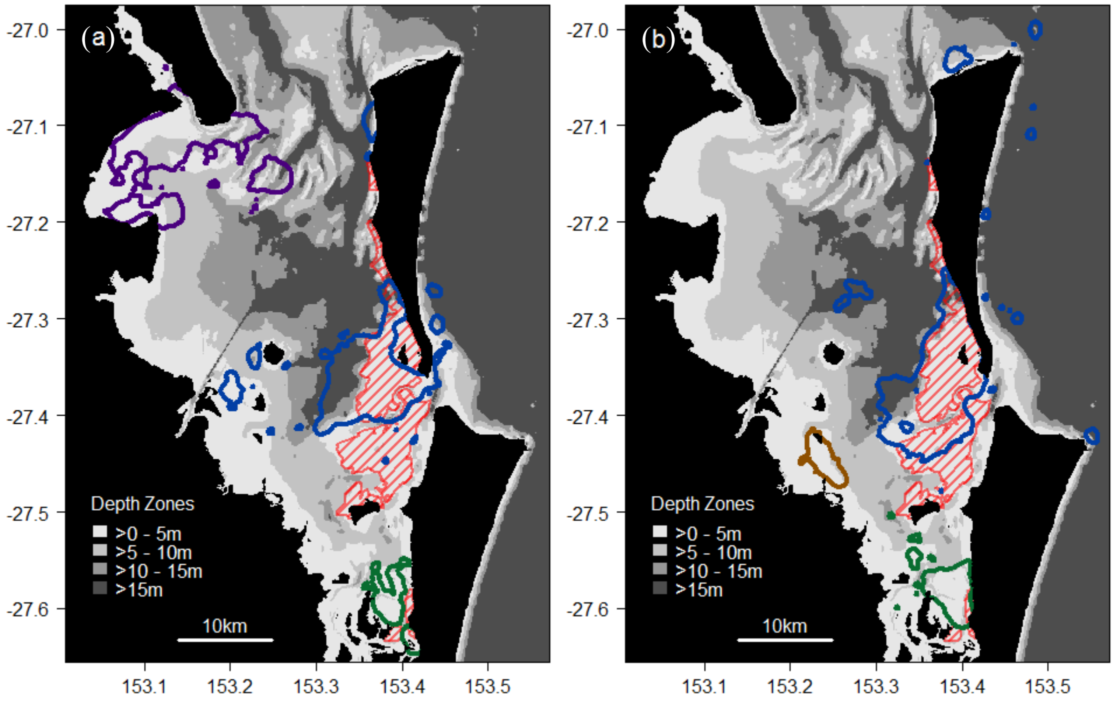

Figure 6.3 Foraging habitats (95% UDs) of (a) green turtles and (b) loggerhead turtles in Moreton Bay, tracked in the east *blue*, the south *green*, the west *brown* and the north *purple*. Red hatched polygons denote the Go Slow Zones for turtles and dugongs.

Loggerhead turtles used 155.8 km^2 in eastern Moreton Bay, 32.7 km^2 in southern Moreton Bay and 15.6 km^2 in western Moreton Bay. The proportion of their habitat lying within the Go Slow Zones was 55% in eastern Moreton Bay and lower in both the southern (7%) and western (0%) areas of Moreton Bay (Figure 6.3b).

Most of the habitat used by both green and loggerhead turtles was in water shallower than or equal to 5 m (Figure 6.4). Within eastern Moreton Bay, most of the shallow water habitat used by both species was within the Go Slow Zones, but little or none of the shallow water habitat used by turtles in the other parts of Moreton Bay occurred in the Go Slow Zones (Figure 6.4). Turtle habitats in deeper zones (depth > 5 m) were generally outside of the Go Slow Zones, with the exception being some areas within eastern Moreton Bay (Figure 6.4).

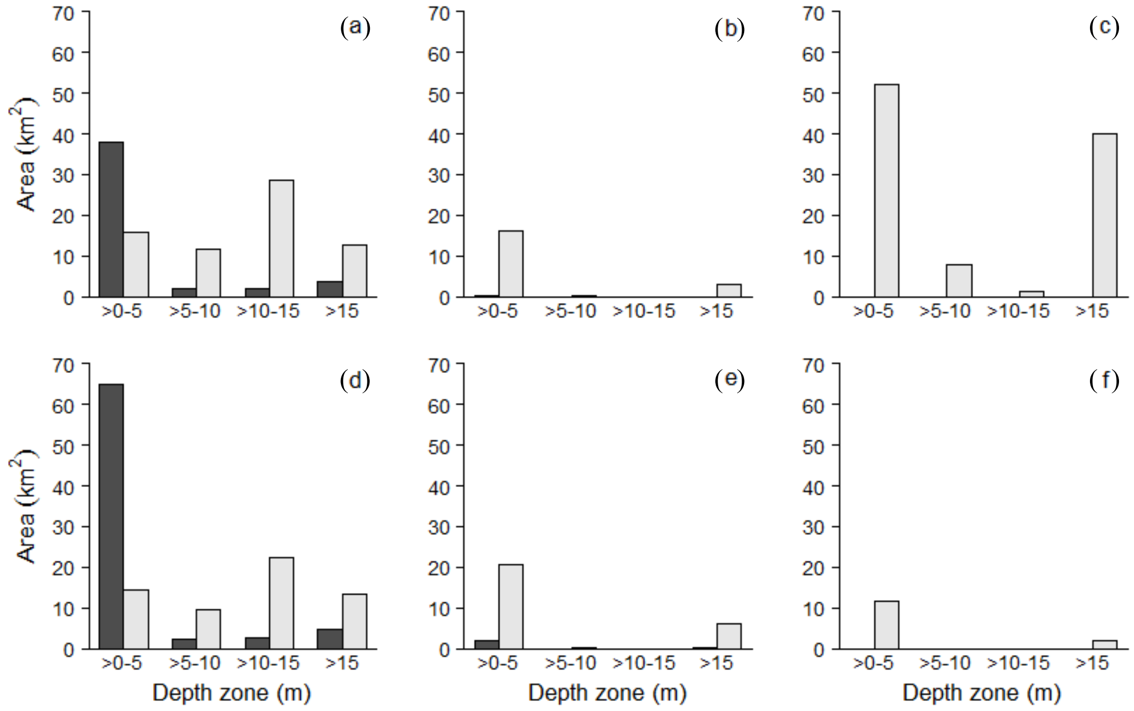

Figure 6.4 Depth zone at turtle habitats within the Go Slow Zones *black* and outside the Go Slow Zones *grey* in Moreton Bay: (a) green turtles in the east, (b) green turtles in the south, (c) green turtles in the north, (d) loggerhead turtles in the east, (e) loggerhead turtles in the south, (f) loggerhead turtles in the west.

Turtle habitats occurring in deeper zones were along the edges of the shallow zone: indeed, the distance between each grid cell of turtle habitats in deeper zones and the nearest shallow zone was <4.2 km (median = 0.5 km) for green turtles and <7.1 km (median = 0.5 km) for loggerhead turtles (Figure 6.5). Therefore I calculated the proportion of habitats inside shallow zones and also inside areas of shallow zones with buffers up to 7.1 km extending toward deeper water.

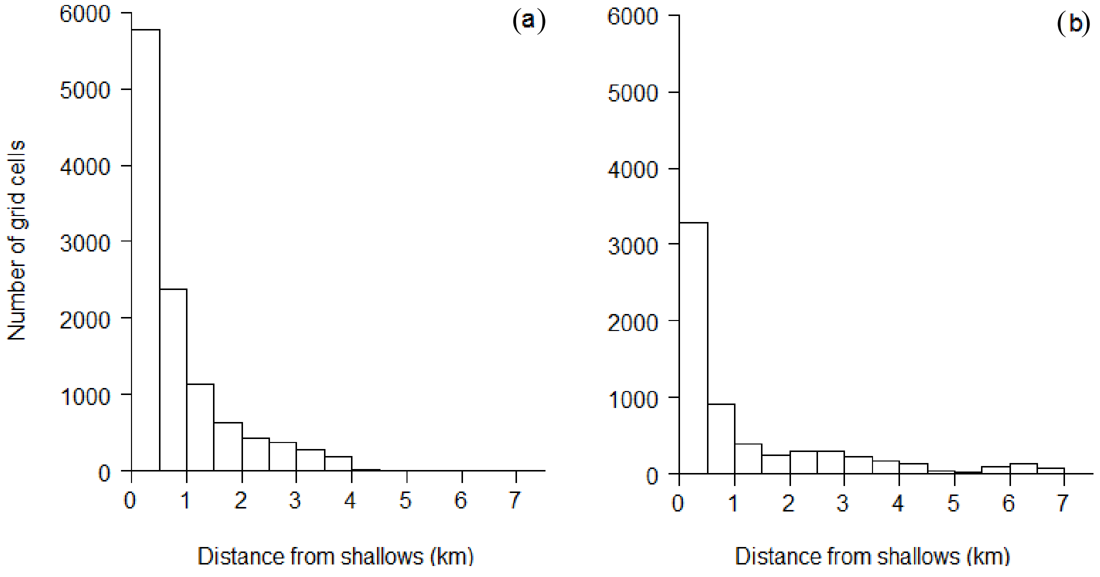

Figure 6.5 Frequency distribution of distance between each grid cell of turtle habitats in deeper zones (>5 m) and the nearest shallow zone (≤5 m) in (a) green turtles and (b) loggerhead turtles.

