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Flatbacks at sea:
Understanding ecology in foraging populations

Thesis submitted by

Natalie E. Wildermann

Lic. Biology, Universidad del Zulia
MSc Biological Sciences (Major: Aquatic Ecology), Universidad del Zulia

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James Cook University

"Look deep into nature, and then you will understand everything better"

Albert Einstein

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"It always seems impossible until it's done"

Nelson Mandela

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Ethics Statement

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Reports

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Barrios-Garrido H., Bolivar J., Benavides L., Viloria J., Dugarte F., Wildermann N (2017). Evaluación de la pesquería de palangre artesanal y su efecto en la raya látigo (*Dasyatis guttata*) en Isla Zapara, Golfo de Venezuela. Lat. Am. J. Aquat. Res, 45(2), 302-310. doi:10.3856/vol45-issue2-fulltext-6

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Espinoza Rodríguez N., Vernet P., Morán L., Barrios-Garrido H., Wildermann N (2014). Primer reporte de la actividad de anidación de tortugas marinas en la costa nor-occidental del Golfo de Venezuela. Boletín del Centro de Investigaciones Biológicas, 47(1).

Thesis Abstract

To assess the current conservation status of a species, we first need to have a good understanding of how the individuals are distributed in time and space. The latter is the focus of fields such as biogeography and conservation biogeography when applied to inform conservation decision-making. The distribution of a species will be influenced by innumerable factors, from large-scale processes such as dispersal and migration, to the local variability in environmental parameters, inter- and intra-specific interactions and ultimately the effect and intensity of natural and human-induced changes. In the marine realm, currents and wind promote connectivity among sometimes far-spread habitats. While large physical barriers are limited, the distribution of marine species is often influenced by physic-chemical barriers (i.e. thermoclines, photic zone). As a result, marine habitats tend to be highly dynamic in time and space, which in turn influences the diversity and distribution of marine species.

In tropical environments and in particular in the tropical shallow waters of the Indo-West Pacific region, habitats are characterised by very high diversity of species with relatively broad geographic ranges. This is particularly true for migratory marine megafauna, such as whales and marine turtles, which can distribute across 100 to 1000s of km. Such large-scale movements pose a great challenge to monitor their movements and identify habitats used by the populations. However, the advancement of tracking technologies (i.e. acoustic and satellite tracking), animal borne-videos, accelerometers and molecular techniques such as stable isotope analysis, have enabled great advances in the understanding of marine megafauna biogeography.

The general biogeography of marine turtles has been extensively studied worldwide. The distribution of nesting grounds of all marine turtle species is very well described, and while less is known on their foraging distribution and ecology, there is still an extensive body of work in this field. As migratory species, marine turtles make use of a great variety of coastal and oceanic habitats throughout their life, which vary between and among species and populations. Ontogenic, seasonal and reproductive changes in habitat use have been widely described, and are a common feature in all species. In general, biogeography of marine turtles is influenced by local and oceanic currents, distribution and abundance of prey, presence of predators, availability of shelters and seasonal shifts in water parameters (i.e. temperature). Nevertheless, improving the knowledge on biogeography of local populations, especially on the distribution of non-reproductive turtles, is still one of the global research priorities for marine turtles.

In Australia, the foraging distribution and ecology of green, loggerhead and hawksbill turtles has been well described, because these species inhabit shallow coastal habitats, typically with clear water and relatively easy access for research. In contrast, knowledge on the foraging ecology of leatherback, olive ridley and flatback turtles in Australia is limited. Some aspects of the foraging ecology of leatherback and olive ridley turtles can be inferred from studies on other populations in the world, and recent advances have been published on the migration and foraging distribution for flatback turtles in Western Australia. In my thesis, I provide new and novel information on the distribution of non-reproductive flatback turtles in eastern Australia. In particular, the aim of my thesis was to improve our understanding of the biogeography and ecology of flatback turtle across different life-stages, with the intention to generate scientific information to improve the state of knowledge of the species and provide relevant outputs to inform management actions for conservation.

First, in Chapter 2, I assessed a key process in understanding the biogeography of marine turtles: the early dispersal of post-hatchlings. In particular, I examined the potential mechanisms that underpins the neritic dispersal of post-hatchlings flatback turtles. Long-term records of post-hatchling flatback turtles are evidence of the neritic dispersal of the species, and studies on hatchling swimming behaviour and particle simulation have provided insights on the evolutionary adaptations of this species to turbid coastal waters. To explain the lack of oceanic dispersal of this species, I employed a hydrodynamic advection-diffusion model (called SLIM) to simulate the dispersal of virtual post-hatchlings under different scenarios of passive drift and active swimming behaviour. The results of my simulations suggest that, under the conditions I tested, the retention of flatback turtles in neritic waters of the Great Barrier Reef (GBR) depends on three main factors: (a) the location of the nesting beaches: flatback turtles nest in inshore islands and mainland of eastern Queensland; (b) the local currents, wind-driven waves and the tidal phase when post-hatchlings were released; and (c) swimming behaviour of post-hatchlings, with higher swimming effort dispersing turtles into neritic habitats of the GBR. In this chapter, I also provide future directions for research in the area of early dispersal of marine turtles, and potential approaches to test the cues that induce directional swimming in marine turtles.

Next, in chapters 3 and 4, I examined two other key biogeographical processes: migration and habitat use of foraging adult turtles. Chapter 3 focused on describing the spatial distribution of 44 flatback turtles tracked with high accuracy GPS-linked satellite tags, from eight different nesting beaches to their respective foraging grounds. Home ranges of flatback turtles in eastern Australia were relatively larger than other coastal marine turtle species in the region. I also describe common patterns in the migratory and foraging strategies displayed by the tracked turtles. In this sense, flatback turtles in eastern Australia displayed direct and multi-stop migrations, and flexible and dynamic foraging behaviour (i.e. using more than one foraging ground).

To supplement the understanding of the spatial ecology of foraging turtles, in Chapter 4 I further examined the distribution of the tracked turtles in relation to the environmental parameters of the seabed habitats which they inhabit. Such studies are not common in marine environments, given the challenge that represents comprehensively surveying the habitat used by individuals. However, data on the biotic (prey) and abiotic characteristics of the seabed habitats used by flatback turtles in the Great Barrier Reef were available and accessible through the GBR Seabed Biodiversity Project. Employing a Random Forest analysis, I was able to assess how the tracked turtles respond to abiotic parameters in the environment, as well as to the distribution and abundance of potential prey groups. The results confirm that flatback turtles inhabit inshore subtidal habitats, with a preference for mud-rich inshore environments. In addition, the tracked flatback turtles were associated with distribution of soft-bodied invertebrates such as sea pens and soft corals; however, flatback turtles might as well be associated with a wider variety of benthic prey than previously reported. The flexibility observed in foraging behaviour, combined with the large size of home ranges and the association of the tracked turtles to multiple habitat types and prey items suggest that flatback turtles in eastern Australia are generalist and opportunistic feeders. Nevertheless, some turtles displayed high affinity for just one of the three habitat types, which might suggest some degree of individual specialisation within the population, a hypothesis that warrants further research.

Finally, in chapter 5 focused on quantifying the exposure of flatback turtles to different threats and the level of protection in their foraging habitats within the Great Barrier Reef Marine Park (GBRMP). To achieve this, I performed a spatial analysis overlapping the foraging area identified for the tracked flatback turtles (Chapter 3) with the distribution of marine protected areas, as well as with two potential threats known to occur in the GBRMP, shipping and trawling. I also considered the cumulative exposure of flatback turtles to the combined threats. The results indicate that half (52.2%) of the foraging area of the tracked turtles is within a marine protected area, 47.3% was located in “General Use” areas, and 0.5% were located within ports. In addition, the overall exposure of the tracked turtles to the individual and cumulative effect of shipping and trawling was low, with some foraging locations in the northern section of the GBRMP displaying medium exposure to the threats. I strongly suggest that future research should aim to include the synergistic effect of threats, and include other human-related stressors, such as water quality and marine debris.

Overall, my thesis provides detailed and novel information which improves the knowledge base on the spatial distribution of flatback turtles in eastern Australia, including aspects on their dispersal, migratory and foraging behaviour and ecology. My thesis is relevant to several priority action areas required to maintain/recover the eastern Australia flatback stock. In this sense, I have already been able to provide copies of my data, shapefiles and written work to the GBR Marine Park Authority and the Australian Government and my data has informed the revised Marine Turtle Recovery Plan 2017. In conclusion, my study provides a comprehensive baseline on the spatial and movement ecology of flatback turtles at sea, and will hopefully provide the guidelines to address further gaps that need to be addressed to gain a better understanding of the status, vulnerability and adaptive capacity of flatbacks of the eAus stock.

Table of Contents

List of Tables

List of Figures

Chapter 1

General Introduction

Image of a flatback hatchling heading towards the sea at Mon Repos in December 2013.

Photo credits: Hector Barrios-Garrido

1.1. Biogeography in an ecological and conservation context.

Environmental management decisions are driven by the need to mitigate the impact of natural and anthropic pressures on the ecosystem's values and functions (Guisan *et al.*, 2013). Decision-making relies on the appropriate identification of areas where conservation problems might be in place. Conservation biogeography aims at providing scientific foundation on the distribution of species for conservation decision-making. Whittaker *et al.* (2005) defined this field as "the application of biogeographical principles, theories, and analyses, being those concerned with the distributional dynamic of taxa individually and collectively, to problems concerning the conservation of biodiversity".

Biogeography entails all possible processes that drive the spatial distribution of species, and can be focused at a variety of spatial and temporal scales (Whittaker *et al.*, 2005). Studies on biogeography have been approached from two main perspectives: the historical and ecological distribution of species. Historical biogeography focuses on species distribution at evolutionary time-scales and how it influenced the known distribution of species (Crisci *et al.*, 2009). In contrast, ecological biogeography focuses on the current distribution of species and how present environmental factors drive patterns in distribution (Crisci *et al.*, 2009).

In the marine realm, vicariance and dispersal are considered as two of the main forces that shape biogeographical patterns (Carpenter, 1998; Kohn, 1983). Vicariance acts at evolutionary scales (historical biogeography) often resulting in allopatric speciation (Ronquist, 1997); vicariant events in the ocean include geo-tectonic movements, and changes in the climate (i.e. winds) and currents which can restrict the distribution of a species (Carpenter, 1998). Dispersal and migration have a larger effect on the ecological biogeography of marine species and are of great importance in colonisation-extinction relationships (Kohn, 1983).

Based on the current biogeographical features and patterns in marine biodiversity, the world's oceans have been classified in distinctive biogeographic regions (Briggs & Bowen, 2012). Relevant to this study is the Indo-West Pacific (IWP) region. Within the IWP, tropical shallow water habitats are characterised by very high diversity of species with relatively broad geographic ranges (Kohn, 1983). The ecological biogeography of marine species can be however particularly challenging to assess. The limited physical barriers within the aquatic realm provide a world of extensive connectivity among habitats. Instead, physic-chemical barriers, such as thermoclines, pycnoclines, haloclines, photic/aphotic zones, among others, limit marine species. As a result, marine habitats are highly dynamic in both spatial and temporal scales, and this variability can directly influence the diversity and distribution of marine species.

In addition to the complexity of the physical environment, it is often difficult to directly observe and monitor the interactions between marine species and their environment, especially in the case of highly mobile species. Migratory marine megafauna, such as whales and marine turtles, typically display wide-spread distributions (over 100 to 1000s of km). Factors that limit their distribution can vary throughout their life-cycle and include complex interactions among physical parameters (e.g. salinity, temperature), physical forces (e.g. currents, winds), ecological processes (e.g. dispersal, foraging, competition) and ultimately the effect of natural and human-induced changes in the environment (Benoit-Bird *et al.*, 2013; Block *et al.*, 2011; Sequeira *et al.*, 2014; Wolanski, 2016). Indeed, improving the knowledge on biogeography has been identified as one of the global research priorities for marine turtles (Hamann *et al.*, 2010).

As migratory species, the ecological biogeography of marine turtles includes a diversity of coastal and/or oceanic habitats, including but not limited to breeding areas, foraging grounds and migratory pathways. The distance between such habitats varies between and among species and populations, and can range from a few tens to thousands of kilometres. Furthermore, ontogenic changes in the migration and foraging habitat use are also evident across marine turtle species (Musick & Limpus, 1997; Okuyama *et al.*, 2009; Scott *et al.*, 2014). In general, some of the variables that influence the biogeography of marine turtle are the local and oceanic currents during the early life-stages (Hays *et al.*, 2010; Lohmann *et al.*, 2013; Luschi *et al.*, 2003), availability and abundance of prey, presence of predators (Heithaus, 2013) and shelter (Christiansen *et al.*, 2017), and seasonal shifts in water temperature (Hawkes *et al.*, 2007; Hawkes *et al.*, 2011; Shimada *et al.*, 2016a). Some of these aspects have been explored for marine turtles of Australia (i.e. Hazel *et al.* (2012); Shimada *et al.* (2016a)), but more in-depth studies on what drives the distribution of non-reproductive turtles is still needed for multiple species.

In Australia, there is extensive scientific information on the distribution and ecology of reproductive (specially nesting and inter-nesting) life-stages of the six marine turtle species -green (*Chelonia mydas*), loggerhead (*Caretta caretta*), hawksbill (*Eretmochelys imbricata*), leatherback (*Dermochelys coriacea*), olive ridley (*Lepidochelys olivacea*) and flatback turtles (*Natator depressus*)- distributed across the country (Limpus, 2009a). In addition, the diet and population dynamics of green, loggerhead and hawksbill turtles has been well described because they live in shallow near-shore habitats with clear water and thus capture-mark-recapture studies are possible (all species: Limpus (2009a); hawksbill turtles: Bell and Pike (2012)). However, there are still significant knowledge gaps on the distribution and ecology of foraging turtles of leatherback, olive ridley and flatback turtles (Commonwealth of Australia, 2017; Limpus, 2009a). Because the leatherback and olive ridley turtle are global species, an understanding of the biology of Australian populations can be inferred from studies elsewhere in the world. The flatback turtle is an

Australian endemic species and thus there is a need for Australian-based research. Relevant to flatback turtles in eastern Australia, the 2014 Vulnerability Assessment developed by the GBR Marine Park Authority (GBRMPA, 2014b) and the 2017 Recovery Plan for Marine Turtles in Australian Waters (Commonwealth of Australia, 2017) both highlight the need of improving the knowledge on migratory, foraging and breeding areas of the population. Thus, improving our understanding on flatback dispersal, distribution, migratory and foraging ecology, exposure/vulnerability to threats and protection coverage is essential to inform management actions relevant to the species at national, regional and local scales.

In the following sections, I provide a summary of the current knowledge on flatback turtles highlighting the most relevant information gaps, and describe the theoretical framework to understand the rationale of my PhD research. In particular, I will assess the ecological biogeography of the flatback turtle through spatial analysis approaches, focusing on how environmental parameters and animal behaviour influence ecological processes like dispersal, migration and foraging.

1.2. The flatback turtle: synthesis of current knowledge and gaps

Flatback turtles are the only marine turtle endemic to the Australian continental shelf. Their rookeries (nesting sites) are restricted to the tropical coast of Australia, from Exmouth in northern Western Australia across northern and eastern Australia to Mon Repos in southern Queensland (Figure 1.1) (Limpus, 2007). Foraging flatback turtles of all life-stages have been recorded mostly in Australian neritic (inshore) waters, with scattered records of adult turtles feeding in Indonesia and the Gulf of Papua (Dermawan, 2002; Hamann *et al.*, 2015; Limpus, 2007; Spring, 1982). Flatback turtles display an entirely neritic life-cycle, a unique aspect among marine turtles (Limpus, 2007; Walker & Parmenter, 1990). All other marine turtle species exhibit developmental stages in oceanic waters at least during part of their life-cycle (Bolten, 2003a).

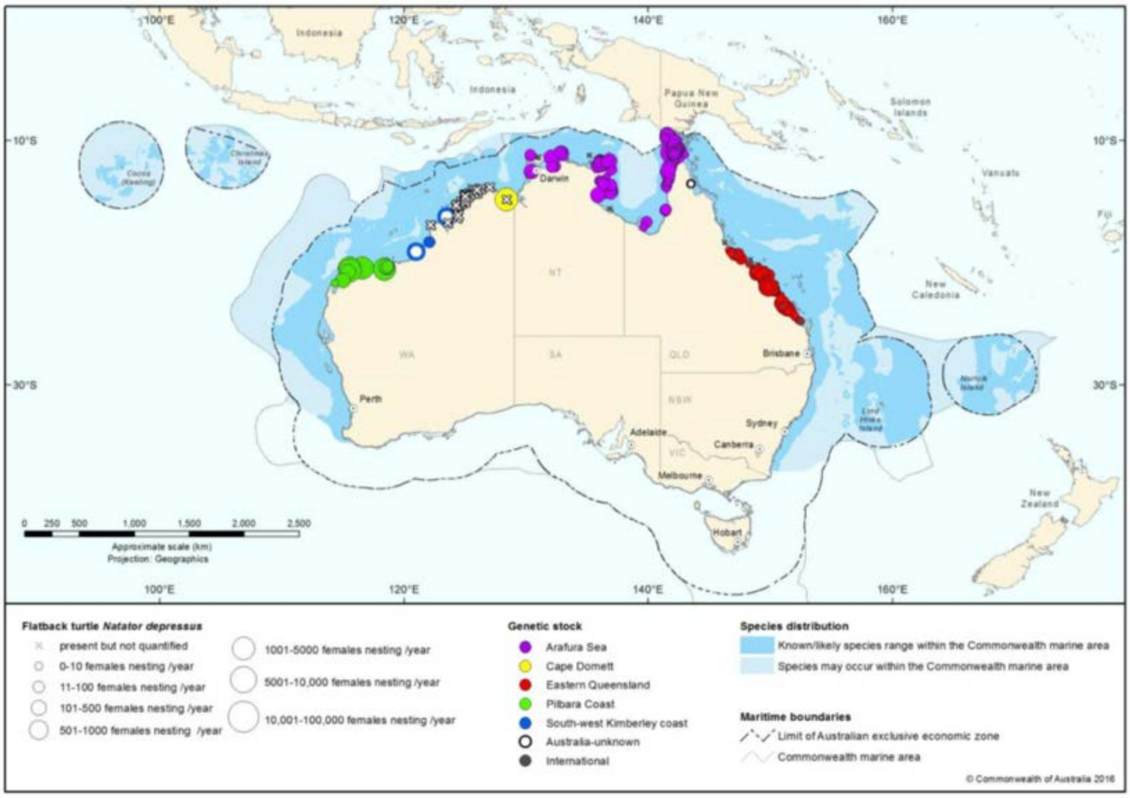

Figure 1.1. Spatial distribution of flatback rookeries in Australia. Colours indicate each genetic stock. Size of circles indicate the number of nesting females per year. Extracted from: (Commonwealth of Australia, 2017).

Flatback turtles display a variety of phenotypic and behavioural traits consistent with adaptations to an inshore living. For example, the body size of hatchlings is relatively larger compared to other marine turtles (Figure 1.2), resulting in larger energy reserves stored in their yolk sac. Hence, they develop a longer swimming frenzy (2-3 days) (Salmon *et al.*, 2009) but with less stroke power than other turtle species (Pereira *et al.*, 2011), probably favouring a short-distance neritic distribution. Flatback turtle hatchlings also display behavioural traits that could potentially result from adaptations to habitats with low visibility (typical of inshore habitats in the Great Barrier Reef), such as short exposures to the surface, slow dives, and higher reaction capacity relative to green, which could increase their chance of escaping predators (Salmon *et al.*, 2010).

Figure 1.2. Hatchlings of three different marine turtle species (from left to right): loggerhead, green and flatback turtles.

Marine turtles spend most their life-cycle at in-water habitats, where they use a diversity of habitats for foraging. Thus, identifying the distribution of marine turtle foraging grounds as well as understanding their foraging ecology is crucial to effectively manage and protect their populations. For flatback turtles, the distribution and ecology of foraging turtles remains largely unknown. To date, the characteristics of flatbacks' foraging grounds have been qualitatively described as sandy and/or muddy grounds in shallow waters. Diet items collected from a small number of stranded adult flatbacks include a variety of soft-bodied invertebrates (e.g. members of the classes Holothuroidea (sea cucumbers), Anthozoa (soft corals), Gastropoda (cuttlefish), among others), suggesting mainly benthic feeding habits for this species (Chatto *et al.*, 1995; Zangerl *et al.*, 1988); nevertheless, they have been reported to feed occasionally on Scyphozoa (jellyfishes). Less information is known about the diet of immature flatbacks; post-hatchlings (up to 22 cm carapace length) seem to feed primarily on pelagic invertebrates of the macrozooplankton (Zangerl *et al.*, 1988) and stranded post-hatchlings have been found with pumice in the stomach, suggesting a degree of surface foraging (Hamann, unpublished data). Presumably, after ceasing pelagic feeding habits post-hatchlings recruit to benthic foraging grounds with similar, if not the same, feeding preferences as adults.

According to genetic and demographic analysis there are five distinctive stocks for flatback turtles (FitzSimmons & Limpus, 2014): eastern Australia (eAus), Arafura Sea, Cape Domett, south-west Kimberley Coast and Pilbara Coast (Figure 1.1). The lack of long-distance oceanic migrations has resulted in a low genetic diversity and limited gene flow among these stocks (Pittard, 2010). As a consequence, flatback turtles display a noticeable spatial differentiation and isolation of rookeries, with restricted connectivity among some of them (Pittard, 2010). This is highly important for management purposes, as each unit is both genetically and ecologically unique and therefore irreplaceable. Considering that each management unit represents an independent genetic and demographic stock, it is important to take into account that small populations with narrow geographic ranges are particularly vulnerable and susceptible to intermediate disturbances and stochastic events (e.g. cyclones), which can lead to local extinctions and reductions in the population size and genetic diversity (Sutherland, 2000).

1.3. Flatbacks at sea: current state of knowledge on the in-water ecology of the species.

The first records of in-water knowledge on flatback turtles date back to 1967 (Williams *et al.*, 1967). In 1983 the first reports on flatback turtle foraging grounds in eastern Australia were published (Limpus *et al.*, 1983), followed in 1988 by a compilation of the general knowledge on flatback turtles across Australia, including information on the diet and general foraging habitat (Zangerl *et al.*, 1988), and an updated compilation on the species in 2007 (Limpus, 2007). Even though extended efforts were undertaken to monitor flatback turtles in in-water habitats, the encounter rate of individuals at sea remains extremely low. Thus, historic information on the migratory and foraging ecology of the species available for eastern Australia had been typically drawn from opportunistic encounters, such as records of animals accidentally caught in prawn trawlers (prior to the introduction of TEDS in the 2000s) (Robins, 1995; Robins, 2002), stranding events, direct observation and tag recovery (EHP Queensland Turtle Research database) (Limpus *et al.*, 2013a; Limpus, 2007). With the improvement of acoustic and satellite tracking techniques in the last decade there has been a myriad of initiatives focused on tracking flatback turtles and delivering information on their movement and distribution. A search of satellite tracking projects registered at seaturtle.org resulted in around 250 flatback turtles tracked from all management units since 2005; 52 were deployed on flatback turtles in eastern Australia, and 44 of these are included in the analyses of this thesis.

Out of the five flatback turtle genetic stocks in Australia (FitzSimmons & Limpus, 2014), foraging grounds have been identified for the Pilbara (Pb) stock (Whittock *et al.*, 2016). However, information on flatback turtle foraging grounds for the Arafura Sea (ArS), Cape Domett (CD), south west Kimberley (swKim) and eastern Australia (eAus) stocks are still unknown (Commonwealth of Australia, 2017). An undergoing PhD project is aiming at identifying migratory routes and key foraging grounds for the ArS stock (Justin Smith, pers.com.). No information is currently available on past or current projects focusing on the migration and/or foraging ecology of flatback turtles in the CD and swKim stocks. By-catch records have been long used as a surrogate to infer the relative spatial distribution of foraging turtles across broad geographic extents in Australia (Robins, 2002). For example, historic data on the relative spatial distribution of foraging flatback turtles in eastern Queensland was estimated from trawl by-catch (Robins, 2002), EHP Queensland Turtle Research database. More recently, some in-water locations of flatback turtles have been estimated from fisheries by-catch records, indicating the presence of flatback turtles mostly in northern Australia and a minor proportion in the Far Northern region of Queensland (Riskas *et al.*, 2016).

Foraging grounds for the Pb stock are widely dispersed across the western and northern coast of Australia (Whittock *et al.*, 2016). Flatback turtles tracked from different nesting beaches in the Pilbara region display consistent migratory patterns across a narrow coastal strip covering the north-west to north neritic waters of Australia (Pendoley *et al.*, 2014). While most foraging grounds are located across Western Australia State, turtles from the Pb stock have been tracked as far away as the Northern Territory State and the Queensland coast of the Gulf of Carpentaria (2511 km away). Behaviour of foraging flatback turtles in western and northern Australia is described as variable, given that some turtles use more than one foraging area with pathways inter-connecting the disparate foraging areas (Whittock *et al.*, 2016). Lastly, the exposure of foraging grounds to several threats (fisheries and resource sector activities) has been assessed for this stock enabling the identification of important areas for conservation in the Kimberly and Pilbara regions (Whittock *et al.*, 2016).

Flatback turtles from different nesting beaches of the ArS have been tracked in the last 10 years. In 2008, four satellite tags were deployed on nesting flatback turtles and tracked to various locations in the Gulf of Carpentaria and the Arafura Sea (http://www.seaturtle.org/tracking/?project_id=330, accessed online 20/07/2017). Furthermore, preliminary results of the migration and foraging ecology of the ArS stock (Hamann *et al.*, 2015) indicate that post-nesting flatback turtles migrate to foraging grounds in the Arafura Sea, Gulf of Carpentaria and the Bonaparte Gulf (Northern Territory State). Turtles were tracked from Deliverance Island in Torres Strait (northern Queensland) in 2013 and 2014, and migrated up to 1652 km away from the nesting island. Importantly, none of the 11 turtles tracked from Torres Strait nesting sites migrated into the waters of the GBR. This could mean that a dispersal barrier exists separating the two stocks. Further information on this project is expected to be available by 2018 (Justin Smith, pers.com).

1.4. Flatbacks at sea: theoretical framework

1.4.1. Dispersal

In the marine environment, where physical boundaries are scarce, dispersal is often widespread and influenced by the combination of physical forces and the active behaviour of individuals (Wolanski, 2016). Dispersal plays a crucial role in the distribution of a species, by enabling the discovery and settlement of individuals in new suitable, and sometimes previously considered unsuitable, habitats (Pulliam, 2000). Most marine turtle species are known to disperse into oceanic currents as hatchlings when they first enter the sea from the nesting beaches. However, the lack of evidence of flatback turtles of any life-stage in oceanic locations, where individuals of other species of the same region of origin have been encountered, strongly suggests that flatback turtles have a neritic development. This is supported by long-term records of post-hatchlings in coastal waters of Australia. Chapter 2 of this dissertation focuses on using oceanographic models to simulate the dispersal of flatback post-hatchlings in eastern Australia and understand the mechanisms that drive the neritic distribution of this species. Research of hatchling flatback turtle behaviour has provided essential facts about the swimming performance and dispersal strategies of flatbacks during their first weeks at sea (Hamann *et al.*, 2011; Pereira *et al.*, 2011; Salmon *et al.*, 2010; Salmon *et al.*, 2009). As shown by oceanographic modelling, hatchling dispersal of this species is limited to coastal, predator-rich waters and is driven mainly by the swimming activity and local water circulation (Hamann *et al.*, 2011).

1.4.2. Migration

Dispersal and migration are fundamental processes in shaping the distribution range of species. Long-distance migration is widespread across numerous taxa and is typically resource-driven. Resources include any type of component needed for development and/or reproduction of an individual, ranging from prey to suitable environmental conditions (e.g. temperature) and mating partners. For example, the decrease in water quantity and quality (e.g. excessive salinity) at the end of the wet season triggers the long-distance migrations of zebras and wildebeest in the Serengeti National Park (Gereta & Wolanski, 1998). Apart from resource-driven, migrations can also be modelled by ancient genetically and/or culturally inherited behaviours (i.e. zebras between Namibia and Botswana, Naidoo *et al.* (2014)), as well as by imprinting processes during early life-stages (i.e. all marine turtles species, see review in (Lohmann *et al.*, 2013)). In the marine realm, long-distance migrations are largely influenced by coastal boundaries and major oceanic currents, and are an important source of connectivity among populations. With the advance of satellite telemetry technologies, it has become evident that in many cases one or multiple species travel through migratory corridors, which are important focal areas for conservation (Pendoley *et al.*, 2014).

The nature and purpose of migrations can vary throughout the life-cycle of an individual. Marine turtles display ontogenetic, breeding and seasonal migrations. Chapter 3 of this dissertation focuses on the post-breeding migration of post-nesting flatback turtles, which covers the movement of the turtles from nesting beaches to foraging grounds. Post-breeding migratory patterns vary from one species to another, and between individuals of the same species. For example, olive ridley turtles display a nomadic behaviour, with no clear migratory pathways or spatio-temporal patterns, and a high degree of differentiation among individuals (Plotkin, 2003). In contrast, green and hawksbill turtles typically display coastal migrations with relatively direct movements from the nesting beaches to the foraging grounds (see review in Godley *et al.* (2008)). As for flatback turtles, the patterns seem to follow the coastal behaviour observed in green and hawksbill turtles; a study in Western Australia showed that satellite tracked flatback turtles undertook migrations of variable length (10 to >1500 kilometres distance between nesting beach and foraging ground) with consistent patterns along a coastal corridor (Pendoley *et al.*, 2014).

1.4.3. Foraging habitat use

While “habitat” is one of the most common terminologies in ecology, understanding the selection and use of habitat by individuals is a very complex field of study. Classical definitions of habitat are based on the ecological niche theory, and imply that the spatial area occupied by individuals is the result of the selection of resources, under certain limits and conditions, that will ultimately increase the individual’s fitness (Jones, 2001). Thus, to simplify the study of species-habitat relationships, researchers assume that the habitat in which an individual is observed, reflects a portion of the suitable conditions for its survival, reproduction or persistence (Garshelis, 2000). While the distribution of a species is also influenced by other processes, such as dispersal, predation and competition, in Chapters 3 and 4 I will focus exclusively on the habitat use of flatback turtles in foraging grounds.

Habitat selection and habitat use are two important principles often approached in species-habitat studies. Habitat selection is the process through which an individual chooses and exploits the resources of a specific habitat. It involves decision-making processes, which are influenced by the available resources and the individual’s decision-making on preference of one resource over another. The end result of this process is the habitat use. Habitat use can be measured by observing or recording how an individual uses the abiotic (environmental factors) and biotic (prey) resources in space and time. A habitat can be used for one or more purposes (i.e. nursery, foraging, resting, mating), and in some cases individuals shift habitats depending on the purpose as well. In particular, many species of marine megafauna display ontogenetic changes in habitat use. Sharks are well known to occupy nearshore nursery areas during the juvenile stages, and then recruit to larger home ranges which often include offshore environments (Munroe *et al.*, 2016). All species of marine turtles display a highly-differentiated habitat use between reproductive and foraging periods, in particular in terms of geographic location (separate areas for foraging and nesting) and behaviour.

As capital breeders, marine turtles tend to fast during reproductive periods (Bonnet *et al.*, 1998; Hamann *et al.*, 2002a). Thus, energy intake in adult turtles during the foraging periods is invested in foraging (i.e. searching, chasing/escaping, digesting), but also to restore and build somatic energy reserves required for the following reproductive periods (Bjorndal *et al.*, 1997; Hatase & Tsukamoto, 2008; Wallace *et al.*, 2006). There are multiple foraging patterns observed between species, including foraging in coastal neritic habitats (i.e. green, hawksbill turtles), foraging in oceanic habitats (i.e. leatherback, olive ridley turtles), and foraging in both neritic and oceanic habitats (i.e. loggerhead turtles). The current knowledge on flatback turtle foraging ecology is limited. Foraging flatback turtles have been recorded in sub-tidal turbid coastal waters and are considered opportunistic foragers, with an apparent preference to soft-bodied benthic invertebrates (Limpus, 2007). In addition, a recent study in Western Australia revealed that flatback turtles in this region display flexible foraging strategies, making use of one or more foraging grounds (Whittock *et al.*, 2016). Chapter 3 and 4 of this dissertation focus on identifying and describing the migratory and foraging ecology of flatback turtles in eastern Australia, and assessing potential associations between the turtles and the habitats they occupy.

1.4.4. Threats and conservation of foraging flatback turtles in the Great Barrier Reef Marine Park (GBRMP)

In Australia, flatback turtles are listed nationally as a threatened species [*Vulnerable*] and a marine and migratory species, hence they are considered by the Australian Government as a *Matter of National Environmental Significance* (MNES) (Environment Protection and Biodiversity Conservation Act, 1999). In Queensland, the species is classified as *Vulnerable* (Nature Conservation Act 1992) and considered as a *Critical Priority* in Queensland under the “Back on Track species prioritisation framework” (Department of Environment and Heritage Protection). The understanding of the threats and the magnitude of their impact on foraging flatback turtle populations in the GBRMP are limited. However, some of the potential threats that have been identified to affect flatback turtles in the GBRMP include habitat loss and degradation, decreasing water quality, incidental capture in commercial fisheries, boat strike and ingestion/entanglement of marine debris (GBRMPA, 2014a).

There is an extensive array of legal frameworks and management actions that aim to protect marine turtles and their habitats in the GBRMP (see Outlook Report (GBRMPA, 2014b) for detailed information). Recent recovery plans, such as the “Reef 2050 Long-Term Sustainability Plan” (Commonwealth of Australia, 2015) and the “Recovery Plan for Marine Turtles in Australian Waters” (Commonwealth of Australia, 2017), have both identified flatback turtles as species of conservation concern and highlighted the necessity to improve the current knowledge on their foraging ecology in the GBRMP. This dissertation aims to address these gaps and provide new information to inform future management actions of the species in the GBRMP.

1.5. Thesis outline

1.5.1. Research aims and objectives

The aim of my thesis was to improve our understanding of the biogeography and ecology of flatback turtle across different life-stages, with the intention to generate scientific information to improve the state of knowledge of the species and provide relevant outputs to inform management actions for conservation. To achieve this, I addressed three main objectives:

1. To improve the understanding of the mechanisms that drive the neritic dispersal of post-hatchlings flatback turtles.

2. To improve the knowledge on the ecological biogeography of foraging flatback turtles in eastern Australia.

3. To assess the protection level of foraging habitats for flatback turtles in the Great Barrier Reef Marine Park.

1.5.2. Thesis structure

The structure of the thesis is schematically represented in Figure 1.3

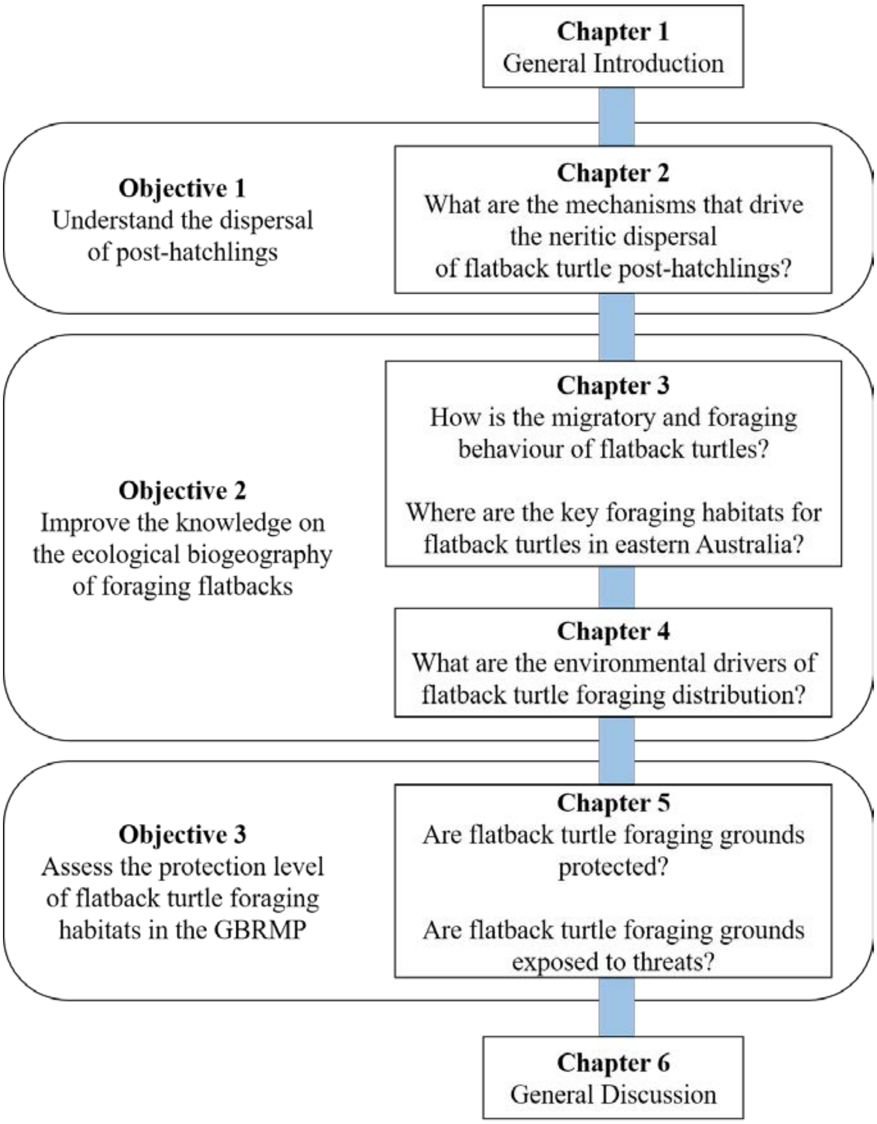

Figure 1.3. Schematic diagram of thesis structure.

In **Chapter 1**, I provide a general introduction to understand the context and rationale of my research. I begin with an overview of some concepts relevant to biogeographical studies and the ecology of flatback turtles. Then, I introduce further ecological concepts relevant to the data chapters, relating each of them to the current knowledge on marine turtles and, when existing, on flatbacks specifically.

Chapter 2 aims to understand why flatback post-hatchling flatback turtles remain in neritic waters, instead of dispersing into oceanic habitats similar to all other marine turtle species. There are no current technologies to track and monitor recently hatched turtles during the first months of life at sea. Therefore, I use a high-resolution oceanographic model to simulate the water circulation and turtle dispersal in the GBR. Through this approach, I assess the effect of a selection of oceanographic features and different swimming behaviours in the retention or export of turtles in the GBR. Associated publication:

> Wildermann N, Critchell K, Fuentes MMPB, Limpus C, Wolanski E, Hamann M (2017) Does behaviour affect the dispersal of flatback post-hatchlings in the Great Barrier Reef? Royal Society open science. 4: 170164. http://dx.doi.org/10.1098/rsos.170164

In **Chapter 3**, I explore the behaviour and distribution of flatback turtles in eastern Australia. More specifically, I analyse the fine-scale changes in behaviour to objectively classify migratory and foraging events, and describe different migratory and foraging patterns displayed by the tracked flatback turtles. I also determine the foraging area of tracked flatback turtles in eastern Australia, describe general characteristics of the foraging home ranges of the turtles and identify foraging hotspots within the region. The following chapters are focused only on the foraging area identified in this chapter, without considering the migratory pathways of the turtles. I aim to submit this chapter as a manuscript to Endangered Species Research.

Chapter 4 aims to explore the environmental drivers of the distribution of foraging flatback turtles in eastern Australia. In this chapter I evaluate the potential associations between the habitat use by tracked flatback turtles and the spatial distribution of environmental variables. The results provide new insights on the types of habitat used by flatback turtles, the physical variables that drive the distribution of the tracked turtles, and some likely associations with potential prey groups. I aim to submit this chapter as a manuscript to Diversity and Distributions

Chapter 5 focuses on quantifying the protection coverage and exposure to threats of flatback turtles at the foraging grounds identified in chapter 3. First, I evaluate the extent to which current management actions within the GBRMP provide protection to the newly identified flatback foraging grounds. Second, I evaluate the exposure of turtles to two threats known to affect foraging turtles or their habitats: shipping and trawling. Finally, I highlight the importance of further assessing the exposure to other threats at specific foraging grounds, which might need improvement in their protection coverage in future management assessments. I aim to submit this chapter as a manuscript to Biological Conservation.

In **Chapter 6**, I summarise the key findings of my four data chapters within the context of the known distribution and foraging ecology of flatback turtles at a national scale. I also consider how my results can inform the management of flatback turtles in the GBRMP. To finalise, I identify further gaps in the knowledge of the in-water ecology of flatback turtles and propose a selection of approaches to assess these gaps.

Chapter 2

Does behaviour affect the dispersal of flatback post-hatchlings in the Great Barrier Reef?[1]

Three-month old reared flatback post-hatchling released at sea in the Whitsunday region.
Photo credits: Matt Curnock

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[1] Wildermann N, Critchell K, Fuentes MMPB, Limpus C, Wolanski E, Hamann M (2017) Does behaviour affect the dispersal of flatback post-hatchlings in the Great Barrier Reef? Royal Society open science. 4: 170164. http://dx.doi.org/10.1098/rsos.170164

Abstract

The ability of individuals to actively control their movements, especially during the early life-stages, can significantly influence the distribution of their population. Most marine turtle species develop oceanic foraging habitats during different life-stages. However, flatback turtles (*Natator depressus*) are endemic to Australia and are the only marine turtle species with an exclusive neritic development. To explain the lack of oceanic dispersal of this species, I predicted the dispersal of post-hatchlings in the Great Barrier Reef (GBR), Australia, using oceanographic advection-dispersal models. I included directional swimming in my models and calibrated them against the observed distribution of post-hatchling and adult turtles. I simulated the dispersal of green and loggerhead turtles since they also breed in the same region. My study suggests that the neritic distribution of flatback post-hatchlings is favoured by the inshore distribution of nesting beaches, the local water circulation and, directional swimming during their early dispersal. This combination of factors is important because, under the conditions tested, if flatback post-hatchlings were entirely passively transported they would be advected into oceanic habitats after 40 days. My results reinforce the importance of oceanography and directional swimming in the early life-stages and its influence on the distribution of a marine turtle species.

Keywords: Great Barrier Reef, marine turtles, flatback turtle, neritic dispersal, SLIM oceanographic model, directional swimming.

2.1. Introduction

Dispersal strategies during the early developmental stages of an organism can have a profound effect on individual survivorship, fitness and distribution range (Hansson, 1991; Matthysen, 2012; Wolanski, 2016; Wolanski & Elliott, 2015; Wolanski & Kingsford, 2014). In the ocean, physical boundaries are scarce and ocean currents promote long-distance transportation; thus, active and directional swimming, both horizontal and vertical, is of special relevance for self-recruitment of species from plankton to fish and turtles (Cobb *et al.*, 1997; Criales *et al.*, 2013; Dao *et al.*, 2015; Wolanski, 2016; Wolanski *et al.*, 1997). In particular, the fate of aquatic species greatly relies on passive and active dispersal mechanisms. It is common for species to display multiple mechanisms of dispersal throughout their lifecycle, adapting specific strategies to different biological and ecological requirements. Passive transport relies on external forces (e.g. wind, tides, currents) and can be regarded as an uncontrolled transport mechanism with low energetic costs for individuals (Burgess *et al.*, 2016; Matthysen, 2012). Active dispersal results from the autonomous movement of an organism and depends on its capacity to respond to a variety of cues based on complex social and physical interactions with the environment (Matthysen, 2012).

Marine turtles begin their life at sea, after emerging from nests on land, with one to several days of hyperactive swimming, in which hatchlings constantly swim away from the coastline to reach offshore waters (Carr, 1962; Lohmann & Lohmann, 2003; Wyneken & Salmon, 1992). Following this period, somatic energy reserves are diminished and until recently, it was believed that turtles of several species predominantly dispersed by drifting with the oceanic currents (Bolten, 2003a). However, new studies have indicated that the dispersal of young turtles is not likely to be entirely passive (i.e. Christiansen *et al.* (2016); Gaspar *et al.* (2012); Lohmann *et al.* (2012)). In particular, research in the Gulf of Mexico suggested that young green and Kemp's ridley turtles at estimated age of one year are active swimmers in their natural environment (Putman & Mansfield, 2015). Indeed, directional swimming during the early dispersal stages could benefit turtles when orientating themselves in open ocean (Lohmann *et al.*, 2012; Putman *et al.*, 2014), for example, moving away from cold waters, shelf seas or strong currents (Putman & Mansfield, 2015; Putman *et al.*, 2012a) and this also improves their probability of survival and protection (Bolten, 2003b; Lohmann & Lohmann, 2003; Salmon *et al.*, 2009).

The swimming behaviour of turtle hatchlings and post-hatchlings varies between species (Wyneken, 1997) and could reflect different strategies to reach oceanic waters (Chung *et al.*, 2009). Active swimming during their early life stages could lead to very distinctive dispersal trajectories (Putman *et al.*, 2014) and life history patterns (Bolten, 2003a). In south and central-eastern Queensland three species of marine turtle nest concurrently along the mainland coast and islands of the southern Great Barrier Reef (GBR). Yet despite the three species breeding in the same geographic area they have different dispersal patterns. Most notably, post-hatchlings of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles originating from this region have an oceanic dispersal and are not commonly found in the GBR Lagoon (Boyle, 2007; Jensen *et al.*, 2016). In contrast, flatback turtle (*Natator depressus*) post-hatchlings display a completely neritic (non-oceanic) developmental stage (Limpus, 2007; Walker & Parmenter, 1990). Their neritic stage is assumed to be mainly driven by swimming behaviour and the local water circulation (Hamann *et al.*, 2011). Nevertheless, our knowledge of behaviour of hatchling and early post-hatchling marine turtles is generally limited to the first days, and in some cases weeks, of their life (Hamann *et al.*, 2011; Pereira *et al.*, 2012; Salmon *et al.*, 2009; Salmon & Wyneken, 1987; Wyneken & Salmon, 1992), and the dispersal strategies of post-hatchling turtles remain poorly known.

Most of our current knowledge on early swimming behaviour of marine turtles is based on laboratory experiments and oceanographic models (Booth, 2009; Gaspar *et al.*, 2012; Hamann *et al.*, 2011; Lohmann *et al.*, 2001; Okuyama *et al.*, 2009; Okuyama *et al.*, 2011; Pereira *et al.*, 2012; Putman *et al.*, 2012b; Salmon *et al.*, 2009; Wyneken *et al.*, 2008; Wyneken & Salmon, 1992). Oceanographic advection-diffusion modelling combined with animal biology and behaviour offer a useful means of exploring the likely dispersal and migration trajectories of marine turtles (Briscoe *et al.*, 2016; Casale & Mariani, 2014; Collard & Ogren, 1990; Gaspar *et al.*, 2012; Hamann *et al.*, 2011; Okuyama *et al.*, 2009; Putman *et al.*, 2012a; Wolanski, 2016). Thus, I used oceanographic modelling verified by field data on the distribution of young and adult animals, to improve the understanding of dispersal of post-hatchling flatback turtles, with a special focus on how swimming behaviour can influence their dispersal patterns. I suggest there are three main drivers that favour the neritic distribution of simulated post-hatchling flatback turtles under typical oceanographic conditions, namely: (a) the inshore location of nesting beaches, (b) local water circulation and net currents, and (c) directional swimming of post-hatchlings.

2.2. Methods

2.2.1. Study population and area

The eastern Australia (eAus) flatback population nests on continental islands and mainland beaches in southern and central Queensland (Limpus, 2007). There are records of at least 104 rookeries (nesting beaches), the majority of them distributed within two local regions with high nesting abundance: Broad Sound and Capricornia (Figure 2.1a). Two major rookeries (>100 nesting females/season) have been identified for this population: Peak Island located in Broad Sound, and Wild Duck Island located in Capricornia (Figure 2.1a) (Limpus *et al.*, 2013a). The remaining of the nesting is distributed among intermediate (11-100 nesting females/season) rookeries, such as Curtis Island and, minor (<10 nesting females/season) rookeries, such as Mon Repos. Most flatback turtle rookeries in eastern Australia are located on the continental islands within the southern GBR, and to a limited extent on mainland beaches along the central Queensland coast. There are also major rookeries for green and loggerhead turtles within the same geographical extent of the southern GBR. However, they are distributed on the outer shelf coral cays and islands of the Capricorn Bunker Group and Swain Reefs (Figure 2.1a). The nesting season for marine turtles in eastern Australia begins in mid-October until late January for flatbacks, and early May for green and loggerheads; the peak emergence of hatchlings for all species is in February (Limpus, 2007).

