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Life history and spatial ecology of sharks and rays in mangrove habitats

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For the degree of Doctor of Philosophy

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Abstract

Elasmobranchs (sharks and rays) are a group of cartilaginous fish, mostly marine predators occurring in tropical to boreal, shallow to deep waters of the world. With diverse morphologies and ecological niches, the group has adopted to a wide range of habitat types. While the importance of their ecological roles as predators is well recognised, elasmobranchs are one of the most threatened taxa in the world mainly due to overexploitation and habitat degradation. Particularly, loss and degradation of coastal habitats, including mangroves, seagrasses and coral reefs has a severe impact on coastal species. Despite their importance, the habitat function of mangroves for elasmobranchs is poorly studied and undervalued. This thesis aimed to define the functional roles and importance of mangrove habitats to elasmobranchs by investigating how elasmobranchs use mangrove habitats. To achieve this goal, the present study focused on the four specific objectives: (1) review and assess current knowledge on the relationship between mangrove systems and elasmobranchs, (2) examine the life history parameters of a data-deficient mangrove-associated species, (3) test if acoustic telemetry can be used to track animal movement in mangrove habitats and (4) investigate patterns in habitat use and movement of elasmobranch species within mangrove habitats on daily and seasonal timescales.

Mangroves are one of the most productive components in coastal ecosystems. Mangroves are highly productive due to high biodiversity, primary production and nutrient recycling. Mangrove habitats are typically considered to offer elasmobranchs feeding opportunities, refuge from predators, and serve as nursery areas for juveniles, though such functions have rarely been tested. In particular, as their feeding ecology is understudied, trophic linkages between mangroves and elasmobranchs remains unclear. Dense mangrove roots and trunks create complex structures, likely offering effective shelter from large predators, yet direct observations of elasmobranch behaviour in mangrove habitats are scarce. The use of mangrove systems (mangrove and adjacent habitats) as elasmobranch nursery areas is relatively well examined, although there are taxonomic and regional biases in research. Given ongoing loss of global mangroves, better understandings of how this loss affects elasmobranch populations is required, particularly in those regions where losses are greatest and for elasmobranch species that are at risk of extinction.

Life history data, such as age and growth characteristics provide important information for population status, productivity and extinction risk of a species. Collection of this information is particularly important for data deficient species or species that occur in degraded habitats or have fragmented geographical distributions. This study examined age-at-length data of data-deficient graceful sharks *Carcharhinus amblyrhynchoides* from the Kimberley Region, Western Australia and estimated growth

parameters using growth models. The results highlighted slow growth of this medium-sized species. Growth completion parameters were $g_{\text{Log}} = 0.28$ for female and $g_{\text{Log}} = 0.34$ for male; size at birth was estimated to be 54.5 ± 1.5 cm TL and asymptotic length L_∞ was 132.7 cm TL for females and 119.5 cm TL for males in this study. The length results suggest that the body size of the Kimberley population of graceful sharks are small compared to the maximum size known for this species from other locations. Maturity data of the species also supported the findings of their slow growth, suggesting their high vulnerability to exploitation. The life history data of a data-deficient species is often extrapolated based on biologically similar species, but this study emphasises the importance of species-specific life history data for improving management since smaller-bodied carcharhinid sharks are typically fast growing. Slow growth and smaller body size of this population may be attributed to low oxygen levels in mangrove habitats that this species is known to regularly occupy. The life history data of graceful sharks will help guide population management particularly outside of Australian waters since the global population is threatened.