The shallow zone included 47%, 84% and 51% of habitats used by my tracked green turtles in eastern, southern and northern Moreton Bay respectively. Similarly, 59%, 77% and 85% of my tracked loggerheads' habitat were within the shallow zone in eastern, southern and western Moreton Bay respectively. My data indicate buffer widths required to increase the spatial extent of habitat protection to 80%, 90% and 95% of turtles' habitats were 1.2 km, 2.3 km or 2.9 km for green turtles, and 0.7 km, 2.4 km or 3.6 km for loggerhead turtles (Figure 6.6 & 6.7).

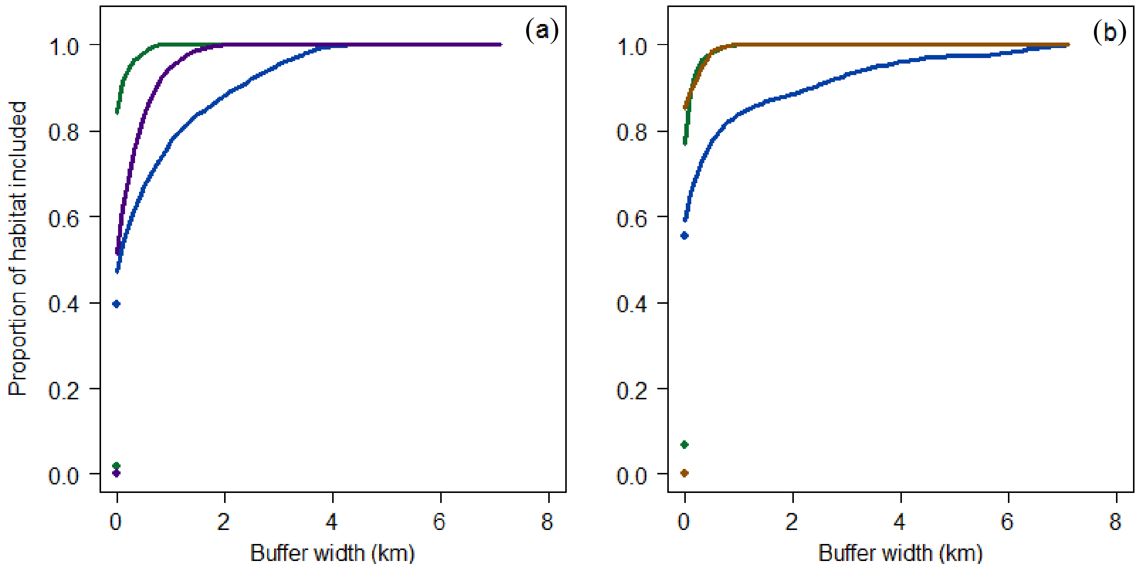

Figure 6.6 Proportion of home ranges within the Go Slow Zones (circles) and shallow zone (depth ≤ 5 m) with buffers ranging from 0 to 7.1 km (lines): (a) green turtles, (b) loggerhead turtles. Symbols are colour coded for different areas of Moreton Bay: east *blue*, south *green*, west *brown*, and north *purple*.

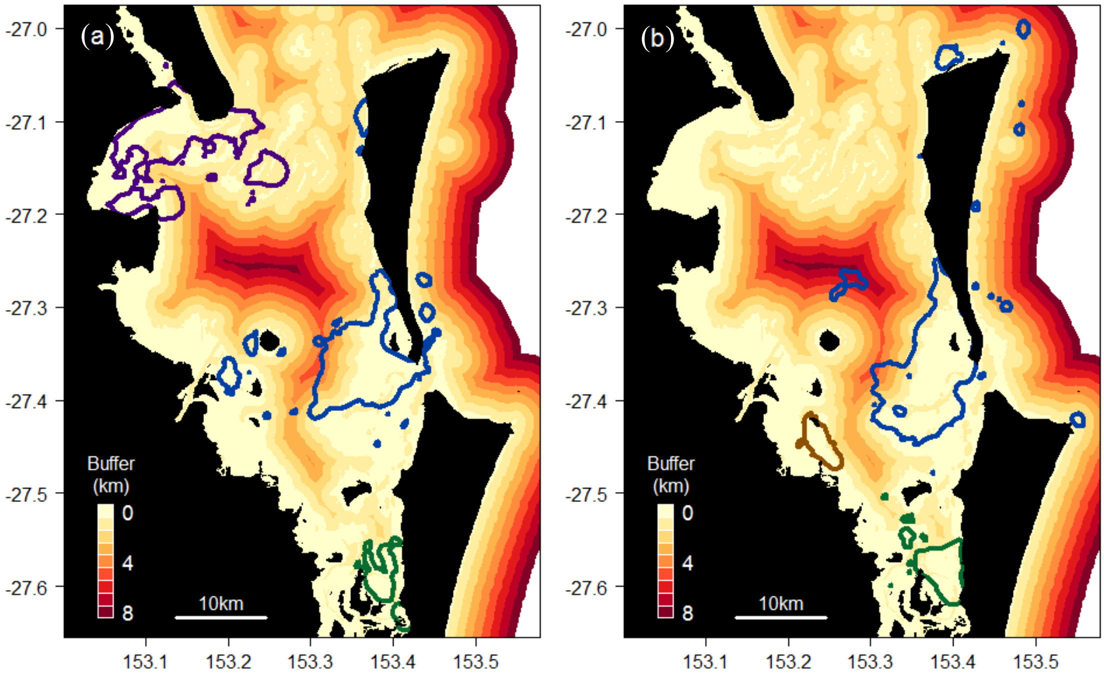

Figure 6.7 Foraging habitats (95% UDs) of (a) green turtles and (b) loggerhead turtles tracked in Moreton Bay, with relation to the shallow zones with buffer widths ranging from 0 km lightest yellow to 8 km darkest red. Contours are colour coded by turtles tracked in different areas of Moreton Bay: east blue, south green, west brown, and north purple.

6.4 Discussion

Moreton Bay is a significant foraging area for green and loggerhead turtles of eastern Australia (Limpus and Limpus 2001, Limpus 2008, Hazel et al. 2009) but the risk of boat strikes is high because of extensive recreational and commercial vessel traffic within the Bay. While exact locations of most vessel-related incidents are not known, management systems are in place in some shallow areas where high densities of foraging turtles and dugong (*Dugong dugon*) were known to occur and where animals with signs of vessel-related injuries were regularly recorded (Haines and Limpus 2001, Meager and Limpus 2012). Further, the Go Slow Zones intentionally were not declared over recognised navigation channels. Therefore current legislation only protects turtles that forage in some shallow water zones in eastern and southern Moreton Bay against vessel collisions. My findings highlighted that their home ranges extend beyond the protected shallow water zone and turtles residing outside of the Go Slow Zone remain exposed to boat strike. These, together with their high site fidelity (Chapters 3, 5), could explain why despite implementation of management restrictions, turtle-vessel interactions still occur in Moreton Bay.

Among turtles foraging outside the Go Slow Zones, those in the western side of Moreton Bay may be particularly vulnerable to boat strikes because various vessels travel in and out the large ports (e.g. Port of Brisbane) and marinas (e.g. Wynnum, Manly and Cleveland Bay). Additionally, water turbidity in the western Moreton Bay is often very high relative to the eastern side of Moreton Bay (Shimada, Limpus and Hamann, field observations), which, coupled with shallow waters, is likely to reduce the vessel operators' ability to avoid collision with turtles.

High use of shallow water zones by the study turtles may be associated with their diets. Herbivorous green turtles are likely to feed in shallow waters where seagrass (their main diet at the study site) is generally most abundant (Rasheed et al. 2014) particularly in turbid waters such as those in western Moreton Bay (Abal and Dennison 1996). Loggerhead turtles may forage in deeper waters but current evidence indicates their main habitats in Moreton Bay are situated within the shallow zones. For example, one loggerhead turtle with no prior capture history that was released at Mon Repos nesting beach, travelled to Moreton Bay and settled in the shallow zones of western Moreton Bay (Figure 6.3b). In another study, a loggerhead turtle, which was rescued while floating in Moreton Bay and so its precise foraging habitat was unknown, was released in north of Moreton Bay after rehabilitation and tracked back as it settled in the shallow areas of eastern Moreton Bay (Chapter 3). Therefore my tracked data are likely to represent general habitat use of green and loggerhead turtles in Moreton Bay.