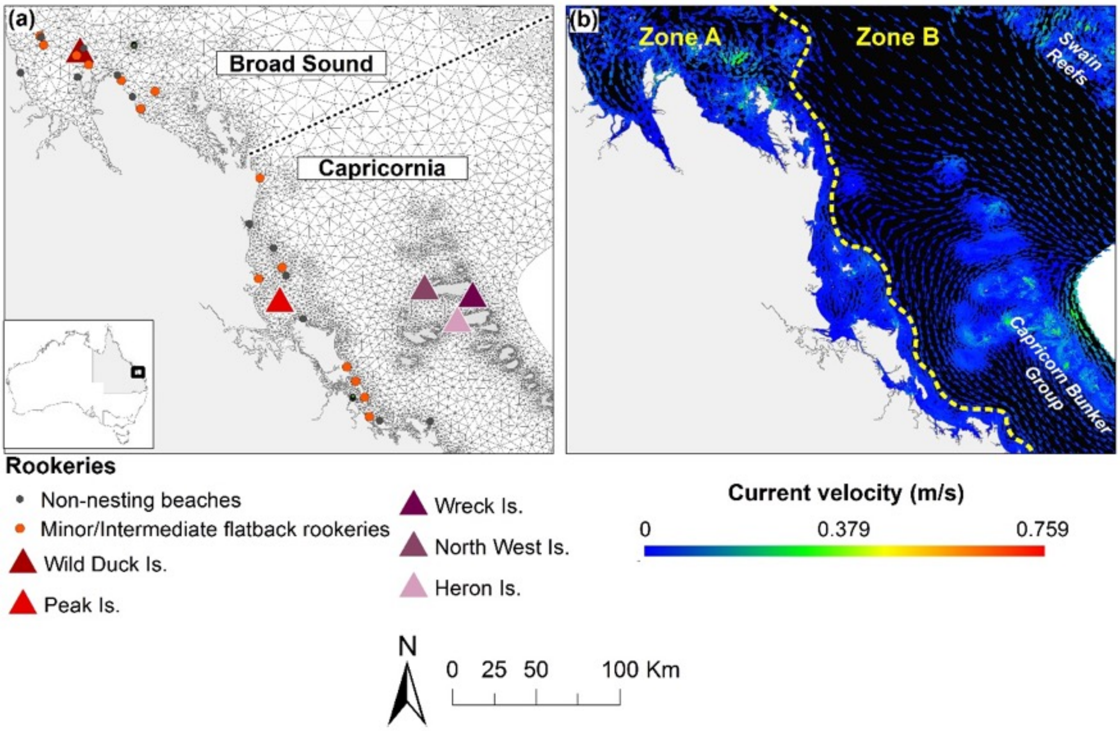

Figure 2.1.Geographical extent of the study area and model domain: (a) Distribution of releasing sites (rookeries) of s-turtles in each region (Broad Sound and Capricornia), background exemplifies the triangular mesh used for the SLIM model; (b) The net, tidal-averaged water circulation in the modelled study area: “Zone A” is the wind-driven coastal boundary layer and represents areas where the currents favour a neritic dispersal, while “Zone B” is the Coral Sea Lagoonal current which flows seaward to the Pacific Ocean.

2.2.2. Mean water circulation in the Great Barrier Reef

The southern GBR has two areas with distinct oceanography (Figure 2.1b): Zone A is located inshore, which is the wind-driven coastal boundary layer where the longshore northward current is highly macro-turbulent with numerous eddies, jets and stagnation zones; Zone B is located further offshore and has a general southward current trend, which is the Coral Sea Lagoonal current formed by the intrusion of the East Australian Current (EAC) on the GBR continental shelf. This current is permanent but it waxes and wanes with the periodic formation and disappearance of the Capricorn Eddy, a cyclonic eddy which forms on the seaward side of the Capricorn channel (Griffin *et al.*, 1987; Kingsford & Wolanski, 2008; Weeks *et al.*, 2010; Wolanski *et al.*, 2013). The currents and the seaward water export are larger during the austral spring and summer months, in which the turtle nesting season takes place (Limpus, 2007).

2.2.3. Methods overview

I compared the observed distribution of flatback turtles in the GBR (field evidence) to an array of scenarios in which I simulated the dispersal of turtles using a hydrodynamic advection-dispersal model. Compared to ocean simulation models, high resolution hydrodynamic models have proven to be a useful technique to depict physical processes relevant to organismal movements in nearshore waters (Putman & He, 2013; Wolanski & Kingsford, 2014). Hereafter, simulated post-hatchling turtles will be identified with an "s-" prefix (e.g. s-turtles, s-flatbacks, s-greens and s-loggerheads). In a first step, I assessed the passive dispersal of the s-turtles accounting for the effect of the geographic location of nesting beaches, and the tidal phase (spring/neap) when the s-turtles entered the sea. In a later step, I added a swimming behaviour component to my simulations, and created a sensitivity analysis based on changing swimming speeds and directions, as well as the length of the passive dispersal phase.

My dispersal simulations were based on releasing s-turtles in January 2012. This date was chosen as the climatic and oceanographic features in January 2012 were representative of the average hatching season, and the currents and wind values I used were <1 SD of the average long-term conditions for the month. The variability in current velocity/direction (Figure 2.2a) and wind speed/direction (Figure 2.2b) in the southern GBR during the months that hatchlings disperse from beaches (December-February) fluctuates within a narrow range across years, with some exceptions due to extreme weather events. Thus, my modelling approach is based on assessing the variability in the dispersal due to (a) a selection of geographic/oceanographic parameters under typical climatic conditions, and (b) a range of hypothetical swimming behaviours of the animals. The main focus of my study was to assess how behaviour influences dispersal patterns, and I acknowledge that different oceanic conditions such as monthly/yearly variability, especially those related to atypical weather events, might provide different dispersal predictions and it would be a worthy hypothesis to test in further studies.

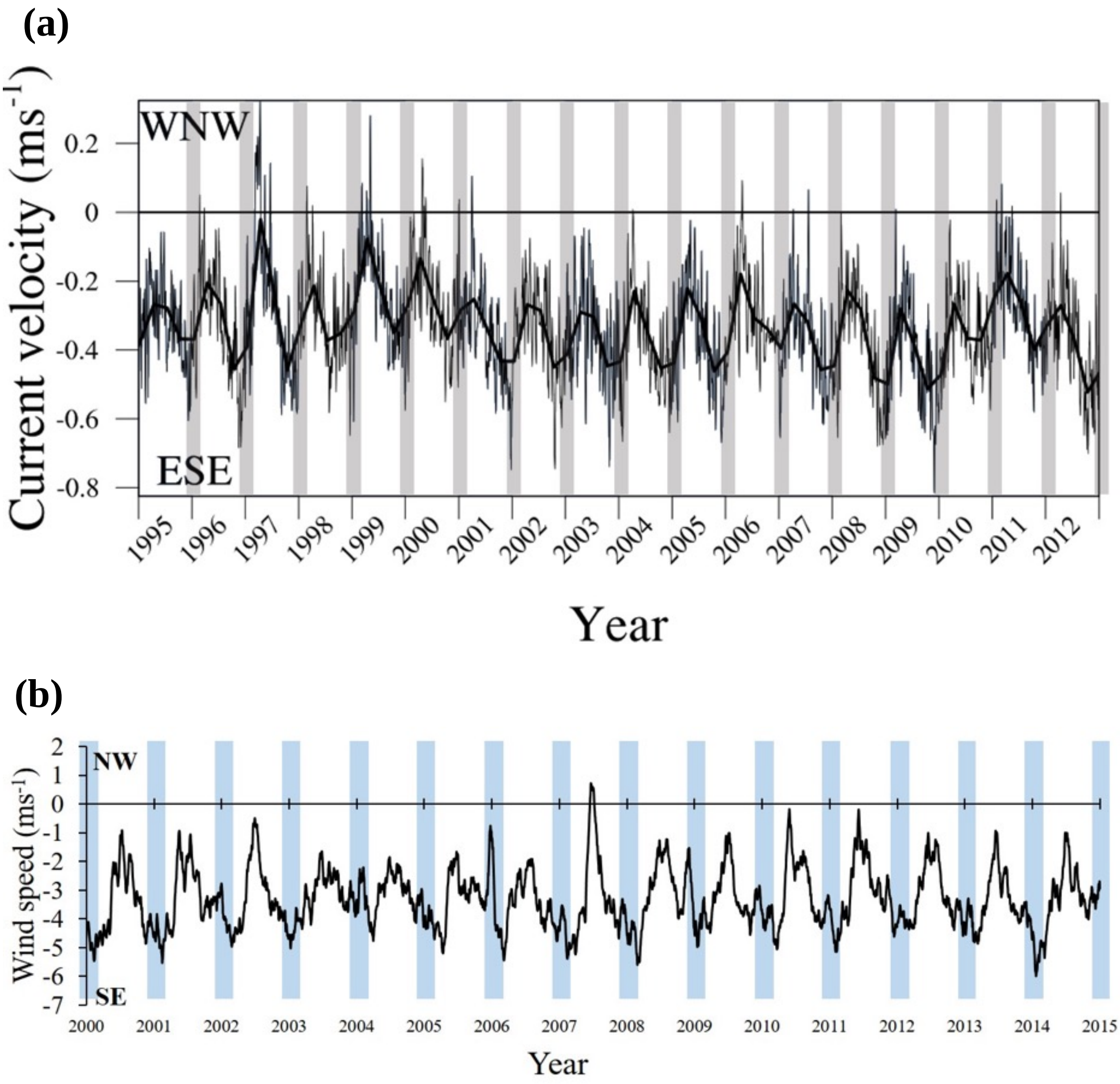

Figure 2.2. Time series of currents and winds in the GBR. (a) Time series of current velocity and direction between 1995 and 2012. Grey areas represent the flatback turtle hatching season (December – February). Current data provided by Jodie Schlaefer. (b) Time series of wind speed and direction between 1995 and 2012. Blue areas represent the flatback turtle hatching season (December – February). Wind data provided by the Australian Bureau of Meteorology (BoM).

2.2.4. Direct evidence of distribution of turtles

Data on the observed distribution of flatback turtles was used to quantitatively delineate the known distribution range of the population. Field evidence was gathered from the long-term recorded distribution of flatback turtle post-hatchlings (N=120) along the eastern coast of Australia and foraging adults (N=121) from the eastern Australia stock (Figure 2.3 a, c). The database includes a comprehensive set of records based on strandings, predation, fisheries, in-water captures and satellite telemetry, between 1969 and 2016 (EHP Queensland Turtle Research database). In addition, prior to the introduction of turtle excluder devices (TEDs) there was evidence of juvenile and adult flatback turtle by-catch in the East Coast Otter Trawl Fishery of Queensland and it occurred along most of the Queensland coast, with higher CPUE within the GBR (Robins, 1995). There is no evidence of flatback turtles of any life-stage outside the continental shelf of Australia. In addition, all life-stages co-occur in similar regions within the inshore waters (Limpus, 2007). The distribution of flatback turtle post-hatchlings has been mostly recorded along the northern coast and inshore waters of eastern Australia, with some records scattered across the southern coast. Conversely, stranded and by-caught green and loggerhead post-hatchlings originating from eastern Australia have been recorded across the Pacific (Boyle, 2007).

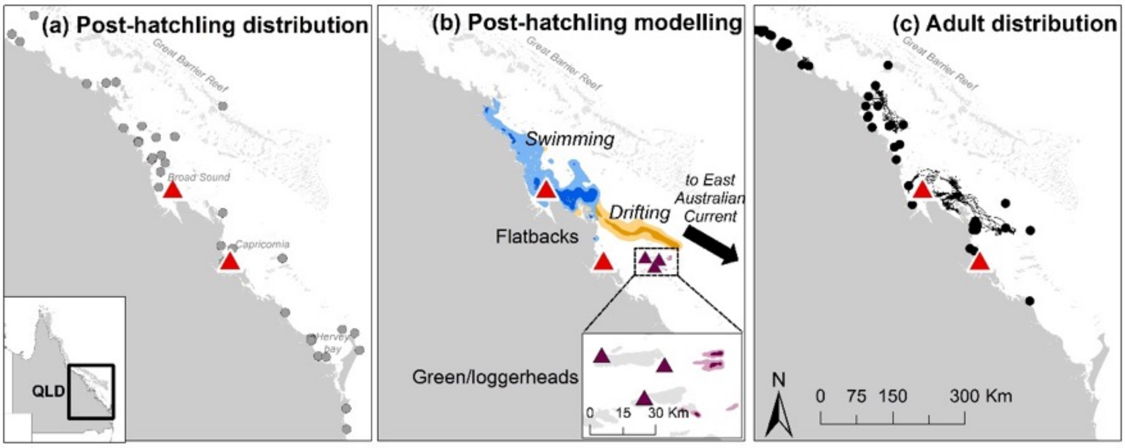

Figure 2.3. Comparison of (a) observed distribution of post-hatchling flatback turtles, (b) simulated dispersal scenarios of s-flatbacks (blue polygons: directional swimming scenario DS-1-SR, orange polygons: passive drift scenario PD-0) and s-green/loggerheads (purple polygons: passive drift scenario PD-GL-species). Polygons represent the probability of distribution of s-turtles, with dark and light colours representing 50% and 95% probability, respectively. S-flatbacks were released from Wild Duck and Peak islands (red triangles from north to the south) and were modelled for 120 days until 00h on 2nd May 2012. S-green/loggerheads were released from North West, Heron and Wreck islands (purple triangles from west to east) and were modelled for 12 days until 00h on 14th January 2012. After 120 days of simulation, the s-flatbacks under active swimming remained inside the GBR displaying a neritic distribution, similar to that of observed flatback turtles (panels a and c). In contrast, most drifting s-flatbacks were advected seaward into the Pacific Ocean by the East Australian Current (EAC).

2.2.5. Oceanographic advection-dispersal model with animal behaviour

The model domain covered the southern extent of the GBR Lagoon (Figure 2.1). I used the unstructured-mesh SLIM model (2D Second-generation Louvain-la-Neuve Ice-ocean Model; www.climate.be/slim) to simulate the hydrodynamics of the region and the dispersal of s-turtles (Lambrechts *et al.*, 2008). The mesh size varied between 150 m near reefs and islands to 10 km in offshore waters (Figure 2.1a). The SLIM model has been calibrated for the GBR by Andutta *et al.* (2012; 2011, 2013) and Thomas *et al.* (2014), and used for ecological applications including the study of the accumulation and movement of marine debris (Critchell *et al.*, 2015; Critchell & Lambrechts, 2016), the nearshore dispersal of flatback turtle hatchlings (Hamann *et al.*, 2011), and the fate of fine sediment in 2D and 3D (Delandmeter *et al.*, 2015; Lambrechts *et al.*, 2010). Forcing parameters for the model included wind stress (wind speed and direction), water circulation in the Coral Sea and the tides and tidal currents at the shelf edge following the model calibrations for the GBR (Andutta *et al.*, 2012; Andutta *et al.*, 2011, 2013; Thomas *et al.*, 2014). Daily wind data between January and April, from 1999-2014, were provided by the Australian Bureau of Meteorology (BOM) and averaged to calculate the monthly mean wind stress during the hatching season.

The dispersal simulation allows for directional swimming of the s-turtles, following the method of Wolanski and Kingsford (2014). Scenarios were designed to test the hypothesis of passive drift (the null scenario), and active swimming dispersal (Table 2.1). In all scenarios, the initial period of swimming frenzy was determined from published data, namely during the first hour the s-turtles swam eastwards at 0.3 m s^{-1}, then swam for 72 hours at 0.08 m s^{-1} (Chevron-Australia, 2010; Hamann *et al.*, 2011; Pereira *et al.*, 2011, 2012; Thums *et al.*, 2013). After the simulated swimming frenzy either their swimming behaviour was stopped and they dispersed passively, or they swam directionally; the parameters behind each scenario are listed in Table 2.1. The simulations lasted for 120 prototype days.

The passive drift was the null scenario (scenario PD-0), in which s-turtles were left to drift with currents with no additional behaviour. To comprehensively test this hypothesis, I designed five scenarios to account for the influence of the geographic location (GL) of rookeries and the tidal phase (TP) on the dispersal of turtles (Table 2.1). To test whether the location of rookeries of the different species result in distinctive dispersal trajectories, I compared the passive dispersal of s-turtles released from a subset of rookeries where only flatback turtles (n=16) and only green/loggerheads (n=3) nest (Figure 2.1a, Table 2.2). I then analysed the s-turtle dispersal within the nesting range of the eAus flatback turtle population. I tested the differences in the passive dispersal of s-flatbacks (a) between regions (n=8 rookeries in each region: Broad Sound and

Capricornia), and (b) within each region, comparing the major rookeries (n=1 in each region; Wild Duck Island for Broad Sound and Peak Island for Capricornia) to a subset of minor/intermediate rookeries (n=7 in each region) and non-nesting beaches (proximal beaches with no records of flatback turtle nesting, n=7 in each region) (Figure 2.1a, Table 2.2). All subsets were randomly selected with the *r.sample* function in GME 0.7.3.0 (Beyer, 2012). In each case 5000 s-turtles were released near the selected rookeries, on the 3rd of January 2012 at 00:00. I used the major rookeries as a proxy for each region, namely Wild Duck Island for Broad Sound and Peak Island for Capricornia. To quantify the importance of the spring-neap tidal cycle at the time when turtles entered the sea at Wild Duck and Peak Islands (Figure 2.1a, Table 2.2), I simulated the dispersal of 5000 s-turtles from each rookery released on two different dates: (a) at neap tide (3-January-2012 15:00), and (b) at spring tide (7-January-2012 12:00).

The effect of behaviour on the dispersal of s-flatbacks was tested through a sensitivity analysis by analogy with modelling fish swimming dispersal (Wolanski & Kingsford, 2014), where I tested different directions and speeds based on the currently known behaviour of flatback turtle post-hatchlings (Hamann *et al.*, 2011; Salmon *et al.*, 2010; Salmon *et al.*, 2009) and expert opinion. A standard run (scenario DS-1-SR) was arbitrarily designed based on my best guest of what is known about the biology and swimming behaviour of flatback turtle post-hatchlings, namely the s-flatbacks swam north-westward at 0.02 m s^{-1} for 75% of the time (the remaining 25% of the time s-turtles drift passively). To test the sensitivity of this solution to other parameters, all other scenarios were arranged by changing one swimming parameter from the standard run (Table 2.1). The parameters that defined the swimming behaviour of s-turtles were: (a) direction: north-west, north, south, east; (b) speed: 0.01 m s-1, 0.02 m s^{-1}, 0.04 m s^{-1}; (c) proportion of time s-turtles spent swimming per day: 25%, 50%, 75%, 100%; and (d) day the post-frenzy swimming behaviour started: day 4 (immediately after end of swimming frenzy), day 30, 60 or 90 (Table 2.1). For all scenarios that tested the influence of the swimming behaviour I released 15000 s-turtles near the major rookeries (Wild Duck and Peak islands), on the 3rd of January 2012 at 00:00.

Table 2.1. Dispersal scenarios and parameters. All scenarios included a period of swimming frenzy during the first three days. For the sensitivity analysis, only one parameter (underlined) was changed from the standard run (DS-1-SR). PD: passive drift, DS: directional swimming, GL: geographic location, TP: tidal phase, SR: standard run, Nd: flatback (*Natator depressus*), Cm: green (*Chelonia mydas*), Cc: loggerhead (*Caretta caretta*), BS: Broad Sound, C: Capricornia, CBG: Capricorn Bunker Group.

					Swimming parameters			
	Scenario type	**Scenario name**	**Species**	**Release locations**	**Swimming direction**	**Swimming speed (m s^{-1})**	**Proportion of time swimming (%)**	**Start of swimming behaviour (day)**
	Passive drift	PD-GL-species	Nd, Cm, Cc	BS, C, CBG	-	-	-	-
	Passive drift	PD-GL-regions	Nd	BS, C	-	-	-	-
	Passive drift	PD-GL-minor/major	Nd	Minor/Intermediate and major rookeries within BS and C	-	-	-	-
	Passive drift	PD-GL-non/major	Nd	Non-nesting beaches and major rookeries within BS and C	-	-	-	-
	Passive drift	PD-TP-neap/spring	Nd	Major rookeries	-	-	-	-
Sensitivity analysis	Passive drift	PD-0	Nd	Major rookeries	-	-	-	-
	Directional swimming	DS-1-SR	Nd	Major rookeries	north-west	0.02	75	4
	Directional swimming	DS-2	Nd	Major rookeries	north	0.02	75	4
	Directional swimming	DS-3	Nd	Major rookeries	south	0.02	75	4
	Directional swimming	DS-4	Nd	Major rookeries	east	0.02	75	4
	Directional swimming	DS-5	Nd	Major rookeries	north-west	0.01	75	4
	Directional swimming	DS-6	Nd	Major rookeries	north-west	0.04	75	4
	Directional swimming	DS-7	Nd	Major rookeries	north-west	0.02	25	4
	Directional swimming	DS-8	Nd	Major rookeries	north-west	0.02	50	4
	Directional swimming	DS-9	Nd	Major rookeries	north-west	0.02	100	4
	Directional swimming	DS-10	Nd	Major rookeries	north-west	0.02	75	30
	Directional swimming	DS-11	Nd	Major rookeries	north-west	0.02	75	60
	Directional swimming	DS-12	Nd	Major rookeries	north-west	0.02	75	90

Table 2.2. Summary of releasing locations of s-turtles. BS: Broad Sound, C: Capricornia, CBG: Capricorn Bunker Group, Nd: flatback (*Natator depressus*), Cm: green (*Chelonia mydas*), Cc: loggerhead (*Caretta caretta*), PD: passive drift, GL: geographic location, minor: minor rookery, major: major rookery, non: non-nesting beach.

Region	**Type of rookery**	**Locality**	**Coordinates**		**Nesting species**	**Scenarios**
BS	Major	Wild Duck Is.	149.859	-22.001	Nd	All (see Table 2.1)
BS	Minor/ Intermediate	Avoid Is.: SE East Beach	149.664	-21.977	Nd	PD-GL-species, PD-GL-regions, PD-GL-minor/major
		Long Is.: East Beach	149.907	-22.083		
		Swb Beach North Side Mcdonald Pt.	150.185	-22.319		
		Swb 2nd Beach South of Stanage Beach	150.082	-22.166		
		Infelix Islets: South	149.841	-22.033		
		Lingham: Northern Beach	150.263	-22.226		
		Red Clay Isle: Western Beach	149.646	-21.930		
BS	Non-nesting	Red Clay Isle: East Beach	149.651	-21.936	-	PD-GL-non/major
		Wild Duck Is.: South Beach	149.864	-22.005		
		Swb Bat Cave Beach,South	150.061	-22.140		
		Swb Sth of Yenyarindle Hut	150.142	-22.255		
		Tin Case Ck Southward	149.541	-22.128		
		West Side Island	149.849	-22.149		
		Marble Island	150.151	-21.980		
C	Major	Peak Is.	150.932	-23.341	Nd	All (see Table 2.1)
C	Minor/ Intermediate	Facing Is.: North Beach	151.341	-23.783	Nd	PD-GL-species, PD-GL-regions, PD-GL-minor/major
		Facing Is.: Settlement Bay	151.388	-23.869		
		Stockyard Point	150.827	-22.691		
		Emu Pt.: Tanby Pt.	150.820	-23.232		
		Wild Cattle Island	151.413	-23.973		
		Curtis Is.: Southend	151.258	-23.665		
		NWGKIs Big Pen – 3rd beach	150.945	-23.171		
C	Non-nesting	Hummock Hill Is.	151.467	-23.996	-	PD-GL-non/major
		Middle Is.	151.740	-24.000		
		Curtis Is: Cape Keppell	151.057	-23.449		
		Humpy Island	150.966	-23.216		
		North Keppell	150.900	-23.070		
		Water Park Point	150.770	-22.940		
		Boyne Island	151.324	-23.873		
CBG	Major/Minor	Wreck Is.	151.968	-23.314	Cm, Cc	PD-GL-species
		North West Is.	151.710	-23.274		
		Heron Is.	151.885	-23.448		

2.2.6. Outputs and data analysis

I calculated the area where 95% of the s-turtles were located (this is called the 95% distribution area), as well as core dispersal zones (area where 20% of the s-turtles were located) using the Kernel Density Estimator tool in ArcMap 10.2.2 and isopleth function in GME 0.7.3.0 (Beyer, 2012). I assessed the degree of overlap between scenarios with the Bhattacharyya's Affinity Index (BAI), computed with the adehabitatHR package in R (Calenge, 2006; R Core Team, 2016). The BAI spans from 0 to 1 (1 being 100% of overlap between two areas).

To quantify the influence of behaviour in the dispersal, I calculated the dispersal success (percentage of s-flatbacks dispersed into inshore habitats of the GBR) for each individual scenario of the sensitivity analysis (26 scenarios in total; one passive drift and 12 directional swimming scenarios for each releasing location) (Table 2.1). Then, for each scenario I averaged the dispersal success over the two releasing locations to obtain the overall dispersal success, which I ranked based on a quantile classification as Very low (≤ 25%), Low (25.01 – 50%), Medium (51.01 – 75%) and High (> 75%). The inshore region was delimited by the wind-driven coastal boundary layer (see “Zone A” in Figure 2.1b). S-turtles located in the Coral Sea Lagoonal current (see “Zone B” in Figure 2.1b) were considered to get swiftly advected outside the GBR, and thus counted as distributed into offshore waters.

2.3. Results

2.3.1. Turtle dispersal under the passive drift hypothesis

The passive dispersal of s-turtles differed greatly between rookeries of the different species. Assuming passive transport for the s-green and s-loggerheads under typical oceanographic conditions, the simulations resulted in 92.5% of the s-turtles leaving the model domain and entering the EAC within 14 days. In contrast, under typical oceanographic conditions s-flatback turtles remained in lagoonal waters for 40 days before starting to leave the domain. Under most passive drift scenarios for s-flatbacks, the core dispersal zones after 120 days of simulation were located within the Coral Sea Lagoonal current flowing towards oceanic waters outside of the GBR (see “Zone B” in Figure 2.1b).

In addition, s-flatback post-hatchling dispersal differed significantly between the two regions (BAI = 0.590); s-flatbacks released from Capricornia under typical conditions reach Zone B sooner and are more likely to get advected into oceanic currents (Figure 2.4). Despite the differences between the regions, the distribution area of s-flatbacks released from non-rookeries, minor rookeries and major rookeries within each region was similar (Broad Sound $\mathrm{BAI}_{\mathrm{minor/major}} = 0.906$, $\mathrm{BAI}_{\mathrm{non/major}} = 0.993$; Capricornia $\mathrm{BAI}_{\mathrm{minor/major}} = 0.942$, $\mathrm{BAI}_{\mathrm{non/major}} = 0.933$) (Figure 2.5).

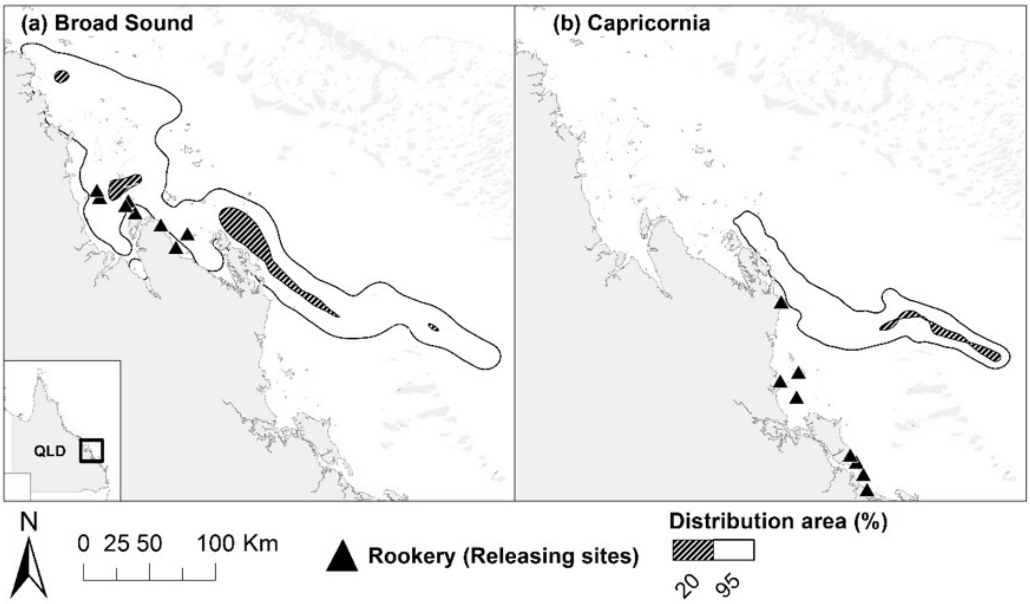

Figure 2.4. S-flatback distribution probabilities after 120 days (02-May-2012/00:00) of passive dispersal (scenarios PD-GL-regions) from (a) Broad Sound, and (b) Capricornia.

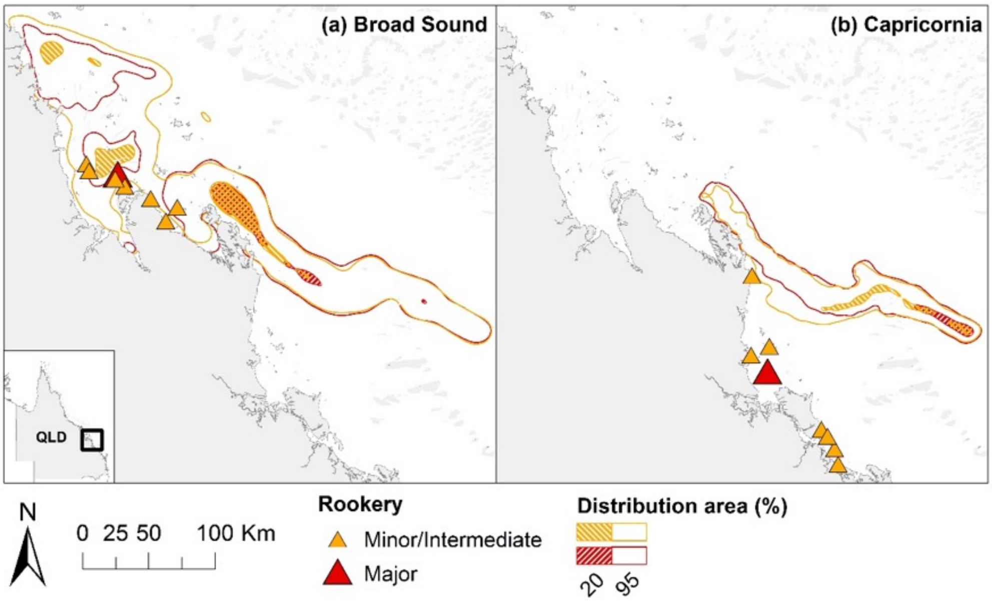

Figure 2.5. S-flatback distribution probabilities after 120 days (02-May-2012/00:00) of passive dispersal (scenarios PD-GL-minor/major) from major and minor/intermediate rookeries in (a) Broad Sound and (b) Capricornia.

Under the conditions that were modelled, the phase of the tidal sea surface elevation (neap/spring) at the time of release had an effect on the short-term (<7 days of dispersal) distribution of passive s-flatbacks. Spring tides favoured a westerly dispersal of s-flatbacks by day 3 (equalling the approximate end of swimming frenzy), while neap tides dispersed s-flatbacks further away from the coast and in an easterly direction (Figure 2.6a, 2.7a). Furthermore, the influence of neap/spring tides on the long-term distribution of s-flatbacks varied between the releasing regions. After 120 days, for Peak Island the distribution of s-flatbacks was not affected by the phase of the tides when they enter the ocean (BAI = 0.973) (Figure 2.7b). In contrast, core dispersal zones of s-flatbacks from Wild Duck Island greatly differed between the two tidal phases (BAI = 0.000), with spring tides favouring the dispersal of s-flatbacks inside the GBR, while neap tides promoted the advection of s-turtles into the EAC (Figure 2.6b).

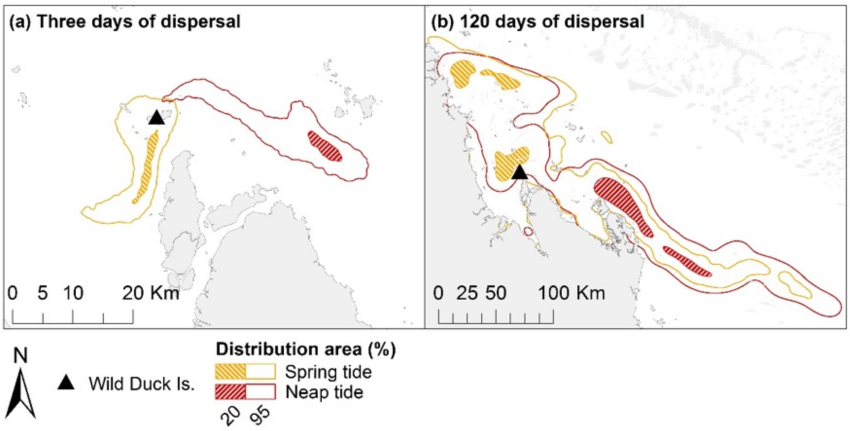

Figure 2.6. S-flatback distribution probabilities from Wild Duck Island after (a) 3 days and (b) 120 days of passive drift (scenarios PD-TP-neap/spring) after entering the sea during neap on 3-January-2012 at 15:00 and spring tide on 7-January-2012 at 12:00.

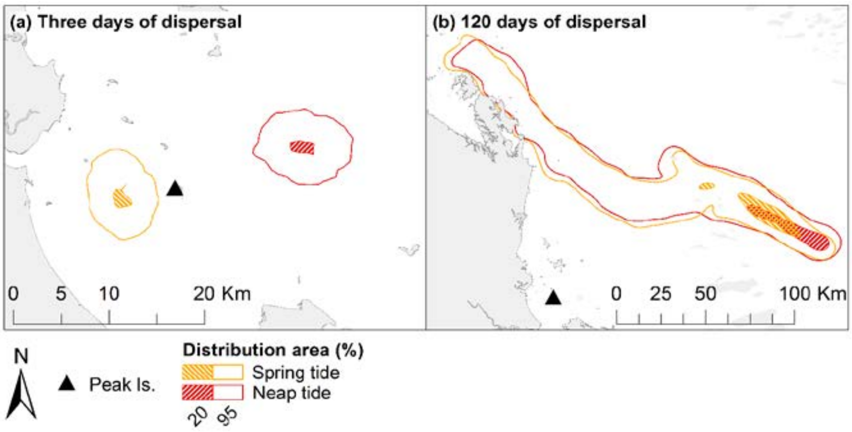

Figure 2.7. S-flatback distribution probabilities from Peak Island after (a) 3 days and (b) 120 days of passive drift (scenarios PD-TP-neap/spring) after entering the sea during neap on 3-January-2012 at 15:00 and spring tide on 7-January-2012 at 12:00

2.3.2. The importance of directional swimming

The standard run (DS-1-SR) scenario displayed a reasonable fit with the sparse data on post-hatchling distribution (Figure 2.3b). Under the passive drift scenario 67.5% for Wild Duck Island and 94.2% for Peak Island of s-flatbacks were transported seaward towards the Coral Sea after 120 days. For the standard run scenario, this loss rate reduced to 7% and 21.7% for Wild Duck Island and Peak Island, respectively. This represents between a 6- and 17-fold increase of s-flatbacks being retained inside the GBR with the addition of swimming behaviour to the simulation.

The dispersal success of each swimming scenario is shown in Table 2.3. Some of the best performing scenarios (high proportion of s-flatbacks in inshore habitats) were DS-6 and DS-3, in which turtles would swim at faster swimming speed (0.04 m s^{-1}) and southwards, respectively. The horizontal swimming favouring s-turtles to remain in the coastal waters (high dispersal success) included (a) swimming at medium-fast speeds (0.02-0.04 m s^{-1}, scenarios DS-1-SR and DS-6) (Figure 2.8, 2.10a), (b) maintaining a swimming direction towards the south or north-west (scenarios DS-3 and DS-1-SR) (Figure 2.10b), (c) developing a short initial drifting phase (start swimming between 4 and 30 days after entering the sea, scenarios DS-1-SR and DS-10) (Figure 2.10c), or (d) spending more than 75% of the day swimming (scenarios DS-1-SR, DS-9) (Figure 2.9, 2.10d).

In contrast, the lowest dispersal success (low proportion of s-flatbacks in inshore habitats) was observed when s-flatbacks were entirely passive (scenario PD-0) or maintaining headings towards the east (leading s-turtles directly into the EAC, scenario DS-4) or north (leading s-turtles into the Coral Sea Lagoonal current, scenario DS-6). Low dispersal success was also related to low swimming efforts by s-flatbacks; namely, scenarios in which s-flatbacks began to swim after >90 days (DS-12) or spent only 25% of the day swimming (DS-7).

Table 2.3. Dispersal success (percentage of s-flatbacks in inshore waters) of each scenario of the sensitivity analysis. The dispersal success for Wild Duck Island, Peak Island, the average over the two locations, and the overall dispersal success are shown for each scenario. Overall dispersal success is based on the average, and ranked as Very low (≤ 25%), Low (25.01 – 50%), Medium (51.01 – 75%) and High (> 75%). S-flatbacks were modelled for 120 days until 00h on 2nd May 2012. PD: passive drift, SR: standard run.

	Dispersal success (% of s-flatbacks in inshore waters)			
Scenario name	**Wild Duck Is.**	**Peak Is.**	**Average**	**Overall dispersal success**
DS-4	5.61	1.8	3.7	Very low
DS-2	24.03	0.0	12.0	Very low
PD-0	29.14	3.4	16.3	Very low
DS-12	66.61	8.6	37.6	Low
DS-7	53.28	26.7	40.0	Low
DS-11	81.32	25.9	53.6	Medium
DS-5	66.31	44.8	55.5	Medium
DS-8	76.25	55.8	66.0	Medium
DS-10	88.65	70.6	79.6	High
DS-1	90.99	75.4	83.2	High
DS-9	97.47	85.8	91.6	High
DS-3	87.38	98.9	93.2	High
DS-6	99.01	96.4	97.7	High

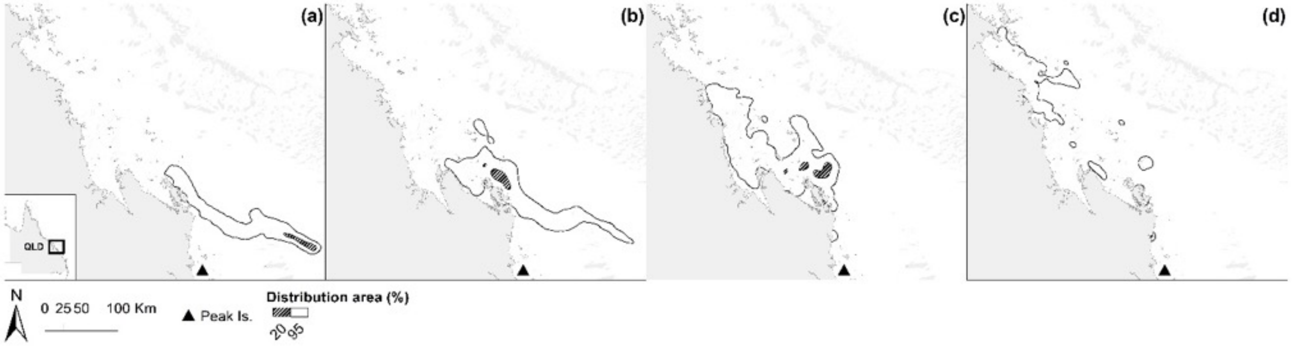

Figure 2.8. S-flatback distribution probabilities from Peak Island after 120 days at sea on 02-May-2012/00:00 under different scenarios: (a) Passive drift (PD-0); and swimming scenarios (b) DS-5 (swimming speed 0.01 m s^{-1}), (c) DS-1-SR (swimming speed 0.02 m s^{-1}), (d) DS-6 (swimming speed 0.04 m s^{-1}).

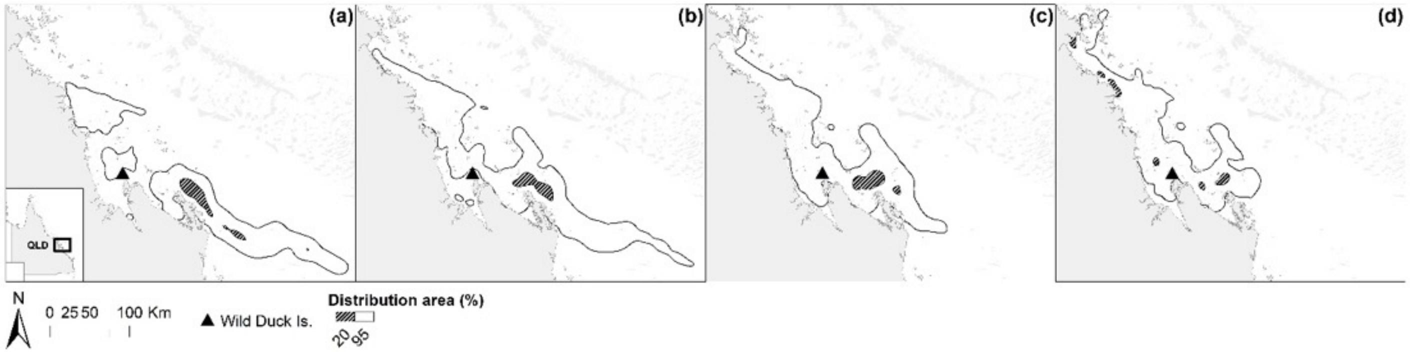

Figure 2.9. S-flatback distribution probabilities from Wild Duck Island after 120 days at sea on 02-May-2012/00:00 under different scenarios: (a) Passive drift (PD-0); and swimming scenarios (b) DS-7 (swimming 25% of the time), (c) DS-8 (swimming 50% of the time) and (d) DS-1-SR (swimming 75% of the time).

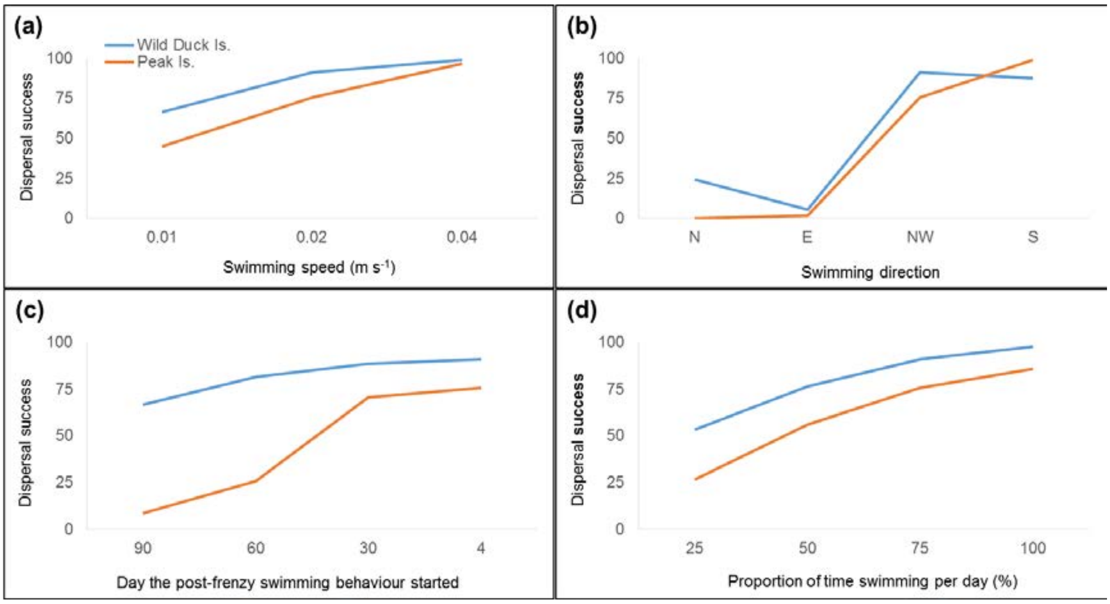

Figure 2.10. Dispersal success (percentage of s-flatbacks in inshore waters) for each of the swimming parameters I evaluated in the sensitivity analysis: (a) swimming speed, (b) swimming direction, (c) proportion of time swimming per day, and (d) the day the post-frenzy swimming behaviour started. For each scenario, the dispersal success for Wild Duck Island, Peak Island. Dispersal success are Very low (≤ 25%), Low (25.01 – 50%), Medium (51.01 – 75%) and High (> 75%). For all scenarios s-flatbacks were modelled for 120 days until 00h on 2nd May 2012.

2.4. Discussion

This study focused on simulating, with a high resolution hydrodynamic model, the effect of behaviour on the dispersal of s-flatback turtles in the GBR, by assessing different scenarios of passive drift and active swimming. I suggest potential mechanisms that could drive the neritic development of flatback turtles. In particular, my models indicate that s-flatback post-hatchling distribution during the first months of their life is likely to be defined by the combination of (a) inshore location of nesting beaches, (b) local tides and net currents and, just as important, (c) the turtle's active and directed swimming behaviour. Finally, I suggest that wind-driven waves might have an important effect in the orientation of s-flatbacks in the GBR, a hypothesis that warrants further testing.

2.4.1. The effect of nesting selection on post-hatchling dispersal patterns in the southern GBR

Major rookeries of green and loggerhead turtles in the southern GBR are nearly all located along the islands of the outer edge (Figure 2.1a) and in close proximity to the EAC, which is the dominant oceanic current of eastern Australia. My modelling confirmed that, even under passive drift scenarios and typical oceanographic conditions, s-green and s-loggerhead turtles are advected into the EAC within the first two weeks of life and thus are likely to have an oceanic developmental stage (e.g. Boyle (2007)) (Figure 2.3b). If swimming behaviour of green and loggerhead turtles is accounted for in the model, I could expect it to further facilitate an expeditious dispersal into oceanic waters. In contrast, flatback turtle nesting sites are predominately located along the islands and beaches of two regions (Broad Sound and Capricornia) of the inshore GBR (Figure 2.1a) and my models suggest that the inshore location of flatback turtle rookeries favours the retention of s-flatbacks in the GBR lagoon during the first month of dispersal. After this period, my models indicate that s-flatbacks under typical oceanographic conditions and with no swimming behaviour eventually get advected into the EAC and exported to the ocean (Figure 2.3b). It is feasible that some proportion of flatback turtle post-hatchlings do reach the EAC, which could help explain the presence of scattered post-hatchlings records around the Hervey Bay region (Figure 2.3a) and some small foraging aggregations which occur in southern Queensland.

It is also important to consider the oceanographic processes in this region, as well as their interaction with variable turtle behaviour. If the post-hatchlings were spending most of the time drifting near the surface, they would be swept directly into the EAC and dispersed into the Coral Sea. In contrast, if they were developing prolonged dives near reefs, the internal currents could increase their retention, as it happens with fish larvae and other small organisms (Snyder *et al.*, 2014). However, if this was the case, it would be expected to find more records of predated or stranded flatback turtles within the adjacent coral cays and islands of the Capricorn Bunker Group and Swain Reefs (Figure 2.1b) – both of which are areas with high rates of reef-based dive and fishing operations.

My results indicate that the advection rate of s-flatback turtle post-hatchlings was similar among inshore major, minor and non-rookeries, as well as between tides. Combined, these results suggest that some of the evolutionary drivers that have favoured the selection of the larger flatback turtle rookeries appear to be related to broad regional scale differences (e.g. selection of inshore versus outer edge beaches). A previous study in the GBR suggested that nesting distribution might be related to the exposure of rookeries to wind and wind-generated waves that assist hatchlings' movement during the swimming frenzy, and indicated that flatback turtles seem to prefer sheltered beaches (Garcon *et al.*, 2010). At a local scale, the nesting distribution of flatback turtles could also be influenced by other biophysical features (e.g. access to beach, presence of fringing reefs) which are not accounted for in my simulations.

Local water circulation patterns seem to have an important effect on the dispersal of post-hatchlings in coastal waters (Hamann *et al.*, 2011). Based on my models, spring tides promote a near-shore dispersal during the first week and might prolong the retention of s-flatbacks in the GBR (Figure 2.6a, 2.7a). This finding is consistent with a previous study (Hamann *et al.*, 2011) which revealed that the tides and currents around nesting islands can influence the direction and spread of flatback turtle hatchling dispersal during the first two weeks at sea. In other regions of the world (e.g. Atlantic Ocean) with small tidal ranges, tides do not seem to be an influential parameter for hatchling dispersal. However, in eastern Australia, the large tidal currents coupled with relatively shallow water act together to deflect the southward flowing EAC further offshore (Hamann et al. 2011). Distribution in near-shore areas might affect the probability of survival of post-hatchlings given that marine predators are likely to be more abundant in these areas (Gyuris, 1994; Stewart & Wyneken, 2004), yet flatback turtle post-hatchlings seem to have phenotype and behavioural adaptations which potentially decrease the risk of predation in coastal waters (Salmon *et al.*, 2009).

The region of origin also had an effect on the export/retention rate of s-flatbacks (Figure 2.4). There was an increased seaward export of s-flatbacks from rookeries in the Capricornia region, likely to be related to the closer location of these rookeries to the Capricorn Eddy (situated around the Capricorn Bunker Group, Figure 2.1b). While it has been suggested that the nesting distribution of other species of marine turtles is strongly associated with the proximity to favourable ocean currents (Putman *et al.*, 2010), it is possible that conversely the nesting distribution of flatback turtles has been shaped by the selection of beaches with favourable local water circulation patterns (Hamann *et al.*, 2011), but distant from the main currents leading into the ocean.