Acoustic telemetry has been used to monitor the movement of sharks and rays in a broad range of aquatic environments. Despite their importance, mangrove habitats are understudied for spatial ecology of elasmobranchs, and acoustic telemetry is rarely used inside mangrove habitats. One reasons may be a general assumption that acoustic signal would not be detectable by the receivers in such shallow water, structurally complex, environments. This study tested whether acoustic receivers can be used in mangrove habitats to track the movement of sharks and rays. Thirty-eight receivers were deployed in a mangrove system in Pioneer Bay, Orpheus Island, Great Barrier Reef, including inside mangroves, mangrove edges and adjacent reef flat areas. The detection range and receiver performance metrics, such as code detection efficiency, rejection coefficient and noise quotient were examined and tested among habitats. Results highlighted that the signal from transmitters were successfully detected inside mangrove habitats as well as on the adjacent reef flat. The detection range of at least 50% of detections was up to 20 m inside mangrove areas and up to 120 m outside mangrove areas. The receiver performance metrics showed low background noise, low rejection rates and reasonably high code detection efficiency in mangrove habitats. Finally, this study applied this method to tracking of juvenile sharks and rays in the mangrove system and demonstrated that acoustic telemetry can be used to successfully track animals inside mangrove habitat.

Mangrove habitats are used by a wide range of organisms, but how elasmobranchs use mangrove habitats remains poorly understood due to sampling difficulty and thus the importance of mangroves is undervalued for this taxon. This study investigated movement patterns of juvenile sharks and rays in a mangrove-fringed intertidal system using passive acoustic telemetry over a one-year period. An array of acoustic receivers was designed to track animal movements inside mangrove stands. Juvenile blacktip reef sharks *Carcharhinus melanopterus,* mangrove whiprays *Urogymnus granulatus* and cowtail stingrays *Pastinachus ater* were equipped with acoustic transmitters and released in Pioneer Bay, Orpheus Island between October 2020 and December 2021. The results demonstrated that the focal species used the intertidal mangrove system differently, with blacktip reef sharks and mangrove whiprays showing close association with mangroves. Seasonal change in mangrove use was observed where the presence of blacktip reef sharks and mangrove whiprays inside mangrove habitats increased between September and November, possibly related to the presence of adult sharks for pupping. Juvenile blacktip reef sharks were detected inside mangroves during the day and were rarely detected at night. Mangrove habitats are possibly too structurally complex to allow easy navigation in darkness. Cowtail stingrays showed little association with mangrove habitats compared to the other species. The results suggest that mangrove habitats offer predation refuge for some species, but species have individually adapted to using mangroves and adjacent habitats depending on their ecological needs and trade-offs.

Given the ecological services that mangroves offer, particularly to species at the vulnerable juvenile life stage, loss of mangrove habitats most likely affects a range of elasmobranch species. However, there is hope as conservation of mangroves and their ecological function will benefit elasmobranch species, and in turn, conservation of elasmobranch species and well-balanced populations will benefit the health of coastal ecosystems and communities, including mangroves. To protect fundamental components of healthy coastal communities, conservation effort of both mangroves and elasmobranchs is a key. From a broader perspective, wetlands including mangroves and megafauna including elasmobranchs are interrelated and both play important roles in the ecological functions within coastal ecosystems. The outcome of this research will add knowledge on the relationship between wetlands and megafauna and inform protection and conservation priorities of both that are highly threatened.

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CHAPTER 1

General Introduction

Elasmobranchs (sharks and rays) are a monophyletic group of mostly marine predators, with approximately 1250 species known from tropical to boreal, shallow to deep waters of the world. They use a wide range of habitats and have diverse morphologies and ecological niches (Ebert *et al.* 2013; Last *et al.* 2016). Elasmobranchs play important ecological roles in the ecosystem mainly as higher order predators or mesopredators, regulating prey populations through direct predation or fear effects (Heupel *et al.* 2014; Roff *et al.* 2016). The presence of predatory sharks can change the diet of mesopredators, and that in turn changes abundance and composition of organisms at the lower trophic level (Barley *et al.* 2017). Many ray species are bottom feeders, and their feeding behaviour modifies and changes the physical state and biological composition of sandflat habitats (O'Shea *et al.* 2012; Takeuchi and Tamaki 2014). In addition, some elasmobranch species are important nutrient vectors between systems by transferring nutrients and egesting materials, ultimately enhancing trophic connectivity between offshore and inshore systems (Williams *et al.* 2018; Peel *et al.* 2019). The functional roles of elasmobranchs are highly diverse, and they contribute to connecting trophic levels and creating trophic linkages across a wide range of marine systems (e.g. coral reefs, offshore, wetlands) (McCauley *et al.* 2012; Shipley *et al.* 2023).