If all shallow areas in Moreton Bay were designed as Go Slow Zones, we could expect approximately a half or more of the habitats of green and loggerhead turtles to be protected from vessel collisions in Moreton Bay. This proportion of protection is similar to that recommended for dugongs (Dobbs et al. 2008) which also feed on seagrass like green turtles and reside in Moreton Bay. Additionally a small increase in buffer areas around the shallow zones could provide more comprehensive protection. For example, shallow zones with a 1.2 km buffer showed to protect 80% or more of habitats of both species by covering deeper zones adjacent to the shallow zones. The addition of areas to the shallow zones will ensure more comprehensive protection for turtles from potential threats by vessel collisions in deeper zones adjacent to shallow zones.

However the benefit of additional areas around shallow zones cannot be estimated precisely because the risk of boat strike on turtles may be lower in the deeper zones (>5 m depth). In that case constraining vessel operation may not contribute to turtle conservation but substantially affect human activities. This is an important aspect to be considered because the intention of the Go Slow Zones is to provide protection to animals while minimising constraints to human activities. For example, the Go Slow Zones intentionally were not declared over recognised navigation channels adjacent to shallow zones such as Rous channel and the dredged channel into Toondah Harbour at Cleveland for the vehicle ferries and water taxis. My results identified some of those channels were within turtles' home ranges, so clearly the risk to turtles in those deeper zones must be assessed with particular caution when making legislative decisions.

Assessing the risk of vessel collisions on turtles in deeper zones requires horizontal and vertical movement data of turtles at fine-scale. Seasons and life stage of animals needs to be considered when collecting such data because surfacing behaviour of sea turtles may vary among seasons (Southwood et al. 2003, Hochscheid et al. 2005, Hochscheid et al. 2007, Hazel et al. 2009) or among different life stages, e.g. foraging and migration (James et al. 2006).

The FGPS tags can provide high resolution of horizontal movement data and a depth recorder can provide fine-scale dive data. However true horizontal positions of most dive recordings cannot be known because FGPS locations can be only acquired when a turtle surfaces to breath. Future research may use accelerometers coupled with FGPS tags and depth recorders, and employ dead-reckoning techniques to estimate the horizontal position of each dive recording (Bidder et al. 2015, Walker et al. 2015, Wensveen et al. 2015). Alternatively acoustic telemetry can provide concurrent horizontal and vertical information to recreate three-dimensional movements of sea turtles (Hindell et al. 2002, Simpfendorfer et al. 2012, Udyawer et al. 2015) provided that acoustic receivers are stationed across the range of interest (e.g. deeper zones adjacent to shallow zones).

To balance protection of species with human use, the Go Slow Zones may be refined by focusing on protection to species which require most conservation efforts. The green turtle population in eastern Moreton bay is increasing, although there is boat strike mortality in the channels and adjacent deeper zones to the go-slow zones (Limpus, unpublished data). Therefore conservation management of the species can be considered to be working. Contrarily loggerhead turtles are in decline in eastern Moreton Bay (Limpus, unpublished data), so more protection is required to improve the conservation outlook for loggerhead turtles. My findings provide an evidence-based guidance for prioritised conservation management.

Other species of sea turtles may occupy the deeper zones of Moreton Bay but their risks of boat strikes are unknown. An olive ridley turtle (*Lepidochelys olivacea*) rescued from Moreton Bay was released in north of the capture site but settled in deeper zones of Moreton Bay adjacent to the capture location (Chapter 3). Other olive ridley, flatback turtles (*Natator depressus*) and hawksbill turtles (*Eretmochelys imbricata*) have been also captured in deeper zones of Moreton Bay by trawling (Robins and Mayer 1998). Future studies can use acoustic telemetry or FGPS tags coupled with depth and acceleration sensors to assess potential vulnerability of olive ridley, flatback and hawksbille turtles in Moreton Bay, which are species of conservation concern (Chapter 1).

Dugongs are also victims of vessel collisions in Moreton Bay (Marsh et al. 2011) although the current Go Slow Zones aim to protect both sea turtles and dugongs (Queensland Government 2008). While both green turtles and dugongs feed on seagrass in shallow coastal waters, dugongs tend to use larger areas of habitat than green turtles along the Queensland coast (Gredzens et al. 2014). The wider home range may increase the risk of collisions between vessels and dugongs. Given the increasing need to protect dugong (Marsh 2008), future studies may simultaneously track both species, or collate tracking data from both species to determine and compare how much protection is given to dugongs and green turtles by the current Go Slow Zones, and how they can be improved as a management tool if adequate protection is not provided.

Lastly the Go Slow Zone policy may need to be adaptive to accommodate new data and to acknowledge temporal changes in trend of species abundance, habitat environment and anthropogenic activities (Pressey et al. 2007). Continuous assessment of those parameters combined with habitat use is vital to maintain the optimal balance between human use and conservation of marine resources in Moreton Bay including threatened sea turtle species.

6.5 Chapter Summary

- Vessel collision is a major threat to sea turtles residing in coastal waters. Moreton Bay in southeast Queensland, Australia is an important foraging habitat for several species of threatened sea turtles, but being situated adjacent to the largest urban population of Queensland, vessel operations in the bay are high.
- To mitigate vessel collision some of the Bay’s shallow water zones (water depth ≤ 5 m) are legislated as vessel “Go Slow Zones” to protect turtles from vessel collision. Yet despite this legislation most vessel collision incidences in Queensland still come from Moreton Bay indicating the current Go Slow Zones may not be providing adequate spatial protection to sea turtles.
- To examine the efficiency of the Go Slow Zones to protect sea turtles in Moreton Bay I tracked green and loggerhead turtles using Argos-linked FGPS tag and investigated their space use in relation to the Go Slow Zones and water depth.
- I found most habitats used by my tracked turtles were in the shallow waters and up to 55% of their habitats were included within the Go Slow Zones in the eastern Moreton Bay.
- However, turtles are not protected from vessel collisions in the deeper zones (water depth > 5 m), which lie adjacent to the Go Slow Zones, or in other shallow water zones in Moreton Bay. In particular, little or no protection is given to sea turtles in southern, western and northern Moreton Bay.
- By designating all shallow areas in Moreton Bay as Go Slow Zones, we could expect nearly a half or more of the Bay’s turtle habitats to be protected from vessel collisions. Additionally my data indicate that shallow zones plus a 1.2 km, 2.4 km, or 3.6 km buffer would protect ≥80%, ≥90% or ≥95% habitats used by both species because they cover the deeper zones adjacent to the shallow zones.
- The results of this study are highly informative to conservation managers when revising the current Go Slow Zones for improved management of these threatened sea turtle populations.

Chapter 7

General Discussion

Spatial ecology investigates mechanisms of nature by examining the spatial patterns (Tilman and Kareiva 1997, Collinge 2010, Rai 2013), and empirical-based knowledge in spatial ecology will improve our approaches to conservation management of wild animals (Pressey et al. 2007, Agardy et al. 2011). Historically, investigation on spatial ecology of wild animals have been challenging due to methodological limits particularly in the marine environment. In the early 1970s a technological breakthrough was made by the emergence of satellite telemetry, which provided researchers with almost unlimited temporal and spatial range to monitor animal movements (Gillespie 2001, Godley et al. 2008, Hazen et al. 2012). Additionally state-of-the-art analytical techniques, coupled with software and hardware to execute them, have enhanced our capacity to improve accuracy of location estimates, and to explore animal movements and their association with various environmental and biological factors in depth (e.g. Barraquand and Benhamou 2008, Bailey et al. 2012, Jonsen et al. 2013). In my research, I was able to build upon existing systems and technologies to advance the ability of animal telemetry to improve our knowledge of spatial ecology of sea turtles and inform conservation planning.

The first substantial advances into satellite-linked telemetry used PTTs (Seegar et al. 1996). These tags provided location accuracy from <250 m out to over a kilometre (CLS 2011). These crude location estimates made them useful tools for investigating broad scale movement such as animal migration and less useful for researchers investigating movements at finer scales. Although locations were crude, analytical techniques such as Bayesian state-space models were developed to improve accuracy of location estimates (Jonsen et al. 2013). In the late 2000s location accuracy was substantially improved with FGPS tags. However while FGPS tags provided more accurate location data some FGPS fixes are inaccurate (Hazel 2009). In chapters 2 and 3 I overcame this challenge by developing a data-driven filter with additional filtering options to objectively screen FGPS data in a biologically and technologically sensible manner. As a result FGPS locations with high error can now be identified and removed while accurate positions are retained. The advance in processing satellite-derived data delivers an improved ability to analyse fine-scale movements of animals.

Understanding fine-scale patterns of animal movement is important because once movement patterns are identified, we can explore the ecological meaning of their behaviour by investigating what factors are affecting them. Recently there have been substantial efforts by ecologists to objectively identify fine-scale patterns of animal movements such as residence time analysis and Bayesian state-space models (Jonsen et al. 2005, Barraquand and Benhamou 2008). Essentially some techniques are more suitable than others according to the type of data collected and its resolution. After I improved data processing I used various spatial and statistical techniques to analyse movement patterns and their relationship with various environmental and biological factors (Chapters 3, 4, 5), and applied my knowledge of sea turtle behaviour to conservation planning (Chapter 6).