2.4.2. Directional swimming in flatback turtle post-hatchlings

The swimming behaviour appears to play a major role in the post-hatchlings' distribution during the first few months of their life. As mentioned before, my results provide evidence that the location of flatback turtle nesting beaches favours the retention of s-flatback post-hatchlings during the first 40 days of dispersal. However, my simulations also suggest that under typical climatic conditions, after 40 days s-flatback post-hatchlings with no swimming are likely to be swiftly advected towards the Coral Sea into oceanic habitats where they have not been historically encountered. I tested a variety of hypothetical swimming scenarios, and conclude that directional swimming greatly decreased the seaward export of s-flatbacks, and further increased the likelihood of retention of s-flatbacks in inshore waters. This result was qualitatively validated with long-term field evidence given that, like my results, they also show that immature and adult flatback turtles in eastern Australia occur within the Great Barrier Reef and coastal waters of southern Queensland (Figure 2.3) (Limpus, 2007; Robins, 2002). Furthermore, the similarity among the modelled dispersal paths of s-flatbacks and the actual migration routes of existent tracked adult turtles (Figure 2.3 b-c) supports the theory that post-hatchlings might be able to imprint the location of habitats they pass through during their development, which can potentially influence the later migrations and distribution of juvenile and adult turtles (Hays *et al.*, 2014; Scott *et al.*, 2014; Shillinger & Bailey, 2015).

In particular, s-flatbacks with active and directed swimming behaviour during the first months after entering the sea are more likely to disperse into neritic habitats. The range of horizontal swimming that favours s-turtle dispersal within the GBR (Table 2.3, Figure 2.10) reveals that the more time and effort s-flatbacks invest in swimming, the higher their chance of maintaining a neritic dispersal. Overall, my results suggest that, under typical oceanographic conditions, flatback turtle post-hatchlings can have a short initial drifting phase, but afterwards they need to actively swim to increase the likelihood of a neritic distribution. According to my simulations, sustained speeds (> 0.02 m s^{-1}) and time spent swimming (> 75% of the day) are influential parameters that increase the inshore dispersal success. In addition, my simulations show that accounting for directionality causes substantial differences in the dispersal outputs (Table 2.3). For turtles released from the two major rookeries, a north-west heading (DS-1-SR) resulted in the best fit with the observed post-hatchling distribution (Figure 2.3 a-b). The scenario with a south heading (DS-3) also favoured a coastal retention of s-flatbacks, leading them to southern areas where reports of wild post-hatchlings occur but are scarce. The results of my study are based on hypothetical swimming parameters and provide valuable baseline criterions to experimentally test the orientation and swimming efforts of flatback turtles in the GBR.

While my study highlights the importance of considering swimming behaviour when simulating the early dispersal of marine turtles, numerous studies have showed that annual variability in oceanic conditions can greatly influence dispersal predictions (Hays *et al.*, 2010; Okuyama *et al.*, 2011; Putman *et al.*, 2012b). As an example of this, simulations of the dispersal of young loggerheads in eastern Florida evidenced that not only the spread in dispersal patterns, but also the magnitude of the influence of navigational behaviour varied greatly among different years (Putman *et al.*, 2012b). Future extensions of my modelling would be greatly enhanced by considering the influence of seasonal and inter-annual variability of the oceanographic conditions in the dispersal of post-hatchlings in the GBR.

2.4.3. Cues for directional swimming in marine species

There is a great array of sensory interactions between marine animals and their environment that likely play an important part in their behaviour, spanning from visual, olfactory or sound stimuli, to the detection of hydrodynamic and magnetic features (Lohmann *et al.*, 2008; Wolanski, 2016; Wolanski & Kingsford, 2014). For example, in the GBR in order to self-recruit to their natal reefs coral reef fish larvae orient themselves to swim against concentration gradients in plumes from their natal reef until they were within reach of sound cues produced from near reefs (<1 km from reef) (Wolanski & Kingsford, 2014). This is also the case for coastal post-larvae crab in New Zealand which use sound cues to find suitable environments to recruit (Radford *et al.*, 2007). The external cues that marine turtles may use to guide behaviour such as directional swimming during dispersal warrants further attention.

Directional swimming using Selective Tidal Stream Transport (STST) (Criales *et al.*, 2013) is unlikely for turtle hatchlings because they would need to remain on the bottom for long periods to enable them to detect pressure changes and judge whether the water pressure (i.e. the tide) is rising or falling. There are however orientation cues that marine turtles are known to use, including the detection of wave direction during the swimming frenzy (Lohmann *et al.*, 1997; Lohmann & Lohmann, 1992; Salmon & Lohmann, 1989) and a combination of visual and magnetic signals to orient themselves in the open ocean (Avens & Lohmann, 2003; Lohmann *et al.*, 1997; Lohmann, 1991; Lohmann *et al.*, 2008; Lohmann *et al.*, 2013; Mott & Salmon, 2011; Putman *et al.*, 2015). A hypothesis that has not been tested so far is the capacity of post-hatchlings to adjust their movements based on the direction of wind-driven waves in coastal waters: for example, this direction is primarily northwestwardly in the GBR, which if adopted for directional swimming, my simulations show favours self-recruitment of flatback turtles. The use of sound or olfactory cues remain unknown. Thus, my understanding of the early dispersal of flatback turtles would be greatly enhanced by experimentally testing the orientation of hatchlings as a response of wind-driven waves, smell/sound plumes, magnetic fields (Lohmann, 1991; Lohmann *et al.*, 2001; Putman *et al.*, 2015), or directly tracking neonates with acoustic (Thums *et al.*, 2013) or satellite tags (Putman & Mansfield, 2015).

2.5. Conclusions

I provide a potential explanation to the differences observed historically in the dispersal strategies (oceanic versus neritic) of co-existing marine turtle species in the GBR. The neritic distribution of s-flatback turtles was favoured by the inshore location of nesting beaches. In contrast, the outer location of reef cays and beaches where s-greens and s-loggerheads nest, favoured a swift dispersal of these species into oceanic waters. The local water circulation in the different regions (Broad Sound and Capricornia) also seems to play an important role in the retention/advection of flatback turtle post-hatchlings, especially during the first month of dispersal. S-turtles released during spring tides displayed a near-shore dispersal during the first week, which could have potential effects on their survival rates. Finally, under typical oceanographic conditions the inshore dispersal is further favoured if directional swimming of s-turtles is added to the models. In particular, my models suggest that high swimming efforts (in terms of speed and sustained swimming) and directionality could be important parameters to consider in future studies of flatback turtle dispersal. My results highlight the value of integrating knowledge and applications from biological and physical sciences to improve knowledge of animal behaviour. High-resolution hydrodynamic models are a valuable tool to understand the influences of physical processes on the distribution of cryptic marine species and to infer potential pathways of dispersal (Hamann *et al.*, 2011; Lambrechts *et al.*, 2008; Putman & He, 2013; Wolanski, 2016). Further advances in the resolution and numerical functions of hydrodynamic models, coupled with improved knowledge of species biology and navigation, are clearly needed. These kinds of improvements will enhance the understanding of the impact that small and large scale oceanographic events might have on the autonomous horizontal and vertical movement of species, and consequently on the behaviour and distribution of species; especially on the face of the current changing conditions in the world’s seas and oceans.

Chapter 3

Dynamic migratory and foraging strategies of flatback turtles in eastern Australia

An adult female flatback turtle equipped with a satellite tag on Curtis Island in November 2013.
Photo credits: Hector Barrios-Garrido

Abstract

Knowledge of the foraging ecology of marine turtles has significantly increased in the past decades. However, for flatback turtles (*Natator depressus*) in eastern Australia (eAus), the migratory routes and foraging areas are poorly known. Flatback turtles are endemic to the continental shelf of Australia and remain mainly in tropical coastal waters within the continental shelf. Based on direct observation, recaptures of tagged turtles and bycatch records, it is known that eAus flatback turtles prefer sub-tidal turbid waters; however, there are limited data on habitat use and foraging behaviour for the eAus flatback turtle stock. Using GPS-linked satellite telemetry technology, I aimed to understand fine- and large-scale movement of flatback turtles, and in doing so describe the migratory and foraging strategies of adult female flatback turtles from the eAus stock. Between 2009-2015, 44 Argos-linked Fastloc GPS tags were deployed on adult female flatback turtles from eight different nesting grounds on the Queensland coast. Data were filtered and analysed with a behavioural point change analysis to identify shifts in the migration and foraging behaviour of turtles. In addition, utilisation distributions (UD) were estimated at 50% (core area) and 95% (home range), with a movement-based kernel density estimator based on a random bridge model (MKDE-BRB). The migration of turtles in this study spanned across 8 degrees of latitude with straight line travel distances ranging between 35 and 1295 km. All tracked turtles remained in coastal waters within the boundaries of the Great Barrier Reef World Marine Park (GBRMP), excepting a small proportion of foraging sites (0.5%) located in ports adjacent to the marine park. I identified two types of distinctive migratory behaviour: (a) Direct migration (N=22), in which turtles migrated directly to their foraging grounds; and (b) Multi-stop travel (n=22), characterised by multiple temporary areas where turtles spent between 5 and 30 days before resuming migration. I also identified four foraging strategies: (a) Single area-fixed foraging (n=22), indicating usage of a single, well-defined foraging area; (b) Single area-wandering (n=5), in which the turtle used a specific foraging ground, but frequently undertook short journeys (up to a week) around that area; (c) Multiple area-shifting (n=10), in which turtles use different foraging grounds, without returning to a previously visited area; and (d) Multiple area-recurring (n=18), typically consisting of two or more well-defined foraging grounds used repeatedly by the turtle. There was no relationship between specific behaviours and nesting location or the year in which the turtles were tagged. Even though tracked turtles from all beaches used in this study were recorded in most management areas of the GBRMP, there was a clear latitudinal trend in the distribution of southernmost nesters foraging in the southern management areas, central nesters foraging across the range, and northernmost nesters foraging in the northern management areas. Overlap in the distribution of home rages was evident in three different regions, which were identified as high use foraging regions in the GBRMP for the tracked flatback turtles. Average size of foraging grounds was larger than reported for other coastal marine turtle species, with average core areas of 68.2 ± 64.1 km^2 and home ranges of 455.5 ± 359.7 km^2. To the best of our understanding, migration routes displaying multiple stops and dynamic foraging strategies such as the ones described in this study are unusual in other marine turtle species, but appear to be a common pattern among flatback turtles tracked in this study. The variability observed in foraging behaviour, as well as the large size of home ranges reported herein, indicate flatback turtles develop a dynamic, opportunistic foraging strategy.

Keywords: flatback turtle, *Natator depressus*, behavioural ecology, movement ecology, migration, foraging, Great Barrier Reef World Heritage Area.

3.1. Introduction

Understanding the distribution of a species is inherently linked to their behavioural ecology, which in turn is greatly shaped by the spatial ecology and habitat use at individual and population levels (Liedvogel et al., 2013). As a complex discipline, behavioural ecology has been typically investigated through phenotypic (observed traits or behaviours), genetic (molecular basis of behaviour) and comparative (trait comparisons between species) approaches (Cézilly *et al.*, 2008). Under this description, telemetry is regarded as a phenotypic approach (Cézilly *et al.*, 2008), and is commonly used to assess species with cryptic life stages or wide spatial distribution, such as marine mammals, turtles and birds (i.e. Costa *et al.* (2010); Fossette *et al.* (2010); Le Corre *et al.* (2012)). While the spatial ecology of a population is frequently used to inform management actions, the importance of addressing differences due to independence and distinctiveness in individual behaviour has progressively been recognised (Liedvogel *et al.*, 2013).

Habitat selection is closely related to individual behaviour through feedback loops. The behaviour of an animal, especially highly mobile ones, will influence the selection of a specific habitat; conversely, the characteristics of the selected habitat will influence the animal’s behaviour and interaction with its surroundings (Dugatkin, 2014). Habitat selection is also dependent on the spatial and temporal distribution of resources (i.e. food, environmental conditions, areas for resting/sleeping) and intra-/inter-specific interactions (i.e. predation risk, breeding) (Dugatkin, 2014; Limpus & Reed, 1985). Furthermore, the process of selecting a habitat and its subsequent use is central in the definition of an individual’s home range. A simple and widely used concept of home range is “that area traversed by the individual in its normal activities of food gathering, mating, and caring for young” (Burt, 1943). Home range can be considered as a high-use area where an animal spends a substantial portion of its time, and is typically used for specific purposes such as foraging, sleeping/resting, sheltering, among other behaviours. In spatial ecology, home ranges are often represented by utilisation distributions (UD).

There are limited methods to accurately determine home ranges of mobile marine megafauna (i.e. marine mammals, sharks, marine turtles), largely because these methods rely on telemetry or remote technologies to indirectly monitor individual-based movements and behaviour (Bestley *et al.*, 2015). Fortunately, the increasing quality of remote sensing, tracking and computing technologies (e.g. acoustic or satellite telemetry, animal-borne videos) have proved to be useful tools with which to make inferences about population behaviour and spatial habitat use of marine species (Godley *et al.*, 2008; Wadsworth & Treweek, 1999). For example, the behavioural plasticity of marine turtles has now been well documented (Godley *et al.*, 2008; Hawkes *et al.*, 2011; Rees *et al.*, 2010; Schofield *et al.*, 2010), largely due to recent improvements in high accuracy Argos-linked Fastloc GPS (FGPS) transmitters and the development of behaviour-specific statistical approaches (Gurarie *et al.*, 2009; Jonsen *et al.*, 2005; Patel *et al.*, 2015). In addition, it is now possible to use high resolution tracking data to improve conservation initiatives. For example, home range analysis and the continuing understanding of the migratory and foraging behaviour of marine turtles have been widely used as a tool to inform management of endangered populations (Gredzens *et al.*, 2014; Shimada *et al.*, 2017).

Despite recent advances in our knowledge on the habitat use of most marine turtle species, there are substantial gaps in the understanding of the spatial and behavioural ecology of flatback turtles (*Natator depressus*). The flatback turtle is the only marine turtle species that lacks an oceanic life stage, instead spending its complete life cycle within neritic habitats on the Australian continental shelf (Limpus, 2007). There are two distinct genetic stocks breeding within the state of Queensland: the Arafura Sea population and the eastern Australia (eAus) population (Figure 1.1) (FitzSimmons & Limpus, 2014). Foraging grounds of the eastern Australian genetic stock are believed to occur from Torres Strait in the north, throughout the Great Barrier Reef and as far south as Moreton Bay (Limpus, 2007). Within this region, non-breeding activities (e.g. migration, foraging, resting, etc.) of flatback turtles have been recorded since 1967 (Williams *et al.*, 1967) through direct observation (EHP Queensland Turtle Research database), trawling data (Robins, 1995; Robins, 2002) and several records of tag recovery data (Limpus *et al.*, 2013a). These data provide a valuable long-term perspective on the distribution of individuals during their non-reproductive life stages in the region. In particular, it indicates that flatback turtles generally prefer the sub-tidal, soft-bottom environments of continental shelf waters (Limpus *et al.*, 2013a). However, compared to the data on other marine turtles in Queensland, current knowledge of flatback turtle foraging ecology and habitat use is limited. This information gap is acknowledged by the Australian Government in their Reef 2050 Long Term Sustainability Plan (Commonwealth of Australia, 2015).

To improve the current knowledge of the foraging ecology of flatback turtles in Queensland, I tracked female turtles from multiple locations across the Queensland coast and analysed their migration to the foraging grounds. I employed high accuracy satellite technology location estimates of the turtles, which I then analysed to describe the large- and fine-scale movement of each individual tracked turtle and test the hypothesis that Great Barrier Reef (GBR) turtles remain in eastern Australian waters. This enabled me to identify foraging hot spots in eastern Australia for the tracked flatback turtles, as well as enhance our understanding on the movement ecology and habitat use of this species. In particular, based on the migratory and foraging behaviour of the individual turtles, I identified different travelling and foraging strategies that seem to be common within the population. These new insights on the distribution and spatial ecology of flatback turtles in the GBRMP which can inform several priority action areas required to recover the eAus flatback turtle stock as identified in the latest Recovery plan for marine turtles in Australian waters (Commonwealth of Australia, 2017).

3.2. Methods

3.2.1. Data collection and filtering

Between 2009 and 2016, 44 adult female flatback turtles were tracked using Argos-linked Fastloc GPS (FGPS) tags (Wildlife Computers) between their nesting beach and foraging area. I tracked 26 turtles from Curtis Island and six from the Mackay Region, and data from the other turtles was provided to me to add value to my thesis data. Details on the deployment of tags are described in Table 3.1. The turtles were caught and tracked from nesting beaches distributed within most of the flatback turtle nesting range in eastern Australia. From north to south: Wunjunga (19.777ºS, 147.616ºE) (n=9), Halliday Bay (20.894ºS, 148.990ºE) (n=3), Ball Bay (20.907ºS, 149.000ºE) (n=1), Eimeo (21.036ºS, 149.180ºE) (n=1), Blacks beach (21.044ºS, 149.187ºE) (n=1), Peak Island (23.342ºS, 150.934ºE) (n=2), Curtis Island (23.741ºS, 151.300ºE) (n=26) and Mon Repos (24.798ºS, 152.443ºE) (n=1) (Figure 3.1). Information on the individual turtles and tag deployment events are detailed in Table 3.2. After a successful nesting event, a FGPS tag was deployed using a harness designed specifically for use on flatback turtles (Sperling & Guinea, 2004). Turtles were tracked during the inter-nesting period (not included in this Dissertation), and as each turtle completed its breeding season, it was tracked from the nesting beach to the foraging area (Chapter 2).

Table 3.1. Tag deployment information and performance of the satellite tags.

Releasing location	**Tagging Year-month**	**Number of tags**	**Transmission length (mean days ± SD)**
Peak Island	*2009-Dec*	*2*	*245.2 ± 93.4*
Curtis Island	*2009-Dec*	*1*	*575.9*
	2013-Nov	*9*	*86.6 ± 13.8*
	2014-Nov	*9*	*164.9 ± 77*
	2015-Nov	*7*	*120.8 ± 47.7*
Mackay region (includes: Halliday Bay, Ball Bay, Eimeo and Blacks beach)	*2014-Nov/Dec*	*4*	*148 ± 67.1*
	2015-Dec	*2*	*158 ± 7*
Wunjunga	*2013-Nov*	*4*	*131.3 ± 56.1*
	2014-Dec	*5*	*359.9 ±174*
Mon Repos	*2015-Dec*	*1*	*142.6*
All		*44*	*171.6 ±124*

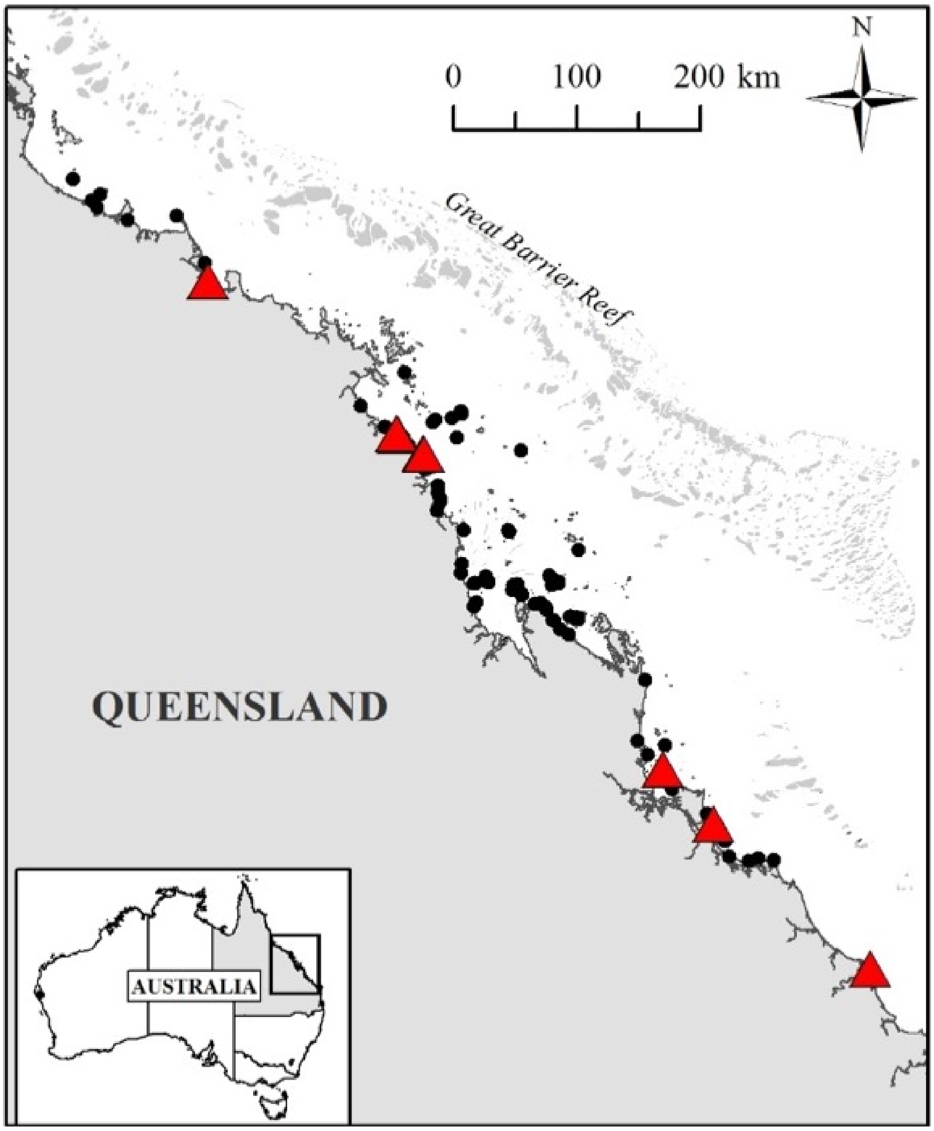

Figure 3.1. Tagging locations of tracked turtles. Red triangles represent nesting beaches where turtles were tracked. From north to south: Wunjunga (n=9), Halliday Bay/Ball Bay (n=3/1), Blacks beach/Eimeo (n=1/1), Peak Island (n=2), Curtis Island (n=26) and Mon Repos (n=1). Black points represent beaches where flatback turtles have been recorded nesting in eastern Queensland.

Table 3.2. Summary of the deployment of satellite tags on 44 nesting flatback turtles in eastern Australia. Deployment location codes: Wunjunga (W), Halliday Bay (HB), Ball Bay (BaB), Eimeo (EB), Blacks beach (BlB), Peak Island (PI), Curtis Island (CI) and Mon Repos (MR).

Turtle ID (satellite tag)	*Flipper tag number*	*CCL (cm)*	*Deployment location*	*Deployment date*	*Transmission length (days)*
54528	K39708	91.0	EB	1-Dec-2014	187.59
54531	T73236	95.5	HB	2-Dec-2014	63.13
96774	T86911	92.3	PI	23-Dec-2009	179.14
96776	-	95.5	PI	23-Dec-2009	311.36
96779	T20453	95.9	CI	23-Dec-2009	575.90
108471	K39709	91.4	BlB	2-Dec-2014	127.43
120641	T73235	93.5	BaB	23-Nov-2014	213.86
133399	-	-	W	15-Nov-2013	210.55
133400	-	-	W	15-Nov-2013	131.05
133401	-	-	W	15-Nov-2013	86.11
133402	-	-	W	16-Nov-2013	97.73
133758	X23103	-	MR	11-Dec-2015	142.64
134189	QA30770	95.7	CI	26-Nov-2013	101.77
134190	K43635	94.6	CI	27-Nov-2013	85.47
134191	T85646	-	CI	26-Nov-2013	81.51
134192	T97108	98.7	CI	25-Nov-2013	100.75
134194	T20452	95.5	CI	26-Nov-2013	80.42
134195	T97111	99.4	CI	26-Nov-2013	59.56
134196	K44384	97.7	CI	26-Nov-2013	86.43
134198	T97125	-	CI	25-Nov-2013	80.72
134199	T85652	91.8	CI	25-Nov-2013	103.36
141738	QA20377	91.6	CI	14-Nov-2014	123.81
141739	QA20379	93.2	CI	15-Nov-2014	164.76
141740	T85633	98.9	CI	13-Nov-2014	55.03
141741	QA20400	99.0	CI	13-Nov-2014	277.46
141742	QA20381	94.2	CI	17-Nov-2014	195.51
141744	K43572	89.4	CI	18-Nov-2014	283.42
141746	QA20383	93.1	CI	18-Nov-2014	165.26
141747	T97209	97.8	CI	18-Nov-2014	112.79
141748	QA20388	93.8	CI	18-Nov-2014	106.42
141758	-	-	W	4-Dec-2014	479.35

141759	-	-	W	5-Dec-2014	477.34
141760	-	-	W	5-Dec-2014	275.29
141762	-	-	W	6-Dec-2014	477.90
141763	-	-	W	7-Dec-2014	89.99
152711	K33707	93.3	CI	9-Nov-2015	55.28
152712	T85690	93.5	CI	6-Nov-2015	73.60
152713	QA30727	-	CI	10-Nov-2015	186.35
152714	QA46070	91.3	CI	6-Nov-2015	127.27
152715	K43686	92.1	CI	6-Nov-2015	144.78
152718	QA30747	-	CI	8-Nov-2015	97.15
152720	T97111	-	CI	4-Nov-2015	161.77
154296	K39714	91	HB	15-Dec-2015	153.26
154297	K39724	97	HB	5-Dec-2015	163.21

Once the tags ceased transmitting data, I extracted the satellite-derived locations for each turtle from the date they departed the nesting beach until the last location received. All data were screened with a data-driven filter (Shimada *et al.*, 2012; Shimada *et al.*, 2016c) to remove temporal and spatial duplicates, and locations marked by biologically unlikely swimming behaviour (> 7.6 km/h) and turning speeds (> 1.8 km/h), using the R package SDLfilter (available from https://github.com/TakahiroShimada/SDLfilter). Results are presented as the range (minimum and maximum recorded values) and/or the mean ± standard deviation.

3.2.2. *Behavioural analysis*

A Behavioral Change Point Analysis (BCPA) (Gurarie *et al.*, 2009) was employed to look at the fine-scale movements (shifts in behaviour) of the turtles and objectively categorise the filtered movements of each turtle as (a) travelling or (b) foraging, using the R package BCPA (Gurarie, 2013). The BCPA was designed to identify shifts in heterogeneous behaviour with irregular temporal sampling, typical of marine organisms. Animal movement is characterised mainly by its speed as well as the persistence and variability in direction; the BCPA combines these features in a parameter called persistence velocity ($Vp = V \cos(\theta)$, where V = speed and θ = turning angle), which “captures the tendency and magnitude of a movement to persist in a given direction” (Gurarie *et al.*, 2009). I used Vp as the response parameter for the BCPA. The analysis is based on a likelihood estimation method which swipes a window across the time series and identifies the most likely “change point” where the mean ($\hat{\mu}$), standard deviation ($\hat{\sigma}$) and/or time-scale of autocorrelation ($\hat{\tau}$) values of the response differ significantly (Gurarie *et al.*, 2009; Gurarie *et al.*, 2016). Within a biological context, $\hat{\mu}$ provides a measure of the mean magnitude and direction of the animal’s movement, $\hat{\sigma}$ describes how much this parameter varies, and $\hat{\tau}$ provides a measure of the tortuosity (how much the animal turns) of the movement, with higher values indicating straighter movements. Given that tracking length and resolution differs among individuals, the window size (*ws* = number of observations covering the minimum time in which a biologically relevant change in behaviour can occur) and sensitivity parameter (*K* = higher values account for differences between more parameters) were tuned for each turtle (Table 3.3).

Table 3.3. Parameters used to tune the BCPA analysis for each turtle. Temporal resolution = the minimum temporal range covered by the window size; K = sensitivity parameter.

Turtle ID	***Window size (number of observations)***	***Temporal resolution (days)***	***K***
54528	22	3	2
54531	32	3	3
96774	24	3	2
96776	21	5	2
96779	21	6	2
108471	39	3	2
120641	21	4	2
133399	30	3	2
133400	38	3	2
133401	42	3	2
133402	48	3	2
133758	26	3	2
134189	21	5	2
134190	21	6	2
134191	21	4	2
134192	21	4	2
134194	21	5	2
134195	21	4	2
134196	21	4	2
134198	21	5	2
134199	21	5	4
141738	21	4	2
141739	21	5	2
141740	21	4	2
141741	21	6	2
141742	21	4	4
141744	21	4	2

141746	21	4	3
141747	21	3	2
141748	21	4	2
141758	32	3	2
141759	31	3	2
141760	28	3	2
141762	29	3	2
141763	44	3	2
152711	57	7	2
152712	25	3	2
152713	21	3	2
152714	25	3	2
152715	22	3	2
152718	23	3	2
152720	29	3	3
154296	21	4	2
154297	21	4	2

The BCPA provides a summary of the different change points, their position in the time series, the significant parameters used to identify them, and the associated parameters ($\hat{\mu}$, $\hat{\sigma}$, $\hat{\tau}$) for each phase (the periods before and after a change point). I categorised these phases as migration or foraging events by defining thresholds (Table 3.4) based on the general patterns in mean ($\hat{\mu}$) and time-scale of autocorrelation ($\hat{\tau}$) parameters.

Table 3.4. Thresholds of *persistence velocity* ($\hat{\mu}$) *and tortuosity* ($\hat{\tau}$) used to categorize movement as travelling, slow travelling and foraging. The “General” threshold was used for all turtles, except for those listed in this table.

Turtle ID	***Travelling***	***Slow travelling***		***Foraging***		***Comments***
	$\hat{\mu}$	$\hat{\mu}$	$\hat{\tau}$	$\hat{\mu}$	$\hat{\tau}$	
General	> 0.15	$0.15 \leq \hat{\mu} > 0.07$	> 0.06	≤ 0.15	≤ 0.06	
96774	> 0.10	$0.10 \leq \hat{\mu} > 0.07$	> 0.06	≤ 0.10	≤ 0.06	Slow travelling speeds
141748	> 0.10	$0.10 \leq \hat{\mu} > 0.07$	> 0.06	≤ 0.10	≤ 0.06	Slow travelling speeds
152711	> 0.15	$0.15 \leq \hat{\mu} > 0.07$	> 0.07	≤ 0.15	≤ 0.07	
154296	-	-	> 0.05	≤ 0.05	-	Very slow and tortuous
152720	> 0.16	$0.16 \leq \hat{\mu} > 0.07$	> 0.06	≤ 0.16	≤ 0.06	Faster foraging movements

A Fisher’s exact test was employed to assess the relationship between travelling/foraging strategies and the location and year of deployment.

3.2.3. *Estimation of home ranges*

I computed utilisation distributions (UD) to estimate the home range and core use areas of each turtle using a movement-based kernel density estimation (MKDE) based on a biased random bridge model (BRB) (Benhamou, 2011). I used the R package adehabitatHR (Calenge, 2011) to compute the UDs and calculate the 95% home range and 50% core areas. The parameters used to estimate the UDs are listed in Table 3.5. The MKDE-BRB incorporates the movement of the animal by interpolating consecutive real fixes at regular time steps, and allowing for variable smoothing depending on the time difference between the real and interpolated fixes (being greater as the time difference increases (Calenge, 2011). Given that the MKDE works under the BRB theoretical concept, the model accounts not only for a diffusion (transport based on random motions) component in the movement but also and advection (transport by the flow of a fluid) component; thus, considering it a more realistic estimation to the real movement of an animal (Calenge, 2011). A Fisher's exact test was employed to assess the relationship between the release location of the turtles (i.e. nesting beach of origin) and the location of the foraging grounds according to the four management areas of the GBRMP (shown in Figure 3.2). All maps were created using ArcMap 10.2.2

Table 3.5. Parameters specified in the R script used to estimate the utilisation distribution (UD) using the MKDE-BRB analysis.

Parameter	***Value***
D	Estimated using the BRB.likD function
Tmax	16 hours
Lmin	50 m
hmin	100 m
type	"UD"
grid	50 m

3.3. Results

3.3.1. General features of the turtles' tracks

All foraging sites of the tracked turtles were located within the boundaries of the GBRMP, with the exception of a small proportion (0.5%) located within ports adjacent to the marine park (Figure 3.2). The straight-line distance between an individual's nesting beach and its main foraging ground ranged between 35 and 1295 km. Total tracking durations lasted between 55 and 576 days, with an average of 6.08 ± 1.02 fixes/day. All turtles were tracked to at least one foraging ground; however, the tracking transmission of eight turtles stopped before arriving to a main foraging ground (residency < 30 days) (Table 3.6).

There were no significant differences between the travelling/foraging strategies and the release location ($p = 0.83$ / $p = 0.57$, Fisher's exact test) or year of tag application ($p = 0.44$ / $p = 0.14$, Fisher's exact test). More than half of the turtles (63.63%) travelled to foraging grounds in the Mackay/Capricorn management region of the GBRMP. The Townsville/Whitsunday management area was the second most-used used of the GBRMP management areas, with 15 turtles (34.09%), seven turtles (15.9%) and eight turtles (18.18%) migrating into the Cairns/Cooktown and Far Northern management areas, respectively. Nearly one third (27.27%) of the turtles tracked were observed to use foraging grounds in two or more management areas (Figure 3.2, Table 3.6).

Furthermore, the proportion of foraging turtles originating from each nesting beach varied significantly among management areas ($p = 0.03$, Fisher's exact test) (Figure 3.3). Turtles foraging in the Far Northern management area were more likely to have been tagged while nesting at Wunjunga Beach (northernmost sampling site), while turtles foraging in the southern management areas were more likely to originate from Curtis Island (a southern sampling site). Turtles tagged while nesting in the Mackay region (i.e. Halliday bay/Ball bay, Blacks beach/Eimeo) were tracked to foraging sites spread all along the extent of the GBRMP.

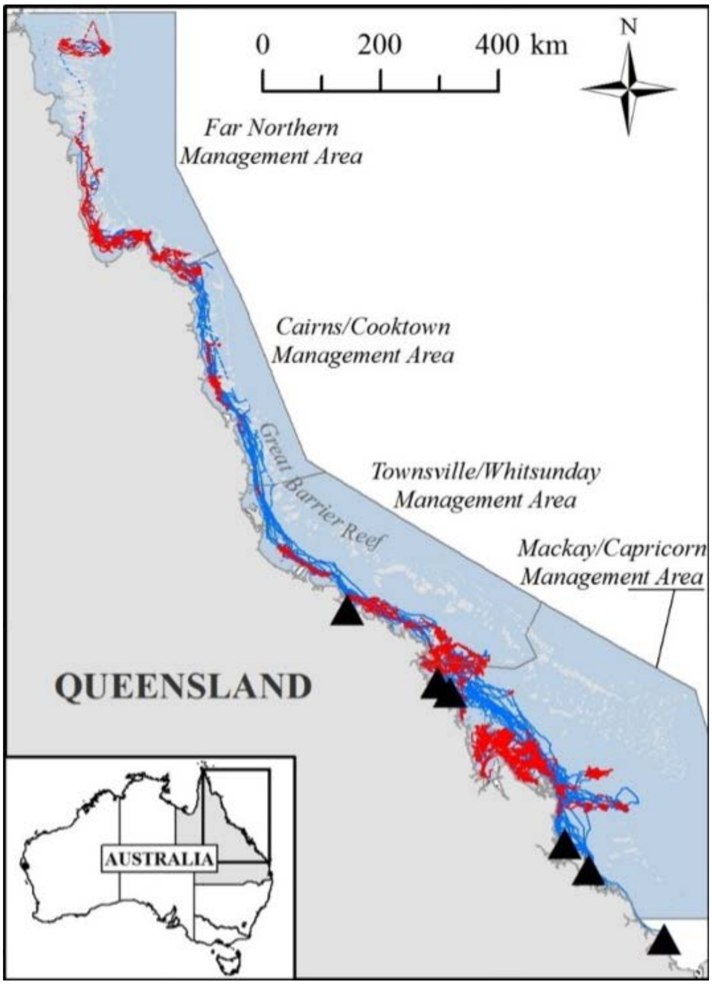

Figure 3.2. Travelling (blue lines) and foraging (red lines) tracks for all tagged turtles. Black triangles represent releasing locations, from north to south: Wunjunga (n=9); Mackay region: Halliday Bay/Ball Bay (n=3/1), Blacks beach/Eimeo (n=1/1); Peak Island (n=2); Curtis Island (n=26) and Mon Repos (n=1).

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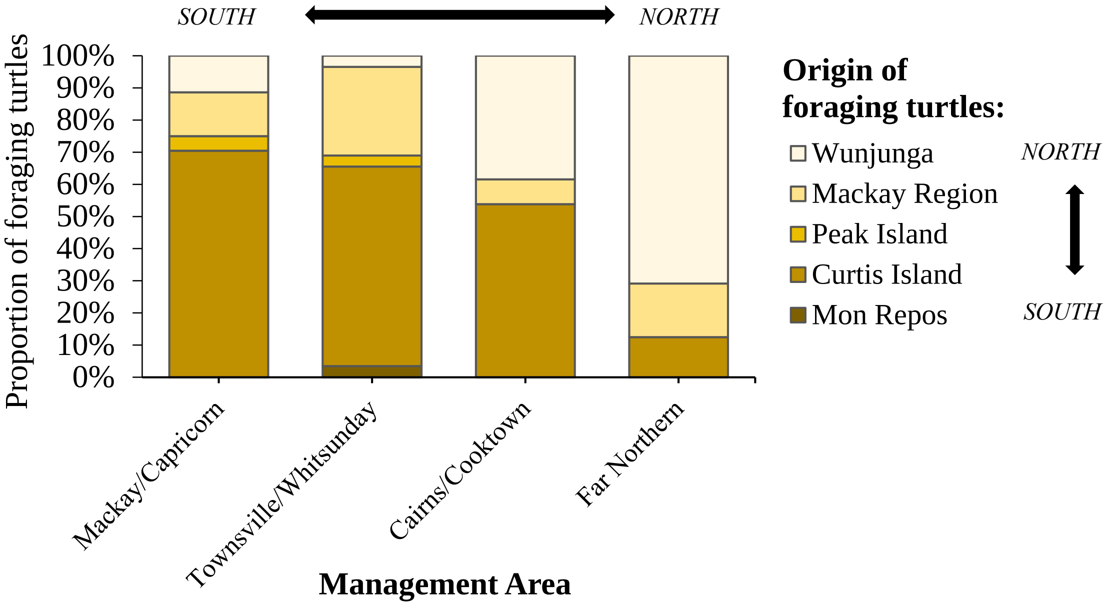


Figure 3.3. Proportion of turtles from each nesting beach which are foraging in each management area.

Table 3.6. Summary of general features of each turtle track. Nesting beach codes: Eimeo (EB), Halliday Bay (HB), Peak Island (PI), Curtis Island (CI), Blacks beach (BlB), Ball Bay (BaB), Wunjunga (W), Mon Repos (MR). Travelling strategy codes: Multi-stop (M-s), Direct migration (D-m). Foraging Management Area codes: 1 = Mackay/Capricorn, 2 = Townsville/Whitsunday, 3 = Cairns/Cooktown, 4 = Far Northern. Foraging strategy codes: Multi-recurring (M-r), Multi-shifting (M-sh), Single-fixed (S-f), Single-wandering (S-w). * = transmission stopped before arriving to a main foraging ground.

Turtle ID	***Nesting beach***	***Travelling strategy***	***Foraging Management Area***	***Foraging strategy***	***No. foraging grounds***	***Total straight line distance in km***	***Total distance in km***	***Total time in days***	***Mean speed in km/h (SD)***
54528	EB	M-s	2, 3, 4	M-r	5	930.26	2160.58	187.59	0.69 ± 0.66
54531	HB	M-s	1, 2	M-sh	3*	93.75	974.87	63.13	0.72 ± 0.66
96774	PI	M-s	1	M-r	2	127.53	2691.82	179.14	0.74 ± 0.59
96776	PI	D-m	2	S-f	1	378.56	2234.95	311.36	0.76 ± 0.68
96779	CI	D-m	1	M-r	3	267.76	5622.71	575.90	0.86 ± 0.86
108471	BlB	D-m	1	S-w	1	331.83	2315.44	127.43	0.95 ± 0.79
120641	BaB	D-m	1, 2	M-r	3	35.67	1991.96	213.86	0.61 ± 0.62
133399	W	M-s	2, 3, 4	M-sh	5	659.54	1689.92	210.55	0.46 ± 0.64
133400	W	D-m	1	S-w	1	389.48	2498.71	131.05	1.13 ± 0.96
133401	W	D-m	1	S-w	1	406.87	1440.29	86.11	0.92 ± 0.73
133402	W	D-m	1	S-f	1	348.98	1947.19	97.73	1.11 ± 0.98
133758	MR	D-m	2	S-f	1	602.94	1501.60	142.64	0.69 ± 0.76
134189	CI	M-s	1	M-sh	2	197.35	1397.73	101.77	0.75 ± 0.76
134190	CI	D-m	1	S-f	1	183.10	654.31	85.47	0.53 ± 0.58
134191	CI	M-s	1	M-r	2	199.67	1108.81	81.51	0.66 ± 0.55

134192	CI	M-s	1, 2	M-r	4	467.24	1396.93	100.75	0.73 ± 0.77
134194	CI	M-s	1	M-sh	2*	272.2	1143.48	80.42	0.79 ± 0.85
134195	CI	D-m	1	S-f	1	223.58	1008.44	59.56	0.82 ± 0.70
134196	CI	D-m	1	M-r	2	194.85	1385.82	86.43	0.90 ± 0.88
134198	CI	D-m	1	S-w	1	403.13	1149.42	80.72	0.82 ± 0.92
134199	CI	M-s	1	M-r	3	199.57	1329.40	103.36	0.65 ± 0.68
141738	CI	M-s	1	M-r	2	212.70	1377.09	123.81	0.70 ± 0.80
141739	CI	M-s	4	M-r	3	1294.74	2159.73	164.76	0.71 ± 0.69
141740	CI	D-m	1	S-f	1*	224.74	810.98	55.03	0.79 ± 0.70
141741	CI	D-m	1	S-f	1	168.81	1211.18	277.46	0.37 ± 0.46
141742	CI	M-s	2, 3	M-sh	4	1197.20	1969.59	195.51	0.77 ± 0.82
141744	CI	D-m	2	M-r	2	453.50	2971.03	283.42	0.75 ± 0.69
141746	CI	M-s	3	M-sh	5	1192.74	2385.36	165.26	0.81 ± 0.75
141747	CI	M-s	2, 3	M-sh	2*	1018.43	1701.88	112.79	0.79 ± 0.73
141748	CI	M-s	2	M-sh	4*	591.11	1245.50	106.42	0.70 ± 0.74
141758	W	M-s	3, 4	M-r	6	1047.53	4624.14	479.35	0.65 ± 0.59
141759	W	M-s	4	M-r	7	821.76	3767.19	477.34	0.50 ± 0.52
141760	W	M-s	3, 4	M-r	4	744.18	2565.82	275.29	0.55 ± 0.57
141762	W	D-m	4	S-w	1	673.65	2909.96	477.90	0.43 ± 0.49
141763	W	M-s	1	M-r	2	396.32	1546.03	89.99	0.86 ± 0.76
152711	CI	D-m	1	S-f	1*	226.58	568.18	55.28	0.58 ± 0.77
152712	CI	D-m	1	S-f	1*	268.66	1457.22	73.60	1.18 ± 1.09
152713	CI	D-m	1	S-f	1	285.53	2760.32	186.35	0.79 ± 0.76
152714	CI	D-m	2	M-r	4	554.96	1636.33	127.27	0.83 ± 0.81
152715	CI	D-m	1	M-r	2	228.81	1400.23	144.78	0.52 ± 0.60

152718	CI	D-m	1	S-f	1*	229.44	1536.71	97.15	0.93 ± 0.93
152720	CI	M-s	1, 2	M-sh	4	426.92	2880.27	161.77	1.01 ± 0.89
154296	HB	M-s	1, 2	M-r	3	81.33	2554.99	153.26	0.94 ± 0.74
154297	HB	M-s	2, 4	M-sh	3	829.36	2274.50	163.21	0.77 ± 0.74

3.3.2. Classifying turtle movement based on behaviour

The behavioural thresholds identified in this study appear to be a realistic representation of the behaviour of the tracked individuals, except for six turtles (13.63%), which displayed distinctive individual behaviours (Table 3.4). Travelling behaviours were identified by the presence of fast and direct movements (high $\hat{\mu}$ and high $\hat{\tau}$) (Table 3.4, Figure 3.4d, e). Detailed inspection of the BCPA plots and maps revealed an additional travelling behaviour, which I named "slow travelling". The slow travelling movements are characterised by intermediate mean speed values (medium $\hat{\mu}$) and straight paths (high $\hat{\tau}$) (Table 3.4, Figure 3.4d, e), and are typically short in duration (Figure 3.4b). A slow travelling movement could represent, for example, a chasing/escaping event or slow, meandering movements between foraging grounds. Within the definition of foraging I considered different potential types of behaviour, such as searching (slightly faster but tortuous movements; medium $\hat{\mu}$ and low $\hat{\tau}$), resting or feeding (slow and very tortuous movements; low $\hat{\mu}$ and low $\hat{\tau}$) (Table 3.4, Figure 3.4).

Travelling phases had a mean duration of 22.5 ± 15.4 days and covered distances up to 1522 km (560 ± 378.9 km) (Figure 3.4a, b). In contrast, slow travelling movements were typically the shortest in duration (13.46 ± 12.56 days) and distance (214.83 ± 183.81 km), while movements of turtles in foraging grounds recorded the largest values (1058.53 ± 902.37 km; 118.11 ± 121.04. days) (Figure 3.4a, b). A summary of the main behavioural features of the travelling and foraging phases for each turtle is shown in Appendix Table A1.

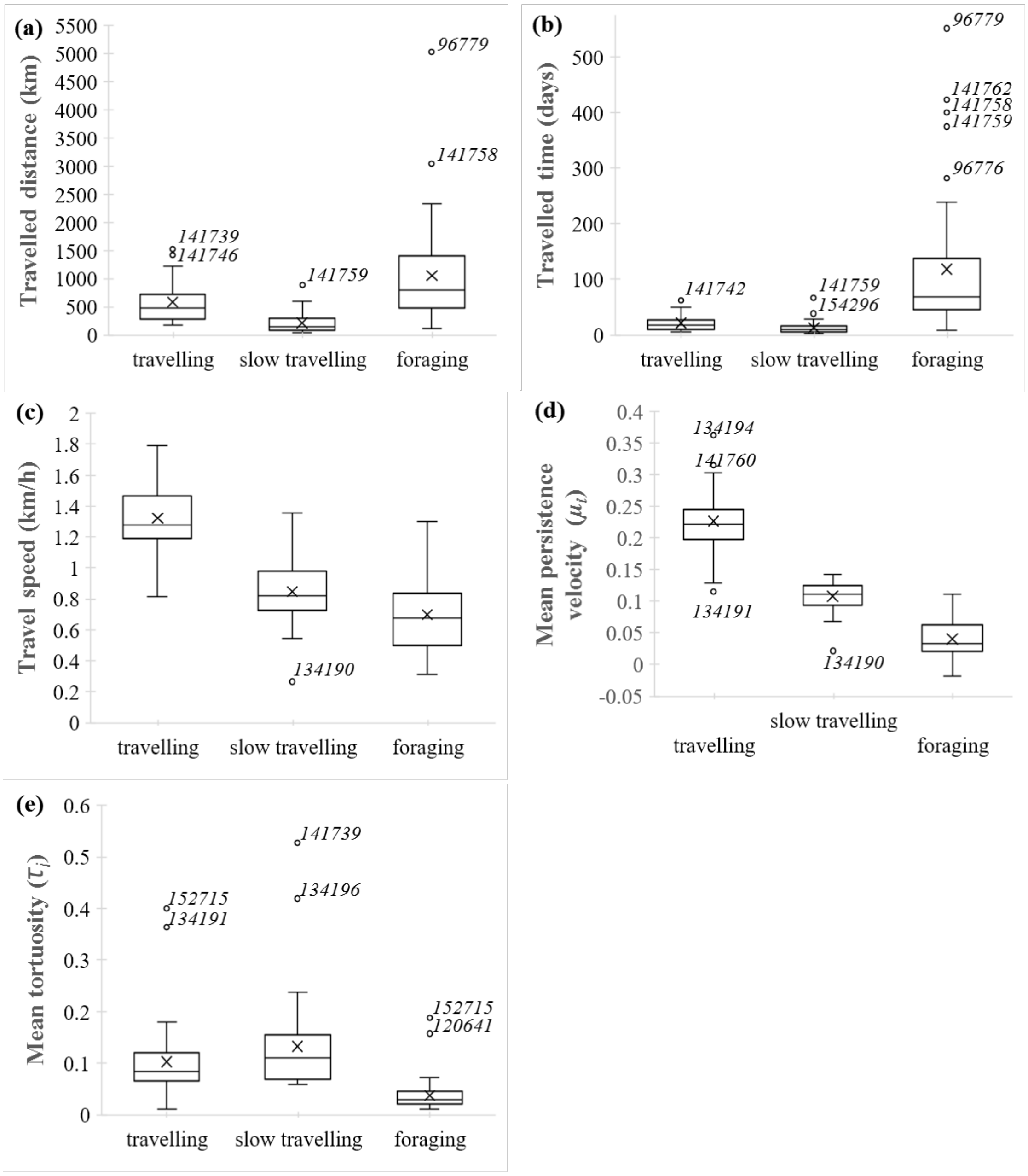


Figure 3.4. Box-plots of (a) total travelled distance, (b) total travelled time, (c) mean travelling speed, (d) mean persistence velocity ($\hat{\mu}$), and (e) mean tortuosity ($\hat{\tau}$) for each behavioural state: travelling, slow travelling and foraging. Box-plot description: whiskers represent the minimum and maximum values, box represents values in the second and third quantiles, line inside the box represents the median, X inside the box represents the mean, circles represent outliers. Outliers are identified with the respective turtle ID.