For the remainder of this chapter, I first provide summary of key findings of this thesis. I then discuss synthesis of turtle behaviour, followed by its conservation implications. Finally I outline opportunities for future research.

7.1 Summary of thesis findings

7.1.1 Thesis objective 1

To improve tracking data by developing an objective method to identify and remove FGPS fixes with high error

To achieve this objective, I explored potential filtering approaches and tested the performance of each option by comparing the differences between filtered FGPS locations and true locations. I found the data-driven approach based on the speed between successive locations, angles created by three consecutive locations, manufacturer's quality index, and number of satellites used for location calculation provided a screening method which significantly improved accuracy of my FGSP data set while retaining most accurate estimates (Chapter 2). The data-driven filter was used in the subsequent chapters prior to any ecological and conservation-based analyses. I also developed the R package SDLfilter to execute the screening techniques, and made the package available to the public (https://github.com/TakahiroShimada/SDLfilter).

7.1.2 Thesis objective 2

To examine the effects of human-induced displacement on sea turtles for their selection of foraging habitat, and to investigate the underlying mechanism of their homing navigation by a detailed examination of their tracks

I first investigated whether or not displaced sea turtles normally return to the foraging habitat where they were first captured, and the factors that influence turtle behaviour following their displacement and release (Chapter 3). After documenting the tracks of each turtle as it returned to its area of capture following displacement, I analysed track data to investigate how homing navigation might work as turtles swam through unfamiliar waters (Chapter 4).

To enable the analysis I used data from my field research in combination with satellite telemetry data made available to me from other researchers and rehabilitation centres. The combined dataset allowed me to investigate turtles' behaviour following displacement while observing the behaviour of non-displaced turtles as controls.

Some of the extra data, especially that collected from southern Queensland areas, introduced additional analytical challenges because many data were low resolution Argos fixes. I overcame the issue by improving the accuracy of Argos location estimates using Bayesian state-space models (Jonsen et al. 2006). The extensive amount of satellite telemetry data obtained from four species of sea turtles (113 tracks) confirmed that displacement up to 117.4 km and captivity up to 514 days did not disrupt homing ability nor diminish fidelity to the home area.

An additional analysis challenge I faced in Chapter 3 was to allow for the influence of tides because many of the turtles were using the inter-tidal habitats. To address this, I developed additional methods for screening FGPS fixes which were estimated to be landward of high tide lines. I also introduced an objective way to select a fix from temporally or spatially duplicated fixes. The new filtering functions were added to the SDLfilter package.

In Chapter 3, I also demonstrated an objective way to delineate tracks of displaced turtles before and after they returned to their home foraging habitats. The FGPS data obtained during homing journey (tracks before arriving at resettlement area) enabled me to analyse their behaviour in relation to the environmental and biological factors. The analyses used GLMs and GLMMs to demonstrate that displaced green and loggerhead turtles travelled faster and followed straighter paths in cooler water (Chapter 3).

In Chapter 4, I further analysed the homing tracks of displaced turtles to gain insight into their navigation mechanisms through waters presumably unknown to them. Using the residence time method (Barraquand and Benhamou 2008), I first identified sea turtles tended to alternate stationary and travelling phases during their trip home. I then conducted a chain of analyses to investigate the patterns of individuals homing movements in spatial and temporal perspectives. My novel analytical approach revealed that sea turtles tended to halt and reassess before making course corrections, with corrections predominantly occurring at sunrise. This was the first study to demonstrate time-restricted orientation by sea turtles and provided a new insight into their sophisticated navigational abilities.

7.1.3 Thesis objective 3

To investigate home range and site fidelity by sea turtles in their coastal foraging habitat, and how the current Go Slow Zones are related to their habitats in Moreton Bay

Fidelity to foraging habitat is clearly demonstrated by sea turtles (Chapters 1, 3). In Chapter 5, I investigated the size of foraging habitats, how long they maintain site fidelity, and what factors may affect size of home range and site fidelity. Based on satellite telemetry data coupled with mark-recapture history, I confirmed that green and loggerhead turtles foraging along Queensland coast can maintain high fidelity to their foraging habitats for 16 years or possibly more. Analyses using GAMMs also revealed that those turtles generally shifted their main foraging areas on a seasonal basis within their long-term foraging habitats. During my research, a series of tropical cyclones and higher than average rainfalls occurred along the Queensland coast, and sea turtle strandings (dead or alive) increased around five-fold when compared to that of previous years since 2000 (Meager and Limpus 2012). However I found turtles in eastern Moreton Bay and eastern Port Curtis maintained their home range size and site fidelity regardless of the extreme weather events, indicating the high conservation values of those habitats.

High density of foraging sea turtles can be found in Moreton Bay (Limpus 2008). The Bay is also known as a hotspot for boat strikes although vessel operation is regulated in some areas (Hazel and Gyuris 2006, Limpus 2008). In Chapter 6, I investigated whether the current Go Slow Zones are providing adequate protection to sea turtles foraging in Moreton Bay. I found up to 55% of habitats were included within the Go Slow Zones in eastern Moreton Bay but turtles in the deeper zones (water depth >5 m) adjacent to the Go Slow Zones and other shallow zones in Moreton Bay are not protected. Since turtle habitats are mainly in shallow zones and deep zones adjacent to the shallow zones, I estimated shallow zones with a 1.2 km, 2.4 km, or 3.6 km buffer would protect ≥80%, ≥90% or ≥95% habitats of green and loggerhead turtles in Moreton Bay.

7.2 Synthesis of turtle behaviour

In chapters 3 to 5, my thesis focused on (1) behaviour after displacement and mechanisms of homing behaviour, and (2) fidelity to, and seasonal shifts in habitats for sea turtles foraging in subtropical and tropical coastal habitats. In this section, I will discuss my findings in the context of broader literature. I will also provide some hypotheses to potentially explain the movement patterns.

7.2.1 Homing behaviour and navigation

Sea turtles remain in their foraging habitats for many decades, often only moving out to undertake breeding migrations. The ability of sea turtles to migrate between foraging and nesting habitats with a high degree of accuracy and repeatability among years is now well established (Plotkin 2003). Less well known are the factors that underpin an individual's ability to navigate over short distances, to remain in familiar habitats and to return to familiar habitat if displaced. Staying within familiar habitats appears a high priority for sea turtles tracked in my study sites given the long-term site fidelity and their persistence to returning to their 'home' habitats after displacement and long-term retention (Chapters 3, 5). Their ability to accurately identify their position and a direction to their habitat is clearly important for maintaining their site fidelity among dispersed habitats, and also to returning to their home habitat when displaced.

In Chapter 4, I identified that green and possibly loggerhead turtles may use sunrise-related navigational cues to pinpoint directions toward their target destination. If the sun's position on the horizon is used for sea turtles' navigation, it might be expected that sea turtles obtain similar navigational cues at sunset as seen in some birds and bats (Alerstam 1990, Bovet 1992). However cues acquired at sunrise are likely to be more useful to sea turtles than sunset-related cues because turtles tend to be more active during the day than at night (Hazel 2009, Chapters 3, 4), and directional corrections were predominantly made around sunrise (Chapter 4).

One of the potential sunrise-related cues is the obvious eastwards marker. Many other animals also obtain directional cues from the sun position but terrestrial and avian animals can use sun compass throughout a day by compensating for the sun's daily movement (Wiltschko and Wiltschko 2009, Guilford and Taylor 2014). There was no evidence that sea turtles made directional corrections during the day except at sunrise. This difference indicates either sea turtles do not have the time compensation ability or they use other sunrise related cues rather than simply an eastwards marker.

If turtles use sunrise as an eastwards marker, they may make better corrections around the equinoxes than around the solstices. This is particularly true in higher latitudes because the sun rises exactly east on the equinoxes whereas it rises north of true east during summer or south of true east during winter where deviation from true east is largest on the solstices, due to the tilt of the Earth's axis relative to its orbit around the sun. My sample size was too small to test the relationship between corrections and time of year. Nonetheless if directional corrections were related to latitude and time of year, it would be a strong indication of turtles' use of sunrise as eastwards marker.

If corrections at sunrise do not vary throughout a year it would indicate sea turtles could compensate the seasonal drift of sunrise direction by referring to their internal biological clock, or they could use other cues that occur at sunrise irrespective of seasons. Turtles might also use multiple navigational cues to compensate inaccuracy or lack of preferred cues (Avens and Lohmann 2003, Lohmann et al. 2013).

In addition to potential navigational cues as discussed in Chapter 4 (i.e. acoustic, polarized light and chemical cues), sea turtles may also use underwater features such as submerged reefs as navigational cues in shallow coastal waters. However it is difficult to imagine how sea turtles would obtain directional or positional cues from features which they have never seen. Nonetheless testing this hypothesis with the data set used in my PhD research would require higher resolution of bathymetry models to represent the complex benthic structure at my study sites.

7.2.2 Site fidelity and seasonal shifts in foraging habitats

My research has confirmed that green and loggerhead turtles residing in coastal Queensland waters show strong fidelity to their foraging habitat, and that, olive ridley and hawksbill turtles may show the same trend (Chapter 3). Moreover, fidelity of green, loggerhead and olive ridley turtles persisted even after human-induced displacement and long-term retention (Chapters 3, 5). My findings strongly support the hypothesis of long-term fidelity to foraging habitat by sea turtles in Queensland waters.

Site fidelity of Queensland sea turtles appear to be substantially stronger than that of sea turtles residing in other regions, in which turtles make long-distance seasonal or/and developmental movements (Chapter 1). Although seasonal shifts in habitats occurred in green and loggerhead turtles foraging in Queensland waters (Chapter 5), the extent of the shifts seen in my study were very small compared to hundreds to thousands of kilometres of seasonal movements which have been documented in other population of sea turtles (Morreale and Standora 2005, Mansfield et al. 2009, Narazaki et al. 2015).

Long-distance seasonal movements are often seen in temperate waters (Musick and Limpus 1997, Morreale and Standora 2005, Mansfield et al. 2009, Narazaki et al. 2015), and there is accumulating evidence of relationship between water temperature and sea turtle movements in temperate foraging habitats (Hawkes et al. 2007, Hawkes et al. 2011, Schofield et al. 2013a). The current theory hypothesises that sea turtles in temperate climate move to higher latitudes during warmer months to look for “better” feeding opportunities, and leave for warmer habitats at the end of summer to avoid cold water (Morreale and Standora 2005, Mansfield et al. 2009, Narazaki et al. 2015). However this theory does not explain why seasonal migration predominantly occurs in turtles foraging in temperate waters. If food resources and water temperature are the drivers of turtle’s seasonal movements, turtles in tropics and subtropics would also be expected to make latitudinal movements between summer and winter to acquire “better” feeding opportunities, but long-distance seasonal movements are much less common in turtles foraging in those warmer waters.

Here I propose an alternative hypothesis to potentially explain why long-distance seasonal movements of sea turtles occur predominantly in temperate waters. Rather than assuming that seasonal migration is driven by cold stress and geographical variation of food resources (often positively related with latitude), it could be driven by combination of cold stress and behaviour related to imprinting; i.e. perhaps turtles remain in their “home” foraging habitat unless they are forced to move away. If a sea turtle is imprinted to foraging habitat in temperate waters of high latitude, the turtle would need to move toward warmer waters during winter to avoid cold syndrome, dormancy or death (Schwartz 1978, Ogren and McVea 1995). As water temperature rises, they would return to the original temperate foraging habitat to which they are likely “imprinted”. This may also explain why sea turtles in subtropical and tropical waters generally do not make long-distance foraging movements, simply because the warm climates allow turtles to remain in the same “home” foraging habitat throughout a year.

7.3 Conservation implications

Many populations of marine turtles, including those in Australia, are conservation-dependent due to past and present anthropogenic threats (Chapter 1). Those threats vary among locations and species, and thus effective conservation planning requires empirical-based knowledge for each species at specific location (Hooker and Gerber 2004, Lourie and Vincent 2004).

Through investigating the spatial ecology of sea turtles, I demonstrated the importance of understanding turtle behaviour in relation to conservation initiatives. In addition, protecting their important foraging habitats should be a priority for long-term conservation management because sea turtles in Queensland will remain in particular foraging habitats for many years (Chapter 5) and their behaviour will persist even after displacement into unknown waters following short and long-term retention (Chapter 3). The long-term site fidelity and lack of response to adverse environmental events also indicate turtles can persist through periods of lower productivity of Queensland coastal waters and unpredictable weather events that influence habitat.

Spatially based management, such as MPAs, can be a powerful approach to achieve conservation goals while providing sustainable use of the environments by humans. However conservation goals of protected areas are compromised in many cases because protected areas are often (1) not established using empirical data as a base and consequently spatial extent of protected areas and the habitat or species they aim to protect do not match, (2) not established specifically to protect single species, even those of conservation concern, and (3) struggle to balance environment protection with human use. Using foraging sea turtles in Moreton Bay as a case study, I demonstrated how spatial analyses on empirical data can improve our understanding of issues related to existing regulations and offer ways to improve the protection by adjusting the protected areas according to the patterns of animal use and the spatial distribution of habitats as functions of environmental and biological factors (Chapters 5, 6).

I identified seasonal shifts in foraging habitat for green and loggerhead turtles in the subtropical waters along Queensland coast (Chapter 5). This is an important point to be considered for ecological research, particularly in the climates where seasons can significantly affect environmental variables such as temperature and food abundance. For these reasons, conservation management should ideally be based on studies which use data collected across all seasons, or over a range of environmental gradients to identify habitats of animals required for protection, otherwise adequate protection may not be provided during unstudied seasons.

Recent satellite-transmitters have capacity to remain operable for 1 year or even more (e.g. Hays et al. 2014b, Chapter 5), but transmission from satellite tags can be unexpectedly ceased within a shorter period of time (Hays et al. 2007). The latter was also the case for some tracks used in this thesis. I overcame the issue by tracking turtles in different seasons so my tracking data generally cover all seasons. I also demonstrated an approach to estimate representative UDs by incorporating differences among individuals and seasons while minimising the potential effects of sample size on UD estimation (Chapter 6). My approach may be applicable to other research which aim to estimate representative UDs of animal habitats for both conservation and research purposes.

7.4 Future research

My thesis revealed some behavioural patterns of sea turtles and their association with some environmental and biological factors. I have also highlighted their application for conservation. However there were limitation in my research, which future research could investigate further to enhance our knowledge of sea turtle ecology. Suggested research directions are outlined below.

7.4.1 Turtle behaviour

Human-induced displacement

I provided strong evidence that sea turtles return to their home foraging habitat after human-induced displacement (Chapter 3) but some questions remain unanswered. The risk to vessel collision may increase if a turtle was released in an area with high vessel traffic. Extra energy expenditure required for their homing trip may have affected their fitness during the trip and after resettlement. Although almost all turtles released in multiple location along Queensland waters, including Moreton Bay and Port Curtis where vessel traffic is known to be high, successfully returned to their home foraging habitat and survived during the tracking period, future research is encouraged to quantify the risk and energy expenditure related to human-induced displacement, and how it may affect turtle fitness such as survivorship and reproduction.

Navigation

Animal navigation is a hot topic in biology but the underlying mechanisms are still cryptic for many groups of animals. I analysed movement patterns of green and loggerhead turtles in detail and, for the first time, found sunrise-related cues to be crucial components of fine-scale navigation of green turtles (Chapter 4). Similar results were inferred for loggerhead turtles but larger sample size is required to be conclusive. It would be valuable to analyse tracks with known target destinations to examine whether other species of sea turtles or any other animals use similar environmental cues.

Multiple potential cues have been proposed to aid turtles for their navigation in addition to well-studied geomagnetic cues (Papi 1992, Lohmann et al. 2013, Chapter 4). To test potential navigational cues, future study needs to use laboratory experiments to test each potential variable in control environments as demonstrated by previous studies (e.g. Lohmann et al. 1999, Avens and Lohmann 2003, 2004, Lohmann et al. 2004). Most importantly, geomagnetic field needs to be controlled to delineate the effects of geomagnetic cues from other potential navigational cues.

I also suggested a potential influence of benthic features in sea turtle navigation. This hypothesis can be tested once high resolution of bathymetry data becomes available to researchers. Alternatively, researchers could experimentally track turtles in shallow coastal waters where structure of substrata is less complex and resolution of existing bathymetry data is suitable to represent the benthic feature of the study site.

Seasonal effects on homing behaviour

Displaced sea turtles travelled faster in cooler water during their trip home (Chapter 3). This finding was unexpected because the studied sea turtle species are ectothermic animals whose metabolisms slowdown in cooler waters (Spotila et al. 1997). As discussed in Chapter 3, I could not conclude whether the behaviour was driven by water temperature or other seasonally varied variables such as food availability. The effects of potential variables can be also tested in indoor environments by controlling geomagnetic field, water temperature, timing of sunrise, photoperiod and amount of food.

Seasonal shifts in foraging habitat in subtropics

The large amount of FGPS dataset enabled me to find evidence for high fidelity and seasonal shifts in foraging habitat by adult green and loggerhead turtles (Chapter 5). High fidelity behaviour of juvenile turtles has been also inferred based on previous mark-recapture studies (Chapter 1). Juvenile sea turtles may respond more sensitively to cooler water due to their smaller body mass and so may show less fidelity behaviour than adult turtles. Quantification of fidelity behaviour and seasonal shifts in foraging habitat for juvenile sea turtles require more samples of their detailed movement data as used in Chapter 5 (e.g. FGPS data).