3.3.3. Identifying travelling and foraging strategies

Detailed visual inspection of the behavioural phases (Figure 3.4 and Appendix Table A1) revealed that flatback turtles display a variety of travelling and foraging strategies. I used the data from the BCPA analysis to categorise these strategies based on characteristics such as residency time, location of foraging grounds and timing of the visits, as follows:

Travelling:

(a) Direct migration: characterised by a single travelling movement from the nesting beach to a foraging ground and time spent at the foraging ground (greater than 30 days) (Figure 3.5a-b).

(b) Multi-stop migration: characterised by at least one (and up to 4) stop of variable lengths (less than 30 days long) before arriving to the main foraging ground (Figure 3.5c-d).

Foraging:

(a) Single area-fixed: turtle spent the complete tracking period within one foraging area, from which the turtle did not leave (Figure 3.5a).

(b) Single area-wandering: turtle spent the majority of the tracking period within one foraging area from which it made wandering loops and always returned to its original foraging ground (Figure 3.5b).

(c) Multiple area-recurring: turtle alternated between two or more well-defined areas, and undertook one or more visits to a previously used foraging ground (Figure 3.5c).

(d) Multiple area-shifting: turtle moved consecutively from one foraging ground to the next, without returning to a previously used area (Figure 3.5d).

Based on these categories, there was an even spread of direct and multi-stop migration among the turtles, with similar tracking durations and distances (Table 3.7*).* The mean travelled distances during multi-stop migrations (881.4 ± 432.5 km) did not significantly differ (U =157, p = 0.113, Mann-Whitney test) from the mean travelled distances during direct migrations (561.3 ± 294.3 km), suggesting that turtles that travelling strategy was not linked to the distance between nesting beaches and foraging grounds. Within the foraging strategies, the combined multiple-area categories (recurring and shifting) were the most common, describing 63.6 % of the observed behaviours (Table 3.7). Despite being the less common, the single area-wandering strategy exhibited the second longest average time span and distance (Table 3.7). Travelling and foraging strategies for each turtle are listed in Appendix Table A1.

Table 3.7. Summary of proportion of turtles, mean tracking duration and mean tracking distances for each behavioural strategy.

Strategy type	**Number of turtles (%)**	**Days spent (Mean ± SD)**	**Travelled distance in km (Mean ± SD)**
Travelling			
Direct migration	22	23.41 ± 13.44	561.30 ± 294.33
Multi-stop	22	38.82 ± 19.53	881.36 ± 432.47
Total	44 (100)	31.11 ± 18.31	721.33 ± 399.82
Foraging			
Single area-fixed	11 (25)	87.34 ± 90.95	780.29 ± 488.59
Single area-wandering	5 (11.4)	131.35 ± 164.90	1089.72 ± 636.81
Multiple area-shifting	10 (22.7)	64.07 ± 40.31	598.21 ± 429.41
Multiple area-recurring	18 (40.9)	163.26 ± 142.82	1475.64 ± 1169.17
Total	44 (100)	118.11 ± 121.05	1058.53 ± 902.38

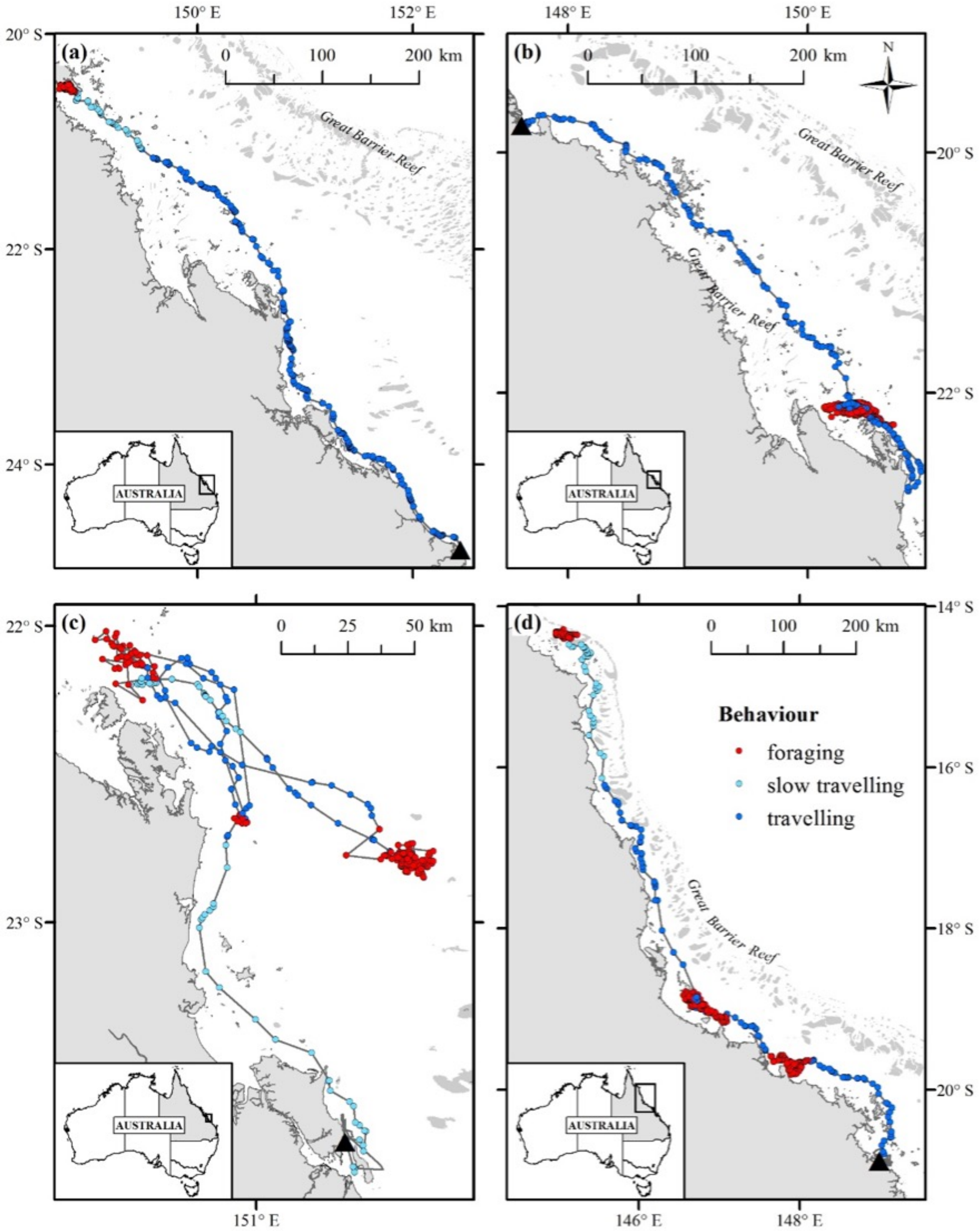


Figure 3.5. Examples of the different travelling and foraging strategies undertaken by tagged turtles: (a) direct migration and single area-fixed strategies displayed by turtle 133578 tracked from Mon Repos (triangle); (b) direct migration and single area-wandering strategies displayed by turtle 133400 tracked from Wunjunga (triangle); (c) multi-stop migration and multiple area-recurring strategies displayed by turtle 134199 tracked from Curtis Island (triangle); (d) multi-stop migration and multiple area-shifting strategies displayed by turtle 154297 tracked from Halliday Bay (triangle).

3.3.4. *General patterns of flatback turtle home ranges in eastern Australia.*

A combined home range of all turtles revealed the presence of three foraging hot spots for the tracked flatback turtles within the GBRMP, namely Broad Sound within the Mackay/Capricorn management area, Whitsundays/Repulse Bay within the Townsville/Whitsunday management area, and Princess Charlotte Bay/east off Cape Melville within the Far Northern management area (Figure 3.6). Foraging grounds located in the Cairns/Cooktown management area were mostly transient habitats.

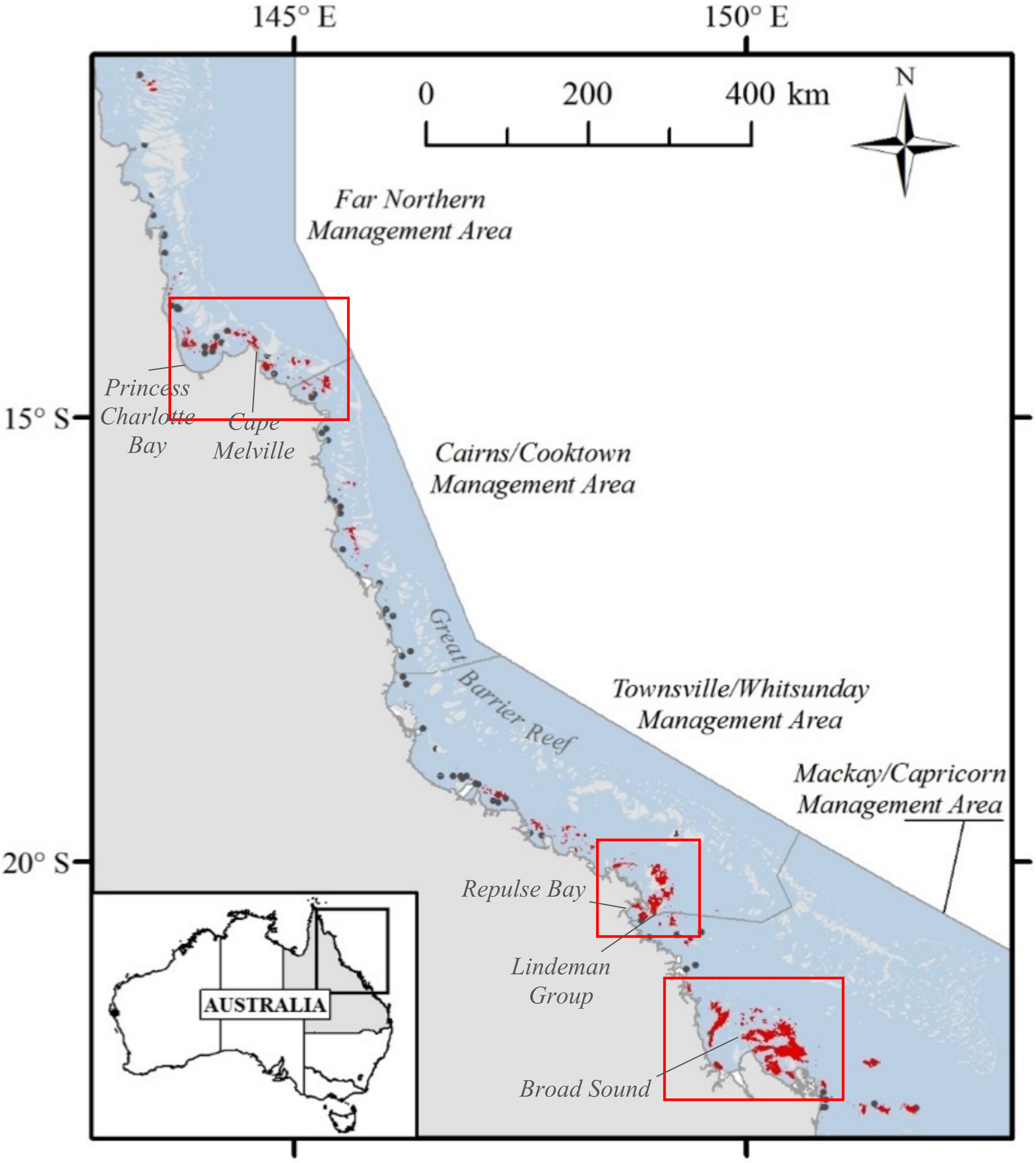


Figure 3.6. Distribution of combined home ranges (red areas) of all tracked turtles and long-term tag-recapture records (grey dots) in the GBRMP management Areas. Red squares represent hot spots foraging regions for the tracked turtles, from north to south: Princess Charlotte Bay/east off Cape Melville, Whitsundays/Repulse Bay, and Broad Sound.

Home range estimates varied greatly among individuals (Appendix Table A2), with total home range areas (95% UD) spanning between 59.3 and 2003.2 km^2 (455.5 ± 359.7 km^2), and total core areas (50% UD) ranging between 13.5 and 415 km^2 (68.2 ± 64.1 km^2). Of the 44 turtles tracked 16 had both main and transient foraging areas. For these turtles, the main foraging areas (236.5 ± 131.9 km^2) were significantly larger (U = 664, p = 1.05 e-05, Mann-Whitney test) than transient foraging areas (97.7 ± 100.2 km^2) (Appendix Table A2), and only one turtle (141742) had a single transient foraging area (192.8 km^2) relatively larger than its main foraging area (35.9 km^2) (Appendix Table A2). Moreover, there were also differences in the size of the home ranges among foraging strategies. Turtles displaying single area strategies (n = 16, 270.17 ± 171.64 km^2) displayed significantly larger home areas (U = 401, p = 0.003, Mann-Whitney test) than turtles displaying multiple area strategies (n = 28, 167.9 ± 213.5 km^2) (Figure 3.7a)

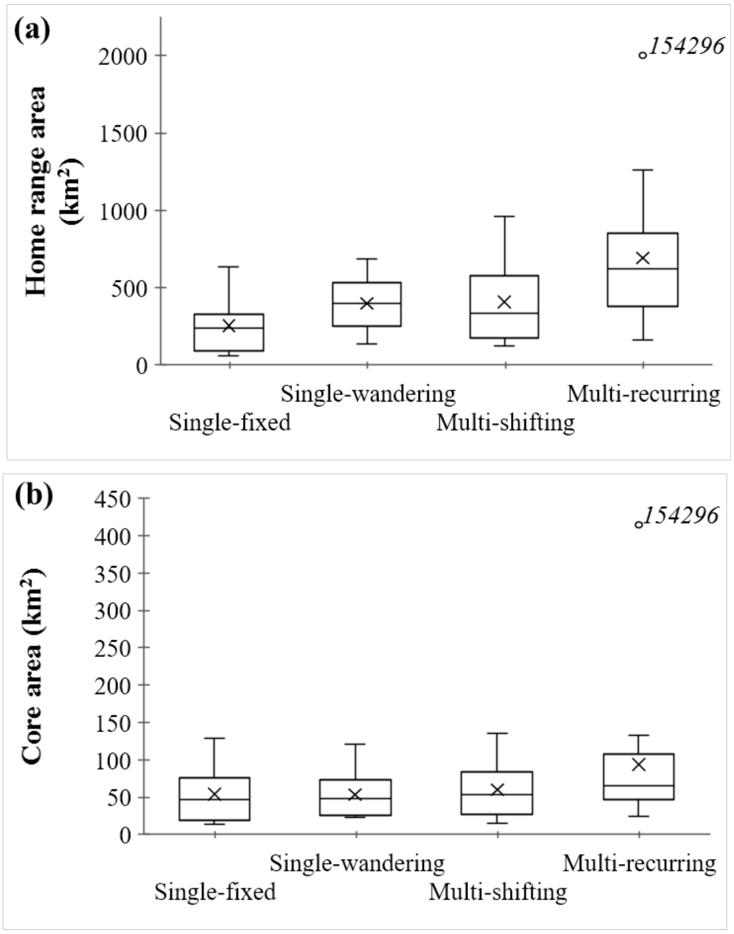


Figure 3.7. Box-plots of (a) home range areas (95% UD) and (b) core areas (50% UD) based on each identified foraging strategy. Box-plot description: whiskers represent the minimum and maximum values, box represents values in the second and third quantiles, line inside the box represents the median, X inside the box represents the mean, circles represent outliers. Outliers are identified with the respective turtle ID.

3.4. Discussion

In this chapter I analyse the behavioural strategies displayed by adult female flatback turtles in eastern Australia and provide further evidence of the characteristic neritic distribution of this species (Chapter 2). This study reveals new migratory and foraging strategies displayed by flatback turtles in eastern Australia (Figure 3.5), as well as identifying three foraging regions of high use by the tracked flatback turtles (Figure 3.6). These results characterise flatback turtles as having dynamic behavioural strategies as they display a variety of behaviours during migration and foraging phases. Such behaviours range from constrained movements in small foraging areas, to moving long distances within and between foraging areas.

Post-nesting flatback turtles tracked in this study revealed a widespread distribution of foraging grounds throughout the neritic habitats of the GBRMP. All turtles remained within the boundaries of the GBRMP, corresponding with the broad distribution of the long-term tag recapture records (EHP Queensland Turtle Research database) (Figure 3.6). The analysis of the foraging behaviour of the tracked turtles revealed previously unknown hot spot areas of higher use within the GBRMP (Figure 3.6), in particular the Broad Sound (south), Whitsundays/Repulse Bay (central) and Princess Charlotte Bay (north) regions.

Individual home ranges were generally smaller than those reported for flatback turtles tracked in Western Australia (Whittock *et al.*, 2016). Although the difference between our studies could be an artefact of us using different kernel based UD estimators, the habitats and climate are also likely to be very different to each other, which can also influence the home range sizes of animals. Nevertheless, home ranges of the flatback turtles tracked in my study (median 342.8 km^2, range 59.3 - 2003.2 km^2) were relatively large when compared to those of green (median 31.3 km^2, range 2.8 - 166.3 km^2) and loggerhead turtles (median 24.0 km^2, range 10.3 - 350.6 km^2) tracked in the same region of Queensland (Shimada *et al.*, 2016a). As an example of the inter-specific variation in habitat use and foraging behaviour at a local scale, female green turtles tracked in Shoalwater Bay in two different studies (Gredzens *et al.*, 2014; Shimada *et al.*, 2016a) report home range sizes between 2.8 and 25.1 km^2, while flatback turtles tracked in the same region displayed average home range sizes of 172.4 km^2 (range 1.1 - 684.2 km^2).

Dynamic migration and foraging strategies seem to be a common pattern for at least two flatback turtle management units: Eastern Australia (this study) and Western Australia (Pendoley *et al.*, 2014; Whittock *et al.*, 2016). The variability in behaviour observed in the tracked flatback turtles was not dependent on neither the origin of the turtles (releasing location) nor the year they were tagged, suggesting that the observed behaviours are a consolidated trait of the population. While other hard-shelled marine turtle species in Queensland, like green and loggerheads, typically undertake direct post-nesting migrations to their foraging grounds (Shimada *et al.*, 2016a; Shimada *et al.*, 2016c), half of the flatback turtles tracked in this study stopped for moderate lengths of time (mean ± SD = 11.2 ± 8.2 days, range = 2.3 – 28.7 days) in transient foraging grounds during their migrations. I have described such movements as the multi-stop migration strategy. The multi-stop strategy was most frequently observed in turtles that undertook migrations of longer distance. By the end of a nesting cycle, energy reserves of female turtles are extremely depleted (Hamann *et al.*, 2002b) as they do not feed during the breeding season; thus, there is a trade-off between migrating directly to a foraging ground through a shorter pathway, or foraging along the migration route at the cost of longer travelling distances and time (Godley *et al.*, 2002).

In terms of the foraging strategies, the flatback turtles tracked in this study were seen to portray a unique combination of behaviours. Flatback turtles in eastern Australia were observed to use one or multiple foraging areas, undertaking loop trips, shifting from one area to another, or even returning multiple times to a specific foraging area. Flexible foraging has been described for leatherback turtles (Hays *et al.*, 2006), which adjust their foraging behaviours while travelling and as a diel response, and flatback turtles in Western Australia (Whittock *et al.*, 2016), where approximately half of the tracked turtles were recorded to use more than one main foraging area. Godley *et al.* (2008) characterised the movements of post-nesting female marine turtles in two broad categories: those which travel to and use neritic foraging areas (type “A”, further subcategorized in three types), and those with a predominantly pelagic foraging pattern (type “B”) characterised by long-distance wandering movements. Based on the current results, flatback turtles would rank within the first group (type “A”), given that both their migrations and foraging phases remain entirely in neritic waters. However, they displayed several foraging strategies, such as the single-area wandering and multiple-area recurring strategies, that seem to be previously unreported if not absent in other Cheloniid turtle species in tropical coastal environments. Dynamic and flexible foraging strategies have also been reported for leatherback turtles, which prey upon mobile gelatinous prey in oceanic waters (Hays *et al.*, 2006; Witt *et al.*, 2007). In addition, if changes to habitats were to occur, they could lead to migration or movement of individual turtles to other profitable known or unknown habitat patches (Giraldeau, 2008). Overtime the compilation of larger tracking tracking datasets will allow this to be tested.

Seasonal movement of loggerhead turtles between foraging grounds in sub-tropical and temperate regions is common, likely as a response to the change in water temperature (Hawkes *et al.*, 2007; Shimada *et al.*, 2016a). In the case of flatback turtles in eastern Australia, there is no evidence that the shifts between foraging grounds are related to seasonal patterns, given that the movements occurred within the same season. Thus, these changes are likely to be related to the distribution and availability of resources, i.e. the profitability of the habitat, or habitat shifts due to individual diet preferences.

The identification of fine-scale movements provides a better understanding of the foraging ecology of flatback turtles. Potential feeding during post-nesting migrations has been reported for several species of marine turtles (Godley *et al.*, 2002; Pendoley *et al.*, 2014; Rees *et al.*, 2012); however, the core results of most studies focus only on the migration pathways or the final foraging areas, overlooking the smaller transient areas that are used less intensively. By considering the distribution of these transient areas and combining it with long-term tag-recapture records, it was possible to identify the higher use regions, fill in the gaps of the regional distribution of the species (Figure 3.6) and provide evidence for the flexible utilisation of habitats all along the Queensland coast. For example, within the Broad Sound region there were four foraging turtles that stopped and/or travelled southeast to visit an area with known high-density patches of holothurians (sea pens) (Pitcher *et al.*, 2007). The identification of transient behaviours between foraging grounds provides further insight into flatback turtle habitat use. In the simplest scenario, short stops might result from opportunistic encounters with food resources, thereby replenishing energy stores during travelling. However, turtles might shift between foraging grounds due to unstable resource availability, or to travel to a previously encountered area to make use of a known resource. Thus, the flexibility in the foraging behaviour of this species could potentially represent an advantage for adaptation to environmental variability, food availability and habitat degradation, especially in face of the rapid rate of global climate change. Repeated tracking of the same individual turtles across multiple return migrations would be a useful experiment to test whether they use the same strategies each time.

3.5. Conclusion

Flatback turtles can be considered habitat generalists, given the large sizes of their home ranges and the diversity in observed behavioural strategies. There were no trends in the behavioural strategies used among turtles from different nesting beaches or tagged during different years, which suggests the ability of flatback turtles to use multiple resources and to adjust to environmental variability. In addition, while the foraging strategies described in this study are based on the observed behaviours of flatback turtles in eastern Australia, they may be used globally as guidelines to identify the variety of behavioural states that may potentially be displayed by other marine turtle species. Future research should include, but not be limited to: re-tagging of individuals during successive nesting seasons to assess the degree of fidelity to migration routes and foraging grounds; the inclusion of diving profiles in foraging areas to better understand the behavioural foraging and/or resting patterns as well as diel patterns; tracking of male flatback turtles from breeding and/or foraging grounds; and assessment of the fitness of individual turtles and exploring any potential relationship between fitness and different foraging strategies.

Chapter 4

Environmental drivers of the foraging distribution of flatback turtles in the Great Barrier Reef

Adult flatback turtle in Northern Australia.

Photo credits: Doug Perrine/Australian Geographic. Source: The Daily Telegraph

Abstract

Assessing the distribution, habitat use and diet of individuals can provide important insights into the relationship between a species and its environment. In particular, studies that quantify the association of individuals with bio-physical parameters are highly informative but particularly challenging when working with marine megafauna. Marine megafauna and marine turtles specifically, typically display long-distance movements and relatively large home ranges, making it difficult to measure the bio-physical parameters over the complete distribution range. In Australia, such assessments are possible in the Great Barrier Reef (GBR) region because of the extensive research and sampling efforts conducted in the region. One project in particular, the GBR Biodiversity Project, mapped the bio-physical characteristics of the non-reef benthic areas of the GBR, which include the habitats used by flatback turtles. Thus, the aim of this chapter is to improve the understanding of which environmental parameters might be associated with the distribution of flatback turtles in eastern Australia. To achieve this, I employed a Random Forest analysis to measure the response of the presence of the tracked flatback turtles (chapter 3) to sets of 25 physical and 29 biological predictors. The results confirm that flatback turtles are associated to predominantly muddy inshore habitats, but can also occur in less muddy environments with low levels of light (typically turbid waters). As reported in previous studies, my results indicate that flatback turtles are associated to soft-bodied invertebrates; however, I also identified an association to other biological groups, such as sponges, ascidians, bivalves, echinoderms and seagrass. Association to the latter is not likely to be because turtles are eating seagrass, but rather be linked to the distribution of invertebrates preyed upon by flatback turtles. Collectively, the results of this chapter provide further evidence that flatback turtles are generalist and opportunistic species. Nevertheless, differences in the individual behaviour reported in Chapter 3 combined with evidence of individual turtles using almost exclusively one of three very different habitats, suggests that the species might display some degree of individual specialisation.

Keywords: flatback turtle, *Natator depressus*, Great Barrier Reef World Heritage Area, random forest, species-habitat association, habitat use.

4.1. Introduction

Habitat selection and use are central components of foraging ecology. A fundamental assumption in the study of habitat selection is that the observed behaviours of a species for selecting and exploiting resources have been shaped by the selection of strategies that maximise fitness and survival (Mitchell & Hebblewhite, 2012). This arises because the use of habitat by foraging animals is shaped by trade-offs among multiple factors such as shelter requirements, availability and quality of food resources, predation risk, inter- and intra-specific competition, individual phenotypic capacity (e.g. physiological limits to environmental parameters, prior learning, vulnerability to diseases) and the carrying capacity of the environment (Bolnick *et al.*, 2003; Christiansen *et al.*, 2017; Morrison *et al.*, 2012). A comprehensive assessment of all these factors would be extremely challenging; thus, to understand habitat use and the drivers of habitat selection by species, researchers typically focus on evaluating some surrogates of the habitat coupled with direct or indirect observations of individual behaviour (Morrison *et al.*, 2012).

The variability in the types of habitats used between individuals defines the habitat breadth of a population (Morrison *et al.*, 2012). The habitat breadth is dynamic, and it can expand or reduce in dimensions following changes in resource availability and accessibility (Araujo *et al.*, 2011). These dynamics are influenced by the plasticity in habitat use within and between individuals. From a foraging perspective, species can be categorised within a generalist-specialist spectrum based on the variability in foraging strategies and/or the resources they use. More specialist species (e.g. herbivorous species such as dugongs) have developed efficient and narrow foraging strategies that enhance energy intake at lower costs. In contrast, generalist species use a broader array of resources within or across trophic levels, enhancing their greater capacity to respond to acute and/or chronic alterations to the environment. In recent years, there has been an increasing attention on identifying the degree of individual specialisation in generalist species (e.g. in sharks, Matich *et al.* (2011); loggerhead turtles, Pajuelo *et al.* (2016); Vander Zanden *et al.* (2010); octopus, (Mather *et al.*, 2012)). Ultimately, the degree of specialisation or generalisation of a species will shape the selection and use of habitat by individuals, and consequently the habitat breadth and distribution of the population.

All species of marine turtles are thought to be opportunistic during their early development, later adopting more specialised (e.g. adult leatherbacks feed on jellyfishes and tunicates) or generalist (e.g. adult loggerheads feed on a variety of benthic organisms) foraging behaviours (Bjorndal *et al.*, 1997). Information on the diet of flatback turtles (*Natator depressus*) is limited, and the existing literature so far indicates they can be considered opportunistic foragers (Limpus, 2007). Diet items collected from a small number of individuals include a variety of soft-bodied invertebrates such as sea cucumbers, sea pens, soft corals and jellyfish, suggesting that adult flatback turtles primarily display benthic feeding habits (Chatto *et al.*, 1995; Limpus, 2007; Zangerl *et al.*, 1988). In addition, immature turtles have been reported to feed occasionally on Scyphozoa (jellyfishes) (Limpus, 2007). Unlike green and loggerhead turtles foraging in coastal habitats off eastern Australia (Gredzens *et al.*, 2014; Shimada *et al.*, 2016a), flatback turtles in Western Australian foraging grounds (Whittock *et al.*, 2016) and eastern Australia (Chapter 3) have large home ranges, with individuals often moving between two or more separate foraging areas. Given that flatback turtles are endemic to Australia and are listed as 'Vulnerable' under Australian biodiversity legislation (EPBC Act, 1999), a better understanding of the species-habitat associations is desirable in order to improve local management of the different populations (Whittock *et al.*, 2016; Whittock *et al.*, 2017).

The eastern Australia (eAus) flatback turtle population is a demographically and genetically distinctive management unit. Foraging grounds of adult eAus flatback turtles span 17 degrees of latitude, from Torres Strait in northern Queensland to Moreton Bay in southern Queensland, and are largely situated within the GBR region, typically in soft-bottom sub-tidal habitats (Chapter 2; Limpus (2007)). The ecology of the GBR has been extensively studied, in particular through the GBR Seabed Biodiversity Project (Pitcher *et al.*, 2007). The project focused on improving knowledge of the biodiversity of the less-studied, non-reef areas of the GBR, using a combination of techniques from more than 1400 locations. Some of its main outputs include a geo-referenced inventory of more than 5300 species and the development of distribution and abundance maps for ~850 species (Pitcher *et al.*, 2007; Roland Pitcher *et al.*, 2012). The extensive biotic and abiotic characterisation of the benthic habitat of the GBR provides an invaluable baseline to assess interactions and distribution drivers for an extensive diversity of marine species, especially those with predominant benthic foraging habits, such as flatback turtles.

Understanding the drivers of habitat use and selection, especially in the marine environment, can be challenging (Benoit-Bird *et al.*, 2013; Espinoza *et al.*, 2014; Kobayashi *et al.*, 2008; Smith *et al.*, 2012; Witt *et al.*, 2007). There are multiple approaches to assess these processes, including but not limited to resource selection functions (RSF), maximum entropy models (Maxent), habitat suitability models and random forests (Mitchell & Hebblewhite, 2012). Random forests analysis (Breiman, 2001) has been recently used for a variety of ecological studies to assess the response of species to biophysical variables, model species distribution, and assess changes in the distribution of species or natural hazards (Cutler *et al.*, 2007; Evans *et al.*, 2011; Garzon *et al.*, 2006; Oliveira *et al.*, 2012; Pierce *et al.*, 2012; Wei *et al.*, 2010). Ultimately, studying animal-habitat associations can lead to an improved understanding of the parameters influencing fitness and survival of a species.

Identifying the ecological characteristics of flatback turtle foraging habitats and how individuals use the available resources remains a major gap in the knowledge of this species' ecology. Thus, the aim of this chapter was to improve the understanding of the environmental parameters that are associated with the distribution of foraging flatback turtles in eastern Australia. In particular, I used a Random Forest analysis to evaluate the association between the distribution of foraging flatback turtles and environmental predictors (abiotic parameters and biomass of potential prey) in the

GBR. The results of my models provide new insights on the foraging ecology of flatback turtles, in particular about the environmental parameters that might be associated with the distribution of foraging habitats and the apparent variability in resource use by individuals within the population.

4.2. Methods

The details of turtle tagging, tracking and home range analysis were provided in detail in chapter 3. In summary, 44 adult female flatback turtles were tracked between 2009 and 2015 from eight nesting beaches in eastern Queensland (Wunjunga (n=9), Halliday Bay (n=3), Ball Bay (n=1), Eimeo (n=1), Blacks beach (n=1), Peak Island (n=2), Curtis Island (n=26) and Mon Repos (n=1); Figure 3.1 in Chapter 3) along migratory routes to their foraging locations. The turtles were tracked between 55 and 575 days and all of them foraged within the boundaries of the GBR Marine Park (GBRMP). The filtered and categorised foraging tracks from chapter 3 were further processed in this chapter to generate the response variable used as input for RF analysis. The specific methods are provided below.

4.2.1. Introduction to Random Forest analysis

Random forest analysis (RF, Breiman (2001)) is based in a machine learning technique classification and regression tree (CART) suite of models. In the RF analysis, the response is randomly sampled and the output is split between a training (In-Bag, IB) and validation (Out-Of-Bag, OOB) set. At each tree branch, the model selects the predictor for which the split value minimises the sums-of-squares of the IB set in the child branches. To avoid the instability of individual trees, a forest of trees (typically 500) is fitted. In each tree of the forest, a random sample of approximately ⅔ of the observations (the 'in-bag', IB) is fitted, and in each split of the tree a different random subset of one-third of the predictors is used to classify the observations. In RF, the performance of the forest is evaluated by cross-validating each tree against the remaining ⅓ of the observations (the 'out-of-bag', OOB) and calculating the average of OOB variation explained (OOB-%VarExp) from the individual trees; this process produces a robust estimate of generalization error. The importance of each predictor is then evaluated by randomly permuting each predictor and quantifying the degradation in prediction performance on the OOB subset.

A conceptual diagram of the methodology, including pre-processing and merging of variables, and the RF analysis employed in this Chapter is summarised in Figure 4.1.

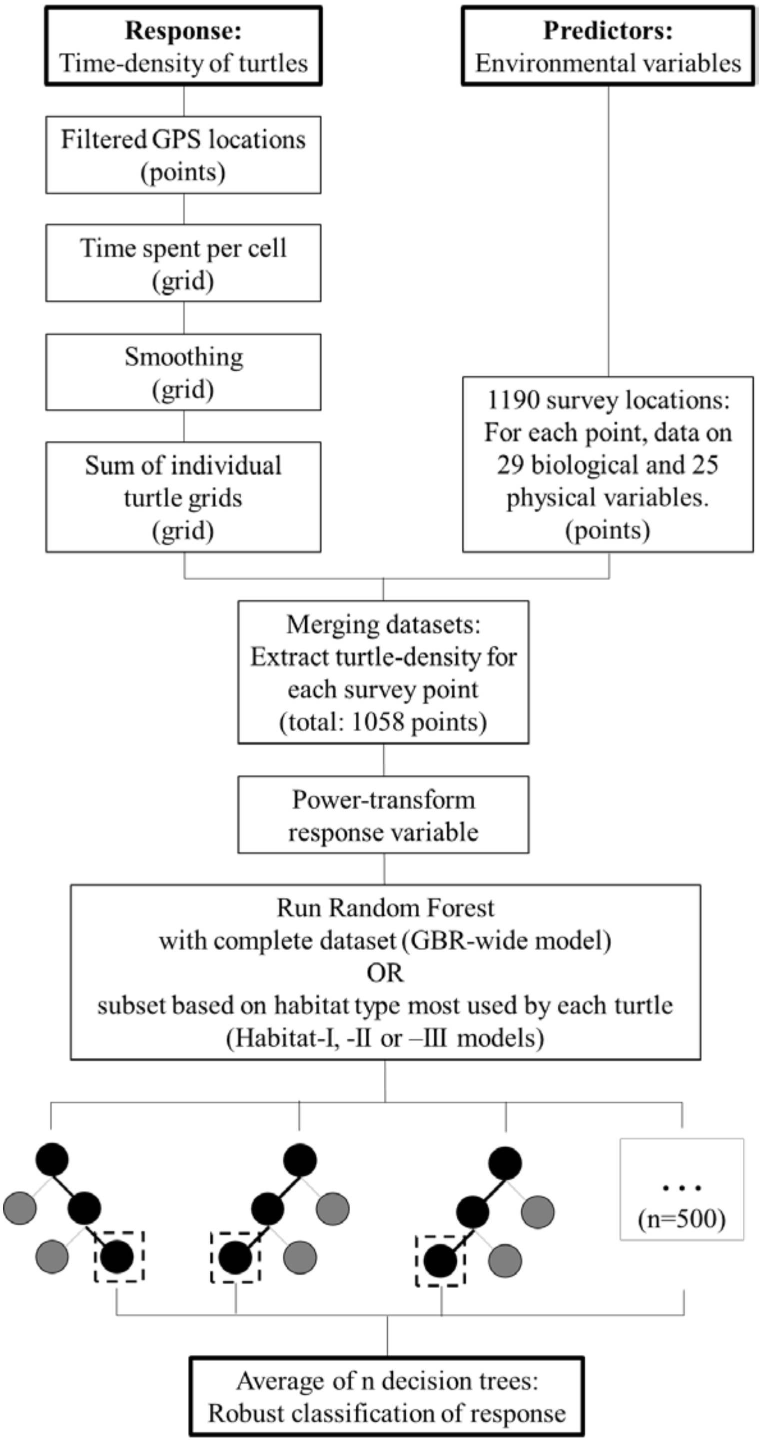


Figure 4.1. Conceptual diagram of the data preparation and RF analysis employed in Chapter 4.

4.2.1.1. Response: time-density of turtles

For this Chapter, all filtered GPS locations of each turtle's individual behavioural events (i.e. each foraging, travelling or slow travelling event) (Chapter 3) were considered, to account for swift occasional feeding events during migrations. Since the distribution of some of the tracked turtles spanned across large geographical extents, I created data subsets for each turtle based on its individual behavioural events (identified in Chapter 3) to decrease computational times. The filtered GPS locations of each event were processed with the R package ‘trip’ (Sumner, 2016) to create a gridded map with 0.01° resolution of time-density (time in seconds spent in each grid-cell by each turtle). Given that the transmission of GPS fixes derived from tracking air-breathing marine species is predicated on the animal spending time at the surface, a kernel density smoothing using the kde2d function of the R package ‘MASS’ (Ripley *et al.*, 2016) was applied to the time density data of each turtle event in order to account for flexibility of underwater movements in the areas adjacent to the tracks. In order to apply a kernel density smoothing to the gridded time-densities, first I had to extract the value of each cell to a point located at the geographic centroid of the cell; the location of these points aligned with the sampling coordinates of the environmental parameters. We modified the kde2d algorithm to define the cell size in degrees and add a parameter for assigning a weight to each point (Appendix Code A1). For the kernel density smoothing I computed the bandwidth using the *ad ho*c method in the package adehabitatHR (Calenge, 2011) and then adjusted the bandwidths to fit the default bandwidth computation of the kde2d algorithm (see Appendix Code A2 for the code to adjust the bandwidths, and Appendix Table A3 for the bandwidth values computed for each turtle event). In addition, I defined a base grid with 0.01º resolution, and I weighted each point by its time-density value. Finally, the smoothed time density grids of each individual event were spatially overlaid and summed to get one single value of the total time density for each cell. All analyses were performed in R v.3.3.1 (R Core Team, 2016) and mapped in ArcMap 10.2.2.

4.2.1.2. Predictors: environmental parameters

The environmental parameters used as predictors for the random forest analysis included physical (25 abiotic parameters; Table 4.1) and biological (biomass of 29 potential prey groups; Table 4.2) variables. Gridded data of physical and biological environmental predictors was obtained from the Great Barrier Reef Seabed Biodiversity Project provided by (Pitcher *et al.*, 2007). This dataset was collected and/or collated between 2003 and 2005.

Table 4.1. List of physical variables used as predictors in the RF analysis. All variables were collated as part of the Great Barrier Reef Seabed Biodiversity Project. Source: (Pitcher *et al.*, 2007).

Physical predictors	***Units***	***Abbreviation***
Bathymetry	m	GBR_BATHY
Aspect		GBR_ASPECT
Slope	degrees	GBR_SLOPE
Bottom stress	Pascals (Nm^{-2})	M_BSTRESS
Carbonate	%	GA_CRBNT
Gravel	%	GA_GRAVEL
Sand	%	GA_SAND
Mud	%	GA_MUD
Nitrate (Ave)	µM	CRS_NO3_AV
Nitrate (SD)	µM	CRS_NO3_SD
Oxygen (Ave)	ml/l	CRS_O2_AV
Oxygen (SD)	ml/l	CRS_O2_SD
Phosphate (Ave)	µM	CRS_PO4_AV
Phosphate (SD)	µM	CRS_PO4_SD
Silicate (Ave)	µM	CRS_SI_AV
Silicate (SD)	µM	CRS_SI_SD
Salinity (Ave)	psu	CRS_S_AV
Salinity (SD)	psu	CRS_S_SD
Temperature (Ave)	ºC	CRS_T_AV
Temperature (SD)	ºC	CRS_T_SD
Chlorophyll-A (Ave)	mg/m^3	CRS_CHLA_AV
Chlorophyll-A (SD)	mg/m^3	CRS_CHLA_SD
K490 (Ave)	m^{-1}	CRS_K490_AV
K490 (SD)	m^{-1}	CRS_K490_SD
Benthic irradiance		SW_K_B_IRR

Table 4.2. List of biological variables used as predictors in the RF analysis. All variables were surveyed as part of the Great Barrier Reef Seabed Biodiversity Project. Source: (Pitcher *et al.*, 2007).

Biological predictors (Class)	***Common name***
Actinaria	Sea anemones
Alcyonacea	Soft corals
Antipatharia	Black wire corals (soft corals)
Ceriantharia	Tube-dwelling anemones
Corallimorpharia	?
Pennatulacea	Sea pens (soft corals)
Scleractinia	Hard corals
Zoantharia	Zoanthids
Hydrozoa	Hydrozoans (soft corals)
Ascidiacea	Ascidians
Gymnolaemata	Bryozoans
Stenolaemata	Bryozoans
Demospongiae	Sponges
Calcarea	Sponges
Asteroidea	Starfish
Crinoidea	Crinoids
Echinoidea	Sea urchins
Holothuroidea	Sea cucumbers
Ophiuroidea	Brittle starfish
Bivalvia	Bivalves
Gastropoda	Gastropods
Cephalopoda	Cephalopods
Crustacea	Crustaceans
Cyanophyceae	Blue-green algae
Chlorophyceae	Green algae
Florideophyceae	Red algae
Phaeophyceae	Brown algae
Rhodophyceae	Red algae
Liliopsida	Seagrass

4.2.1.3. Statistical model

A random forest (RF) approach (Breiman, 2001) was used to quantify the association between the environmental predictors and the time density of all turtles, using the R package randomForest (Liaw & Wiener, 2002). The response variable (SumTime.transformed) was power transformed by raising the summed time density to the power of Z; where Z = 8 (GBR-wide and Habitat-I models) or Z=16 (Habitat-II and -III models); this scaling helped to account for differences in the tracking time length of each turtle. Pairing of the response variable and environmental predictors was based on their geographical coordinates. Only locations with environmental data were included in the RF analysis; thus, time-density cells that did not overlap with sampled habitat locations were not considered. I constructed four RF models, in which the physical and biological predictors were assessed separately and the response included either the complete dataset (GBR-wide model), or a subset based on habitat type (Habitat-I, Habitat -II, Habitat-III model, Figure 4.2). Details on the characterisation of the three habitat types are provided below. The performance of the models was assessed by inspection of the OOB (Out-of-bag) Variance Explained (OOB-%VarExp), which provides a measure of how well the model predicts future data (validation). The IB (In-Bag) Variance Explained (IB-%VarExp) provides a measure of how well the model explains the observed data (training). The influence of the predictors was assessed by inspection of their importance measures (%IncMSE) and partial plots. In order to refine the analysis and reduce the number of variables included, we excluded variables with negative importance or zero importance, one at a time, and re-ran the RF analysis until no negative or zero importance variables were included. Zero importance measures indicate that the predictor does not predict any better than random.

Habitat types were identified with a multivariate regression tree analysis (De'Ath, 2002), using the R package ‘mvpart’, which groups the biological variables into assemblages based on their common response to the physical predictors (Figure 4.2). The multivariate regression tree analysis finds groups in multivariate response data (benthos biomass at taxonomic class level) by finding splits in the environmental predictor variables that minimise sums-of-squares in the response data. Further, a 10-fold cross-validation repeated 10 times was employed to prune the tree to a statistically justifiable level of complexity (number of splits or branches). The three habitat types represent very different benthic environments (Figure 4.3): (a) Habitat-I is characterised by high mud concentration (mean ± SD = 47.2 ± 20.8 %), low relative benthic irradiance (0.07 ± 0.07), low bottom stress (0.1 ± 0.09 Nm^{-2}) and mean depth of -43 m (range -5 to -104 m); (b) Habitat-II is characterised by low mud concentration (6.4 ± 5.9 %), low relative benthic irradiance (0.02 ± 0.01), high bottom stress (0.39 ± 0.42 Nm^{-2}) and mean depth of -56 m (range -15 to -85 m); and (c) Habitat-III is characterised by low mud concentration (7.2 ± 6.4 %), medium relative benthic irradiance (0.13 ± 0.06), medium bottom stress (0.21 ± 0.26 Nm^{-2}) and mean depth of -34 m (range -8 to -73 m). The biomass of the prey classes in each habitat are shown in Figure 4.4. Each turtle was then assigned to one of the habitat types, based on the habitat in which they spent the largest proportion of time.

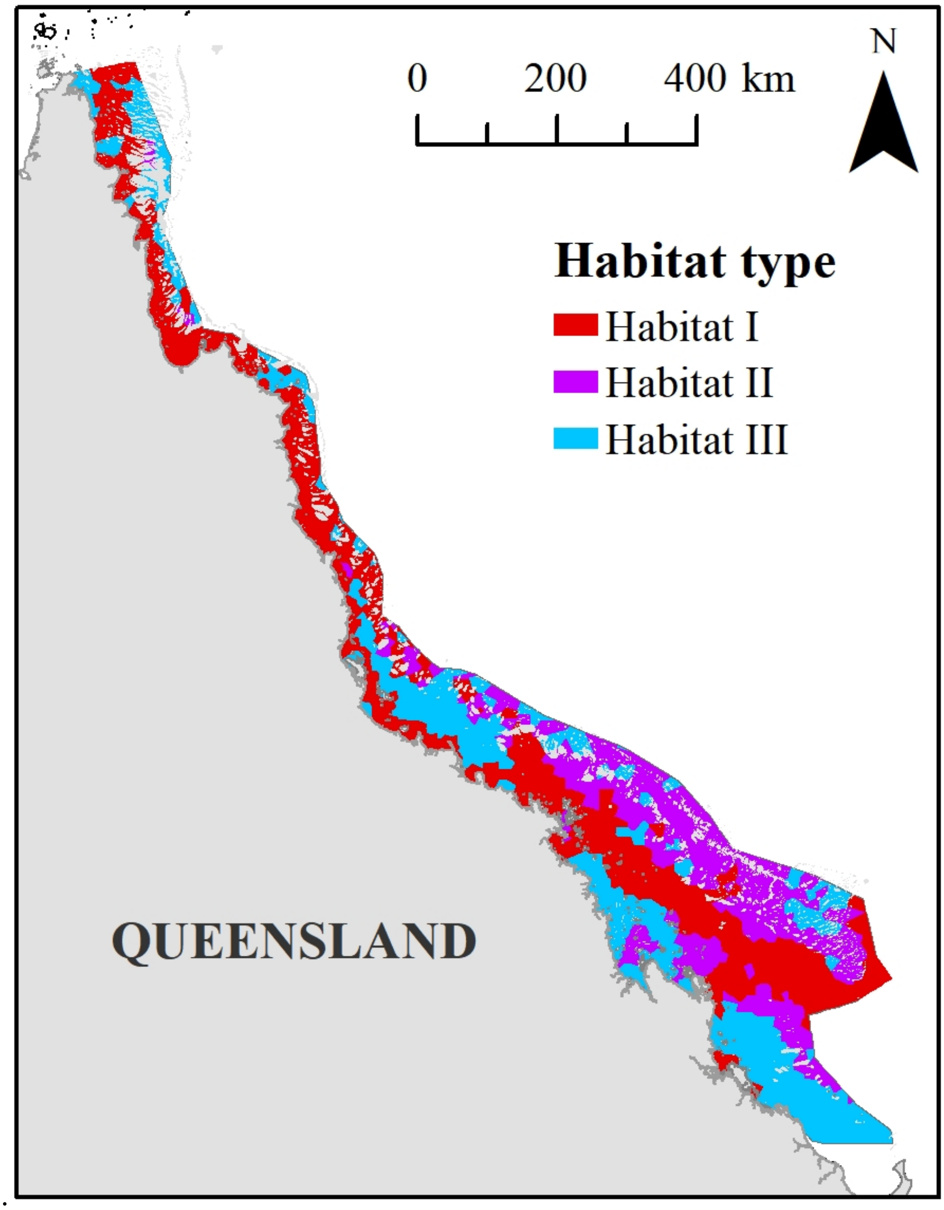


Figure 4.2. Geographical distribution of the three habitat types identified in this study within the GBR. Red polygons (Habitat-I) represent high mud environments, purple polygons (Habitat-II) represent low mud and low relative benthic irradiance environments, and blue polygons (Habitat-III) represent low mud and medium relative benthic irradiance environments. Grey polygons represent the mainland, islands and reefs.