Within the long-term foraging habitats, it is important to understand what causes sea turtles to make seasonal shifts. As discussed in Chapter 5, the turtles’ movement may be dependent on distribution and abundance of food resources which vary among seasons. It is also possible that the behaviour was in response to changes in water temperature (e.g. escaping from cold water) because both acute and seasonal changes in water temperature appear to affect diving behaviour and metabolic rate of sea turtles with an exception of leatherback turtles (see Southwood Williard 2013). Testing these hypotheses on seasonal movements of sea turtles in relation with environmental factors requires concurrent observation of turtle movements, food distribution/abundance, and high resolution water temperature data of their habitat, all ideally at horizontal and vertical scales.

Seasonal shifts in foraging habitat in temperate climate

In eastern Australia, sea turtles are also known to feed in the higher lattitude, along the coast of New South Wales and possibly Victoria (Limpus 2008) but their detailed foraging behaviour such as potential seasonal movements and site fidelity is not known. Except for the northern New South Wales, sea turtles in the higher lattitudes may need to make long-distance seasonal foraging movements to avoid dormancy or death during cold months. Those turtles in temperate waters may migrate northwards to warmer foraging habitats along New South Wales and Queensland waters or to deep off-shore as seen in other temperate waters (Morreale and Standora 2005, Mansfield et al. 2009, González Carman et al. 2012, Narazaki et al. 2015). Monitoring their movements across seasons (e.g. using Argos-linked FGSP) is required to investigate site fidelity and seasonal habitat use of sea turtles residing in the temperate waters of eastern Australia.

Basking behaviour

Some green turtles foraging in south-eastern Queensland are known to remain above water in the intertidal zones at low tide (Limpus et al. 2005, Strydom 2009). This behaviour was also detected in my FGPS data in Cardwell, Shoalwater Bay and Gladstone (Shimada et al. 2013, Shimada et al, unpublished data) but the details of their basking behaviour and its ecological meaning are poorly understood.

Green turtles of Galapagos, Hawaii and Wellesley archipelagos are also known to bask on the beach predominantly during the day (Balazs 1980, Snell and Fritts 1983, Limpus 2008). While factors that underpin basking behaviour are largely unknown, a recent study found that Hawaiian green turtles basked most frequently during winter (Van Houtan et al. 2015). Therefore their basking behaviour is assumed to be related to the sun, potentially to aid thermoregulation, digestive efficiency or synthesis of Vitamin D (Balazs 1980, Van Houtan et al. 2015).

The sun-related reasons are however unlikely for green turtles foraging along Queensland coast because basking behaviour were observed predominantly at night both during winter and summer (Shimada et al. 2013). Other hypothesised reasons for basking behaviour are to (1) avoid predation, (2) rest, (3) conserve energy, (4) eliminate epibiotic parasite, (5) increase immune function, (6) avoid unwanted courtship, or (7) aid egg development (Balazs 1980, Whittow and Balazs 1982, Swimmer 2006). Since the latter two reasons do not apply for foraging turtles, future research should investigate the possibility of the first five potential reasons for the nocturnal basking behaviour of green turtles residing in Queensland coast.

7.4.2 The ecosystem which supports sea turtles

Habitat loss

Habitat loss is a major cause of species extinction in the terrestrial environment (Ehrlich 1994, Pimm and Raven 2000, Purvis et al. 2000). It is expected that loss of foraging habitat may also have negative effects on marine animals but little of it is documented (Millennium Ecosystem Assessment 2005, UNEP 2006) largely due to difficulties in conducting such investigation in marine environments. For example, the seagrass communities of the Great Barrier Reef (GBR) are facing both anthropogenic and natural pressures such as agricultural/urban/industrial catchment runoff, development, increasing intensity of cyclones and rainfall, rise of sea temperature and sea level (Waycott et al. 2005, Waycott et al. 2007, GBRMPA 2011, Petus et al. 2014, York et al. 2015). Seagrass meadows are significant habitats and food resources for variety of species in GBR and other regions but the impacts of changes to seagrass on the resident animals have not been well explored (see Bjorndal and Jackson 2003, Marsh et al. 2011). Understanding the effects of habitat loss on marine species is vital to enhance our ability to manage habitats and to prevent species extinction in marine environments.

Sea turtles may be particularly impacted by habitat destruction in marine environments because they show such strong fidelity to their home habitats (Chapters 3, 5). For example, expansion at the Port of Brisbane required construction of a 4.6 km seawall enclosing 230 ha of sub-tidal land for future reclamation (Ameratunga et al. 2005). This was a foraging area for many green turtles and they had to be captured and displaced to other parts of Moreton Bay (J. Hazel, personal communication). These turtles may have made an attempt to return to the original habitats given their strong fidelity to their “home” habitat (Chapter 3). However their habitat was no longer accessible, so the turtles may have settled near their original habitats which were converted to be part of the port. In that case, turtles would be exposed to new threats such as collisions with vessels going in and out of the ports, and changed locations of food. Another concern is the impact to the ecosystem in the new habitats where displaced turtles settle in. The original residents, not only turtles but also other animals including large herbivores like dugongs, have to compete with the new settlers over limited food. The increased competition may cause exploitation of the food sources, and is likely to disturb the balance of ecosystem. I recommend future research to prioritise the effects of those potential disturbance to ecosystem caused by anthropogenic habitat destruction.

Ecological role of sea turtles

The role of sea turtles in the ecosystems is poorly understood. It was assumed that sea turtles had had significant effects in marine ecosystems before their population severely declined by anthropogenic activities (Bjorndal and Jackson 2003). Yet there have been few experimental studies. Understanding the ecological role of sea turtles is important for ecological and conservational reasons. As large fauna, either an increase or decrease in populations could result in substantial effects on their food sources, predators and competitors (Bjorndal and Jackson 2003) and the condition of their habitat. At least two studies now have highlighted increasing turtle numbers as hindering seagrass recovery and thus having other ecological impacts (Lal et al. 2010, Christianen et al. 2014). Identification of the interaction between sea turtles and the neighbouring environments and organisms will enhance our understanding on marine ecosystems. These ecological knowledge can then assist researchers and conservation managers to improve conservation planning.

In Chapters 3 and 4, I identified high fidelity to foraging habitat by depleted population of sea turtles. Given that growth rate and body condition of green turtles are negatively associated with population density (Bjorndal et al. 2000), fidelity behaviour may not persist once the consumption of food resources exceeds the carrying capacity of their habitats. Long-term studies of population dynamics and movements of foraging sea turtles are required to test the effects of population density on site fidelity and its impact on ecosystems.

7.5 Concluding remarks

Understanding mechanisms of nature is key to appreciating their values and informing effective conservation planning. However it has been challenging to untangle the complex structure of nature particularly in marine environments. The new technology and analytical tools I adopted in this thesis enabled me to overcome the difficulties associated with investigating marine animal movements and consequently to improve our understanding of their relationship with environmental variables. The approach I demonstrated has applications for investigating spatial ecology of other animals including other population of sea turtles. I would recommend research embracing those modern tools and techniques to find ways to improve our relationship with nature, and most excitedly to discover wonders of nature.