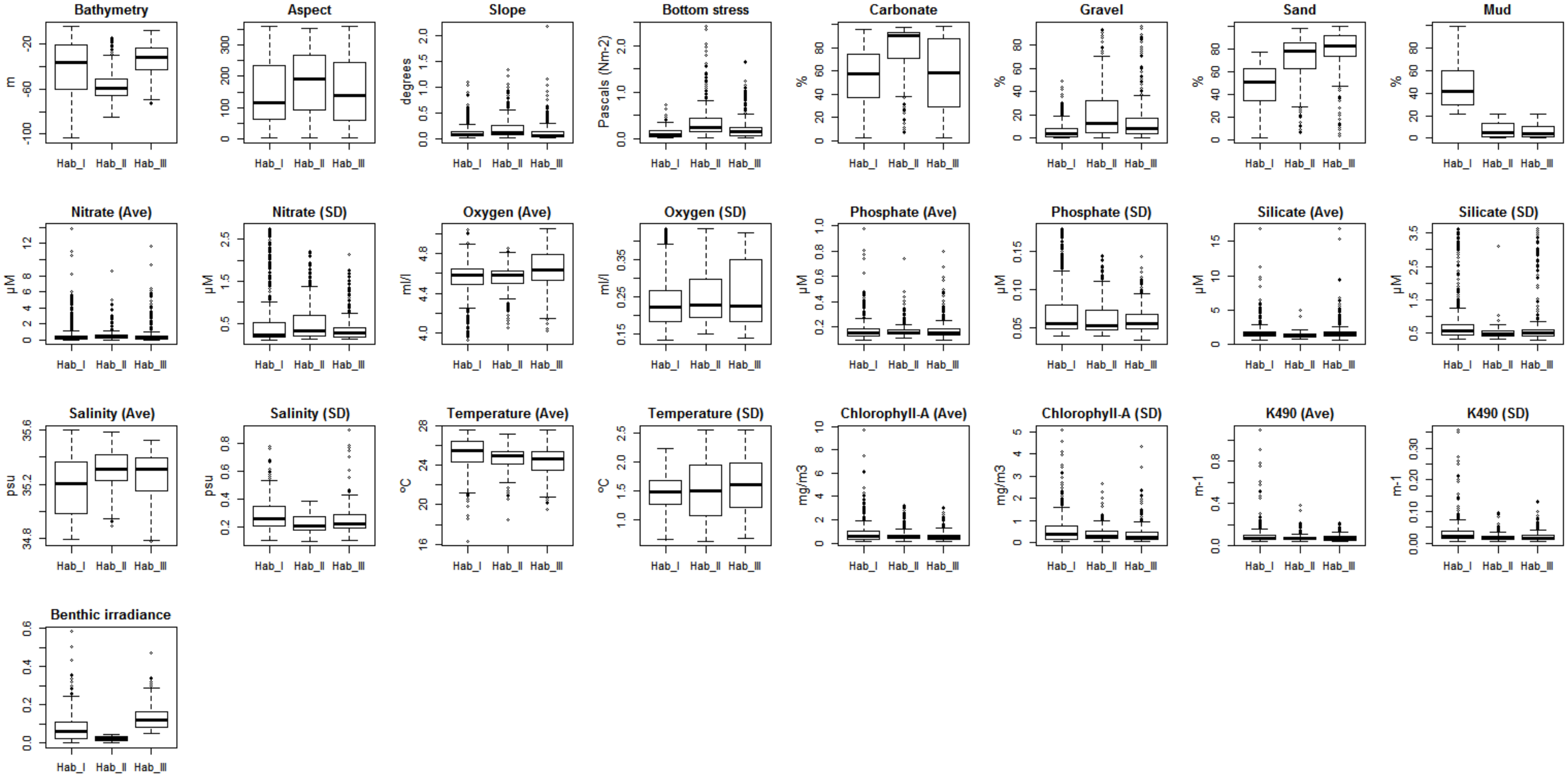


Figure 4.3. Box plots of the distribution of the physical variables in each habitat type (x-axis; I = Habitat I, II = Habitat II, III = Habitat III).

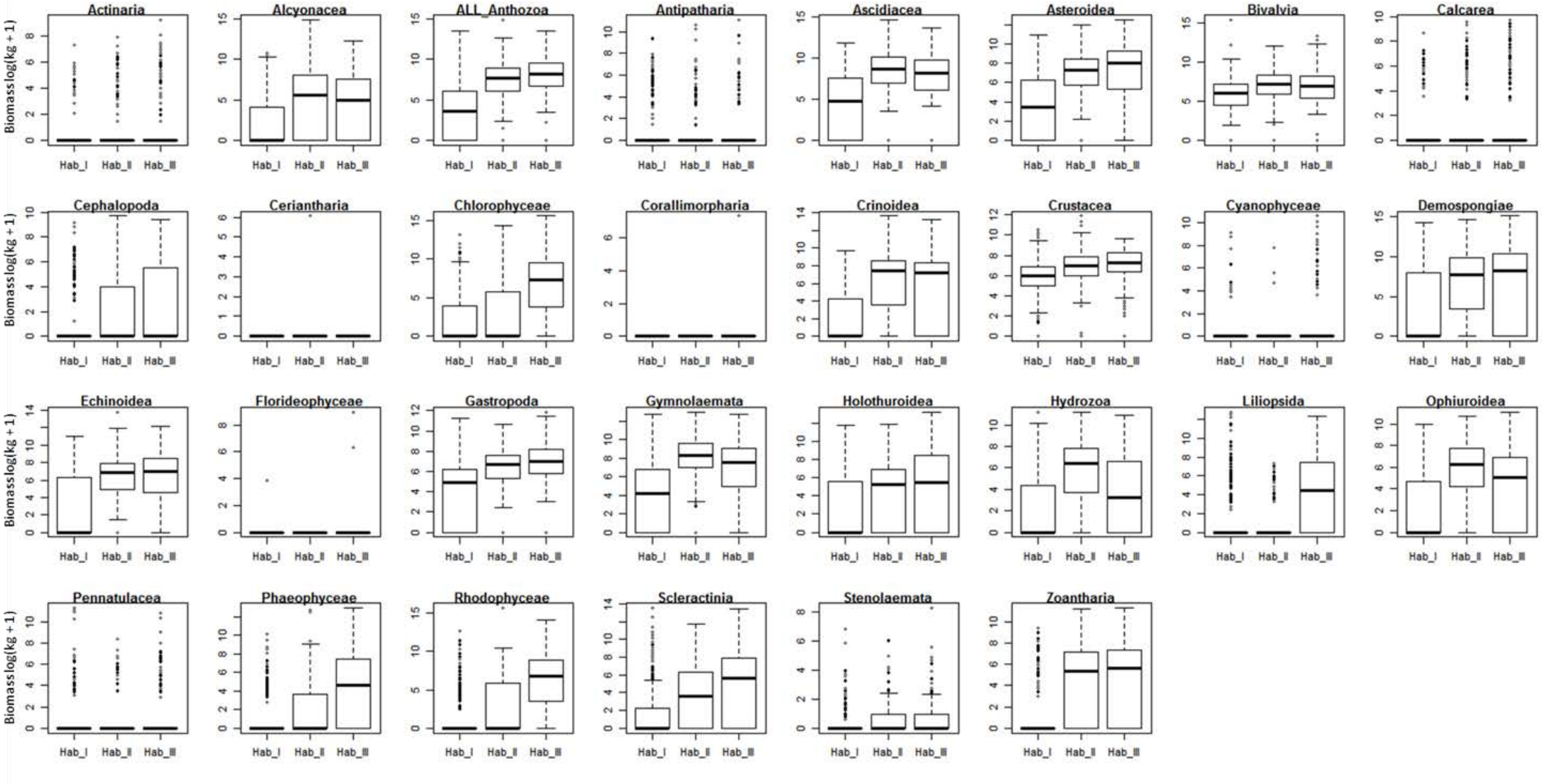


Figure 4.4. Box plots of the log=transformed biomass (log(kg + 1)) of the biological variables in each habitat type (x-axis; I = Habitat I, II = Habitat II, III = Habitat III).

4.2.2. *Constraints and assumptions*

The main constraint in habitat studies, especially in the marine realm, is simultaneously obtaining data on environmental variables where individuals are being observed and/or tracked. *In situ* surveys of one or more environmental variables within a turtle's home range would be an extremely challenging and resource-intensive task, let alone surveying across the total distribution of the population. The environmental variables used in this chapter were collected during benthic habitat surveys conducted between 2003 and 2005 and/or collated as part of the Seabed Biodiversity Project (Pitcher *et al.*, 2007). I acknowledge that the distribution and abundance of benthic species, as well as the values of the physical variables, might have changed by the time the turtles were tracked between 2009 and 2016. However, there is no way of estimating whether this occurred across the turtles' home ranges, or if it did, the degree of change. Therefore, for the purposes of the analysis of this chapter, I assumed that flatback turtles living in the GBR during the period of data collection for the Seabed Biodiversity Project (2003-2005) would use similar geographical areas as the ones tracked herein (Figure 4.5).

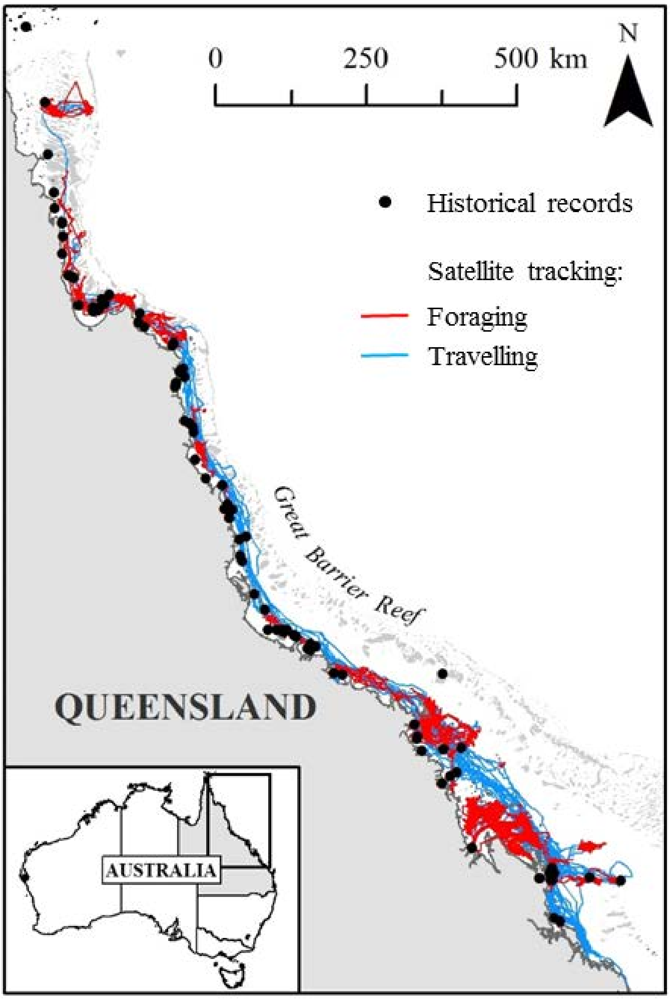


Figure 4.5. Spatial distribution of flatback turtle travelling and foraging records in eastern Australia. Black dots indicate flatback turtle presence as indicated by bycatch records in trawl fisheries.

4.3. Results

The proportion of time spent by the tracked turtles within each of the three habitat types varied among individuals (Figures 4.6, 4.7). Most turtles (ca. 70%) divided their time between more than one of the three habitat types (Figure 4.7a). However, some individuals displayed a high affinity for specific habitats (i.e. turtles 54528 (Figure 4.7b), 108471 and 141738 for Habitat-I, -II and -III, respectively). For the RF analysis, individuals were assigned to the habitat used most frequently by them (Figure 4.6); nearly half of the tracked turtles (43.2%) were assigned to Habitat-I, followed by 31.8% to Habitat-II and 25% to Habitat-III.

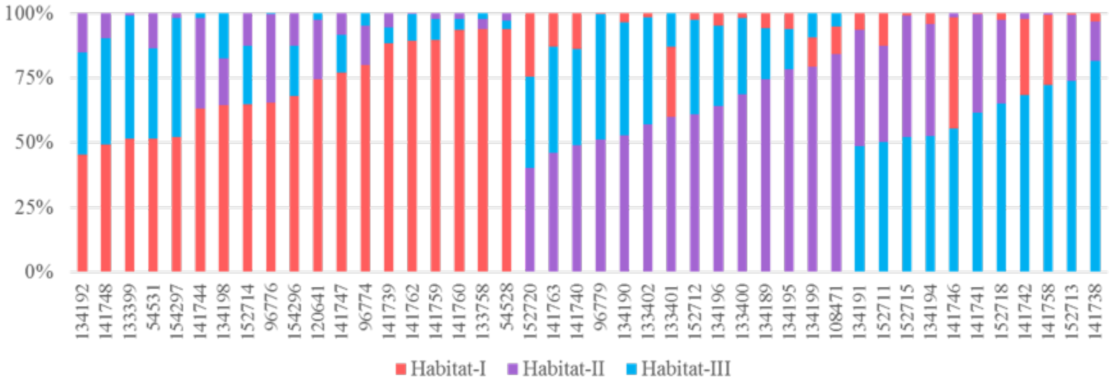


Figure 4.6. Proportion of time spent by individual turtles within each habitat type. For each turtle, bars are ordered from most- to least-frequently used habitat, with the most frequent one displayed at the bottom of the bar.

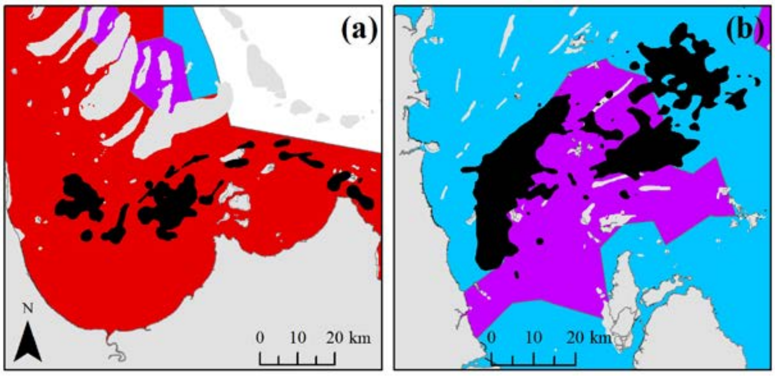


Figure 4.7. Differences in type of habitat used by individual turtles: (a) turtle 96779 split its time evenly between Habitats II and III in Broad Sound, while (b) turtle 54528 predominantly used Habitat I in Princess Charlotte Bay. Home ranges of the turtles are represented by the black areas. Polygons represent the different types of habitat: Habitat I (red), Habitat II (purple), Habitat III (blue). Grey polygons represent the mainland, islands and reefs.

A total of 1058 paired locations (locations with data on turtle time-density AND environmental variables) were included in the RF analysis. Turtles responded to different predictors within each model, with no clear overall pattern of habitat preference (see Appendix Figures A1, A2 for responses in the GBR-wide model; Appendix Figures A3-A8 for responses in the individual habitat models). Model performance varied among general and habitat-specific models, as well as between sets of predictors (Table 4.3). The OOB-%VarExp ranged between 80.52% and 95.16% for the models that used physical predictors, and 10.47% and 30.47% for the models that used biological predictors. All models evaluating the association between turtles and physical variables performed well with high predictive power (> 80%VarExp OOB); the highest predictive power was estimated for turtles in Habitat-II. In contrast, models evaluating the association between turtles and biological variables had a lower predictive power (10.47 - 30.47 %VarExp OOB); the lowest predictive power was estimated for turtles in Habitat-III. The IB-%VarExp was very high (> 95%) and high (>80%) for the physical and biological predictors, respectively.

Table 4.3. Percentage of explained variation in validation (OOB) and training (IB) sets.

Model	***OOB-%VarExp OOB***		***IB-%VarExp***	
	Physical	***Biological***	***Physical***	***Biological***
GBR-wide	82.93	18.77	97.14	85.28
Habitat-I	80.52	16.98	96.70	84.77
Habitat-II	95.16	30.47	99.19	87.72
Habitat-III	84.46	10.47	97.27	83.65

The importance, magnitude and direction of the effects of the variables also differed among models, as evidenced by the importance plots (Figures 4.8, 4.9) and partial plots (Appendix Figures A1, A2 for responses in the GBR-wide model; Appendix Figures A3-A8 for responses in the individual habitat models). The most important physical variables for predicting the presence of turtles in the GBR-wide model (turtles across the complete geographical range) were carbonate (IncMSE = 32.3 %), bottom stress (27.1 %) and the variability in temperature (25.2 %) (Figure 4.8a, Table 4.4). These variables also had high predictive importance in the Habitat-III model (Figure 4.8d), but had a lower predictive importance in Habitat-I and -II (Figure 4.8b-c, Table 4.4). It is also important to consider the direction of the response (turtle presence) to each variable. In this sense, the response of turtles to carbonate was consistently lower in high carbonate sediments across all models, the direction of the response to bottom stress was predominantly positive (excepting in Habitat-III) and the direction of the response to the variability in temperature differed in each model (Table 4.4). There were further consistencies in the response of turtles of other variables across models. For example, there were positive responses to bathymetry (down to ~40m), mud, light attenuation (average and SD), salinity (average and SD), silicate (average and SD) and Chlorophyll-A (average), and negative responses to sand, nitrate (average), phosphate (SD) and slope. In some other cases, such as for temperature (average), nitrate (SD) and phosphate (average) there were mixed responses across models (Table 4.4).

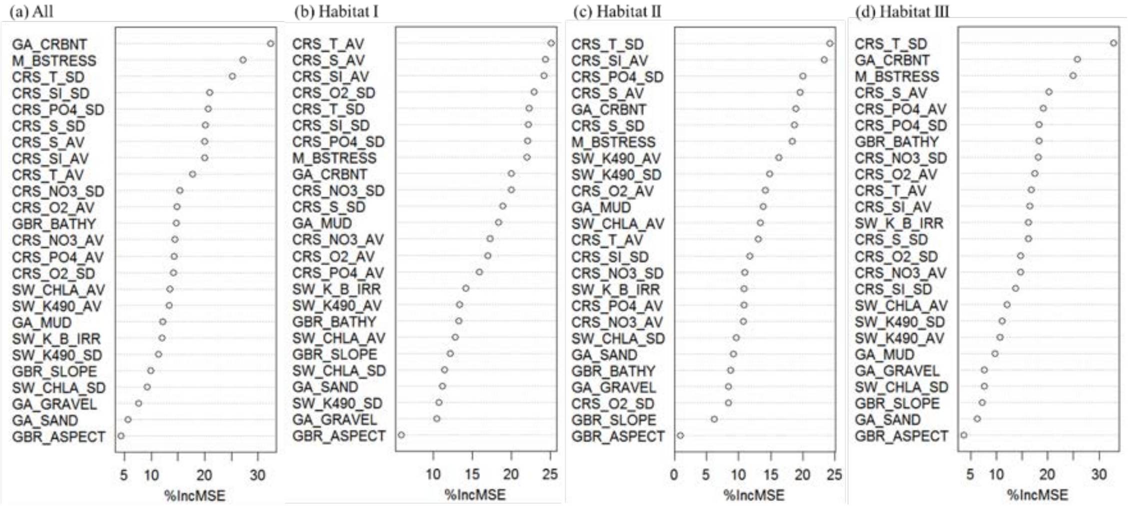


Figure 4.8. Importance plots for each model of the physical variables, representing the importance of each variable to predict the presence of turtles in the GBR.

Table 4.4. Importance of physical predictors for turtle presence in each model. Number and colour of dots represent the ascending importance rank based on values of %IncMSE: < 15% = ●, 15 – 20% = ●, 20 – 25% = ●●, 25 – 30 % = ●●●, >30% = ●●●●. The direction of the response (turtle presence) to each variable is indicated in brackets: (+) = positive response, (–) = negative response, (⋀) or (⋁) = bell-shaped response, (?) = mixed response. Direction of the response is derived from the Partial Plots (Appendix Figures A1, A3, A5, A7)

Physical predictors	***GBR-wide***	***Habitat-I***	***Habitat-II***	***Habitat-III***
Carbonate	●●●● (–)	●● (–)	● (–)	●●● (–)
Bottom stress	●●●● (+)	●● (+)	● (+)	●● (–)
Temperature (SD)	●●● (⋁)	●● (–)	●● (+)	●●●● (+)
Silicate (SD)	●● (⋁)	●● (+)	● (+)	● (+)
Phosphate (SD)	●● (–)	●● (–)	●● (–)	● (⋁)
Salinity (SD)	●● (+)	● (+)	● (+)	● (+)
Salinity (Ave)	●● (+)	●● (⋁)	● (+)	●● (+)
Silicate (Ave)	● (+)	●● (+)	●● (+)	● (+)
Temperature (Ave)	● (⋁)	●●● (+)	● (–)	● (⋁)
Nitrate (SD)	● (+)	●● (–)	● (+)	● (–)
Oxygen (Ave)	● (⋁)	● (⋁)	● (+)	● (+)
Bathymetry	● (+)	● (+)	● (⋀)	● (+)
Nitrate (Ave)	● (–)	● (–)	● (–)	● (–)
Phosphate (Ave)	● (–)	● (+)	● (⋀)	● (–)
Oxygen (SD)	● (⋁)	●● (–)	● (+)	● (⋁)
Chlorophyll A (Ave)	● (+)	● (+)	● (+)	● (⋀)
Light attenuation (Ave)	● (+)	● (+)	● (+)	● (⋀)
Mud	● (+)	● (+)	● (+)	● (⋀)
Benthic irradiance	● (+)	● (+)	● (–)	● (+)
Light attenuation (SD)	● (+)	● (+)	● (+)	● (+)
Slope	● (–)	● (–)	● (–)	● (–)
Chlorophyll-a (SD)	● (⋁)	● (⋁)	● (?)	● (+)
Gravel	● (+)	● (+)	● (⋁)	● (⋁)
Sand	● (–)	● (–)	● (–)	● (⋁)
Aspect	● (⋁)	● (+)	● (+)	● (–)

The response to biological variables differed considerably among models. Tracked turtles displayed strong negative association to Chlorophyceae (green algae) in all models except Habitat-I. Turtles seem to relate to different classes of invertebrates in each habitat (Figure 4.9, Table 4.5). The most important responses to invertebrates per habitat were as follow: (a) Habitat-I: positive response to Zoantharia (zoanthids) and Gymnolaemata (a class of bryozoans); (b) Habitat-II: positive response to Ophiuroidea (brittle stars) and Hydrozoa (hydrozoans); and (c) Habitat-III: negative response to Stenolaemata (a class of bryozoans) and positive response to Hydrozoa. Turtles across all habitats displayed a consistent positive response to Liliopsida (seagrass), Antipatharia (black wire corals), Pennatulacea (sea pens) and Alcyonacea (soft corals), and a negative response to Chlorophyceae (green algae), Stenolaemata (a class of bryozoans) and Asteroidea (asteroids) (Table 4.5).

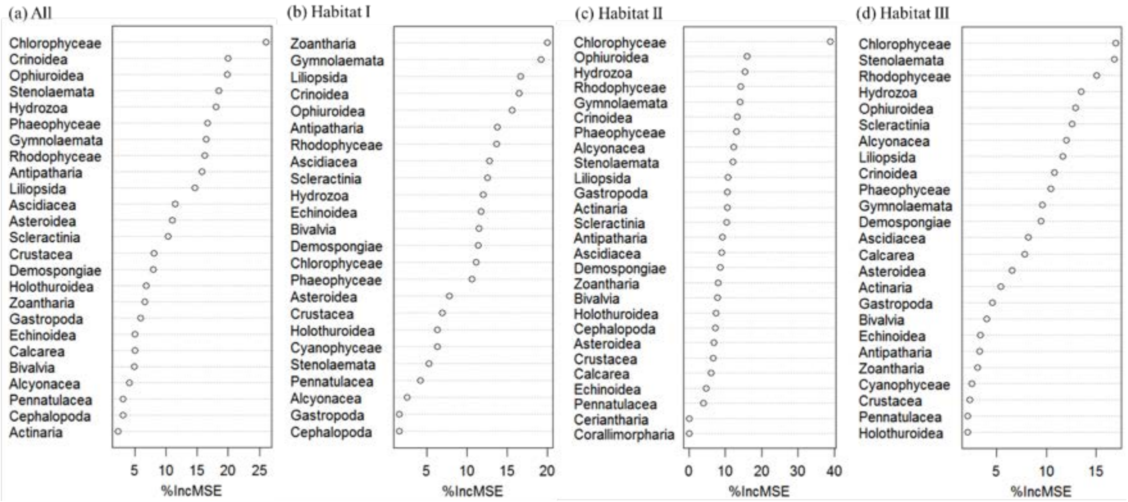


Figure 4.9. Importance plots for each model of the biological variables, representing the importance of each variable to predict the presence of turtles in the GBR.

Table 4.5. Importance of biological predictors for turtle presence in each model. Number and colour of dots represent the ascending importance rank based on values of %IncMSE: < 15% = ⚪, 15 – 20% = ⚫, 20 – 25% = 🔵🔵, 25 – 30 % = 🟡🟡🟡, >30% = 🔴🔴🔴🔴. The direction of the response (turtle presence) to each variable is indicated in brackets: (+) = positive response, (–) = negative response, (/\) or (\/) = bell-shaped response, (?) = mixed response. Direction of the response is derived from the Partial Plots (Appendix Figures A2, A4, A6, A8)

All	***GBR-wide***	***Habitat I***	***Habitat II***	***Habitat III***
Chlorophyceae	🟡🟡🟡 (–)	⚪ (\/)	🔴🔴🔴🔴 (–)	⚫ (\/)
Crinoidea	⚫ (\/)	⚫ (–)	⚪ (–)	⚪ (+)
Ophiuroidea	⚫ (+)	⚫ (+)	⚫ (/\)	⚪ (–)
Stenolaemata	⚫ (–)	⚪ (–)	⚪ (–)	⚫ (–)
Hydrozoa	⚫ (+)	⚪ (\/)	⚫ (+)	⚪ (\/)
Phaeophyceae	⚫ (+)	⚪ (–)	⚪ (+)	⚪ (+)
Gymnolaemata	⚫ (+)	⚫ (\/)	⚪ (+)	⚪ (\/)
Rhodophyceae	⚫ (+)	⚪ (\/)	⚪ (+)	⚫ (+)
Antipatharia	⚫ (+)	⚪ (+)	⚪ (+)	⚪ (+)
Liliopsida	⚪ (+)	⚫ (+)	⚪ (+)	⚪ (+)
Ascidiacea	⚪ (+)	⚪ (/\)	⚪ (+)	⚪ (+)
Asteroidea	⚪ (–)	⚪ (–)	⚪ (–)	⚪ (–)
Scleractinia	⚪ (+)	⚪ (–)	⚪ (+)	⚪ (+)
Crustacea	⚪ (\/)	⚪ (?)	⚪ (–)	⚪ (\/)
Demospongiae	⚪ (\/)	⚪ (+)	⚪ (+)	⚪ (+)
Holothuroidea	⚪ (+)	⚪ (+)	⚪ (–)	⚪ (\/)
Zoantharia	⚪ (+)	🔵🔵 (\/)	⚪ (?)	⚪ (+)
Gastropoda	⚪ (\/)	⚪ (\/)	⚪ (–)	⚪ (\/)
Echinoidea	⚪ (+)	⚪ (+)	⚪ (+)	⚪ (–)
Calcarea	⚪ (+)		⚪ (+)	⚪ (+)
Bivalvia	⚪ (+)	⚪ (+)	⚪ (+)	⚪ (+)
Alcyonacea	⚪ (+)	⚪ (\/)	⚪ (+)	⚪ (+)
Pennatulacea	⚪ (+)	⚪ (+)	⚪ (+)	⚪ (+)
Cephalopoda	⚪ (+)	⚪ (/\)	⚪ (–)	
Actinaria	⚪ (+)		⚪ (+)	⚪ (+)
Cyanophyceae		⚪ (+)		⚪ (+)

4.4. Discussion

This study is the first to describe the biological and physical features of the foraging habitats of flatback turtles and predict the environmental variables that could be associated with their presence in these habitats. Flatback turtles were tracked across different habitats of the GBR, predominantly in muddy (Habitat-I) and low-mud/low-light (Habitat-II) habitats, but also in low-mud/medium-light (Habitat-III) environments. Overall, the presence of the tracked turtles seems to increase at lower levels of carbonate and higher levels of bottom stress. Nevertheless, within each habitat, turtles responded to different sets of environmental predictors (Tables 4.4, 4.5). These results, combined with observations of large home range areas and dynamic foraging strategies (Chapter 3), suggest that flatback turtles are generalist, opportunistic foragers, although some individuals seem to be more specialised in their use of resources.

Flatback turtle foraging grounds have been described as sub-tidal turbid soft-bottom habitats (Limpus *et al.*, 2013a; Limpus, 2007). This corresponds with the inshore high mud areas (Habitat-I) in which nearly half of the turtles were distributed, and the positive response of turtles to mud across all models (Table 4.4). Nevertheless, there was a subset of turtles that foraged in inshore areas with lower mud concentration and coarser seabed in both low-light (Habitat-II), and to a lesser extent medium-light environments (Habitat-III). Light levels can be measured through benthic irradiance, which is closely related to turbidity and Chlorophyll-a concentration (Pitcher *et al.*, 2007), especially in deep inshore waters (Kenneth *et al.*, 2004). Typically, higher benthic irradiance in the GBR is related to the presence of marine plants (Pitcher *et al.*, 2007). Thus, while the results associate most turtles with low-light, likely turbid areas, turtles in Habitat-III might be associated with less turbid waters. The use of diverse habitats by flatback turtles could reflect differences in the composition and availability of resources, as well as potential individual preferences in their diet. An association with turbid waters could also be linked to a predator avoidance technique, especially in younger age classes (Salmon *et al.*, 2009).

Overall, physical variables explained a larger variation of turtle presence in the models than did biological variables. The large difference in the predictive power between the physical and biological variables is likely to be influenced by the sampling methods. Biomass measures of the biological variables were obtained from a single sample from a 300 m^2 sled at ~1200 sites, while physical variables were smoothed from multiple samples averaged cross years and/or spline interpolations of point data (Pitcher *et al.*, 2007). Thus, the biological data are subject to much more sampling noise than the physical variables. The effect of the physical variables could also be related to the range and distribution of potential prey species (biological predictors), which in turn will shape the distribution for individual turtles. At a threshold of 70-80% of carbonate, turtle presence decreased considerably (Appendix Figures A1, A3, A5, A7), suggesting that flatback turtles tend to avoid inter-reef seabed areas which are typically composed by very high levels (80-100%) of carbonate (Pitcher *et al.*, 2007). Increased bottom stress was shown to be an important potential driver of turtle presence, especially in the Broad Sound region. This could be related to stronger currents or vertical water mixing which can promote sediment resuspension and provide potential substrate and nutrients to a large range of sessile invertebrates (Netto *et al.*, 1999; Roland Pitcher *et al.*, 2012). The data in this chapter also shows that turtle presence increased where seasonal variability of temperature is greater than ca. 2.4º. Similarly, the tracked turtles responded to other seasonal ranges of physical predictors, such as salinity and levels of silicate, phosphorus and oxygen. Association with seasonal ranges suggests that environmental variability is an important potential driver of the benthic community diversity and distribution (Roland Pitcher *et al.*, 2012). In terms of turtle presence, this suggests that potential prey species could be represented by groups with higher tolerance to environmental variability, or that turtles are feeding on a variety of prey species that are adapted to a range of different environmental conditions.

The apparent association of turtles to different prey groups (Figure 4.9, Table 4.5) in each habitat has important implications for their ecological role in benthic ecosystems. The limited evidence available of flatback turtle diet indicates that the species feeds on soft-bodied invertebrates, such as sea pens, soft corals, sea cucumbers (Holothuroidea) and jellyfish (Limpus *et al.*, 2013a; Limpus, 2007). These findings are supported by the models of the tracked flatback turtles, which collectively displayed positive responses to sea pens (Pennatulacea) and soft corals (Antipatharia, Hydrozoa, Pennatulacea, Alcyonacea) (Table 4.5). Furthermore, the results of my study provide insights into potential positive association of flatback turtles to a broader range of invertebrates, including sponges, ascidians, bivalves and echinoderms. Unexpectedly, the tracked turtles were positively associated with seagrass; however, this might be linked to the distribution of macro-invertebrates that are preyed by flatback turtles.

My analysis revealed that flatback turtles in the GBR use very different environments across their foraging range, with some individuals displaying a strong affinity for specific habitats (i.e. turtles 141758, 141760, 133758, 108471 in Figure 4.6), and thus different prey groups (Figure 4.9, Table 4.5). In addition, as described in Chapter 3 and reported by Whittock *et al.* (2016) for flatback turtles in Western Australia, the home range of some turtles in the GBR are considerably large (455.5 ± 359.7 km^2), and this could be linked to their preference for prey with wide spatial distributions and/or mobile prey. In some cases, turtles that travelled long distances displayed a multi-stop migration (Figure 3.5d in Chapter 3) during which they are likely to be foraging. These “stops” were in some cases located across different habitats, suggesting that the turtles’ generalist capacity could make use of a variety of prey in each habitat. In other cases, turtles displayed constrained home ranges (Figure 3.5a in Chapter 3), or undertook short trips to specific locations (Figures 3.5b-c in Chapter 3) that might be linked to searching strategies for a preferred prey. Combined, the results of chapters 3 and 4 provide evidence of the complexity of interactions between the species and its habitat, and suggest that flatback turtles in the GBR are generalist and opportunistic foragers, with some degree of individual specialisation.

More often, variability in habitat use among individuals is related to ontogenic, seasonal or gender-specific differences (Cardona *et al.*, 2010; Hawkes *et al.*, 2011; Scott *et al.*, 2014; Shimada *et al.*, 2016a). All flatback turtles tracked during this study belonged to the same reproductive stage (reproductive adults) and sex class (females). Specialisation within individuals of the same age and sex class has been related to cognitive processes (e.g. individual diet preferences, learning from previous foraging experiences) and internal physiology (Woo *et al.*, 2008). The spatial and temporal dynamics in the diversity and density of resources can also have an effect on the level of specialisation or generalisation portrayed by individuals (Rosenblatt *et al.*, 2015). Thus, assessing resource partitioning by flatback turtles and the consistency in resource use over time remains to be determined, and is fundamental to understand the degree of individual specialisation within the population.

My thesis findings provide insights into habitat use by flatback turtles in the GBR benthic ecosystem. The number of foraging flatback turtles in the GBR is estimated to be in the order of several thousand (Colin J. Limpus, pers. comm.). As large-bodied, top-level consumers of benthic invertebrates, adult flatback turtles are likely to feed on substantial amounts of prey biomass, which could potentially influence prey community composition and trophic dynamics. Thus, flatback turtles could potentially influence the abundance of invertebrates through top-down mechanisms, and/or act as ecosystem engineers by shaping the biological diversity and community structure. In addition, at an ecosystem level, flatback turtles could serve as connectors of multiple energy pathways in the food web. This is important because studies of apex marine predators have shown that individual specialisation can also have an important effect on the diversity of energy fluxes in ecosystems, influencing the coupling or compartmentalisation of trophic pathways (Matich *et al.*, 2011). In addition, given the observed dynamic foraging strategies (Chapter 3) and shifts between habitats (Figure 4.6), flatback turtles may contribute to the transfer of nutrients and energy between foraging habitats.

4.5. Conclusion

Flatback turtles in eastern Australia appear to be associated with a variety of inshore subtidal habitats, including but not limited to mud-rich inshore environments and less muddy environments with low levels of light intensity. The results of my study confirm that flatback turtles are associated to soft-bodied invertebrates such as sea pens and soft corals; however, flatback turtles might as well be associated with a wider variety of benthic prey than previously reported. The observed plasticity in foraging behaviour and habitat use suggests that the population as a whole can be classified as generalist and opportunistic; however, my results also suggest that there might be some degree of niche partitioning among individuals. Collectively, the results highlight the potential capacity of flatback turtles as a species to adapt to variation or change to their environments and resources.

My thesis study provides a first insight into the potential associations between flatback turtles and their habitat. Logistical constraints related to the habitat (turbid, deep) and the ecology of flatback turtles (long immersions, fast fleeing response) have made it difficult to encounter and study them directly in the wild. Thus, by combining satellite tracking with habitat modelling, my study sheds light on potential key areas of research for future foraging studies. The next steps to improve our understanding of the foraging ecology of flatback turtles include but are not limited to (a) stomach content analysis of wild foraging individuals to identify a wider range of diet items, (b) stable isotope analysis in foraging and/or nesting populations (see Pajuelo *et al.* (2016); Vander Zanden *et al.* (2010)), (c) the use of animal-borne videos or autonomous underwater vehicles (AUVs) to directly observe the interaction between turtles and the environment, (d) affixing accelerometers to turtles in order to measure feeding activity (Watanabe & Takahashi, 2013). Refining the information on diet and foraging ecology of the individuals will improve the predictive capacity of statistical models (e.g. to generate predictive species distribution maps), and increase the potential applications of such models (e.g. to assess the potential impact of future changes to habitats), which would generate valuable outputs to inform local management and conservation of the species.

Chapter 5

Exposure of flatback turtle foraging habitats to threats and their protection in the Great Barrier Reef Marine Park

Tanker and cargo vessels at Gladstone Port in December 2015.

Photo credits: Natalie Wildermann.

Abstract

Species' vulnerability and risk assessments are greatly enhanced when the cumulative and/or synergistic effect of threats are considered in the process. A cumulative impact refers to the additive effect of two or more threats, while a synergistic impact refers to the augmented effect that results from the interaction among threats. Assessing the distribution and intensity of such effects derived from human activities is of special importance for the efficient management of marine species and habitats. In this sense, by localising and quantifying the effects of human activities, conservation planners and managers can take informed decisions on where to focus the reduction or mitigation of stressors. This is of special relevance for migratory marine megafauna in the Great Barrier Reef Marine Park (GBRMP), such as marine turtles, which are considered a key species of conservation concern in the region. Multiple management documents pertaining to the GBRMP have highlighted the necessity of improving our understanding of the cumulative impact of human threats to marine turtles in the region. Thus, the aim of this chapter is to quantify the individual and cumulative exposure of foraging flatback turtles to two of the human threats (shipping and trawling), as well as the extent to which the tracked turtles were protected within the GBRMP. To achieve this, I overlayed the distribution of the tracked flatback turtles (chapter 3) to layers of mapped intensity of trawling, shipping, and the combined threats, as well as to the layer of protected zones in the GBRMP. The results indicate that 52.2% of the tracked foraging locations were located within marine protected areas, 47.3% in "General Use" areas (limited protection level), and only 0.5% were located within ports (no protection). In addition, the resulting maps suggest there is an overall low exposure of the tracked foraging flatback turtles to the individual and cumulative effect of shipping and trawling across the GBRMP. However, there were also a few foraging locations in the northern half of the GBRMP that displayed medium exposure to the threats. This chapter provides much-needed data on the distribution of potential threats relative to flatback turtle foraging grounds in order to inform future stock and risk assessments. Future studies in this area should include the cumulative and synergistic effect of other human-related stressors, such as water quality and marine debris.

Keywords: Great Barrier Reef World Heritage Area, protection, threats, cumulative impact, marine turtles, flatback turtle.

5.1. Introduction

The importance of understanding the cumulative and synergistic impact of human activities on coastal and marine ecosystems has increasingly been highlighted in the literature (e.g. Ban *et al.* (2010); Crain *et al.* (2008); Fuentes *et al.* (2011); Grech and Marsh (2008); Halpern *et al.* (2008).

Comprehensive assessments of cumulative impacts are vital to gain a holistic understanding of the vulnerability and risk of habitats and species (Fuentes *et al.*, 2011). However, there are multiple constraints to achieving this, including but not limited to: accessibility of available data; the variability in spatial and temporal scales of datasets; and a sound understanding of the relative impact, magnitude of and interactions among different pressures (Grech *et al.*, 2016). In Australia, extensive studies have evaluated the impact of individual stressors on several species (i.e. marine turtles) through strategic assessments as part of the Environment Protection and Biodiversity Conservation Act (EPBC, 1999). These strategic assessments provide the necessary data to undertake comprehensive cumulative impact assessments and are of special importance to the Great Barrier Reef World Heritage Area (GBRWHA) (GBRMPA, 2014b; Grech *et al.*, 2016).

The Great Barrier Reef (GBR) in Queensland, Australia, spans over 2,400 km, covers an area of 348,000 km^2 and is listed as a World Heritage Area for its outstanding universal value, based on multiple ecosystem and heritage values (GBRMPA, 2014b). These values include the presence of natural beauty and natural phenomena, major stages of the Earth’s evolutionary history, outstanding ecological and biological processes and habitats for conservation and biodiversity (GBRMPA, 2014b). The GBR is also an important social and economic resource for human development, contributing approximately $5.6 billion to the Australian economy (between 2011 and 2012) (GBRMPA, 2014b). Even though there is extensive knowledge on the impacts of individual human threats to the GBRMP, the effect of cumulative impacts in the region is still poorly understood (GBRMPA, 2014b). Most of the ecosystems of the GBR are located within the boundaries the GBRMP, and are therefore protected by an extensive array of management actions (see Outlook Report (GBRMPA, 2014b) for detailed information). These actions are focused on managing the direct use of the marine park, external factors that might affect the ecosystems (natural and human) and to protect the region’s values. In particular, the GBR Marine Park Zoning Plan 2003 (GBRMPA, 2004) appears to benefit biodiversity and enhances the ecosystem’s health and resilience, provided compliance is consistently high (GBRMPA, 2014b).

Both the Zoning Plan and the World Heritage listing recognised the distribution and status of marine turtle populations in the GBR as a key feature of the region (Dryden *et al.*, 2008). The latest reported population trends indicate that many nesting populations of marine turtles in the eastern Australia are stable or increasing, while some others are declining and conservation dependent (GBRMPA, 2014b). Yet these assessments are mostly based on numbers of female turtles breeding each year. Less is known about the status and condition of non-breeding turtles. Some of the biggest threats to foraging marine turtles in the GBRMP are habitat loss and degradation, decreasing water quality, incidental capture in commercial fisheries, boat strike and ingestion/entanglement of marine debris (GBRMPA, 2014a).

Knowledge of key marine turtle mating areas, foraging habitat and migratory corridors is still needed to inform management in the GBRMP, and continuous efforts are being made to fill these knowledge gaps (GBRMPA, 2014a). Historic distribution for eAus foraging flatback turtles has been derived from long-term opportunistic in-water records, indicating that the species forages from Moreton Bay in the south of Queensland, to Torres Strait in the north. In addition, in Chapter 3 I identify new foraging aggregations of flatback turtles and foraging hotspots across the GBRMP, based on satellite tracking of adult female turtles. However, to make informed management decisions it is vital to generate knowledge on the spatial distribution of turtles relative to the exposure to potential threats (Fuentes *et al.*, 2011; Maxwell *et al.*, 2013). Animal-borne telemetry has proven to be an effective tool to integrate the spatial ecology and management of a species (Maxwell *et al.*, 2013; McGowan *et al.*, 2017). Thus, the aims of this chapter are to quantify the exposure of foraging flatback turtles to shipping and trawling in the GBRMP, and to generate much-needed data on flatback turtle distribution in order to inform future stock and risk assessments. This chapter also provides base spatial layers of turtle presence and shipping/trawling intensity which can be easily combined with new input data and/or overlayed with additional threats.

5.2. Methods

5.2.1. Turtle tracking dataset

The details of turtle tagging, tracking and home range analysis are provided in detail in Chapter 3. In summary, 44 adult female flatback turtles were tracked between 2009 and 2016 from nesting beaches in eastern Queensland to their foraging locations. The turtles were tracked for a duration between 55 and 575 days each and all turtles remained within the boundaries of the GBRMP. The raster layers of the individual home ranges from Chapter 3 were transformed into a presence/absence grid (0.1º x 0.1º resolution = approx. 114 km^2) using the spatial join tools in ArcMap 10.2.2. All individual presence/absence layers were then converted into raster layers and summed using the raster calculator in ArcMap 10.2.2 to obtain a single raster layer displaying the number of turtles present in each grid cell (Figure 5.1). For the exposure analysis, the turtle dataset was re-scaled (0-1) using the Fuzzy Membership tool in ArcMap 10.2.2.

In this chapter, I use the term “foraging sites” to refer to each individual grid cell in which foraging was recorded, and “foraging area” to the complete extent of all foraging sites for all turtles recorded across the GBRMP. To align the results of this study with the management structure of the GBRMP, foraging sites were analysed based on the four Management Areas (MAs) implemented by the GBRMPA (GBRMPA, 2004), from north to south: Far Northern MA, Cairns/Cooktown MA, Townsville/Whitsundays MA and Mackay/Capricorn MA. The relative importance of each MA for the tracked flatback turtles was calculated multiplying the number of foraging sites (cells) by the mean number of turtles recorded in each MA.

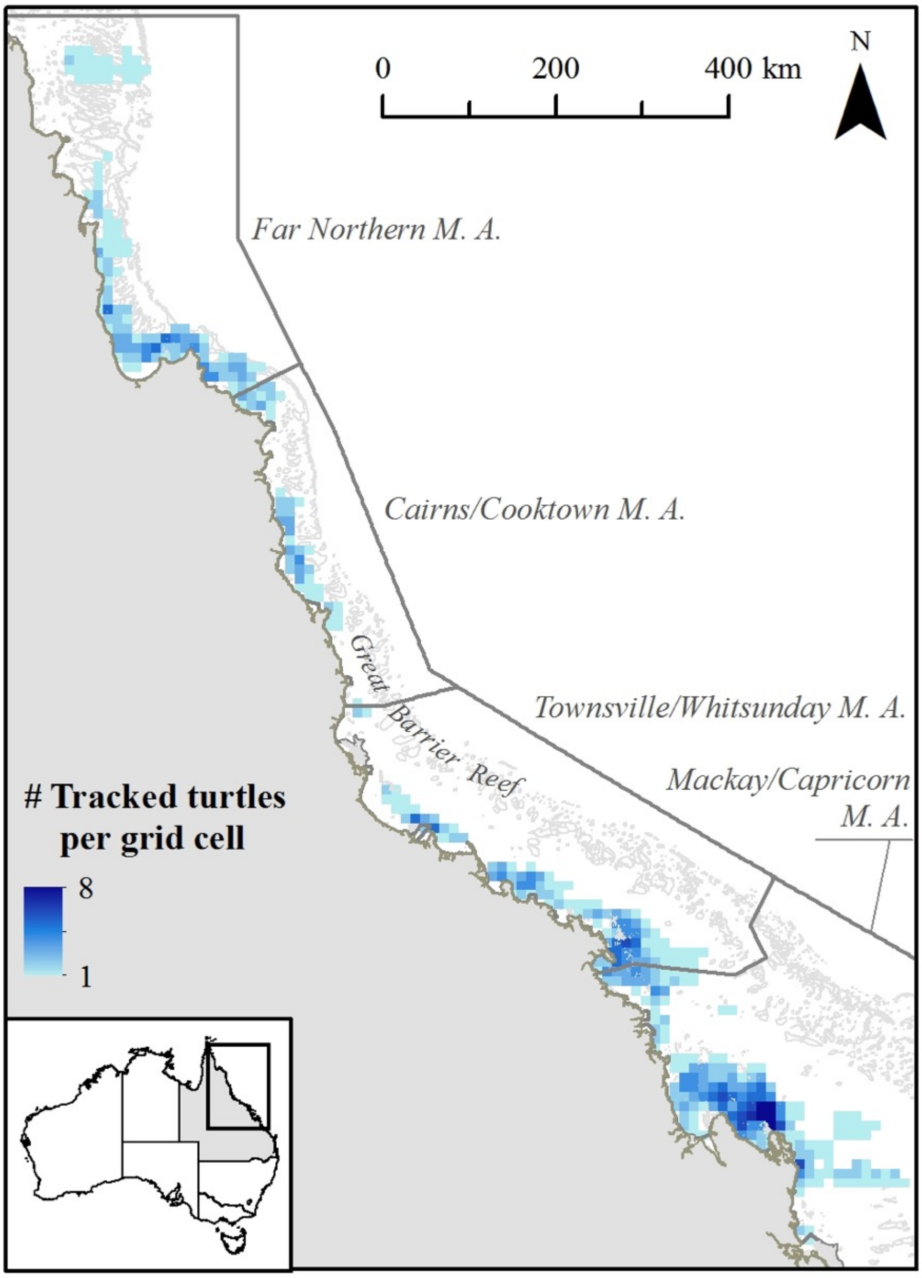
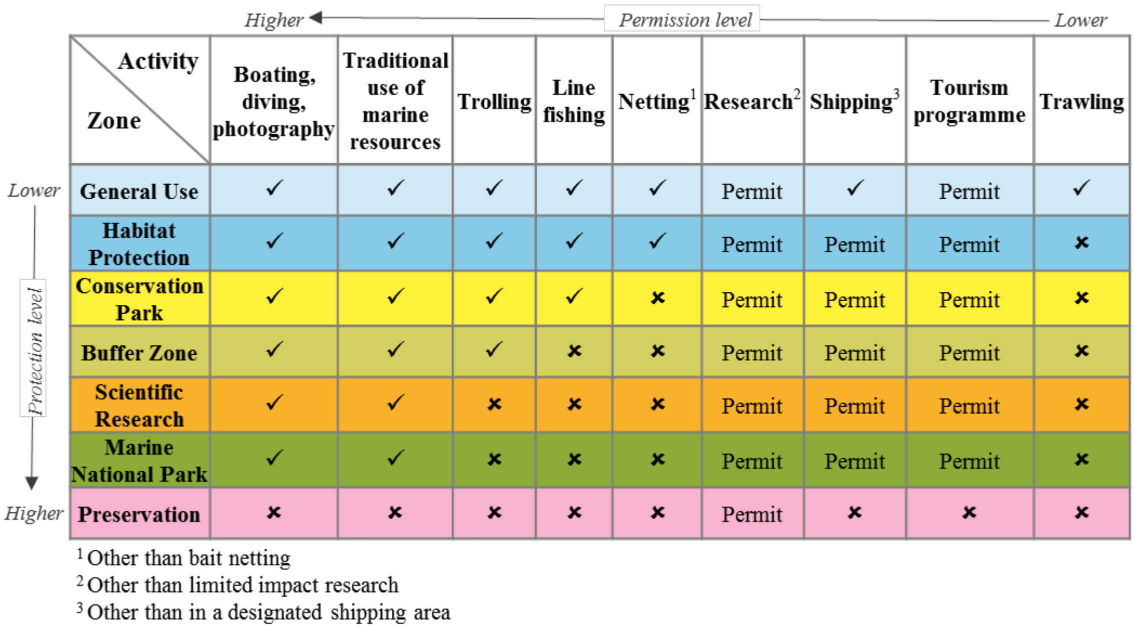


Figure 5.1. Combined foraging area of flatback turtles tracked in this study. Coloured scale indicates the number of turtles per grid cell (0.1° x 0.1° resolution = approx. 114 km^2). Polygons outlined in grey represent the boundaries of each MA of the GBRMP.

5.2.2. *Quantification of protection coverage*

Protection coverage of flatback turtle foraging habitat was measured by calculating the percentage of foraging area located within each zone of the GBRMP. I selected the GBRMP zoning as it is the main instrument in place for management and conservation of the GBR (Zoning Plan 2003). Management of the GBRMP is based on a multiple-use area scheme, providing protection to a range of habitats and allowing for controlled recreational commercial and research activities (Zoning Plan 2003). A summary of permitted activities in each zone is summarised in Table 5.1, and a spatial representation of the zoning is shown in Figure 5.2. For the purposes of this study I consider all zones, except "General Use", to provide high level of protection to turtles. The spatial layer of the GBRMP zoning was obtained online (June 2016) from the spatial data information services section of the GBRMPA (http://www.gbrmpa.gov.au/geoportal/catalog/main/home.page).

Table 5.1. Zones of the GBRMP and permitted activities that could potentially interact with marine turtles. Colours of each zone follow the original colour scheme implemented by the GBRMPA. Adapted from: GBR Marine Park Authority (GBRMPA, 2004).



Activity / Zone	Boating, diving, photography	Traditional use of marine resources	Trolling	Line fishing	Netting[1]	Research[2]	Shipping[3]	Tourism programme	Trawling
General Use	✓	✓	✓	✓	✓	Permit	✓	Permit	✓
Habitat Protection	✓	✓	✓	✓	✓	Permit	Permit	Permit	×
Conservation Park	✓	✓	✓	✓	×	Permit	Permit	Permit	×
Buffer Zone	✓	✓	✓	×	×	Permit	Permit	Permit	×
Scientific Research	✓	✓	×	×	×	Permit	Permit	Permit	×
Marine National Park	✓	✓	×	×	×	Permit	Permit	Permit	×
Preservation	×	×	×	×	×	Permit	×	×	×

[1] Other than bait netting
[2] Other than limited impact research
[3] Other than in a designated shipping area

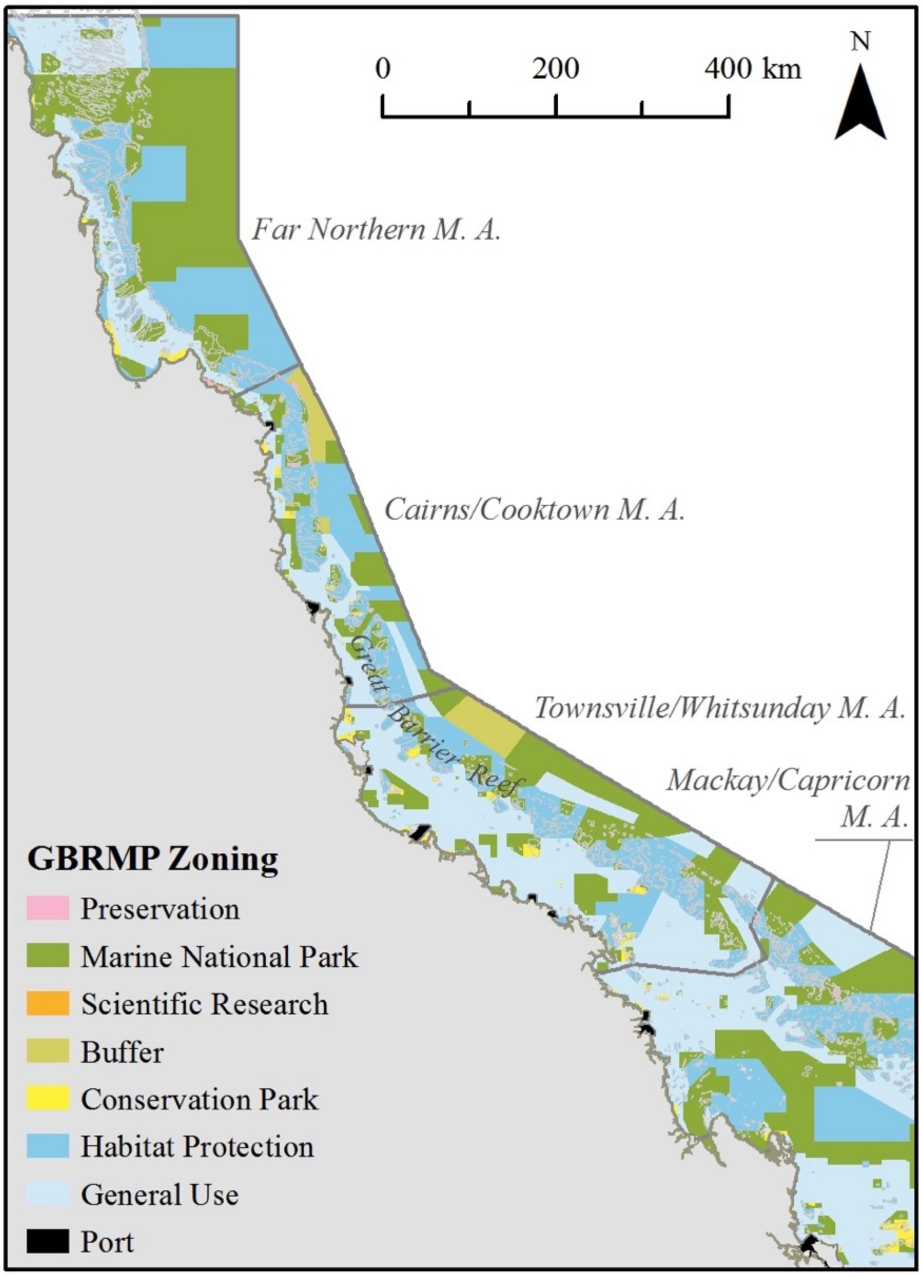


Figure 5.2. Spatial distribution of ports (all ports are located outside the boundaries of the GBRMP) and protection zones of the GBRMP. The description of permitted activities that could potentially interact with marine turtles in each zone is summarised in Table 5.1. Polygons outlined in grey represent the boundaries of each MA of the GBRMP.

5.2.3. Quantification of threat exposure

Quantifying the exposure to threats is the first step to assess their impact on the environment. It is important to consider that exposure does not necessarily imply that an impact is occurring, but rather that the threat is present and could potentially have an effect on the species, population or habitat being studied. In this study, I assess the exposure of flatback turtles to shipping (recreational and commercial vessels), trawling (commercial fishery) and the cumulative exposure of shipping + trawling. These threats were selected from the potential pressures identified in the marine turtles' vulnerability assessment (GBRMPA, 2014a), based on the access and resolution of available datasets. Quantification of exposure of flatback turtles to shipping and trawling in the GBRMP was calculated by overlaying the combined foraging area layer (Figure 5.1) with spatial layers of these two threats (details below). Similar approaches have been employed in other studies assessing the spatial overlap between marine megafauna and different stressors (e.g. marine turtles (Dawson *et al.*, 2017), whales (Rosenbaum *et al.*, 2014)).

Shipping tracking data of all vessels crossing the GBRMP between January 2014 and December 2015 was obtained from the Australian Maritime Safety Authority spatial data website (https://www.operations.amsa.gov.au/Spatial/). To avoid overestimating the spatial extent of shipping, I filtered the raw dataset to only include (a) moving vessels (speed > 1 knot), and (b) vessels with regular transmission of position coordinates (at least one position every 6 hours). This filtering process reduced the number of total vessels from 2398 to 1100 vessels; however, after visually comparing the pre-filtered and filtered datasets, the latter still provides an accurate representation of the shipping intensity across the region. A raster layer of the shipping intensity (Figure 5.3), where the value of each cell (0.1° x 0.1° resolution = approx. 114 km^2) represents the number of vessels crossing per cell, was calculated using the Spatial Join and Polygon to Raster tools in ArcMap 10.2.2.

Average yearly catch (tonnes) of the East Coast Otter Trawl Fishery between 2014 and 2015 was obtained from the Queensland Commercial Fisheries Information System (QFISH) database (http://qfish.fisheries.qld.gov.au/) (State of Queensland, Department of Agriculture, Fisheries and Forestry). The dataset is constructed with self-reported compulsory daily fishing logbooks obtained from trawl fishers, at a 30-minute (0.5 °) resolution scale. This dataset was re-sampled to a 6-minute (0.1 °) resolution scale by breaking the cells into smaller segments and assigning the original cell value to each of the segments. Given the large spatial resolution of the original dataset and in order to reduce overestimation of trawled areas, the re-sampled layer was clipped to "General Use" areas of the GBRMP, in which trawling is permitted (Table 5.1). A raster layer of trawling catch (Figure 5.4), where the value of each cell (0.1° x 0.1° resolution = approx. 114 km^2) represents the average catch in tonnes per cell, was calculated using the Spatial Join and Polygon to Raster tools in ArcMap 10.2.2.

To ensure that the turtle and threats datasets were comparable, each dataset was re-scaled (0-1) using the Fuzzy Membership tool with linear membership in ArcMap 10.2.2. A guide to the un-scaled and re-scaled values for shipping and trawling intensity are shown in Table 5.2. To quantify the individual and cumulative exposure levels of flatback turtles to the threats, the re-scaled combined foraging area was multiplied by each of the re-scaled threat layers using the tool Raster Calculator in ArcMap 10.2.2. The resulting exposure values were classified as no exposure (0), low (< 0.25), medium (0.25 - 0.50), high (0.50 – 0.75) or very high (> 0.75) level of exposure, and represented as individual exposure maps. Finally, for the cumulative exposure analysis, the individual maps of exposure to shipping and exposure to trawling were added with the Raster Calculator tool to generate a map of cumulative exposure, in which values ranged from 0 to 2. Both individual exposure maps were considered to have the same relative impact. The resulting cumulative exposure values were classified as no exposure (0), low (< 0.5), medium (0.5 - 1), high (1 – 1.5) or very high (> 1.5) level of cumulative exposure, and represented as a cumulative exposure map.

Table 5.2. Un-scaled and re-scaled values of filtered shipping and trawling intensity in the GBRMP.

Intensity level	***Un-scaled values***		***Re-scaled values***
	Shipping (number of vessels)	***Trawling (tonnes)***	
Low	< 275	< 422.05	0 - 0.25
Medium	275 - 550	422.05 – 844.1	0.25 - 0.50
High	550 – 825	844.1 – 1266.15	0.50 – 0.75
Very high	> 825	> 1266.15	0.75 - 1

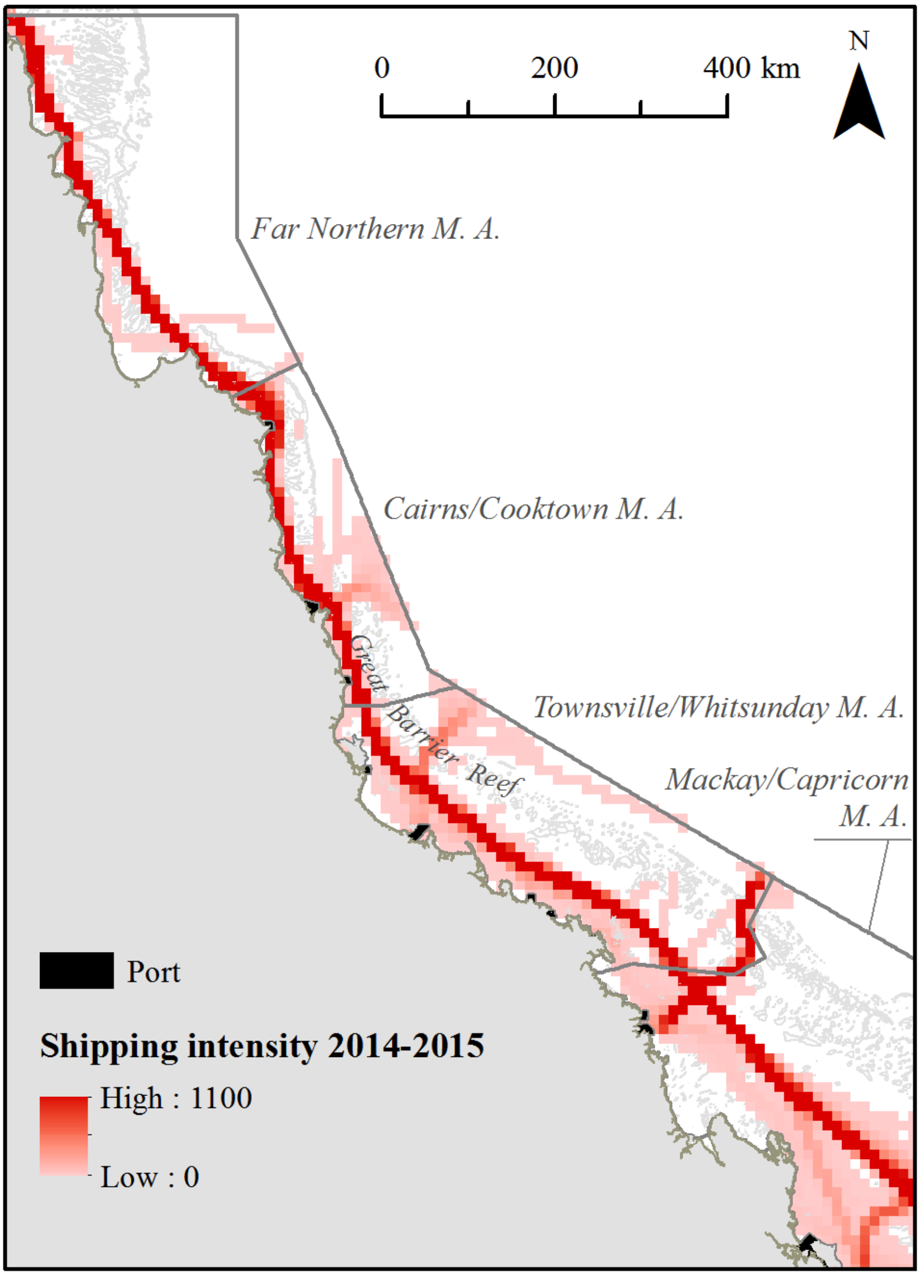


Figure 5.3. Shipping intensity between 2014 and 2015 along the GBRMP. Re-scaled values represent a range from 0 (low) to 1100 (high) vessels.

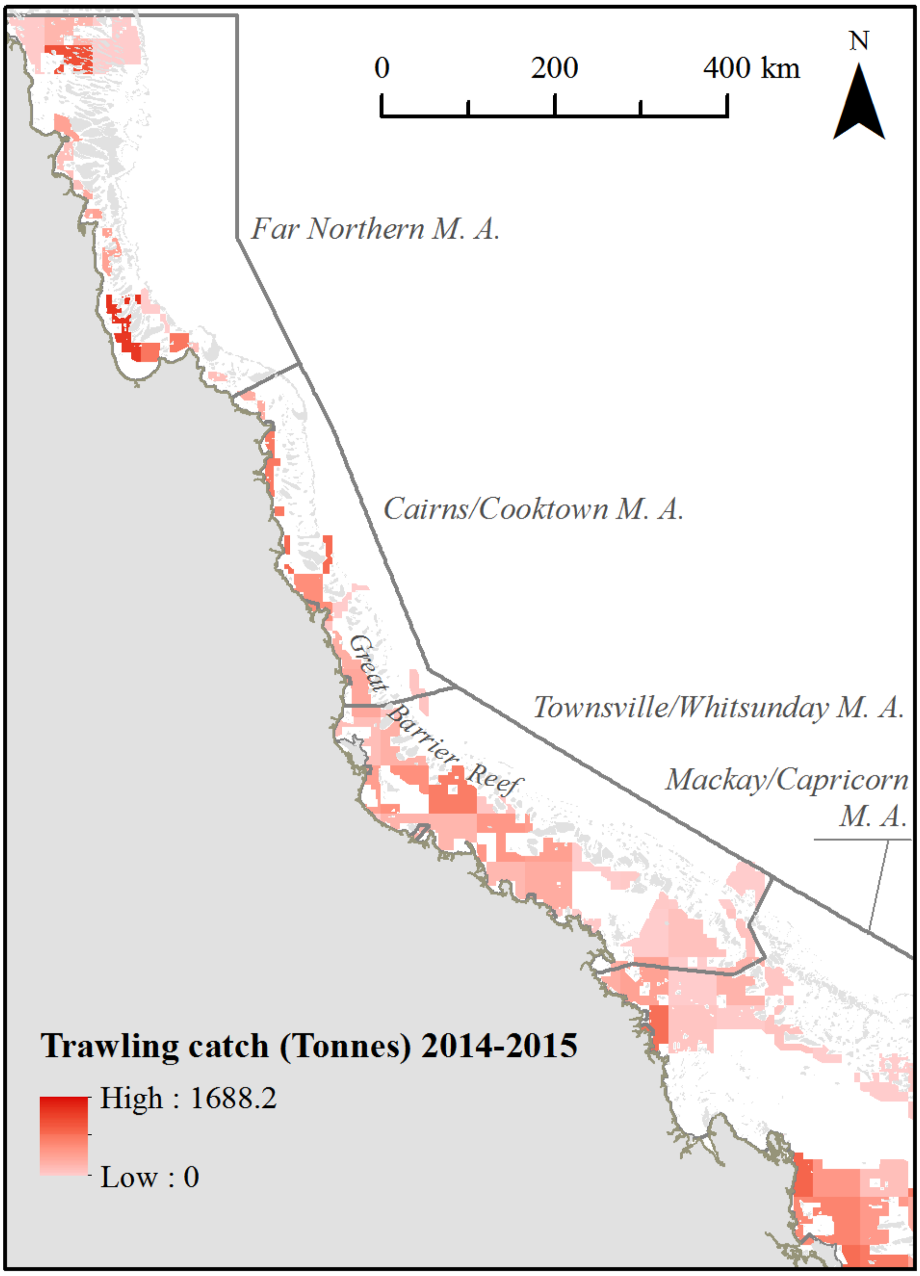


Figure 5.4. Re-scaled trawling catch between 2014 and 2015 along the GBRMP. Re-scaled values represent a range from 0 (low) to 1688.21 (high) tonnes of yearly catch.

5.3. Results

Foraging sites for the tracked turtles spanned close to the entire length the GBRMP and included all MAs, with a higher number of foraging cells in the Mackay/Capricorn (N = 177 cells) and Far Northern (N = 117 cells) MAs (Table 5.3). Nevertheless, the proportion of foraging cells relative to the size of each MA was relatively low (< 5 %). The most important MA, in terms of proportion of foraging sites and recorded turtles, was the Mackay/Capricorn MA, followed by the Townsville/Whitsunday, Far Northern and Cairns/Cooktown MAs (Table 5.3).

Table 5.3. Relative importance of each MA for the tracked flatback turtles, based on the product of foraging sites by the mean number of turtles per cell recorded in each MA.

	Management Area	***Total number of cells***	***Foraging sites (cells)***	***Proportion of foraging sites (cells)***	***Max. turtles per cell***	***Mean ± SD turtles per cell***	***Relative importance (rank)***
North	Far Northern	2833	117	4.1	4	1.6 ± 0.7	187.2 (3)
	Cairns/Cooktown	1260	47	3.7	4	1.5 ± 0.7	70.5 (4)
	Townsville/Whitsunday	2651	99	3.7	6	1.9 ± 1.2	188.1 (2)
South	Mackay/Capricorn	5071	177	3.5	8	2.3 ± 1.7	407.1 (1)

5.3.1. Protection coverage of flatback turtle foraging area

The foraging area of the tracked flatback turtles was located mostly within the boundaries of the GBRMP, with the exception of a very small area located within ports (0.5%) (Figure 5.5). Most of the foraging area occurs within "Habitat Protection" (27.8%) and "Marine National Park" (22.9%) zones, and a smaller percentage is distributed in "Conservation Park" (2.1%) zones (Figure 5.5). The remaining 47.3% of the foraging area is located within General Use zones (Figure 5.5).

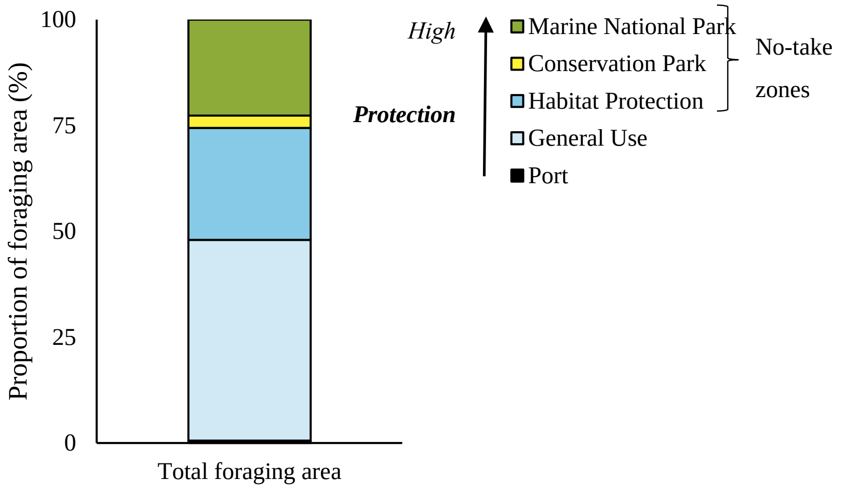


Figure 5.5. Proportion of the total foraging area within ports and each zone of the GBRMP

Foraging sites with high turtle abundance (> 6 turtles per grid cell), although small in extent, were distributed almost entirely in areas with high protection (91.6%) (Column C in Figure 5.6). More than half of the foraging sites (60.6%) with medium turtle abundance (3 – 5 turtles per grid cell) were also located in areas with high protection (Column B in Figure 5.6). Most of the foraging area (75.7%) exhibited low turtle abundance (1 – 2 turtles per grid cell) (Column A in Figure 5.6). Of the grid cells with low turtle abundance, 50.3% were located in General Use zones, and 49.7% in areas with high protection (22.7% in Habitat Protection, 2.1% in Conservation Park, and 24.2% in Marine National Park).

The largest proportion of foraging area within high level of protection (all zones, excepting ports and General Use zone) was recorded for the Mackay/Capricorn (63.5%) and Cairns/Cooktown (61.7%) MA (Figure 5.7). These MAs also recorded the highest proportion of foraging sites in no-take areas (Marine National Parks). The lowest protection coverage was recorded in the Townsville/Whitsunday MA, with nearly 75% of the foraging sites within General Use zones and less than 15% in no-take areas (Figure 5.7).

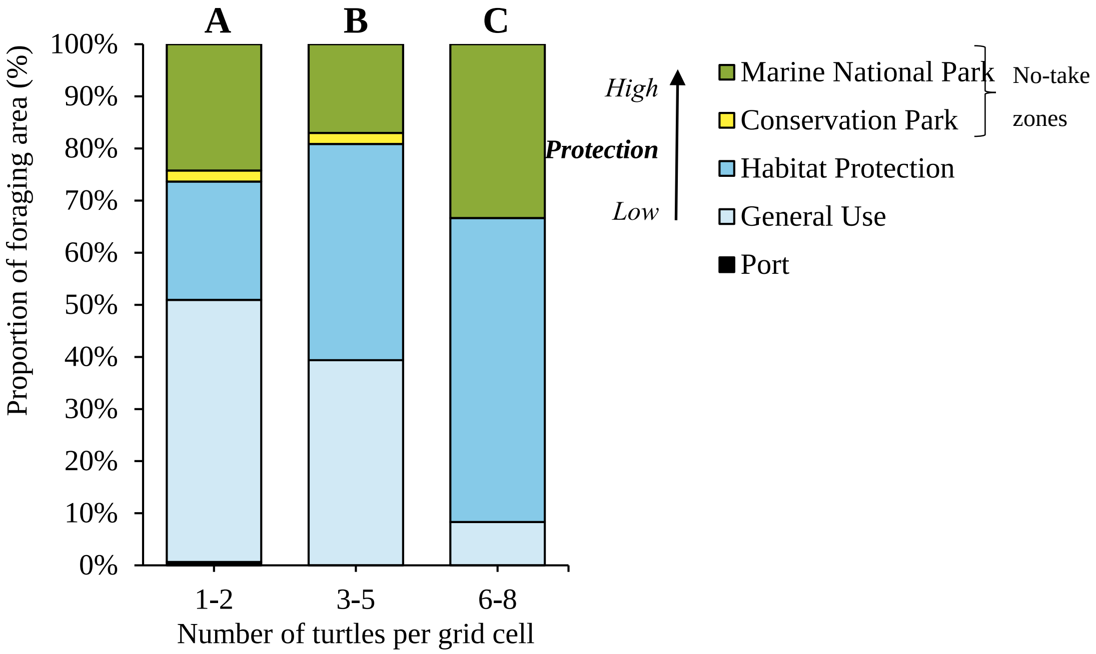


Figure 5.6. Proportion of flatback turtle foraging area used by tracked turtles distributed within different GBRMP zones. Columns represent different levels of turtle abundance: A= low abundance (1 – 2 turtles per grid cell), B= medium abundance (3 -5 turtles per grid cell) and C= high turtle abundance (6 – 8 turtles per grid cell).

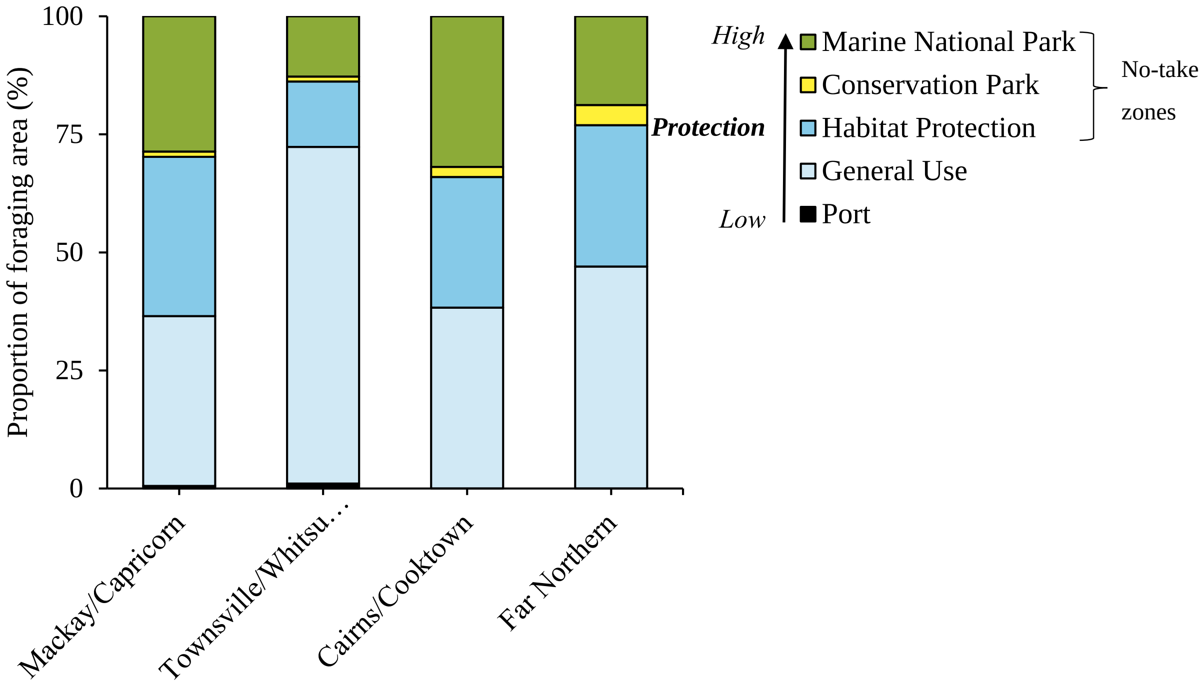


Figure 5.7. Proportion of flatback turtle foraging area within ports and different GBRMP zones. Columns represents each MA of the GBRMP, and are ordered from south (Mackay/Capricorn) to north (Far Northern).

5.3.2. Exposure to shipping

The mean shipping intensity recorded within the foraging area of the tracked turtles was low (< 275 vessels/cell). In addition, 66.3% of the foraging area in the GBRMP displayed low exposure to shipping (< 0.25) (Figure 5.8). Medium exposure (0.25 - 0.5) was recorded for several foraging sites within the Far Northern MA, Cairns/Cooktown MA off the coast from Cairns, and Townsville/Whitsunday MA (Figure 5.8). High or very high exposure levels (> 0.5) were not recorded across the foraging area. Nearly half of the foraging area exposed to shipping was located within highly protected areas, including 17.6% in Marine National Parks (the second highest level of protection in the GBRMP) (Figure 5.9).

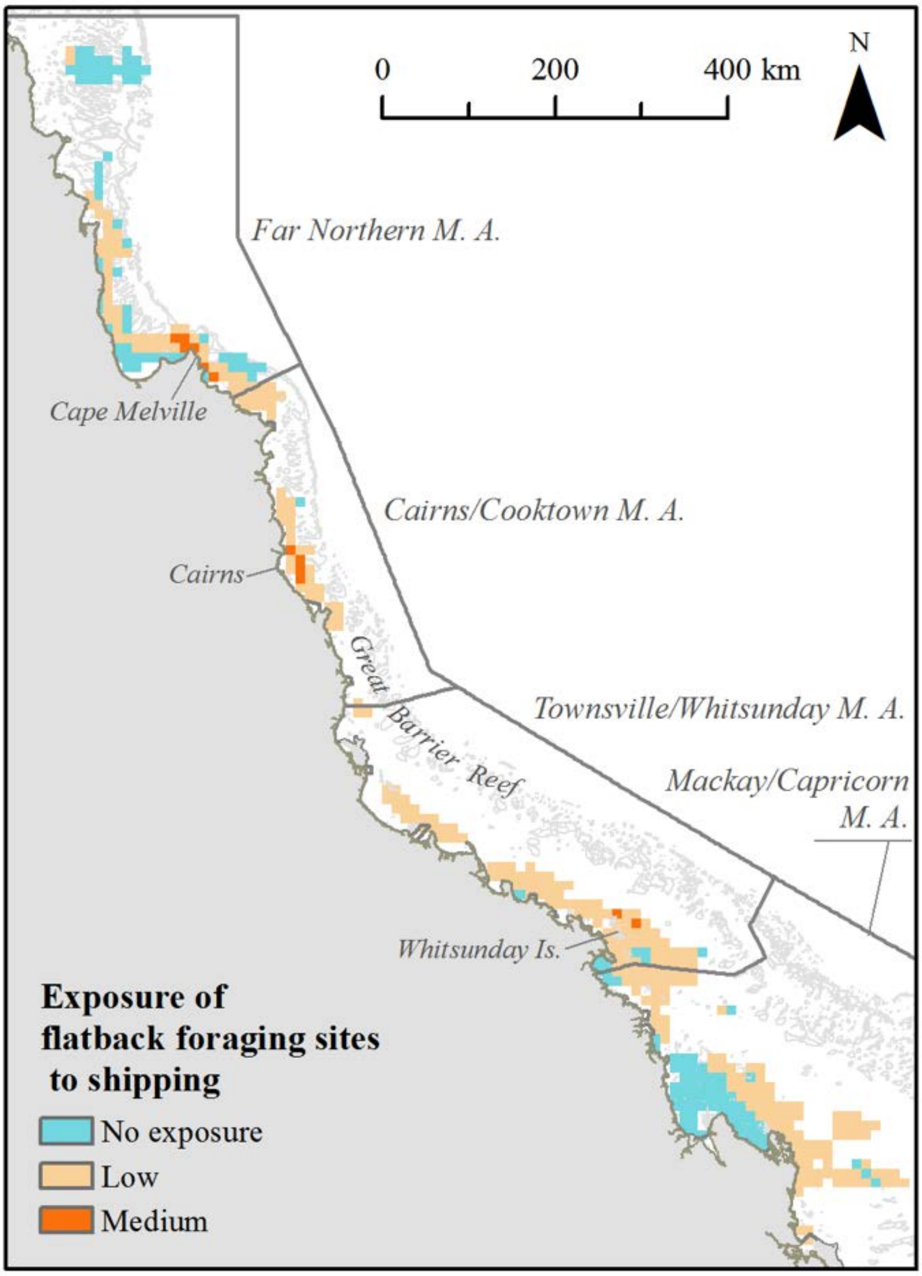


Figure 5.8. Exposure of flatback turtle foraging areas to shipping in each MA of the GBRMP.

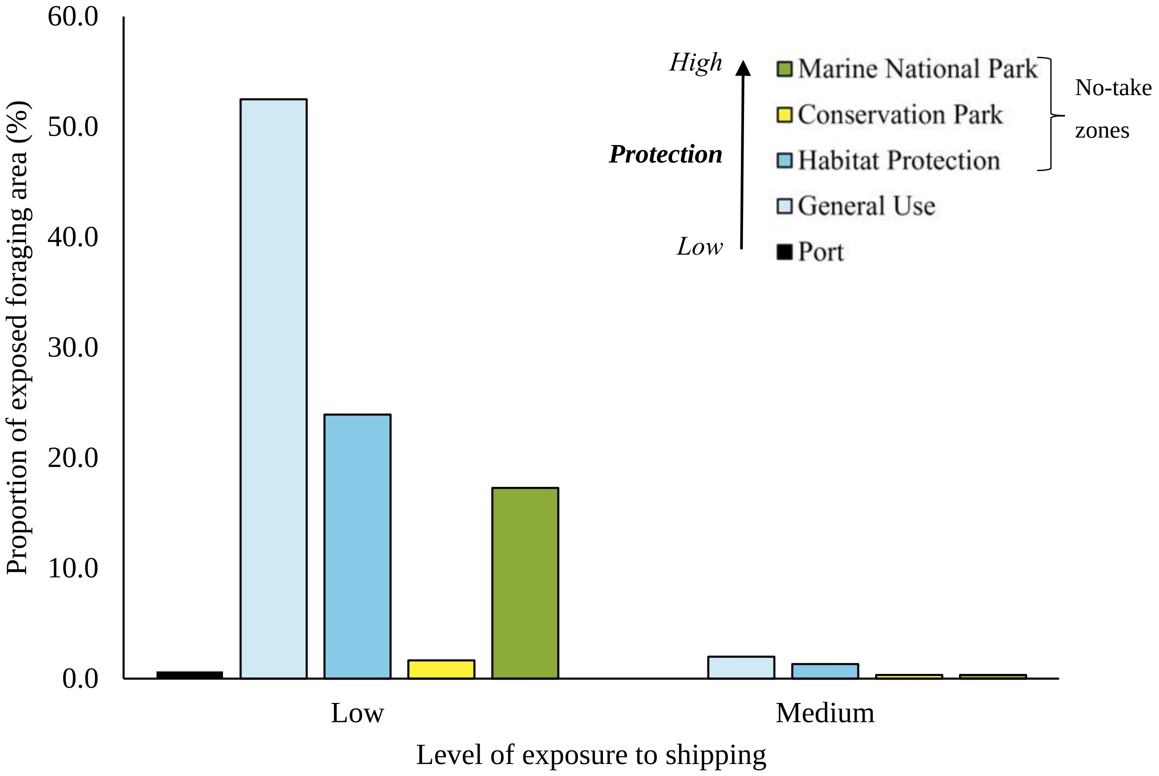


Figure 5.9. Proportion of foraging area exposed to low and medium levels of shipping. Columns represents ports or different GBRMP zones. There was no exposure to high or very high levels of exposure detected.

5.3.3. *Exposure to trawling*

Overall, 43.3% of the flatback turtle foraging area in the GBRMP displayed low exposure to trawling (< 0.25). Medium exposure (0.25 -0.5) was only recorded in a few foraging sites within the Far Northern MA, namely northwest of Princess Charlotte Bay (Figure 5.10). All foraging sites exposed to trawling are located in General Use areas, since trawling is prohibited in all other zones of the GBRMP.

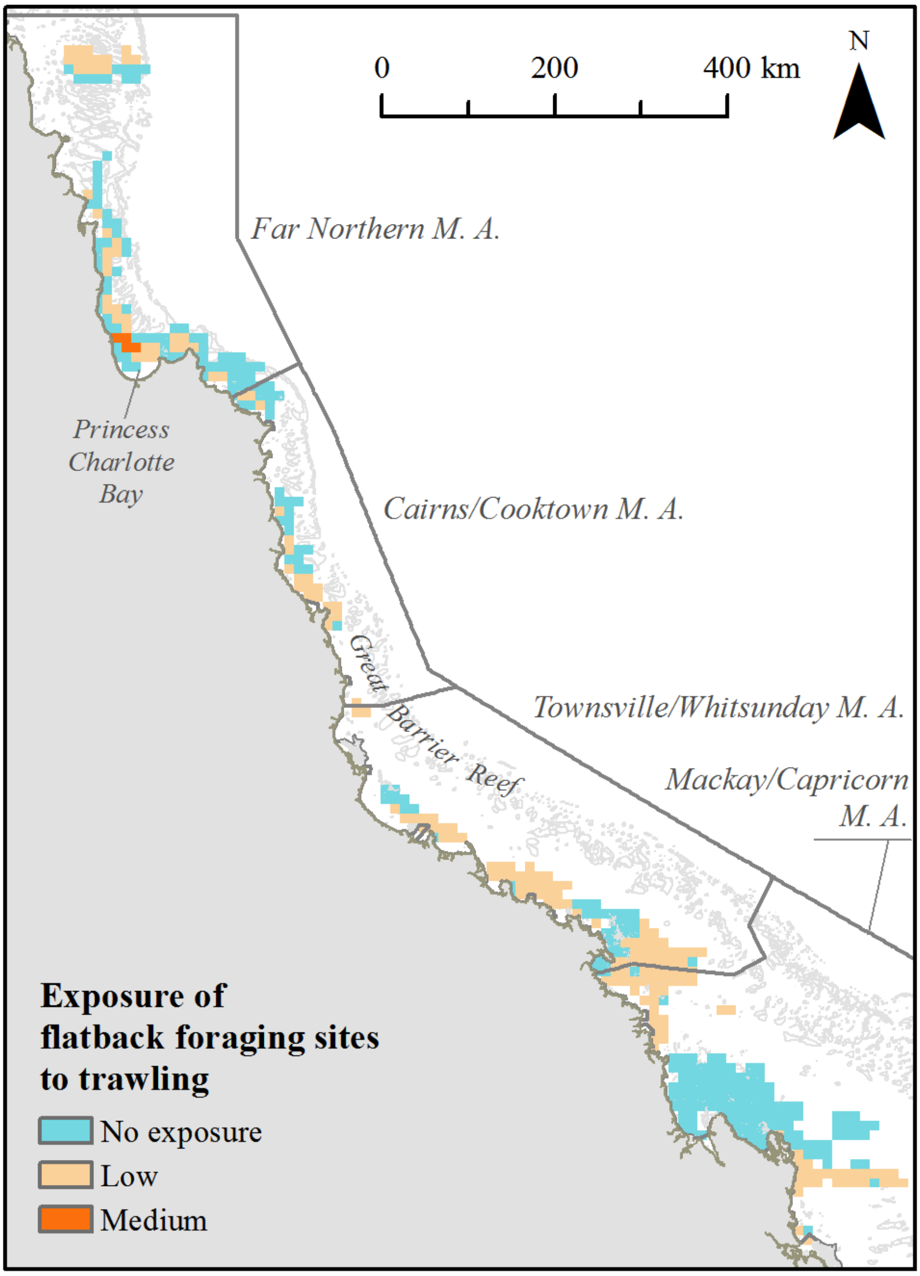


Figure 5.10. Exposure of flatback turtle foraging areas to trawling in each MA of the GBRMP.

5.3.4. Cumulative exposure to threats

Overall, cumulative exposure to shipping and trawling was evident in 76.8% of the total flatback turtle foraging area. Approximately 35% of the foraging sites within the Mackay/Capricorn and Far Northern MAs were not exposed to any threats (Figure 5.11). The Townsville/Whitsunday MA and the Cairns/Cooktown MA displayed the largest proportion of cumulative exposure, with 95.9% and 93.6%, respectively. In addition, medium levels of cumulative exposure were recorded in the two northern MAs (Cairns/Cooktown and Far Northern), off the coast east of Cape Kimberley and northwest of Cape Melville, respectively (Figure 5.12).

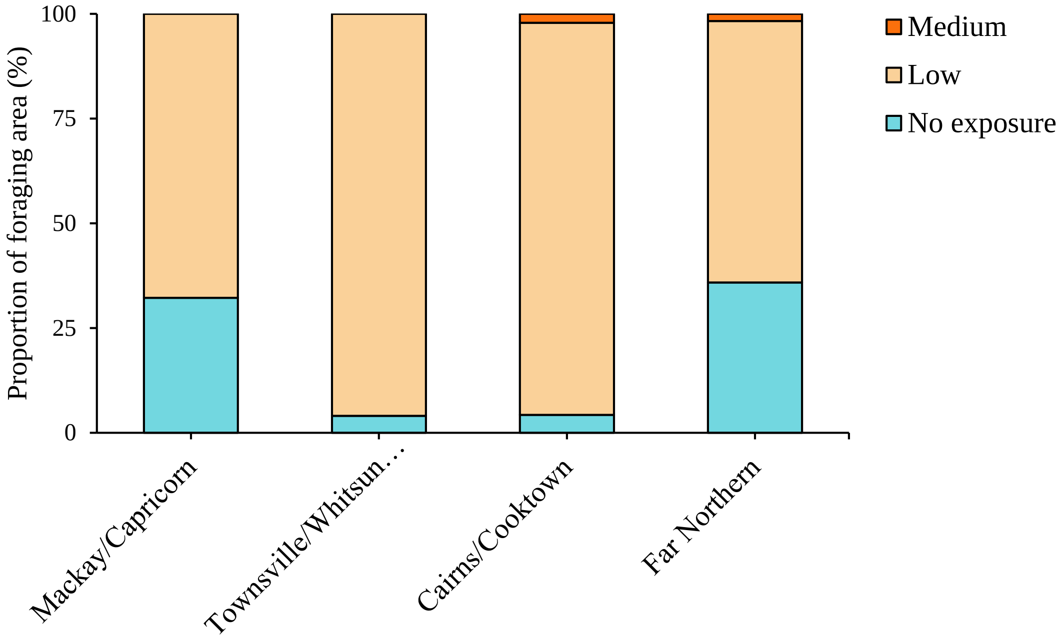


Figure 5.11. Cumulative exposure of flatback turtle foraging areas to shipping and trawling. Columns represent each MA of the GBRMP, and are ordered from south (Mackay/Capricorn) to north (Far Northern).

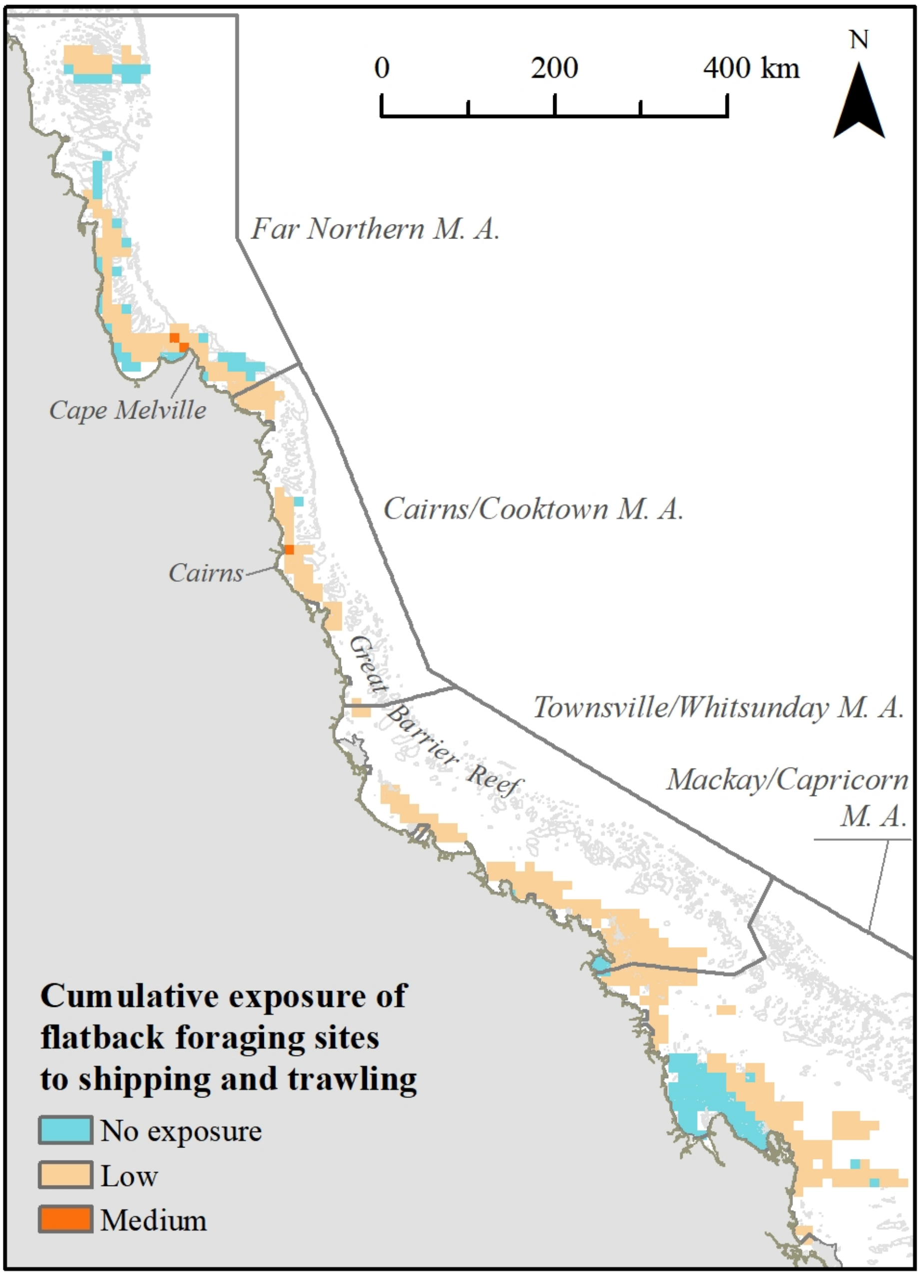


Figure 5.12. Cumulative exposure of flatback turtle foraging areas to shipping and trawling in each MA of the GBRMP.

5.4. Discussion

My study is the first to quantify the protection coverage and exposure of flatback turtle foraging habitats to specific threats in the Great Barrier Reef. Overall, more than half of the foraging area of the tracked turtles were located within a protected area. Exposure to shipping and trawling was low across the region, with some sites displaying medium exposure to the individual threats. In addition, there was medium cumulative exposure to the threats evident in several foraging sites within the northern MAs (i.e. northwest of Cape Melville in the Far Northern MA, Figure 5.12). My study suggests that the current management zoning in most cases provides an adequate level of protection to the foraging flatback turtles I tracked. Current zoning of the Mackay/Capricorn MA provides high levels of protection (Figure 5.7) and low exposure to threats (Figure 5.11) to foraging flatback turtles. However, foraging sites in the Cairns/Cooktown MA displayed both the highest protection (Figure 5.7) and the highest exposure to threats (Figure 5.11), evidencing a mismatch between protected areas and the distribution of flatback turtle foraging sites. Future steps include a more in-depth exposure analysis, including additional threats not accounted for in my thesis, such as dredging, recreational boat strike, water quality and climate change effects.

5.4.1. Protection of flatback turtle foraging habitats in the GBRMP

Current zoning of the GBRMP (GBRMPA, 2004) provides protection to 52.8% of the foraging area used by the turtles tracked in this study, with 22.9% of the foraging habitat located in a no-take protected area (highest protection levels, “Marine National Park” or “Preservation Zone”) (Figure 5.5). In 2007, GBRMPA assessed the proportion of marine turtle nesting and foraging habitats located in each of the current zones of the GBRMP and identified high priority areas for inclusion in no-take zones (Dobbs *et al.*, 2007). However, the assessment did not consider foraging habitats for flatback turtles, because information about known aggregations was absent at the time of zoning plan development. The 2007 assessment found that 20.9% of the overall foraging habitat for green, loggerhead and hawksbill turtles was located within “General Use” zones, with remaining 79.1% of the habitat located in no-take zones. In contrast, my results indicate that 46.8% of the flatback turtle foraging area is located in “General Use”, 52.7% in no-take zones and just 0.5% lies outside the Marine Park (i.e. inside ports) (Figure 5.5). While current management practices in the GBRMP seem to provide an adequate level of protection to the entire flatback turtle foraging area described in this study, I recommend that further research works to identify high priority foraging sites and perform case-by-case assessments of these sites.