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Appendix

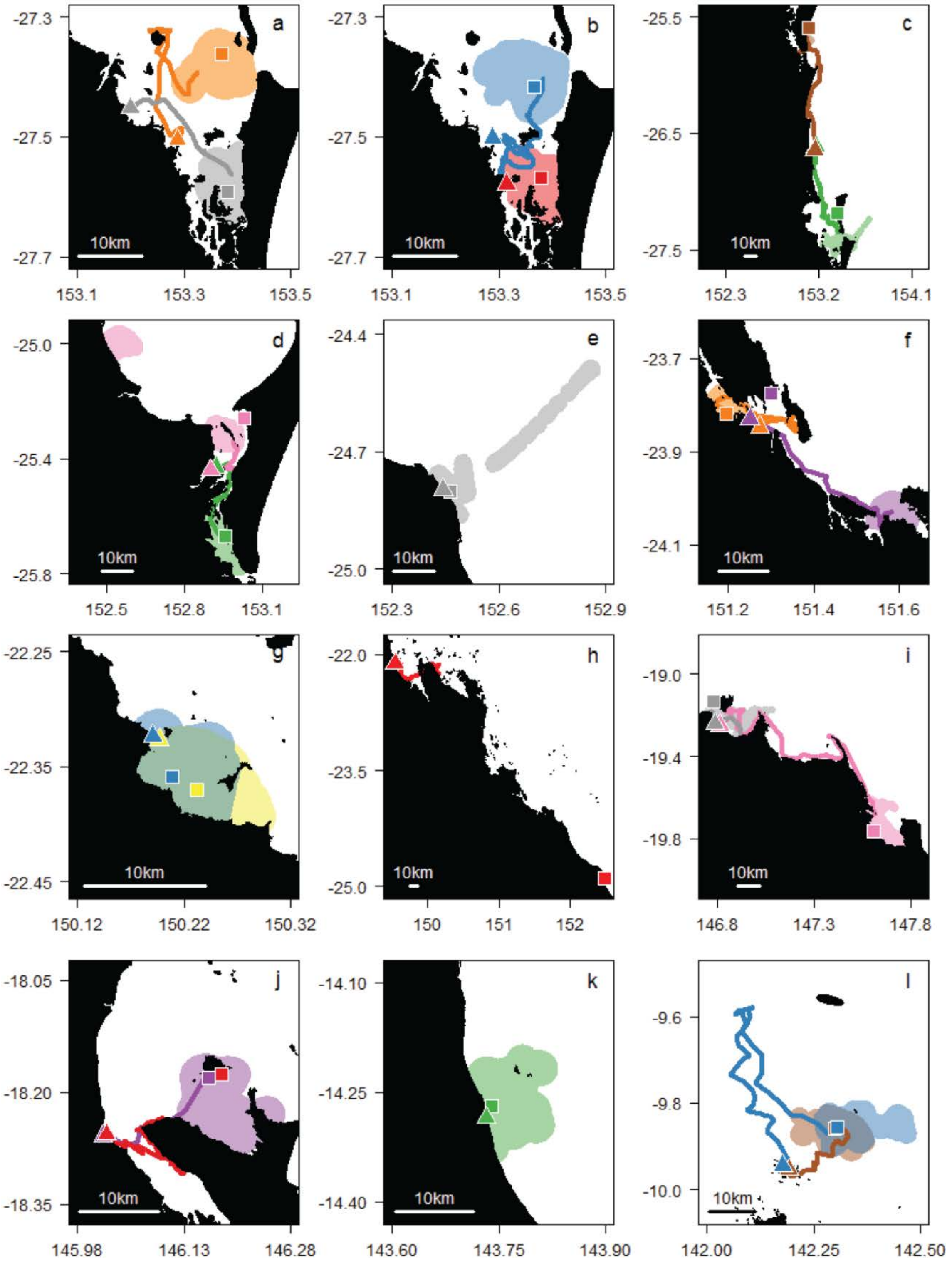

Figure A1 Representative examples of study turtle tracks after release at diverse sites. Square = capture location, triangle = release location, line = travelling path of displaced turtles, coloured polygon =resettlement area. The symbols are colour-coded for each turtle.

At sites where more than two turtles were tracked (i.e. sites 1, 3, 6, 7, 9, 11), only two tracks are presented for clarity. Site numbers correspond to release sites marked in Figure 3.1. **a** [Site 1] Both green turtles were displaced and they travelled back to their areas of capture. **b** [Site 1] One loggerhead turtle *blue* was displaced and travelled back to its the area of capture. Another loggerhead turtle *red* was not displaced and remained within the area of capture. **c** [Site 2] The olive ridley turtle *brown* and the loggerhead turtle *green* were found debilitated and displaced after rehabilitation. Both turtles moved toward their areas of capture but their resettlement areas did not include the capture locations. **d** [Site 3] Both green turtles were displaced. One turtle *green* returned to the area of capture. The other turtle *pink* moved towards the area of capture but the resettlement area did not include capture location. **e** [Site 4] The green turtle was not displaced and remained in the area of capture. **f** [Site 5] Both green turtles were displaced. One green turtle *orange* returned to the area of capture. The other green turtle *purple* resettled away from the capture location. **g** [Site 6] Both green turtles were not displaced and remained in the areas of capture. **h** [Site 7] The loggerhead turtle was displaced. The turtle moved toward the area of capture but the transmission ceased *en route*. **i** [Site 8] Both green turtles were found debilitated and were displaced after rehabilitation. One turtle *pink* returned to its area of capture. Another turtle *grey* moved closer to its capture location but the resettlement area did not include the capture location. **j** [Site 9] Both green turtles were displaced. One turtle *purple* returned to its area of capture. The other turtle red moved toward its area of capture but transmissions abruptly ceased while it was travelling. **k** [Site 10] The green turtle was not displaced and remained in its area of capture. **l** [Site 11] Both green turtles were displaced and returned to their areas of capture.

Table A1 Metadata for sea turtles tracked by satellite tags. CCL is curved carapace length. Age is maturity status (A = sexually mature adult, J = immature juvenile). Site numbers correspond to release sites marked in Figure 3.1. Relocation is a straight-line distance between capture and release sites. Status (D = displaced, ND = not displaced) was inferred by comparing release sites to resettled habitat as described in '3.2.3 Classification of displaced and non-displaced turtles'.

Turtle ID	Argos ID	Tag type	CCL : cm	Sex	Age class	Site	Displacement distance: km	Days retained	Released year/month	Days tracked	Status
Chelonia mydas											
K24369	54553	GPS	96.1	M	A	1	17.2	1	2013/06	132	D
K25713	88073	GPS	114.6	F	A	1	18.5	1	2008/11	23	D
K34861	2858	PTT	66.1	F	J	1	20.0	0	2007/09	113	D
K36347	88076	GPS	115.7	F	A	1	18.0	1	2008/10	66	D
K40305	2859	PTT	100.8	M	A	1	38.3	2	2002/08	338	D
K40464	7222	PTT	105.7	M	A	1	4.5	2	2002/06	59	ND
K63374	88077	GPS	105.3	F	A	1	18.2	2	2008/10	121	D
K86116	88074	GPS	112.0	F	A	1	17.7	1	2008/10	61	D
K90544	41563	PTT	51.0	-	J	1	3.6	<1	2007/10	429	ND
K92598	88075	GPS	110.5	F	A	1	18.6	2	2008/10	71	D
QA11722	48855	GPS	113.0	F	A	1	3.6	2	2010/05	86	ND
QA11747	48861	GPS	101.6	F	A	1	3.9	1	2010/05	428	ND
QA18333	96776	GPS	106.5	F	A	1	23.7	1	2011/08	132	D
QA23607	72448	GPS	108.5	F	A	1	19.2	1	2011/09	157	D
QA23646	48840	GPS	119.9	F	A	1	2.0	1	2011/09	157	ND
QA3228	48862	GPS	107.0	F	A	1	1.8	1	2011/05	262	ND
QA34298	54529	GPS	94.0	M	A	1	15.9	1	2013/06	108	D
QA4279	88075	GPS	107.3	F	A	1	1.4	1	2011/02	328	ND
QA4969	48845	GPS	112.5	F	A	1	19.4	2	2011/04	354	D
T5561	48841	GPS	110.6	F	A	1	19.7	2	2011/04	313	D
T13734	48852	GPS	109.4	F	A	1	0.2	1	2011/05	249	ND
T53786	2858	PTT	100.7	M	A	1	14.2	2	2002/09	134	D
T84474	48855	GPS	111.7	F	A	1	17.5	2	2011/05	320	D
K79044	7224	PTT	107.1	F	A	3	6.3	2	2006/07	177	ND
QA23117	48884	GPS	121.2	F	A	3	23.2	1	2011/07	566	D
QA23188	88077	GPS	106.1	F	A	3	27.0	1	2011/07	512	D
QA23196	96775	GPS	107.8	F	A	3	6.3	1	2011/07	354	ND
QA23200	96774	GPS	106.1	F	A	3	8.1	1	2011/07	260	D
T54322	88072	GPS	108.8	F	A	3	21.9	1	2011/07	250	D
T69943	88074	GPS	113.2	F	A	3	26.8	1	2011/07	187	D
T22737	41563	PTT	68.8	M	J	4	2.0	3	2010/07	131	ND
K70229	133767	GPS	105.7	F	A	5	4.9	1	2013/11	249	ND
K93085	72448	GPS	51.3	-	J	5	8.1	1	2010/07	213	D
K93086	96781	GPS	85.6	M	J	5	14.0	1	2010/07	179	D