The large size of flatback turtle foraging grounds and the high mobility of turtles within and between foraging grounds compared to other marine turtle species in the eastern Australia (Chapter 3) can challenge the management of the population. While the number of turtles tracked in my study is not sufficient to draw conclusions on the density of turtles in foraging grounds, it does provide a proxy of areas that are likely to be important for foraging flatback turtles, especially sites used by multiple turtles during my study. This assumption is supported by the fact that several of the areas used by the tracked turtles coincide with long-term historical in-water records of the species ((Limpus, 2007), Chapter 3). From the data obtained in this study, I derived at least three important flatback turtle aggregation areas to be considered in future management assessments

(Figures 3.6, 5.12): (a) the Broad Sound area in the Mackay/Capricorn MA, including Broad Sound, Broad Sound channel, Shoalwater bay, and particularly off the coast of Townshead Island; (b) the southern extent of the Whitsunday region in the Townsville/Whitsunday MA, in particular the channels north and west of the Lindeman Group; (c) off the coast of Cape Melville in the Far Northern MA, between the Fairway Channel and Bewick Island.

5.4.2. Exposure of foraging flatback turtles to threats in the Great Barrier Reef

Extended efforts have been carried out at national and regional levels to identify the vulnerability and risk of marine turtles in Australia. I considered two of the threats (trawling and shipping) identified to affect marine turtles in the latest Recovery Plan for marine turtles in Australia (Commonwealth of Australia, 2017). While exposure does not necessarily imply direct threat, quantifying it is the first step in assessing the vulnerability and risk of a species (Fuentes *et al.*, 2011). Based on my results, the exposure of foraging flatback turtles to both shipping or trawling was low over most of the GBRMP, with some specific sites displaying medium exposure (Figures 5.8, 5.10). Based on the Marine Turtle Recovery Plan (Commonwealth of Australia, 2017), shipping poses a low risk and trawling (in terms of habitat degradation) a medium risk to the eastern Australia flatback turtle population (which mostly forages within the GBR). However, the risk from trawling has been assessed from the perspective of bycatch, which is now managed through turtle excluder devices, and less is known about the impact of trawling on the status and condition benthic fauna and habitats.

Trawl fisheries can have a detrimental effect on the biodiversity of benthic habitat if not managed properly. The most-trawled bioregion in the GBRMP are non-reef areas (Grech & Coles, 2011), which also happen to be the typical habitats of flatback turtles ((Limpus, 2007), Chapter 4). Fortunately, multiple management practices ranging from the compulsory use of turtle excluder devices (TEDs), effort reduction (spatial and temporal) to buy-back of licenses, have been implemented in the GBRMP since 1999. As a result, prawn trawling in the GBRMP has improved towards an environmentally sustainable fishery. The status of many stocks of benthic sessile fauna has improved considerably, reversing previously recorded, unsustainable trends. Highly relevant to foraging flatback turtles, who appear to forage on a wide diversity of benthic species ((Limpus, 2007), Chapter 4), is the proportion of seabed trawled and the recovery times of sessile and mobile species. The impact rate of the GBR prawn trawl fishery on the seabed has been estimated between 5 and 25% per trawl (Pitcher *et al.*, 2016), and by 2009 less than half of the area was trawled more than once (Grech & Coles, 2011).

Nevertheless, trawling can have an effect on the immediate quantity and quality of prey available. Recovery times have been estimated to range between several years to decades for sessile species in the GBR (Pitcher *et al.*, 2016), and six months to several years for mobile species in the Gulf of Carpentaria in northern Australia (Haywood *et al.*, 2008). Flatback turtles seem to be highly mobile both within a foraging ground and between foraging grounds (Chapter 3), which could mitigate the impact of foraging in trawled habitats. Conversely, the behaviour observed in the tracked turtles could also be interpreted as a response to trawling, by shifting away from a recently trawled area. Thus, the current trawling practices are likely to have a low impact on flatback turtles.

There are multiple effects of recreational and commercial shipping on marine turtles such as disturbance (i.e. collision, noise) and habitat degradation (i.e. physical damage and/or changes in habitat quality) (Commonwealth of Australia, 2017) and noise pollution. Vessel disturbance/collision is an important concern for marine megafauna in shallow waters (Commonwealth of Australia, 2017; Grech & Marsh, 2008; Shimada *et al.*, 2017). As a strategy to minimise the impact of vessel disturbance on marine turtles and dugongs, the Queensland Government has designated “Go Slow Zones” in some highly transited areas of the Marine Park with known turtle and dugong habitat, with the aim of reducing vessel speed and eliminating high-speed motorised sport (Biddle & Limpus, 2011; DERM, 2008). The risk of vessel strike to the eastern Australia flatback turtle population is considered to be low, given that flatback turtles do not commonly inhabit shallow coastal habitats (Commonwealth of Australia, 2017), however the degree to which flatback turtles, and other species of marine turtles, are possibly affected by noise pollution is not known and warrants further research attention.

Flatback turtle foraging habitats are mostly located in deeper waters ((Limpus, 2007), Chapter 3), where the likelihood of interacting with large shipping vessels is very low, but the proximity to major shipping lanes increases their exposure to chronic (continuous) levels of noise, pollutants and marine debris (Commonwealth of Australia, 2017; Critchell *et al.*, 2015; Kroon *et al.*, 2015)). These threats are of special concern in the northern half of the GBRMP, in which the designated shipping lane is constrained to a narrow, near-coast channel (Figure 5.3) overlapping with most of the flatback turtle foraging sites (Figure 5.8). In addition, shipping is predicted to increase in terms of traffic and vessel size in the next 15 years (reviewed in Kroon *et al* 2015), which will undoubtedly increase the exposure of turtles and other marine fauna to the combined impacts of shipping. For the eAus flatback turtle population, understanding the risk of chronic noise interference and the risk of marine debris ingestion and chronic chemical discharge are considered to be important knowledge gaps and avenues for future research. (Commonwealth of Australia, 2017).

5.4.3. Cumulative exposure to threats

The cumulative and synergetic impact of human-related activities to marine turtles has been identified as one of the highest concerns for their survival in the GBRMP (GBRMPA, 2014a). In this study, the cumulative exposure of foraging flatback turtles to shipping and trawling was found to be low to medium across the GBRMP. However, foraging sites exposed to medium levels of combined threats were located in the Far Northern MA (i.e. northwest of Cape Melville) and the Cairns/Cooktown MA (i.e. east of Cape Kimberley) (Figure 5.12). Moreover, these same sites were located mostly in areas of lower protection (i.e. General Use zones) (Figure 5.13), potentially increasing the exposure of the turtles to combined pressures.

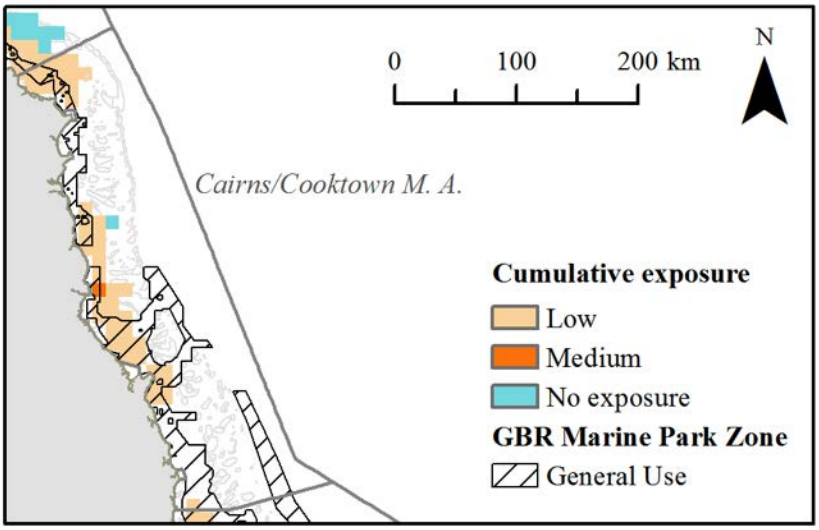


Figure 5.13. Overlap between General Use zones and flatback turtle foraging areas exposed to shipping and trawling in the Cairns/Cooktown MA.

For flatback turtles, the cumulative impact derived from coastal development (i.e. dredging), declining water quality and climate change are of particular high concern (GBRMPA, 2014a). These threats are all likely to affect the sediment, nutrient and/or pollutant composition and concentration in foraging habitats and thus the availability and nutritional quality of potential prey. The magnitude of the effects is also highly variable across the GBRMP, highlighting the importance of developing local assessments and management plans. Water quality studies have shown that decreased water quality is more likely to occur near major rivers and after major weather events, with particular high exposure areas between the Whitsundays and Mackay and further south in the Broad Sound area. However, water quality considerably increases in the northern regions of the GBR (Devlin *et al.*, 2010). Similarly, a qualitative assessment of the risk of emerging contaminants to the GBR revealed that there is a medium risk of pollutants (i.e. PCPs and chronic exposure to antifouling paints) in the southern two-thirds of the region, as well as a high risk of plastic and micro-plastic debris, especially in the northern MAs (Kroon *et al.*, 2015). Impacts resulting from climate change are probably the most difficult to assess and manage due to the high variability and uncertainty of the potential effects. Nevertheless, undertaking a cumulative exposure analysis including spatial layers of the best available data could greatly enhance future vulnerability assessments of the species in the GBRMP (Grech & Marsh, 2008). In addition, further studies should aim to account for the relative impact of each threat as well as the synergistic effect of combined threats. The exposure analysis would be greatly improved by considering the vulnerability of the species to different threats. Some approaches used in previous studies have estimated vulnerability through expert elicitation (Fuentes & Cinner, 2010) or literature reviews (Maxwell *et al.*, 2013). While it can be challenging to measure the absolute impact of threats and mortality rates *in situ*, qualitative methods such as surveys based on expert opinion and pair-wise comparisons have been proven to be informative and applicable to estimate the relative impact of threats in vulnerability and risk assessments (Fuentes & Cinner, 2010; Grech *et al.*, 2011)

5.5. Conclusion

In this chapter, I provide a quantitative assessment on the protection and exposure of flatback turtle foraging habitats in the GBRMP. I conclude that the current zoning of the GBRMP provides adequate protection to the majority of the foraging area used by the tracked turtles (Figure 5.5). In addition, foraging flatback turtles are mostly exposed to low levels of shipping or trawling (Figures 5.8, 5.10). However, there was evidence of medium cumulative exposure in some restricted sites in the Far Northern MA and Cairns/Cooktown MA (Figure 5.12). It is also worth emphasising that while some foraging sites in the Cairns/Cooktown MA were highly protected, others displayed medium cumulative exposure levels (Figure 5.13). The outputs of this chapter are targeted to address gaps in the management of foraging flatback turtles in the GBRMP. The methods can be easily updated to include new data and additional spatial layers of other threats. In particular, I suggest to include water quality and marine debris spatial layers, since qualitative comparisons with published data suggest these threats could constitute an important input in the cumulative exposure analysis.

Chapter 6

General Discussion

Image of a nesting flatback turtle returning to sea at Curtis Island in November 2015.

Photo credits: Natalie Wildermann

6.1 Foraging ecology of marine turtles in the Great Barrier Reef

The management of large and complex ecosystems, such as the Great Barrier Reef (GBR), requires extensive knowledge on the environmental, cultural, social and economic dimensions and how they interact. Evidence of the distribution and population trends of four species of marine turtles that live and breed in the GBR was one of the key features considered by the United Nations when it listed the GBR as a World Heritage Area. Likewise, such trends were also considered when the GBR Marine Park (GBRMP) zoning plan was revised to accommodate the GBR as a multi-use marine park (Dryden *et al.*, 2008). Most of the knowledge on marine turtles used to inform management action in the GBR has focused on the hatchling, nesting and inter-nesting stages. Turtles are particularly vulnerable to human impacts during these stages, since they occur in beaches and near-shore coastal environments where the incidence and intensity of human activities is highest. However, less is known about the foraging ecology, growth, health and condition of non-nesting turtles within the GBR.

In the 1980s research on foraging green, loggerhead and hawksbill turtles in eastern Australia began. Most research was focused on green turtles, because they forage along the near-shore coastline and within human-accessible shallow water seagrass habitats. Green turtles typically forage in a variety of tidal and sub-tidal habitats, from seagrass meadows and reefs to sand and mud flats in a lesser extent (Limpus, 2008a). The list of in-water studies is extensive (see compilation in Limpus 2013) and includes research on the demography (i.e. Chaloupka and Limpus (2005); Limpus *et al.* (2005)), habitat use (i.e. Hazel *et al.* (2012); Shimada *et al.* (2017)), genetics (i.e. FitzSimmons *et al.* (1997a); FitzSimmons *et al.* (1997b), endocrinology (i.e. Hamann *et al.* (2003)), behaviour and navigation (i.e. Shimada *et al.* (2016b); Shimada *et al.* (2016c)), and diet (i.e. Arthur *et al.* (2008); Arthur *et al.* (2009)) of green turtles.

In-water ecology of hawksbill turtles in eastern Australia is also well documented. Hawksbill turtles are largely associated to coral and rocky reefs, and in low density to open seagrass meadows (Limpus, 2009b). Long-term monitoring and research of the species has provided comprehensive knowledge on the demography of the foraging aggregations in eastern Australia, as well as revealed strong fidelity to the coastal foraging grounds (Bell & Pike, 2012; Bell *et al.*, 2012; Chaloupka & Limpus, 1997; Limpus *et al.*, 2008). A study on the diet of hawksbill turtles revealed that turtles in a reef in the northern GBR fed predominantly on red algae, followed by soft corals, green algae, sponges, other small invertebrates and brown algae (Bell, 2013).

As for loggerhead turtles, coastal foraging habitats in eastern Australia are described as tidal and subtidal habitats ranging from reefs and seagrass meadows, to soft-bottom habitats (Limpus, 2008b). A significant portion of their foraging grounds are located within Marine Parks (Limpus, 2008b). In addition, these populations have been reported to feed (Limpus *et al.*, 2013b) mainly on benthic molluscs, but their diet can include species from over 100 different taxa Limpus *et al.*, 2013a). Long-term monitoring has provided valuable information on the recruitment, residency and demography of the species in Australian coastal waters (Limpus *et al.*, 2013b). The foraging populations are consistently structured by large immature and adult turtles, and are strongly biased to male turtles (Limpus *et al.*, 1994).

Although less is known about the in-water ecology of flatback turtles in eastern Australia compared to the other species in the region, the first records of in-water flatback turtles date back to 1967 (Williams *et al.*, 1967). The extensive in-water studies that have been undertaken in the eastern Queensland coast since the 1980's in coral reefs and cays, inshore rocky reefs, seagrass meadows, mangroves and inshore bays, have produced very limited records of flatback turtles and numerous records of green, hawksbill and loggerhead turtles. In contrast, most flatback turtle records have been derived from trawling data (Robins, 1995; Robins, 2002), and limited data from direct observation (EHP Queensland Turtle Research database) and tag recovery data (Limpus *et al.*, 2013a; Limpus, 2007). In the following section I describe in detail the current state of knowledge on foraging ecology of flatback turtles, including the results from this dissertation.

6.2 Flatbacks at sea: updated state of knowledge on the in-water ecology of the species.

In this section I summarise the findings of my thesis in relation to former gaps in foraging ecology of the eAus stock, building upon the review on the current state of knowledge on in-water ecology of flatback turtles in Australia described in section 1.3 of the General Introduction. Despite the long-term in-water records of flatback turtles of the eAus stock, fine-scale information on the distribution and ecology of foraging turtles was poorly known. My study provides novel information, not only on the spatial distribution of foraging turtles of the eAus stock, but also in the early dispersal of post-hatchlings, potential environmental associations between post-nesting adults and their habitats, and insights on the exposure to threats of foraging eAus flatback turtles. The availability of high resolution local oceanographic models and a very comprehensive database of the environmental features of the GBR, enabled me to employ novel approaches to understand the in-water ecology of the turtles, such as testing dispersal scenarios (Chapter 2) and examining foraging grounds in relation to biological and physical drivers (Chapter 4). Such approaches could not have been performed for the other genetic stocks, because of the limited high-resolution environmental and oceanographic data.

Some mechanisms that potentially drive the neritic dispersal of flatback turtle post-hatchlings are described in Chapter 2, and summarised in the forthcoming section “Further contributions to marine turtle ecology”. A recent study tracked reared flatback turtle post-hatchlings with solar-powered satellite tags (Wyneken *et al.*, unpublished data). In terms of the distribution of post-hatchlings, based on my simulations I suggest that the region between the Whitsunday Islands and Broad Sound is likely to be of importance for the dispersal and development of early life-stages of flatback turtles. In addition, simulated pathways of post-hatchling dispersal also coincide with the observed tracks of adult turtles (Figure 2.3 in Chapter 2), which could suggest a potential imprint of migration routes and/or foraging sites during the early developmental stages (Hays *et al.*, 2014; Scott *et al.*, 2014; Shillinger & Bailey, 2015).

The distribution of historic (long-term) and current (from this study, Chapters 3-5) foraging sites of eAus flatback turtles is shown in Figure 6.1. The two datasets coincide in most of the foraging extent, with some previous spatial gaps now filled as a result of the high-resolution tracking data. These former gaps in information are likely to be related to the absence of records in areas where trawling has been long prohibited, such as the Whitsunday Islands and Shoalwater Bay. Based on the current distribution of the tracked turtles (Chapter 3) and the exposure to threats in each region (Chapter 5), I identified three foraging hotspots for the tracked turtles in the GBRMP (Figures 3.6, 5.12): (a) north/north-west of Cape Melville in the Far Northern MA, (b) north of the Lindeman Group in the Townsville/Whitsunday MA and (c) Broad Sound region in the Mackay/Capricorn MA. There are also other important flatback turtle aggregations off the coast from Cairns in the Cairns/Cooktown MA and off the coast from Townsville and north of Upstart Bay in the Townsville/Whitsunday MA. These foraging sites were categorised mostly as transient foraging sites, used by turtles for less than 30 days at a time. Other smaller but stable foraging aggregations have been recorded in the southern region of Queensland (i.e. Hervey Bay and Moreton Bay) (Colin Limpus, pers.com) outside the boundaries of the GBRMP. The extent to which these aggregations are protected and exposed to local threats still needs to be assessed.

Home range sizes of turtles in eAus were the smallest among those reported for the species in western and northern Australia (Table 6.1). While some of this variability could have been derived from using different analysis methods, it might also be related to differences in the foraging ecology of turtles (e.g. different types of prey) and/or environmental domain (e.g. bathymetry) of each region. Flexible foraging behaviour (Whittock *et al.*, 2016) was also evidenced for the eAus stock. A detailed description of the different behavioural patterns displayed by migrating and foraging turtles can be found in Chapter 3. The flexible foraging behaviour of the tracked turtles is likely to be driven by the abundance and distribution of potential prey. Most flatback turtles seem to have a greater affinity to muddy habitats (Limpus (2007), Chapter 4); however, some turtles tracked in this study also displayed a greater affinity to habitats with lower mud concentration. Confirmed prey items of adult turtles include a variety of soft-bodied benthic invertebrates (Limpus, 2007; Zangerl *et al.*, 1988); nevertheless, based on the results of Chapter 4, the range of potential prey is likely to include other invertebrates such as sponges, ascidians, bivalves and echinoderms. Strategies such as foraging over large spatial extents, developing flexible foraging behaviours and the potential foraging specialisation of some individuals are evidence of the plasticity of flatback turtle behaviour, which could enhance the adaptive capacity of the species to acute and chronic changes in the environment.

Table 6.1. Reported average size of home ranges and core areas of foraging flatback turtles from three different stocks.

Stock	***Home range (km^2)***	***Core area (km^2)***	***Reference***
Pilbara (Pb)	2502 ± 5078	515 ± 1172	Whittock *et al.* (2016)
Arafura Sea (ArS)	11724 ± 9756	2334 ± 1410	Hamann *et al.* (2015)
Eastern Queensland (eAus)	455 ± 359	68 ± 64	This study, chapter 3

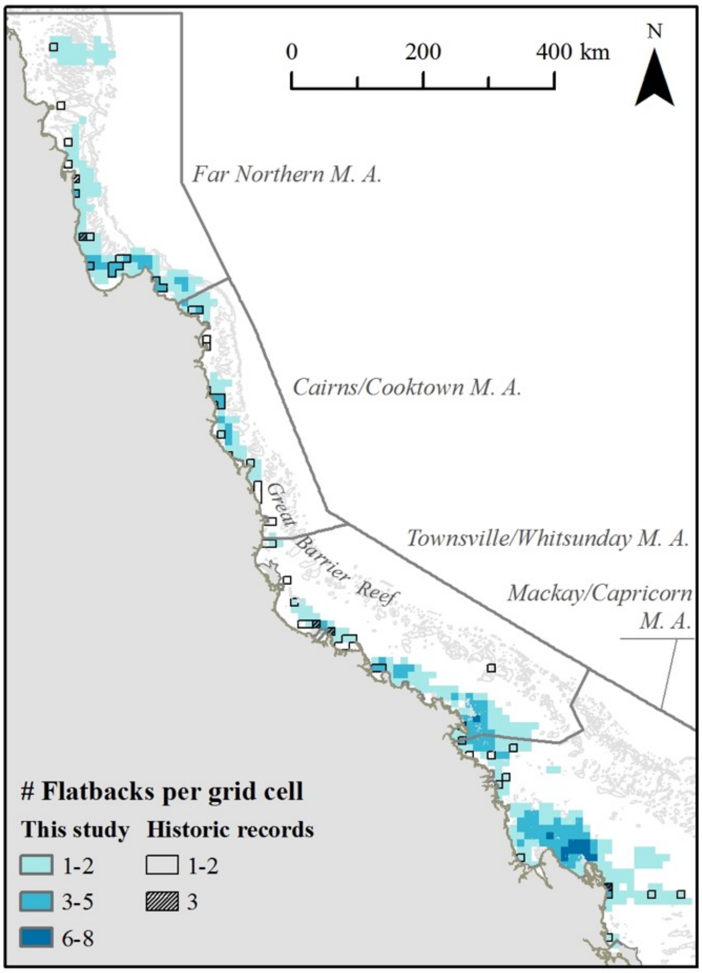


Figure 6.1. Comparison of the spatial distribution of flatback turtles tracked in this study (blue) and historic long-term in-water records (orange) (EHP Queensland Turtle Research database).

Lastly, the eAus stock has been identified as a discrete genetic stock with very limited connectivity with the neighbouring ArS stock (FitzSimmons & Limpus, 2014; Pittard, 2010). This means that, under unlikely extreme scenarios, the population could face local extinctions if external pressures deplete the stock. Most of the eAus flatback turtle nesting stock shows long-term stable demographic trends except for Peak Island (one of two major rookeries) and Curtis Island (one of the minor rookeries) in which declining number of nesting turtles have been recorded in the last decades; the causes of declines are still unknown (Limpus, 2007). The GBRMP provides an adequate level of protection to most tracked flatback turtle foraging grounds in eastern Australia. The exposure of flatback turtle foraging habitats to shipping and trawling in the region is low. However, there was evidence of medium cumulative exposure to these threats in some restricted sites in the Far Northern MA and Cairns/Cooktown MA (Figure 5.11-5.12).

6.3 Further contributions from this thesis to marine turtle ecology

6.3.1. Dispersal of marine turtle post-hatchlings

All life-stages of flatback turtles co-occur in neritic waters of the Australian Continental Shelf, unlike all other species of marine turtles, which for at least part of their life occur in oceanic waters. Understanding the drivers of these different development strategies requires in-depth knowledge of the physical forces that can influence the dispersal of hatchlings, as well as their swimming behaviour. It has been increasingly accepted and tested that marine turtle hatchlings need to engage in at least some amount of swimming throughout the first years at sea to reach favourable areas for their development (Bolten, 2003b; Briscoe *et al.*, 2016; Putman & Mansfield, 2015). Based on advection-diffusion simulations (Chapter 2), the neritic dispersal and distribution of flatback turtle post-hatchlings from the eAus stock are likely to be influenced by three factors: (a) the inshore location of the nesting beaches, (b) the local water circulation of the nesting region and (c) the directional swimming behaviour of the post-hatchlings. Direction in which simulated post-hatchlings were swimming resulted as one of the most influential parameters that favour the retention of turtles in neritic waters of the GBR.

6.3.2. Migratory and foraging movement patterns

Improvement in the resolution of satellite-derived locations and statistical analysis has facilitated the study of fine-scale animal movements in the marine environment (Bestley *et al.*, 2013; Bestley *et al.*, 2015; Dragon *et al.*, 2010; Fossette *et al.*, 2010; Gaspar *et al.*, 2006; Gurarie *et al.*, 2016). Flexible migratory and foraging strategies seem to be a common pattern for the eAus (this study) and Pb (Whittock *et al.*, 2016) stocks. To the best of my knowledge, such behavioural patterns are unusual in other Cheloniid species. I provide a description of the patterns observed in flatback turtles, which can be used as a guideline to identify variations in behaviour that could potentially be displayed by other marine turtle species throughout the world.

6.4. Informing management of flatback turtles in the GBRMP.

The 2014 Vulnerability Assessment developed by the GBR Marine Park Authority and the 2017 Recovery Plan for Marine Turtles in Australia developed by the Australian Government focused on identifying the vulnerability (VA) and risk (RP) of marine turtles to threats. The recovery plan also identifies priority actions to undertake during the next 10 years (2017 - 2027). Both documents identify key nesting and interesting habitats, and highlight the need of improving the state of knowledge of migratory, foraging and breeding areas. This is of particular importance for flatback, olive ridley and hawksbill turtles, for which very limited information on key foraging habitats is known (VA and RP). I have been able to provide copies of my data, shapefiles and written work to the GBR Marine Park Authority and the Australian Government. My thesis results substantially improved the knowledge base on the spatial distribution of flatback turtles in the GBR World Heritage Area (Chapters 3-5), particularly on potential habitats for post-hatchling dispersal and identified important habitats for adult foraging and my data have informed the revised Marine Turtle Recovery Plan. Thus, my thesis is relevant to several priority action areas required to maintain/recover the eastern Australia flatback turtle stock, namely Action Area A1 ("Maintain and improve efficacy of legal and management protection"), Action Area B2 ("Understand population demographics at key foraging grounds") and Action Area B3 ("Address information gaps to better facilitate the recovery of marine turtle stocks").

6.5. Thesis findings by objectives

As mentioned before, prior to my thesis, limited information was available on the ecological biogeography of foraging flatback turtles in eastern Australia. Consequently, the aim of my thesis was to improve our understanding of flatback turtle biogeography and ecology across different life-stages, with the intention being to generate scientific information to improve the state of knowledge of the species and provide relevant outputs to inform management actions for conservation of the species in the GBRMP.

Objective 1: Improve the understanding of the mechanisms that drive the neritic dispersal of flatback post-hatchlings.

This objective targeted the long-lasting question of why flatback turtle post-hatchlings are the only species of marine turtles without an oceanic dispersal. I addressed this objective in Chapter 2, by using a hydrodynamic advection-diffusion model (called SLIM) to simulate the dispersal of virtual post-hatchlings under different scenarios. The outputs of my simulations were qualitatively validated by comparing them to the long-term in-water records of post-hatchlings in Queensland. I developed different hypothesis to test the factors that could influence the neritic dispersal of the species, with a special focus on the effect of the turtles' swimming behaviour. My simulations suggest that there are three main factors that favoured the retention of flatback turtle post-hatchlings under the conditions I tested, namely (a) the location of the nesting beaches: flatback turtles nest in inshore islands and mainland of eastern Queensland, compared to green and loggerheads which nest on the outer reef cays and islands of the GBR; (b) the local oceanography: local currents, wind-driven waves and the tidal phase all influence the dispersal of flatback turtle post-hatchlings; and (c) swimming behaviour of post-hatchlings: this parameters produced the greatest change in the dispersal of post-hatchlings, with higher swimming effort leading turtles to successfully disperse into neritic habitats of the GBR.

Objective 2: Improve the knowledge of the spatial ecology of foraging flatback turtles in eastern Australia.

I focused on three different aspects of spatial ecology to comprehensively target this objective: movement behaviour of individual turtles (n =44), spatial distribution of flatback turtle foraging aggregations and environmental drivers of distribution. The first two components were covered in Chapter 3, and the latter in Chapter 4.

Understanding fine-scale patterns of animal movement relies on the capacity to accurately record the position of individuals at high spatial and temporal resolution. Argos-linked Fastloc GPS (FGPS) provide accurate estimates of the animal's position, and these estimates can be further refined by employing filtering methods that retain only positions which are biologically sensitive (Shimada *et al.*, 2012). I tracked 44 flatback turtles with FGPS tags between their nesting beach and foraging habitat between 2009 and 2016.

The first step of the analysis consisted of describing the migratory and foraging patterns of flatback turtles (Chapter 3). To do this, I used Behavioural Point Change Analysis (Gurarie *et al.*, 2009) and objectively classified each turtle's movement as travelling or foraging. This enabled me to visually assess the different patterns displayed by the turtles. I identified two migratory patterns: (a) direct migration: which is the common pattern described in the literature for other marine turtle species, and is characterised by a single travelling movement from the nesting beach to a foraging ground, and (b) the multi-stop migration: which has not been commonly reported for other marine turtle species, and consisted in migrations with one or more stops of variable lengths before arriving to a main foraging ground. In addition, I identified four foraging patterns: turtles that used one main foraging ground and (a) stayed in that area for all the tracking period (single area-fixed) or (b) undertook wandering loops always returning to its original foraging ground (single area-wandering); and turtles that used more than one foraging ground and (c) alternated between two or more well defined areas (multiple area-recurring) or (d) moved consecutively from one foraging ground to the next with no returns (multiple area-shifting).

Next, I identified and described key foraging habitats of flatback turtles in eastern Australia (Chapter 3). The total foraging area of the turtles I tracked was distributed along ~1600 km of the region. Foraging grounds were identified in each of the Management Areas (MA) of the GBRMP, with key aggregations around Cape Melville in the Far Northern MA, around the southern island of the Whitsunday region in the Townsville/Whitsunday MA, and in the Broad Sound region in the Mackay/Capricorn MA (Figure 3.6). In addition, the average size of foraging home ranges (455.5 ± 359.7 km^2) was larger than those reported for other marine turtle species in coastal habitats of eastern Queensland.

Finally, I assessed potential environmental drivers of the distribution of foraging flatback turtles in the GBR (Chapter 4). I associated the presence of turtles relative to an array of previously available environmental data for benthic seabed habitats of the GBR, gathered during the GBR Seabed Biodiversity Project (Pitcher *et al.*, 2007). To achieve this, I used a Random Forest analysis to assess the response of turtles to biological (biomass of 29 potential prey groups) and physical (25 abiotic variables) predictors. The results suggest that flatback turtles in the GBR might be associated with a broader range of invertebrates than previously reported, extending the range to include brittle stars, crinoids, zoanthids and bryozoans. These findings, combined with the plasticity observed in foraging behaviour (Chapter 3) suggest that the population displays traits consistent with generalist and opportunistic species. However, my results also suggest that there might be some degree of niche partitioning among individuals. It is important to note, that the results of this chapter should be considered carefully as they provide insights into *potential* associations; further in-depth analysis on the diet of flatback turtles should be undertaken to refine the understanding of their foraging ecology and diet preference.

Objective 3: Quantify the exposure to different threats and the level of protection of flatback turtle foraging habitats in the GBRMP.

To address this objective, I investigated the degree of overlap between the identified flatback turtle foraging area (Chapter 3) and two potential threats (Chapter 5): shipping and trawling. Multiple threats have been identified by the GBR Marine Park Authority as posing pressure on marine turtles' foraging habitats (GBRMPA, 2014a). I selected shipping and trawling because they are recognised as pressures to flatback turtles and their data was available, accessible, and could be readily represented in spatial layers. The results indicate that the exposure of flatback turtles to each individual threat is low across the entire GBRMP. However, some foraging sites in the Far Northern region of the GBRMP depicted medium levels of individual and cumulative exposure. I highlight the need to perform further assessments of cumulative exposure, including spatial information on other threats, particularly the distribution of marine debris and pollutants, as well as a better understanding of synergies and relative impact of the potential threats.

6.6. Directions for future research

While my study provides a comprehensive baseline on the distribution and some ecological traits of flatback turtle s at sea, there are further gaps that need to be addressed to gain a better understanding of the status, vulnerability and adaptive capacity of flatback turtles of the eAus stock. A selection of these gaps and proposed methods to address them are described below.

6.6.1. Navigational cues for post-hatchling swimming behaviour

Modelling the dispersal of young turtles has been commonly used to understand the ecology of marine turtles during the first years at sea (also known as "lost years"). To generate accurate simulations, such models need to be complemented with empirical observations on the behaviour of the animals (Wolanski, 2016; Wolanski & Kingsford, 2014). For flatback turtles, several experimental studies have measured the swimming capacity and behaviour of hatchlings during the frenzy and post-frenzy stages (Chevron-Australia, 2010; Hamann *et al.*, 2011; Pereira *et al.*, 2011, 2012; Salmon *et al.*, 2010; Salmon *et al.*, 2009; Thums *et al.*, 2013; Wyneken *et al.*, 2008; Wyneken *et al.*, 2010), but traits such as the navigational orientation of post-hatchlings at sea, travelling speeds and the amount of effort turtles invest in swimming are still unknown. Based on the sensitivity analysis developed in Chapter 2, swimming traits such as orientation and speed of post-hatchlings are likely to favour the neritic dispersal of flatback turtles. I suggest future experiments should focus on assessing the orientation of post-hatchlings towards magnetic headings (e.g. (Avens & Lohmann, 2003; Lohmann *et al.*, 2013; Merrill & Salmon, 2011; Putman *et al.*, 2015)), and a new hypothesis I propose on how post-hatchlings could potentially adjust their orientation based on the direction of wind-driven waves in coastal waters. An ideal but logistically complicated scenario would be to track wild flatback turtle post-hatchlings collected at sea to experimentally test the hypotheses previously described.

6.6.2. Further studies on flatback turtle biogeography.

The largest knowledge gap remaining on flatback turtle biogeography is the in-water distribution of immature turtles and male adults. Acquiring information of these life-stages is extremely challenging, as they do not use any terrestrial habitats. Combining the historical distribution of immature turtles with potential dispersal areas (Chapter 2) could provide some guidelines on where to focus searching efforts. In the case of male adults, with improvements in the performance and retention of satellite tags it could be possible to monitor female adults through two consecutive breeding seasons. If the latter is achieved, it would be possible to identify through behavioural analyses (such as BCPA, Chapter 2) potential breeding areas in which to search for male turtles.

Alternatively, under very rigorous and careful methodologies, scientific trawls (trawl vessels without Turtle Excluder Devices and using short tow times) could be implemented in identified foraging grounds (Chapter 3) to capture flatback turtles of any life-stage. The combination of techniques such as satellite tracking, stomach content analysis, stable isotope and genetic analyses of turtles caught directly in in-water habitats could provide comprehensive information on the demography of flatback turtles in foraging grounds, residence patterns (and site fidelity) of turtles in foraging grounds, and assess ontogenic changes in their foraging ecology.

Further aspects of the foraging ecology of flatback turtles could be inferred from stable isotope analysis. An advantage of this approach is that it can be performed with samples of nesting and stranded turtles. For example, Ceriani *et al.* (2012) were able to infer the location of loggerhead foraging grounds in the eastern coast of United States by coupling satellite tracking and stable isotope analysis of nesting turtles. In addition, diet composition could also be inferred from isotopic signatures (Cardona *et al.*, 2009; Shimada *et al.*, 2014). This approach typically requires comparing isotopic values of turtles and potential prey samples of the foraging grounds. Gaining a better understanding on the habitat preferences and requirement of the turtles can be highly informative to refine analysis such as the ones employed in Chapter 4 and avoid overinterpretation of the results, and ultimately model potential distribution shifts under future changing climate scenarios (Witt *et al.*, 2010)

For flatback turtles in eastern Australia, I particularly suggest to assess the temporal variation in habitat use and the degree of individual specialisation in diet. Changes in habitat use patterns across temporal scales can be assessed both with satellite telemetry (subject to the life length or retention of the satellite tag) and stable isotopes (Shimada *et al.*, 2014). The highly flexible foraging behaviour displayed by flatback turtles (Chapter 3, Whittock *et al.* (2016)) combined with the fact that individual turtles made use of very different habitat types within short time-frames (less than a year) (Chapter 4) suggest that flatback turtles might not display such a strong fidelity to specific foraging grounds (compared to site fidelity in green and loggerheads in eastern Queensland; Gredzens *et al.* (2014); Shimada *et al.* (2016a)). In addition, during my study I was able deploy a satellite tag on the same turtle (flipper tag T97111) in two different breeding seasons (2013 and 2015). Comparison of the turtle's home range each year indicates the use of different areas and different foraging strategies in each year (Figure 6.2). While these data are not conclusive, it generates further questions regarding the degree to which flatback turtles might or not display strong fidelity to foraging grounds. I suggest future studies should aim to assess the temporal variations in habitat use (e.g. studying residence patterns and fidelity to foraging grounds by re-tracking nesting females tagged in previous breeding seasons) and the degree of individual specialisation in diet (e.g. by employing stable isotope analysis, see Pajuelo *et al.* (2016); Vander Zanden *et al.* (2010)) in flatback turtles.

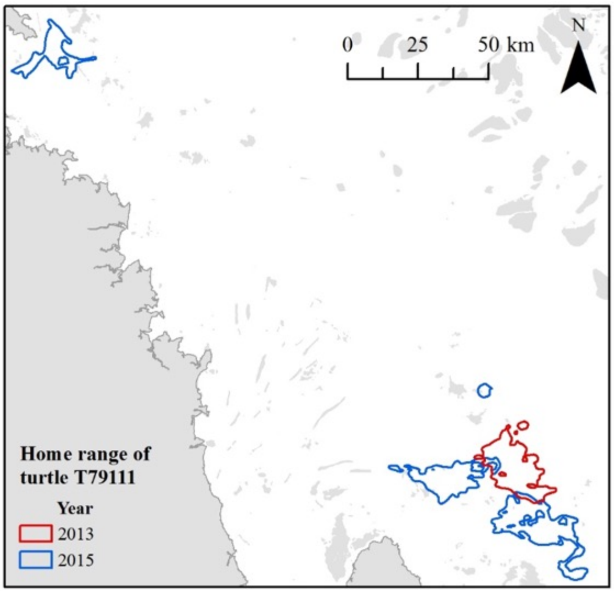


Figure 6.2. Spatial distribution of the home range (95% UD) of turtle T79111 in 2013 (red polygon) and 2015 (blue polygon).

6.6.3. Assessing the local impact of threats in foraging grounds

As demonstrated in previous Chapters, the environmental characteristics (Chapter 4) and the effect of anthropic pressures (Chapter 5) are highly variable across the GBRMP, and foraging flatback turtles are distributed throughout the region (Chapter 3). Thus, it is important to assess the vulnerability and risk of the turtles at local scales. The approach I used in Chapter 5 to quantify the exposure of threats is easily adjustable to include further spatial layers. I suggest that spatial layers on water quality (especially pollutant load) and distribution of marine debris should be included in the analysis. In addition, special attention needs to be granted to the synergistic effect of multiple threats, as well as vulnerability and relative cumulative impact of each threat on marine turtles (during different life-stages) and their habitats (Maxwell *et al.*, 2013). After identifying the threats that can potentially impact a species (Commonwealth of Australia, 2017), quantifying the exposure to threats is one of the first steps to undertake vulnerability (Fuentes *et al.*, 2011), risk assessments (Grech & Marsh, 2008) and cost-effectiveness analysis to prioritise management actions (Dawson *et al.*, 2017; Klein *et al.*, 2016; Maxwell *et al.*, 2011). Thus, further metrics, such as the sensitivity, adaptive capacity and mortality to specific threats still need to be evaluated and if possible quantified.

6.7. Collaborative research

Information on the distribution of adult flatback turtles of the eAus stock was greatly enhanced thanks to collaborative efforts of researchers from multiple institutions. The satellite tracking database collated during my PhD can be used to address many of the future studies I propose. In addition, during my fieldwork I collected tissue samples, which are being analysed as part of undergoing genetic and stable isotope studies leaded by WWF-Australia and the Queensland Department of Environment and Heritage Protection, in conjunction with researchers at James Cook University and other institutions.

6.8. Concluding remarks

Until recently knowledge of the foraging ecology for flatback turtles was poorly understood given the cryptic nature of their in-water behaviour. For example, in eastern Australia information on the distribution of post-hatchlings and foraging adult flatback turtles was available but limited to long-term opportunistic records. My study improved the knowledge on the dispersal, distribution and foraging ecology of flatback turtles in eastern Australia, by adopting a multi-disciplinary approach to study in detail different life-stages of the species. Further studies on flatback turtle behaviour and foraging ecology will enhance understanding of the species, and ultimately understand how flatback turtles could respond and adapt to the impact of increasing anthropogenic pressures and natural changing conditions.

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Appendix

Table A1. Summary of behavioural strategies, distance, time, speed, persistence velocity ($\hat{\mu}$) and tortuosity ($\hat{\tau}$) during travelling and foraging phases for each turtle. Travelling strategies are classified as multi-stop (M-s) and direct migration (D-m). Foraging strategies are classified as single area-fixed (S-f), single area-wandering (S-w), multiple area-recurring (M-r) and multiple area-shifting (M-sh).

	Travelling phases						***Foraging phases***					
Turtle ID	***Travelling strategy***	***Total distance in km***	***Total time in days***	***Speed in km/h (mean ± SD)***	***Persistence velocity $\hat{\mu}$ (mean ± SD)***	***Tortuosity $\hat{\tau}$ (mean ± SD)***	***Foraging strategy***	***Total distance in km***	***Total time in days***	***Speed in km/h (mean ± SD)***	***Persistence velocity $\hat{\mu}$ (mean ± SD)***	***Tortuosity $\hat{\tau}$ (mean ± SD)***
54528	M-s	1003.14	33.42	1.33 ± 0.69	0.26 ± 0.06	0.10 ± 0.07	M-r	936.37	130.96	0.45 ± 0.46	0.03 ± 0.03	0.05 ± 0.10
54531	M-s	279.69	12.02	1.07 ± 0.57	0.17 ± 0.02	0.05 ± 0.01	M-sh	239.15	14.84	0.84 ± 0.64	0.09 ± 0.02	0.05 ± 0.02
96774	M-s	257.85	12.79	0.82 ± 0.52	0.13 ± 0.03	0.06 ± 0.03	M-r	2328.13	159.11	0.73 ± 0.60	0.04 ± 0.02	0.02 ± 0.03
96776	D-m	476.76	19.28	1.15 ± 0.79	0.19 ± 0.04	0.05 ± 0.03	S-f	1658.81	282.20	0.67 ± 0.60	0.04 ± 0.05	0.04 ± 0.07
96779	D-m	314.59	11.44	1.26 ± 0.94	0.22 ± 0.00	0.09 ± 0.00	M-r	5031.63	551.26	0.81 ± 0.81	0.03 ± 0.06	0.05 ± 0.08
108471	D-m	1473.23	68.85	1.13 ± 0.85	0.20 ± 0.05	0.06 ± 0.03	S-w	715.04	44.97	0.82 ± 0.65	0.11 ± 0.03	0.02 ± 0.01
120641	D-m	-	-	-	-	-	M-r	1304.01	164.15	0.55 ± 0.57	0.02 ± 0.03	0.02 ± 0.02
133399	M-s	677.15	25.44	1.15 ± 0.83	0.21 ± 0.09	0.13 ± 0.13	M-sh	782.12	140.14	0.39 ± 0.56	0.03 ± 0.03	0.16 ± 0.30
133400	D-m	826.28	31.47	1.34 ± 0.85	0.23 ± 0.05	0.11 ± 0.04	S-w	1620.09	97.05	1.04 ± 0.99	0.05 ± 0.06	0.02 ± 0.02
133401	D-m	525.26	18.07	1.27 ± 0.64	0.21 ± 0.01	0.07 ± 0.01	S-w	821.12	51.62	0.91 ± 0.75	0.08 ± 0.05	0.03 ± 0.02
133402	D-m	374.15	10.76	1.68 ± 1.01	0.30 ± 0.01	0.07 ± 0.03	S-f	1421.20	69.01	1.13 ± 0.98	0.08 ± 0.05	0.02 ± 0.02
133758	D-m	590.03	23.26	1.20 ± 0.99	0.22 ± 0.04	0.13 ± 0.05	S-f	690.08	106.01	0.49 ± 0.54	0.03 ± 0.02	0.02 ± 0.01

134189	M-s	233.72	8.64	1.25 ± 0.95	0.23 ± 0.04	0.02 ± 0.02	M-sh	828.49	63.03	0.80 ± 0.74	0.00 ± 0.04	0.03 ± 0.03
134190	D-m	195.01	8.03	1.18 ± 0.82	0.16 ± 0.00	0.18 ± 0.00	S-f	331.65	53.92	0.55 ± 0.45	-0.01 ± 0.02	0.05 ± 0.05
134191	M-s	413.09	17.50	0.94 ± 0.60	0.11 ± 0.01	0.36 ± 0.27	M-r	695.71	64.01	0.57 ± 0.50	-0.02 ± 0.02	0.06 ± 0.05
134192	M-s	368.01	11.94	1.51 ± 1.08	0.24 ± 0.05	0.10 ± 0.05	M-r	550.29	62.98	0.48 ± 0.47	0.01 ± 0.01	0.01 ± 0.01
134194	M-s	168.19	5.76	1.74 ± 1.30	0.36 ± 0.05	0.11 ± 0.08	M-sh	433.82	28.92	0.78 ± 0.66	0.03 ± 0.04	0.02 ± 0.02
134195	D-m	234.48	7.23	1.45 ± 0.64	0.29 ± 0.00	0.09 ± 0.00	S-f	662.76	35.29	0.95 ± 0.66	0.04 ± 0.03	0.02 ± 0.04
134196	D-m	183.22	6.70	1.21 ± 0.98	0.19 ± 0.00	0.14 ± 0.00	M-r	914.34	60.80	0.94 ± 0.86	0.05 ± 0.05	0.01 ± 0.02
134198	D-m	381.69	11.12	1.67 ± 1.14	0.30 ± 0.03	0.15 ± 0.06	S-w	397.22	39.59	0.65 ± 0.82	0.02 ± 0.03	0.02 ± 0.02
134199	M-s	424.34	20.73	1.28 ± 1.05	0.23 ± 0.07	0.12 ± 0.06	M-r	586.37	56.77	0.56 ± 0.52	0.02 ± 0.04	0.05 ± 0.10
141738	M-s	312.15	11.94	1.27 ± 0.88	0.19 ± 0.01	0.09 ± 0.07	M-r	899.27	77.97	0.83 ± 0.86	0.04 ± 0.05	0.02 ± 0.02
141739	M-s	1521.88	49.52	1.31 ± 0.69	0.24 ± 0.07	0.18 ± 0.21	M-r	275.42	63.48	0.34 ± 0.41	0.02 ± 0.03	0.02 ± 0.02
141740	D-m	243.74	8.26	1.25 ± 0.80	0.21 ± 0.00	0.12 ± 0.00	S-f	315.29	20.95	0.79 ± 0.64	0.09 ± 0.02	0.03 ± 0.03
141741	D-m	260.52	10.11	1.09 ± 0.74	0.18 ± 0.01	0.07 ± 0.02	S-f	824.80	238.96	0.31 ± 0.35	0.00 ± 0.02	0.03 ± 0.08
141742	M-s	1224.22	61.97	1.22 ± 0.98	0.21 ± 0.06	0.08 ± 0.05	M-sh	458.28	98.73	0.60 ± 0.52	0.07 ± 0.05	0.03 ± 0.02
141744	D-m	632.09	22.52	1.32 ± 0.84	0.22 ± 0.03	0.08 ± 0.04	M-r	2084.93	231.51	0.68 ± 0.58	0.04 ± 0.03	0.03 ± 0.07
141746	M-s	1422.41	48.90	1.34 ± 0.80	0.24 ± 0.05	0.14 ± 0.10	M-sh	293.98	53.66	0.41 ± 0.38	0.01 ± 0.03	0.03 ± 0.02
141747	M-s	1161.26	42.24	1.27 ± 0.77	0.22 ± 0.03	0.08 ± 0.04	M-sh	268.63	30.33	0.51 ± 0.46	0.03 ± 0.04	0.04 ± 0.02
141748	M-s	716.26	36.28	1.05 ± 0.82	0.17 ± 0.04	0.07 ± 0.03	M-sh	196.16	28.79	0.50 ± 0.57	0.05 ± 0.02	0.06 ± 0.05
141758	M-s	1159.85	42.16	1.20 ± 0.69	0.22 ± 0.03	0.07 ± 0.04	M-r	3045.52	400.11	0.53 ± 0.48	0.03 ± 0.04	0.03 ± 0.06
141759	M-s	485.12	19.59	1.14 ± 0.61	0.22 ± 0.08	0.09 ± 0.01	M-r	2261.67	374.93	0.39 ± 0.42	0.02 ± 0.03	0.04 ± 0.07
141760	M-s	674.90	20.01	1.61 ± 0.76	0.32 ± 0.09	0.14 ± 0.20	M-r	1361.07	208.49	0.41 ± 0.39	0.03 ± 0.02	0.07 ± 0.12
141762	D-m	558.38	16.81	1.41 ± 0.65	0.28 ± 0.11	0.08 ± 0.01	S-w	1895.14	423.50	0.31 ± 0.33	0.01 ± 0.02	0.03 ± 0.06
141763	M-s	224.79	7.84	1.55 ± 1.01	0.24 ± 0.03	0.08 ± 0.02	M-r	763.27	46.95	0.78 ± 0.69	0.07 ± 0.05	0.02 ± 0.02
152711	D-m	279.29	9.18	1.32 ± 1.03	0.20 ± 0.01	0.08 ± 0.04	S-f	115.52	8.44	0.80 ± 0.69	0.11 ± 0.00	0.06 ± 0.00
152712	D-m	700.28	20.51	1.79 ± 1.18	0.26 ± 0.06	0.05 ± 0.02	S-f	594.61	23.96	1.30 ± 0.92	0.10 ± 0.02	0.02 ± 0.01

152713	D-m	465.85	17.22	1.55 ± 1.02	0.23 ± 0.04	0.04 ± 0.04	S-f	1303.30	85.57	1.02 ± 0.75	0.05 ± 0.06	0.02 ± 0.01
152714	D-m	662.29	23.85	1.31 ± 0.93	0.21 ± 0.05	0.08 ± 0.04	M-r	620.43	69.15	0.76 ± 0.67	0.04 ± 0.05	0.03 ± 0.03
152715	D-m	222.76	7.90	1.19 ± 0.61	0.19 ± 0.03	0.40 ± 0.74	M-r	953.31	101.47	0.59 ± 0.65	-0.01 ± 0.04	0.19 ± 0.23
152718	D-m	352.37	10.64	1.72 ± 1.15	0.28 ± 0.09	0.05 ± 0.02	S-f	665.20	36.44	1.16 ± 0.91	0.10 ± 0.05	0.03 ± 0.03
152720	M-s	1033.00	36.89	1.43 ± 0.96	0.23 ± 0.02	0.05 ± 0.02	M-sh	1563.71	94.58	1.01 ± 0.86	0.09 ± 0.05	0.02 ± 0.02
154296	M-s	-	-	-	-	-	M-r	1949.73	114.65	0.92 ± 0.71	0.02 ± 0.04	0.02 ± 0.02
154297	M-s	720.94	22.67	1.61 ± 0.95	0.29 ± 0.03	0.01 ± 0.01	M-sh	917.81	87.67	0.66 ± 0.63	0.02 ± 0.05	0.02 ± 0.02
Total		24434.21	911.46	1.30 ± 0.88	0.22 ± 0.06	0.09 ± 0.10		46575.46	5196.89	0.66 ± 0.67	0.04 ± 0.03	0.04 ± 0.03

Table A2. Summary of total home range areas (95% UD) and core areas (50% UD) for each tracked turtle.