K93087	96777	GPS	104.3	M	A	5	14.0	1	2010/07	241	D
K93088	96778	GPS	92.2	M	A	5	14.0	1	2010/07	222	D
QA13938	134182	GPS	95.4	M	A	5	5.9	1	2014/05	174	ND
QA32523	133762	GPS	49.1	-	J	5	3.7	1	2013/11	47	ND
QA33327	133765	GPS	96.5	M	A	5	8.6	1	2013/11	73	ND
QA33335	134180	GPS	89.0	F	A	5	8.0	1	2014/05	96	D
QA33342	133764	GPS	111.0	F	A	5	8.9	1	2013/11	122	ND
QA33348	133769	GPS	107.3	F	A	5	8.6	1	2013/11	58	ND
QA33349	133759	GPS	42.6	-	J	5	7.4	1	2013/11	145	D
QA33350	133763	GPS	42.1	-	J	5	7.0	1	2013/11	46	ND
QA33368	133760	GPS	46.0	-	J	5	8.6	1	2013/11	67	D
QA33394	133758	GPS	43.6	-	J	5	6.6	1	2013/11	105	D
QA34529	133761	GPS	47.9	-	J	5	8.6	1	2013/11	61	D
QA36875	134178	GPS	97.6	M	A	5	8.4	1	2014/05	164	ND
QA43023	133770	GPS	102.7	F	A	5	9.0	1	2013/11	72	D
QA43063	133768	GPS	93.5	M	A	5	5.3	1	2013/11	71	ND
QA43066	133766	GPS	105.7	F	A	5	5.3	1	2013/11	72	ND
QA45408	134179	GPS	103.3	M	A	5	5.3	1	2014/05	88	ND
QA45524	134183	GPS	101.7	F	A	5	6.4	1	2014/05	168	ND
QA45554	134184	GPS	116.6	F	A	5	1.0	1	2014/05	172	ND
QA45566	134188	GPS	110.9	F	A	5	7.8	1	2014/05	101	ND
QA45601	134185	GPS	79.0	-	J	5	8.3	1	2014/05	166	D
QA45627	134181	GPS	63.1	-	J	5	5.8	1	2014/05	173	ND
QA45654	134186	GPS	50.2	-	J	5	1.6	1	2014/05	160	ND
QA45689	134187	GPS	102.5	M	A	5	7.8	1	2014/05	120	D
T83097	96780	GPS	104.4	F	A	5	12.9	1	2010/07	400	D
K55740	96780	GPS	97.3	F	A	6	4.1	1	2012/07	781	ND
QA27532	120641	GPS	95.5	F	A	6	4.6	1	2012/07	144	ND
QA28798	120640	GPS	102.1	F	J	6	6.8	1	2012/06	265	ND
QA30008	108472	GPS	100.5	F	A	6	3.7	1	2012/06	412	ND
QA30012	96777	GPS	96.1	F	A	6	4.3	1	2012/07	582	ND
QA30108	108469	GPS	104.5	F	A	6	4.6	1	2012/06	180	ND
K93022[a]	95890	GPS	107.5	F	A	8	100.9	175	2011/03	253	D
QA29559[a]	108471	GPS	107.0	F	A	8	1.2	170	2012/03	274	ND
QA34823[a]	109194	GPS	98.0	M	A	8	11.8	514	2013/10	116	D
K89289	109193	GPS	95.2	F	A	9	18.0	1	2011/11	57	D
K89296	108470	GPS	89.1	F	A	9	19.2	1	2011/11	31	D
K89297	109194	GPS	92.0	F	A	9	17.4	1	2011/11	40	D
QA7313	108468	GPS	110.0	F	A	9	11.2	<1	2011/10	15	D
QA7335	54527	GPS	100.2	M	A	9	17.4	1	2011/11	68	D
QA39448	140116	GPS	91.4	M	A	10	1.9	1	2014/09	42	ND
QA7011	95891	GPS	102.1	F	A	11	25.6	1	2009/07	204	D
QA7075	95889	GPS	98.0	F	A	11	28.1	1	2009/07	122	D
QA7207	70455	GPS	118.0	F	A	11	16.6	1	2010/09	144	D
QA7435	95892	GPS	105.6	F	A	11	16.0	1	2010/09	164	D

Caretta caretta											
K17100	7222	PTT	99.5	M	A	1	1.4	2	1998/09	122	ND
K24365	54529	GPS	97.5	M	A	1	6.2	1	2010/05	280	ND
K35079	7223	PTT	100.9	M	A	1	15.1	3	2001/10	17	D
K77301	7223	PTT	73.3	F	J	1	2.1	<1	2007/10	599	ND
K77335	45886	PTT	82.3	F	J	1	3.2	<1	2007/10	21	ND
K96000	95889	GPS	92.9	M	A	1	13.7	1	2013/03	177	D
QA14215	54527	GPS	94.4	M	A	1	20.6	1	2010/06	294	D
QA2746	108470	GPS	94.8	M	A	1	17.0	1	2013/03	164	D
QA34296	95890	GPS	85.5	F	A	1	26.9	1	2013/04	220	D
QA34297	95892	GPS	95.2	F	A	1	23.4	1	2013/04	571	D
T462	70455	GPS	98.9	F	A	1	12.3	1	2013/03	71	D
T14914	26040	PTT	91.1	F	A	1	0.0	3	1996/09	292	ND
T23158	48850	GPS	98.6	F	A	1	6.5	1	2010/09	414	ND
T50812	26043	PTT	87.8	F	A	1	6.5	3	1996/09	156	ND
T50968	26039	PTT	91.0	F	A	1	7.7	4	1996/08	67	D
T53732	7224	PTT	90.7	M	A	1	1.4	2	1998/09	150	ND
T53798	41563	PTT	95.0	M	A	1	16.6	4	2003/05	159	D
T53800	7223	PTT	93.5	M	A	1	2.0	2	1998/09	150	ND
T53800	54528	GPS	93.9	M	A	1	18.3	1	2010/06	915	D
T71600	96781	GPS	92.0	M	A	1	1.4	1	2012/05	306	ND
T74361	95890	GPS	100.7	M	A	1	4.3	2	2010/05	133	ND
T74362	88075	GPS	87.4	F	A	1	7.2	1	2009/07	276	ND
T79127	26042	PTT	94.6	M	A	1	2.6	2	1998/09	92	ND
T85300	26041	PTT	98.4	F	A	1	2.4	2	1996/05	516	ND
T89701	54531	GPS	97.0	M	A	1	1.2	1	2010/10	316	ND
T92001	26042	PTT	99.1	F	A	1	0.9	2	1996/05	218	ND
T93045	5196	PTT	94.7	F	A	1	1.7	2	1998/09	4	ND
T94668	95891	GPS	87.9	M	A	1	18.4	1	2013/03	100	D
T94860	26039	PTT	93.5	M	A	1	4.3	2	1998/09	157	ND
K93555[a, b]	88078	PTT	101.1	M	A	2	64.8	69	2009/06	531	D
QA12903	45888	PTT	74.9	F	J	7	432.1	1	2010/01	54	D
Lepidochelys olivacea											
QA34683[a]	127681	PTT	51.5	-	J	2	117.4	198	2013/05	11	D
QA34684[a]	127682	PTT	56.0	-	J	2	64.6	121	2013/05	112	D
Eretmochelys imbricate											
K90512	45888	PTT	38.1	F	J	1	5.4	5	2007/10	166	ND

[a] The turtles were found debilitated and retained in rehabilitation facilities prior to release.

[b] The data was obtained from the open access Zoatrack.org repository (Dwyer et al. 2015).

Table A2 Parameters used in the BRB function of the R pacakge adehabitatHR to estimate the utilisation distribution of study turtles. For details of the function and each parameter, see the vignettes of the package (Calenge 2015a) and the relevant literature as cited in the table.

Parameter	Value	Rationale
D: diffusion coefficient	Estimated using the maximum likelihood method using the BRB.likD function	See Horne et al. (2007).
Tmax: the maximum duration allowed for a step built by successive fixes	14 hours	The 95th percentile of the intervals between successive fixes for 113 tracks used in Chapter 3. Also see Benhamou and Cornélis (2010) and Benhamou (2011).
Lmin: the minimum distance between successive fixes	50 m	The estimated mean error of the filtered high-quality location data (Chapter 2). Also see Benhamou (2011).
hmin: the minimum smoothing parameter	100 m	Greater than the standard deviation of the estimated error of the filtered high-quality location data (Chapter 2) and approximately equal to the resolutions of the bathymetry data used as a boundary of turtle movements. Also see Benhamou and Cornélis (2010) and Benhamou (2011).
type: the type of distribution to return	“UD”	Having the function return the utilization distribution.
grid: the size of the grid	A raster layer specifying the areas below high tide line as plausible turtle habitat	See 3.2.2 Data preparation. Also see Benhamou and Cornélis (2010).

Table A3 Parameters used in the residenceTime and the lavielle functions of the R pacakge adehabitatLT to divide each track of study turtles into travelling or stationary periods. For details of the functions and each parameter, see the vignettes of the package (Calenge 2015b) and the relevant literature as cited in the table.

Parameter	Value	Rationale
Function: residenceTime		
radius: the radius of a given circle centred at each observed location	300 m	Three times "hmin" (100 m - Table A2) as suggested in Barraquand and Benhamou (2008) and Benhamou and Riotte-Lambert (2012) for detailed analyses.
maxt: the maximum time spent by the animal outside the radius before it was considered having left the area	8 hours	The 95th percentile of the intervals between successive fixes for 29 tracks used in Chapter 4. Also see Benhamou and Cornélis (2010) and Benhamou (2011).
Function: lavielle		
Lmin: the minimum number of observations in each track segment	2	I considered each track segment to have more than single observation.
Kmax: the maximum number of segments expected in each track	The number of observations divided by 2 (Lmin)	The maximum number of segments expected in each track (Kmax) is dependent on the minimum number of observations in each track segment (Lmin).
type: the type of contrast function to assess differences among each track segment	"mean"	I assumed that state of each track segment (i.e. travelling or stationary) differs if the means of the segments are statistically different (Lavielle 2005).