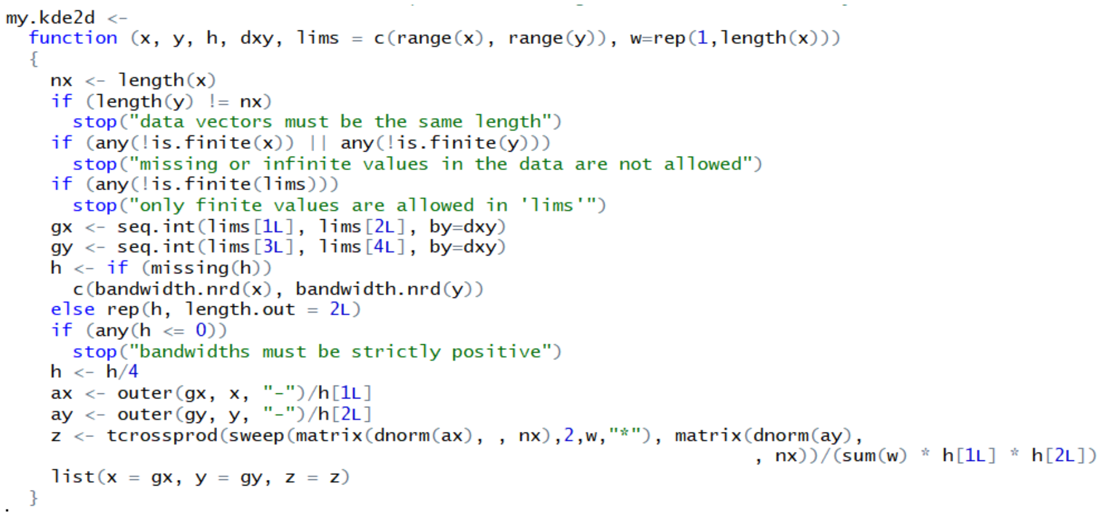
Turtle ID	***Home range area (km^2)***	***Core area (km^2)***
54528	**529.99**	**89.67**
Main 1	165.52	43.97
Main 2	125.07	24.88
Transient 1	77.42	6.05
Transient 2	42.53	0.60
Transient 3	119.45	14.17
54531	**282.36**	**65.17**
Transient 1	60.11	9.73
Transient 2	33.72	5.35
Transient 3	188.52	50.09
96774	**506.87**	**67.07**
Main 1	334.71	51.33
Main 2	172.16	15.74
96776	**238.13**	**45.77**
Main 1	238.13	45.77
96779	**895.52**	**64.77**
Main 1	490.73	0.35
Main 2	404.79	64.42
108471	**134.89**	**22.87**
Main 1	134.89	22.87
120641	**407.81**	**32.94**
Main 1	327.60	32.94
Transient 1	66.90	
Transient 2	13.31	
133399	**417.99**	**48.40**
Main 1	258.71	27.16
Main 2	64.69	15.63
Transient 1	16.05	3.24
Transient 2	40.39	0.55
Transient 3	38.15	1.82
133400	**294.45**	**55.01**
Main 1	294.45	55.01
133401	**684.18**	**120.83**
Main 1	684.18	120.83
133402	**234.14**	**52.12**

Main 1	234.14	52.12
133758	**59.25**	**13.47**
Main 1	59.25	13.47
134189	**352.20**	**65.38**
Main 1	288.26	61.13
Transient 1	63.94	4.24
134190	**141.30**	**37.61**
Main 1	141.30	37.61
134191	**600.40**	**103.80**
Main 1	261.84	36.91
Main 2	338.57	66.90
134192	**269.90**	**53.82**
Main 1	97.95	17.81
Transient 1	13.17	2.98
Transient 2	93.59	15.33
Transient 3	65.19	17.70
134194	**589.54**	**135.57**
Transient 1	343.45	54.13
Transient 2	246.09	81.44
134195	**312.67**	**80.30**
Main 1	312.67	80.30
134196	**632.39**	**128.52**
Main 1	435.89	90.42
Transient 1	196.50	38.10
134198	**483.69**	**41.35**
Main 1	483.69	41.35
134199	**414.13**	**53.28**
Transient 1	219.55	3.56
Transient 2	171.66	49.72
Transient 3	22.92	
141738	**290.12**	**38.74**
Main 1	257.91	38.74
Transient 1	32.21	
141739	**166.59**	**15.39**
Transient 1	49.21	2.03
Transient 2	55.80	12.97
Transient 3	61.58	0.39
141740	**284.43**	**49.16**
Transient 1	284.43	49.16
141741	**78.42**	**14.44**

Main 1	78.42	14.44
141742	**320.85**	**45.85**
Main 1	35.94	11.34
Transient 1	83.97	6.43
Transient 2	192.76	27.85
Transient 3	8.18	0.23
141744	**159.68**	**23.85**
Main 1	112.50	23.85
Transient 1	47.18	
141746	**196.41**	**38.58**
Main 1	116.35	32.95
Transient 1	17.88	2.38
Transient 2	25.54	1.59
Transient 3	7.48	0.53
Transient 4	29.17	1.12
141747	**147.74**	**14.74**
Transient 1	53.67	1.12
Transient 2	94.06	13.62
141748	**126.98**	**23.98**
Transient 1	28.27	5.14
Transient 2	12.03	4.79
Transient 3	13.48	1.18
Transient 4	73.20	12.87
141758	**1261.32**	**133.17**
Main 1	571.55	117.63
Main 2	200.44	4.86
Transient 1	253.05	10.43
Transient 2	55.96	
Transient 3	117.12	0.04
Transient 4	63.20	0.20
141759	**711.80**	**65.46**
Main 1	427.80	62.39
Transient 1	82.31	
Transient 2	43.23	3.07
Transient 3	48.83	
Transient 4	39.51	
Transient 5	45.59	
Transient 6	24.53	
141760	**703.83**	**120.71**
Main 1	343.03	80.48

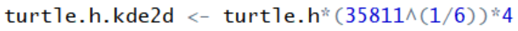
Main 2	245.24	29.76
Transient 1	52.50	9.13
Transient 2	63.06	1.35
141762	**317.08**	**25.82**
Main 1	317.08	25.82
141763	**482.43**	**87.07**
Main 1	254.35	49.77
Transient 1	228.08	37.30
152711	**78.87**	**13.45**
Transient 1	78.87	13.45
152712	**157.70**	**32.35**
Transient 1	157.70	32.35
152713	**490.24**	**116.50**
Main 1	490.24	116.50
152714	**476.50**	**56.09**
Main 1	195.06	36.09
Transient 1	125.64	12.87
Transient 2	113.27	7.14
Transient 3	42.53	
152715	**836.84**	**49.47**
Main 1	274.48	48.39
Main 2	562.36	1.08
152718	**333.37**	**63.33**
Main 1	333.37	63.33
152720	**703.42**	**118.35**
Main 1	220.35	57.55
Main 2	142.95	33.39
Transient 1	325.19	23.88
Transient 2	14.92	3.53
154296	**2003.15**	**414.95**
Transient 1	1723.25	377.02
Transient 2	227.29	27.96
Transient 3	52.62	9.97
154297	**959.74**	**59.51**
Main 1	195.64	52.79
Transient 1	300.18	4.61
Transient 2	463.92	2.11

Code A1. Code for modified kde2d algorithm



```r
my.kde2d <-
  function (x, y, h, dxy, lims = c(range(x), range(y)), w=rep(1,length(x)))
  {
    nx <- length(x)
    if (length(y) != nx)
      stop("data vectors must be the same length")
    if (any(!is.finite(x)) || any(!is.finite(y)))
      stop("missing or infinite values in the data are not allowed")
    if (any(!is.finite(lims)))
      stop("only finite values are allowed in 'lims'")
    gx <- seq.int(lims[1L], lims[2L], by=dxy)
    gy <- seq.int(lims[3L], lims[4L], by=dxy)
    h <- if (missing(h))
      c(bandwidth.nrd(x), bandwidth.nrd(y))
    else rep(h, length.out = 2L)
    if (any(h <= 0))
      stop("bandwidths must be strictly positive")
    h <- h/4
    ax <- outer(gx, x, "-")/h[1L]
    ay <- outer(gy, y, "-")/h[2L]
    z <- tcrossprod(sweep(matrix(dnorm(ax), , nx),2,w,"*"), matrix(dnorm(ay),
                                                                      , nx))/(sum(w) * h[1L] * h[2L])
    list(x = gx, y = gy, z = z)
  }
```

Code A2. Code used to adjust the bandwidth for the kde2d algorithm



```r
turtle.h.kde2d <- turtle.h*(35811^(1/6))*4
```

Table A3. Bandwidth value used for each turtle behavioural event (i.e. each travelling, slow travelling or foraging event) in the kde2d algorithm.

Turtle subset	***Bandwidth adehabitat***	***Bandwidth adjusted for kde2d***
054528_f1	0.019497314	0.44775199
054528_f2	0.026086654	0.599074876
054528_f3	0.021524322	0.494301824
054528_f4	0.035900812	0.824455103
054528_t1	0.064457834	1.480261479
054528_t2	0.283037418	6.499898683
054528_t3	0.188919941	4.338509318
054528_t4	0.016844974	0.386841517
054531_f1	0.00954116	0.219110868
054531_f2	0.033721563	0.774409065
054531_t1	0.050906678	1.169061866
054531_t2	0.072623503	1.667784472
096774_f1	0.010917678	0.250722322
096774_f2	0.020035789	0.460117951
096774_f3	0.010460237	0.240217285
096774_t1	0.055782273	1.281028932

096774_t2	0.05129363	1.17794814
096774_t3	0.055863504	1.282894385
096776_f1	0.007957191	0.182735318
096776_f2	0.005989173	0.137540177
096776_t1	0.227299003	5.219876939
096776_t2	0.012185241	0.279831655
096779_f1	0.034133635	0.783872209
096779_f2	0.016386546	0.3763138
096779_f3	0.016861798	0.387227888
096779_t1	0.161497336	3.708754582
096779_t2	0.031465554	0.722600252
096779_t3	0.035738479	0.820727141
108471_f1	0.013559978	0.311402235
108471_f2	0.019856896	0.456009703
108471_f3	0.007504264	0.172333944
108471_f4	0.009933521	0.228121358
108471_t1	0.158561154	3.641325727
108471_t2	0.01100932	0.252826868
108471_t3	0.076286825	1.751911941
108471_t4	0.008523569	0.195742084
108471_t5	0.008506635	0.195353206
120641_f1	0.009157596	0.210302382
120641_f2	0.007378356	0.169442485
120641_f3	0.016614778	0.381555105
120641_t1	0.036939173	0.848300848
120641_t2	0.025173621	0.57810727
120641_t3	0.016929026	0.388771762
133399_f1	0.004696789	0.107860845
133399_f2	0.023408493	0.537571433
133399_f3	0.0331692	0.761724153
133399_t1	0.072505078	1.665064862
133399_t2	0.172278634	3.956344975
133399_t3	0.156317327	3.589796691
133400_f1	0.026404146	0.606366021
133400_f2	0.010332059	0.237273714
133400_f3	0.012250857	0.281338519

133400_f4	0.011145614	0.255956833
133400_f5	0.005039992	0.115742434
133400_t1	0.249348508	5.726239467
133400_t2	0.068694688	1.577560009
133400_t3	0.013273822	0.304830719
133400_t4	0.010782774	0.247624275
133400_t5	0.013650664	0.313484815
133401_f1	0.026932113	0.618490692
133401_t1	0.277051614	6.362435854
133402_f1	0.012445711	0.285813314
133402_t1	0.234300108	5.380655926
133758_f1	0.005091843	0.116933172
133758_f2	0.005354722	0.122970136
133758_t1	0.334414479	7.679762781
133758_t2	0.006385822	0.146649152
134189_f1	0.022591588	0.518811388
134189_f2	0.011607217	0.266557465
134189_f3	0.014462134	0.332120071
134189_t1	0.079764985	1.831787201
134189_t2	0.068163431	1.565359791
134189_t3	0.015520144	0.35641705
134190_f1	0.006515016	0.149616071
134190_t1	0.113770916	2.612726716
134191_f1	0.023072654	0.529858968
134191_f2	0.008832893	0.202845656
134191_f3	0.020963608	0.481425131
134191_t1	0.08020394	1.841867723
134191_t2	0.067186481	1.542924326
134191_t3	0.10661177	2.448318354
134192_f1	0.012391436	0.284566896
134192_f2	0.007131619	0.163776227
134192_f3	0.012638636	0.29024379
134192_t1	0.243881665	5.600694509
134192_t2	0.054018266	1.240518869
134192_t3	0.069065392	1.586073159
134194_f1	0.030494951	0.700310557

134194_f2	0.019418683	0.44594625
134194_t1	0.155841073	3.57885962
134194_t2	0.031867239	0.731824884
134195_f1	0.012647978	0.290458324
134195_t1	0.118258222	2.715776836
134196_f1	0.024867253	0.571071578
134196_t1	0.154473206	3.547446817
134198_f1	0.031435375	0.721907197
134198_f2	0.004115792	0.094518354
134198_t1	0.268415693	6.164113635
134198_t2	0.030725405	0.705602888
134199_f1	0.010226708	0.234854344
134199_f2	0.011838353	0.271865454
134199_f3	0.003657749	0.083999496
134199_f4	0.011557483	0.265415329
134199_t1	0.132578848	3.044647181
134199_t2	0.056942482	1.3076729
134199_t3	0.04055095	0.931244597
134199_t4	0.045291505	1.040110521
141738_f1	0.008859499	0.203456653
141738_f2	0.020489493	0.470537169
141738_f3	0.010326232	0.237139898
141738_f4	0.007890732	0.181209105
141738_t1	0.04619828	1.060934413
141738_t2	0.126805267	2.912058042
141738_t3	0.006690041	0.153635482
141738_t4	0.007537047	0.173086811
141739_f1	0.017982442	0.412963248
141739_f2	0.003828468	0.087920023
141739_t1	0.633716573	14.55317654
141739_t2	0.02757941	0.633355728
141740_f1	0.01970734	0.452575179
141740_t1	0.114881978	2.638242038
141741_f1	0.006598506	0.151533384
141741_t1	0.1390669	3.193644035
141742_f1	0.037938079	0.871240528

141742_f2	0.026656126	0.612152704
141742_f3	0.009728011	0.223401853
141742_f4	0.006006664	0.137941853
141742_t1	0.31827298	7.309076424
141742_t2	0.040612995	0.932669446
141742_t4	0.186743124	4.288519141
141742_t5	0.095048238	2.182764111
141744_f1	0.010495481	0.241026648
141744_f2	0.009973609	0.229041978
141744_t1	0.254249977	5.838800756
141744_t2	0.010551898	0.242322258
141746_f1	0.003554078	0.081618713
141746_f2	0.024471164	0.561975471
141746_f3	0.008742452	0.200768681
141746_t1	0.490817535	11.27152821
141746_t2	0.02556952	0.587199008
141746_t3	0.119302313	2.739754178
141747_f1	0.010040426	0.230576412
141747_f2	0.006940456	0.159386215
141747_t1	0.312209152	7.169821816
141747_t2	0.245769655	5.644051814
141748_f1	0.011318421	0.259925323
141748_f2	0.015019138	0.344911561
141748_f3	0.010339391	0.237442091
141748_t1	0.230578984	5.295201059
141748_t2	0.042922165	0.985699081
141748_t3	0.035847414	0.823228815
141758_f1	0.036039086	0.827630529
141758_f2	0.03386324	0.777662654
141758_f3	0.043940598	1.009087207
141758_f4	0.010433178	0.239595892
141758_f5	0.044762311	1.027957685
141758_f6	0.046124748	1.059245767
141758_t1	0.207301046	4.760627787
141758_t2	0.172880341	3.970163057
141758_t3	0.056092587	1.288155237

141758_t4	0.072077082	1.655236011
141758_t5	0.024584588	0.56458024
141758_t6	0.04890427	1.123076957
141759_f1	0.015912697	0.36543196
141759_f2	0.00766891	0.176115
141759_f3	0.02788335	0.640335653
141759_f4	0.036563649	0.839677007
141759_f5	0.049165614	1.129078659
141759_t1	0.309379129	7.104830879
141759_t2	0.040524243	0.930631268
141759_t3	0.029516637	0.677843771
141759_t4	0.033453159	0.768245212
141759_t5	0.04567971	1.049025556
141759_t6	0.02003385	0.46007342
141760_f1	0.023012391	0.528475042
141760_f2	0.015971826	0.366789845
141760_f3	0.042764785	0.982084892
141760_t1	0.267237932	6.137066582
141760_t2	0.240730785	5.528335154
141760_t3	0.045835854	1.052611385
141762_f1	0.01834381	0.421261987
141762_t1	0.418076857	9.601052838
141763_f1	0.060622249	1.392178035
141763_f2	0.031721929	0.728487864
141763_f3	0.026400164	0.606274574
141763_t1	0.058612624	1.346027384
141763_t2	0.084615899	1.943187479
141763_t3	0.07079201	1.625724596
152711_f1	0.0195337	0.44858757
152711_t1	0.140827554	3.234077109
152712_f1	0.008507102	0.195363932
152712_f2	0.011019495	0.253060527
152712_f3	0.012519368	0.287504822
152712_t1	0.156889873	3.602945095
152712_t2	0.011964898	0.274771532
152712_t3	0.010739669	0.246634383

152713_f1	0.018359493	0.421622158
152713_f2	0.015698941	0.360523092
152713_f3	0.01765215	0.405378163
152713_t1	0.186512851	4.283230959
152713_t2	0.009353038	0.21479068
152713_t3	0.013397734	0.307676322
152714_f1	0.046512043	1.068139933
152714_t1	0.324469367	7.451375234
152715_f1	0.037454954	0.860145658
152715_f2	0.021870523	0.50225227
152715_f3	0.019327485	0.443851896
152715_t1	0.144550658	3.319577452
152715_t2	0.036936247	0.848233651
152715_t3	0.056120683	1.288800447
152718_f1	0.018979383	0.435857804
152718_f2	0.01250325	0.287134681
152718_t1	0.169501768	3.892574779
152718_t2	0.030573831	0.702122014
152720_f1	0.016581801	0.380797803
152720_f2	0.011398015	0.261753168
152720_f3	0.030511181	0.700683276
152720_f4	0.027401419	0.629268206
152720_f5	0.019868319	0.456272041
152720_t1	0.143224681	3.289126638
152720_t2	0.037041323	0.850646705
152720_t3	0.065926247	1.513983314
152720_t4	0.013557298	0.311340674
152720_t5	0.110704088	2.542297612
154296_f1	0.034562532	0.793721748
154296_f2	0.03396074	0.779901717
154296_f3	0.037461935	0.860305978
154296_f4	0.074264584	1.70547157
154296_f5	0.00746111	0.171342922
154296_t1	0.031324051	0.71935068
154296_t2	0.047023827	1.079892942
154296_t3	0.019093641	0.438481703

154296_t4	0.037135281	0.852804427
154296_t5	0.042707964	0.980780008
154297_f1	0.025689619	0.58995705
154297_f2	0.035057135	0.805080223
154297_f3	0.008522008	0.195706249
154297_t1	0.118416618	2.719414361
154297_t2	0.095020466	2.182126319
154297_t3	0.283016754	6.499424131

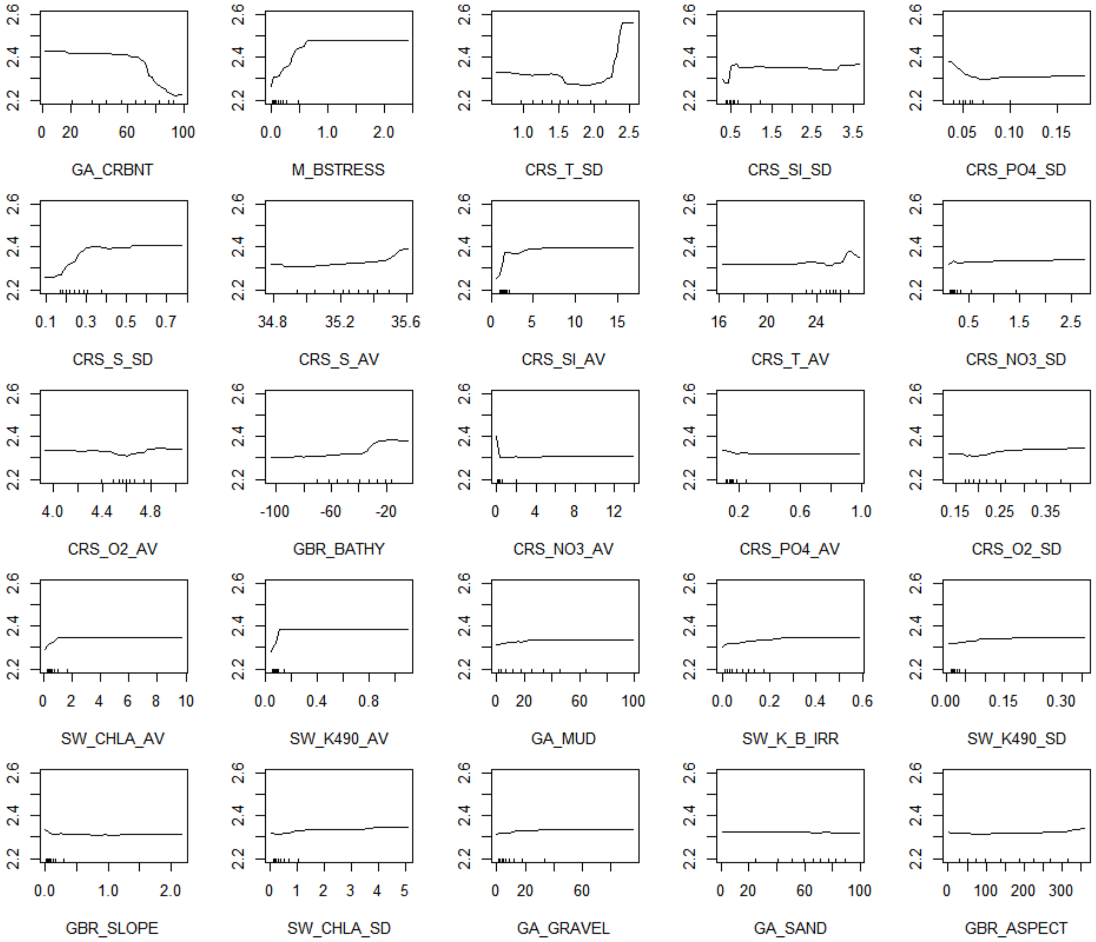


Figure A1. Partial plots displaying the response of turtle presence (y-axis) to each physical predictor (x-axis) in the GBR-wide model. For the relevant units of each physical predictor, please refer to table 4.1.

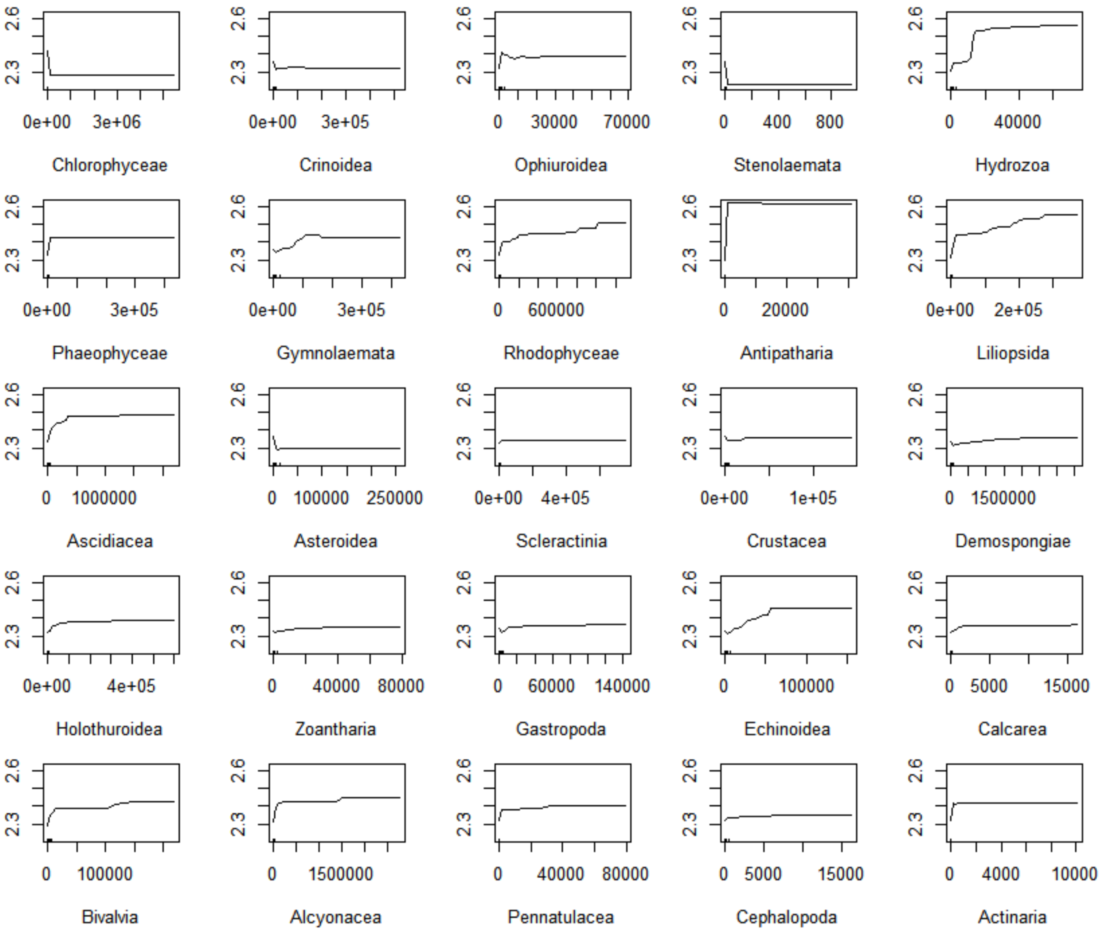


Figure A2. Partial plots displaying the response of turtle presence (y-axis) to each biological predictor (x-axis) in the GBR-wide model. Units of biological predictors are biomass in kg.

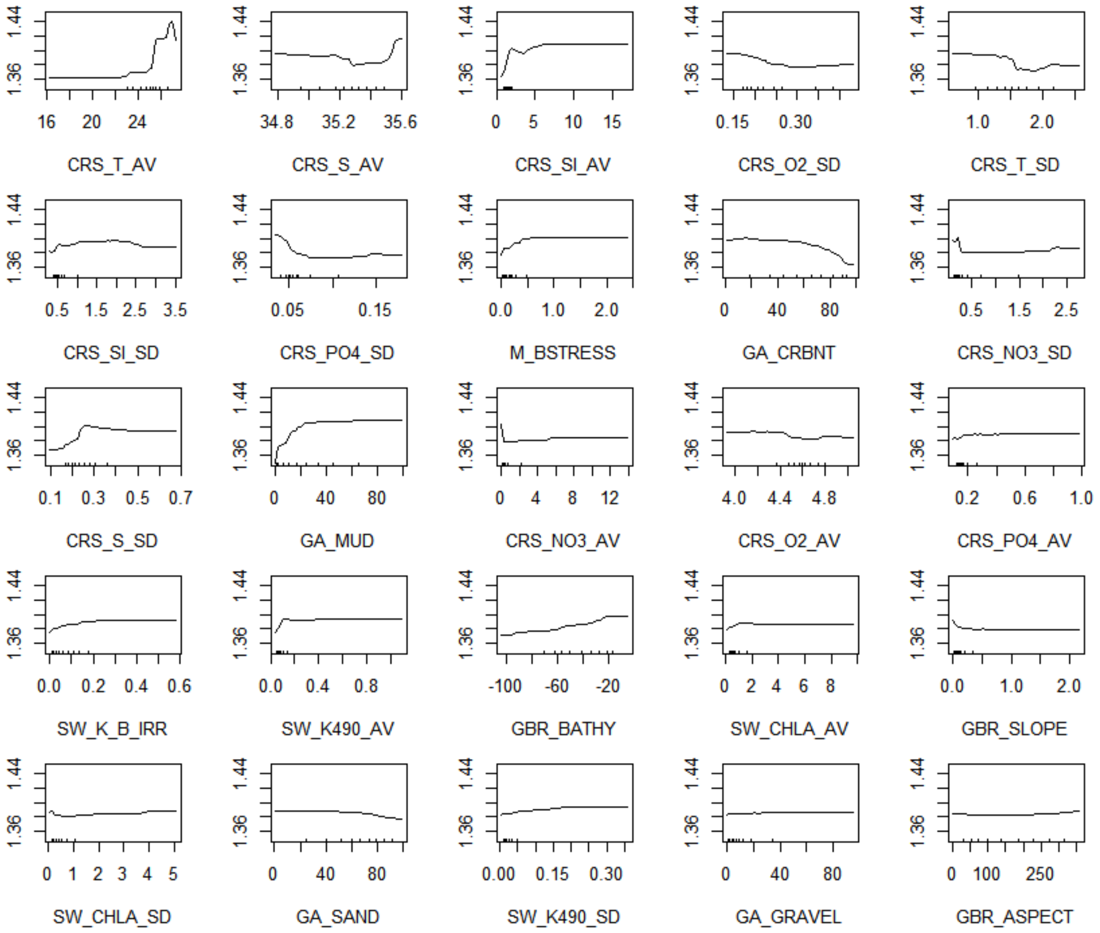


Figure A3. Partial plots displaying the response of turtle presence (y-axis) to each physical predictor (x-axis) in the Habitat-I model. For the relevant units of each physical predictor, please refer to table 4.1.

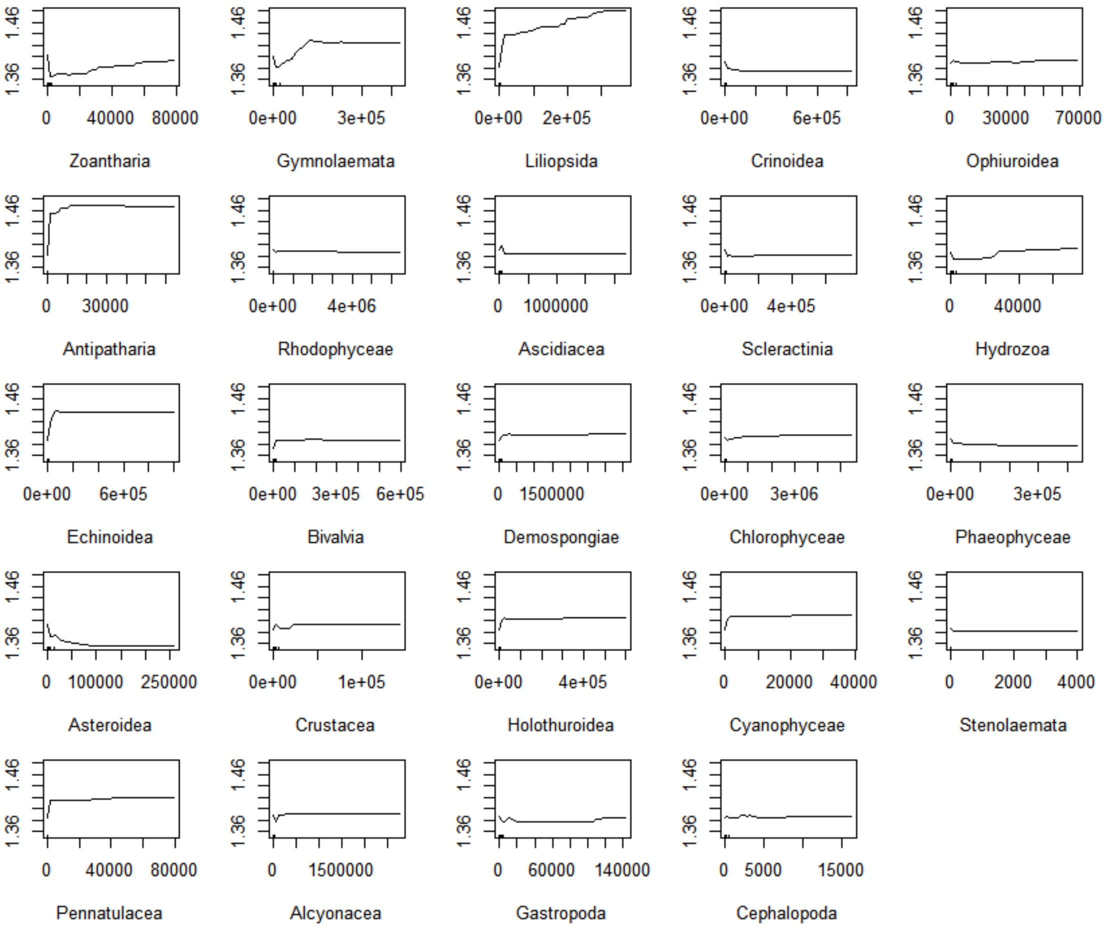


Figure A4. Partial plots displaying the response of turtle presence (y-axis) to each biological predictor (x-axis) in the Habitat-I model. Units of biological predictors are biomass in kg.

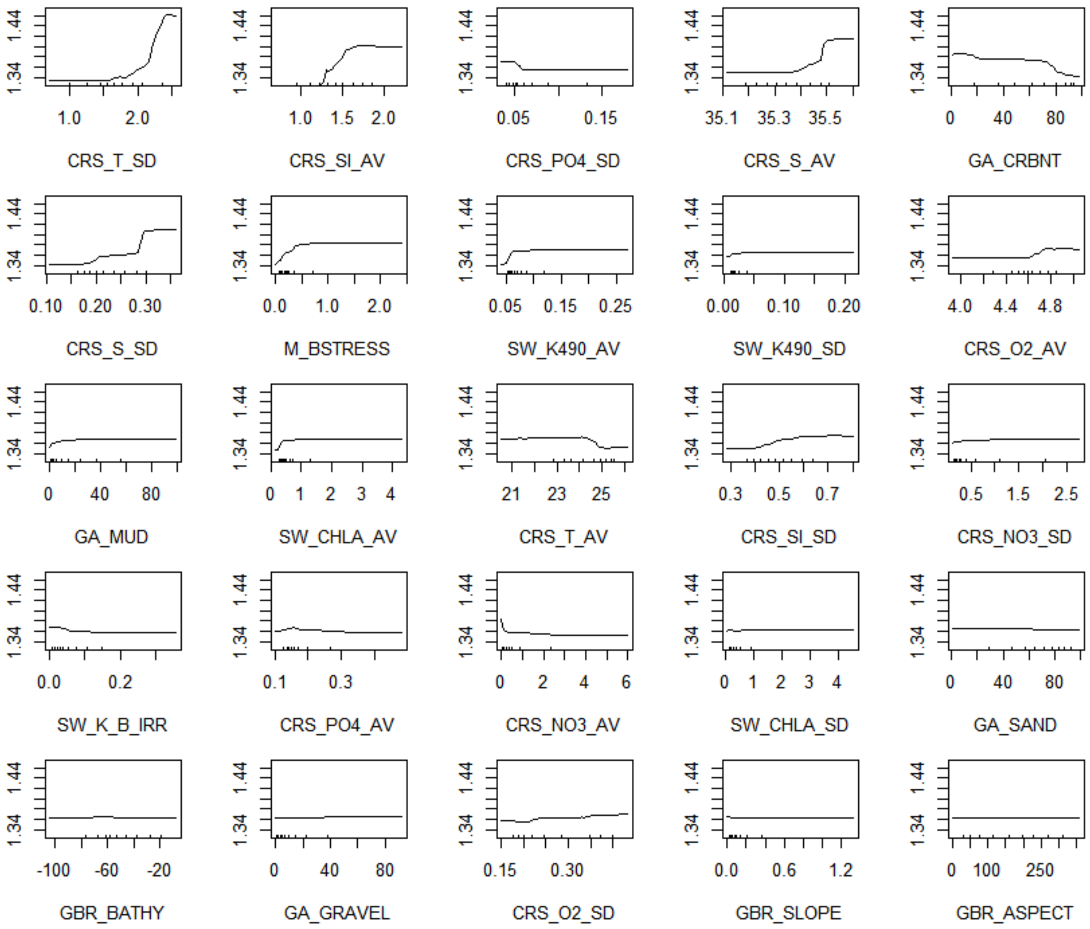


Figure A5. Partial plots displaying the response of turtle presence (y-axis) to each physical predictor (x-axis) in the Habitat-II model. For the relevant units of each physical predictor, please refer to table 4.1.

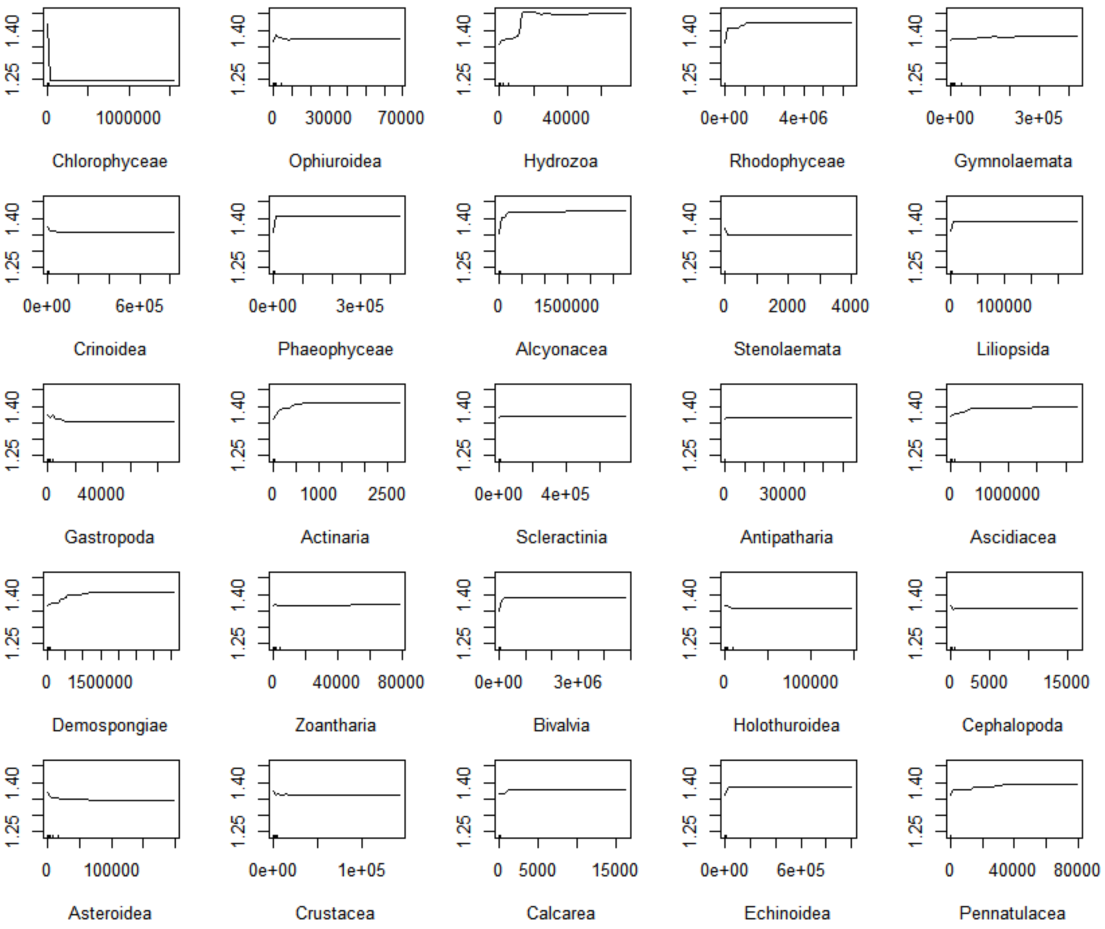


Figure A6. Partial plots displaying the response of turtle presence (y-axis) to each biological predictor (x-axis) in the Habitat-II model. Units of biological predictors are biomass in kg.

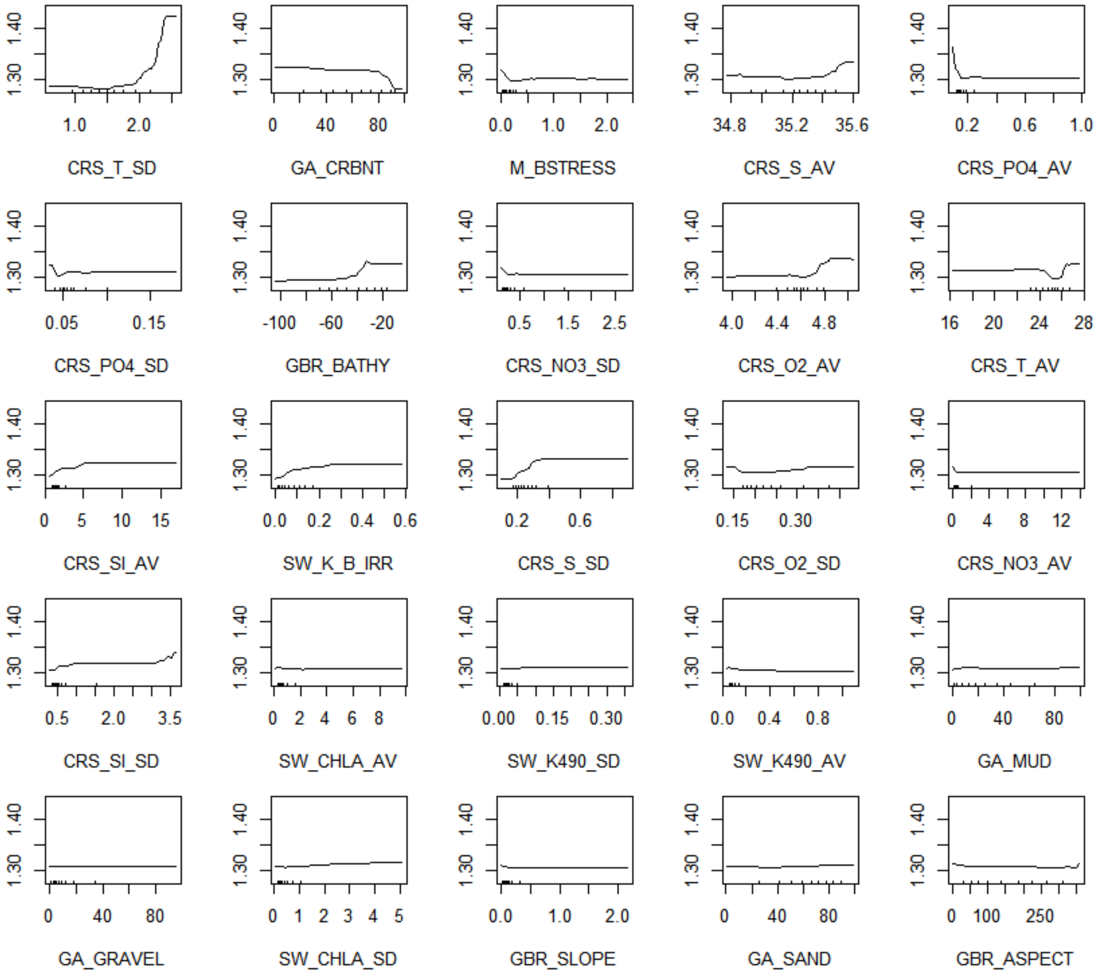


Figure A7. Partial plots displaying the response of turtle presence (y-axis) to each physical predictor (x-axis) in the Habitat-III model. For the relevant units of each physical predictor, please refer to table 4.1.

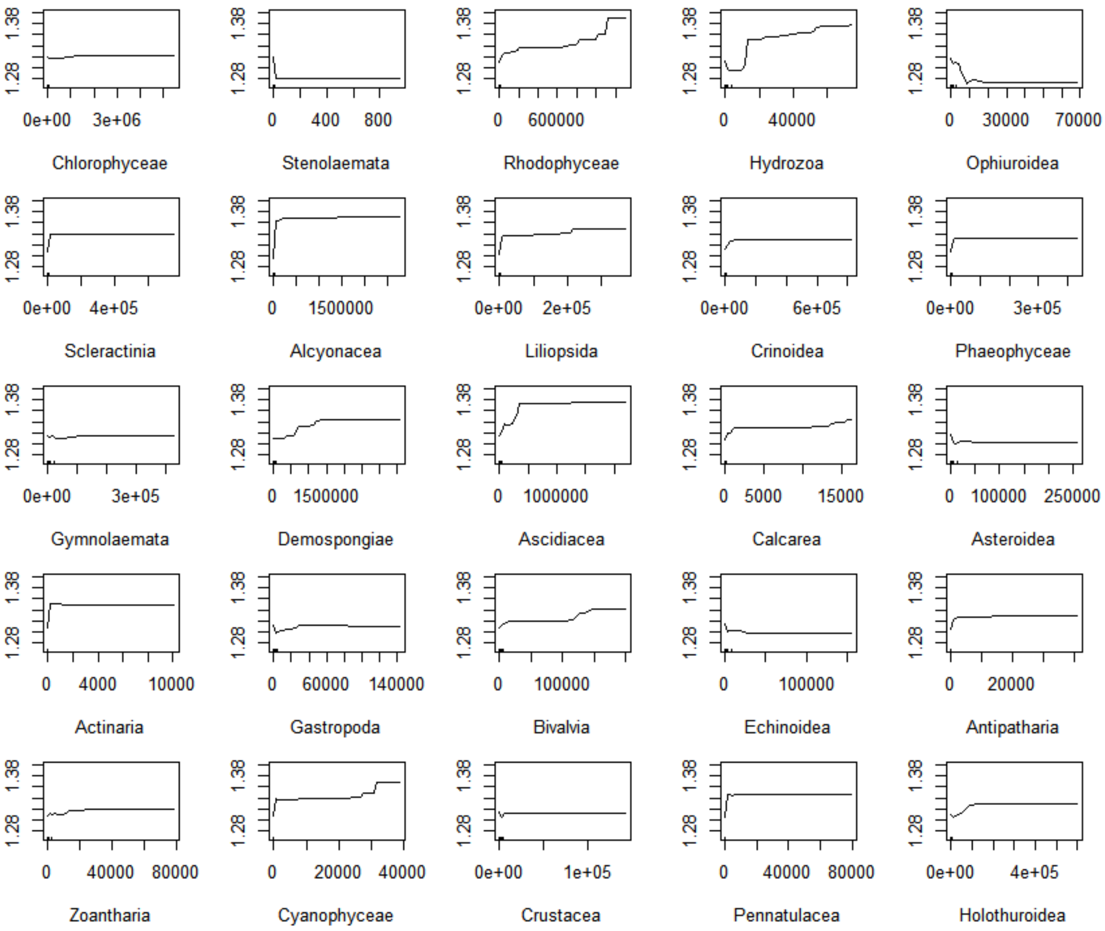


Figure A8. Partial plots displaying the response of turtle presence (y-axis) to each biological predictor (x-axis) in the Habitat-III model. Units of biological predictors are biomass in kg.