Elasmobranchs are one of the most basal groups of vertebrates and have survived for approximately 400 million years. As the group has overcome at least four mass extinction events, they may be the most successful of all fishes in terms of their historical endurance (Grogan *et al.* 2012). Today, in the Anthropocene, however, elasmobranchs are considered to be one of the most threatened faunal groups in the world. One-third of extant species are threatened with extinction and a recent study assessed the three additional species are likely to be extinct (Dulvy *et al.* 2021). The group is characterised by low productivity due to slow growth, late sexual maturity, low fecundity and longevity. These characteristics mean that overexploitation is the biggest threat to species, followed by loss and degradation of habitats and climate change. Particularly, species in tropical and subtropical coastal seas have a very high risk of extinction due to a combination of high levels of intensive fishing and high risk of habitat loss and degradation partly due to ocean warming. As a result, tropical coastal sharks and rays are the most threatened group of elasmobranchs (Dulvy *et al.* 2021). For example, sawfishes (family Pristidae) are among the most threatened marine fish species, living in the shallow coastal and intertidal tropical waters (Last *et al.* 2016). Currently, 4 of 5 sawfish species are listed as Critically Endangered under the International Union for Conservation of Nature (IUCN) Red List (Carlson *et al.* 2022; Espinoza *et al.* 2022; Grant *et al.* 2022; Harry *et al.* 2022) and recent research shows that overfishing and habitat loss have led to extirpation in 55 of 90 nations examined (Yan *et al.* 2021). Extinction of elasmobranch species leads to a loss of the important ecological activities, causing ecological imbalance and damaging healthy functions of the ecosystem (Baum and Worm 2009). Thus, research need is high for elasmobranchs, particularly species that live or spend some part of their life in tropical coastal habitats, and knowledge on how elasmobranch species associate with these habitats will help guide conservation processes that are currently being developed and implemented (Field *et al.* 2009).

While overexploitation is the primary threat to elasmobranchs, the loss and degradation of coastal habitats is the secondary threat to the group (Dulvy *et al.* 2021) and some of the most critical losses of coastal habitats have been in coastal wetlands, such as mangroves, seagrasses and salt marshes (Waycott *et al.* 2009; Davidson 2014; Sievers *et al.* 2019). Mangroves are among the most productive ecosystems occurring on tropical and subtropical coasts, islands and estuaries (e.g. Ewel *et al.* 1998; Kathiresan and Bingham 2001). In the strictest sense, mangroves are woody plants that grow at the interface between terrestrial, estuarine and nearshore marine ecosystems (Kathiresan and Bingham 2001). Mangroves provide a wide range of benefits to coastal communities; they are important sinks and source of carbon (Alongi 2014) and trap sediments and protect shoreline and coastal area from erosion and hydrodynamic events (e.g. tsunami, cyclone) (Mazda *et al.* 2007; Alongi 2008). High productivity of mangrove ecosystems is supported by efficient nutrient recycling and food webs, and net primary production of mangroves rivals that of tropical evergreen forests (Komiyama *et al.* 2008; Reef *et al.* 2010). Mangrove forests are biodiversity hotspots hosting economically and ecologically important terrestrial and aquatic species (Manson *et al.* 2005; Duke *et al.* 2007). Mangrove habitats are unique and prominent components among coastal systems because of their physical complexity, productivity and variable environments. Dense mangrove forests form a structurally complex habitat in nearshore or riverine regions with unique root structures, which offer some degree of protection to inhabitants (Srikanth *et al.* 2015).

A variety of organisms, including barnacles, sponges, molluscs, crustaceans, tunicates, teleost fishes, elasmobranchs, amphibians, reptiles, birds and mammals are reliant on mangrove habitats (Nagelkerken *et al.* 2008; Luther and Greenberg 2009; Rog *et al.* 2017). For example, mangrove use by teleost fish has been studied over the last 50 years and the importance of mangrove habitats for fishes is well recognised (Faunce and Serafy 2006). For example, some teleost species, such as snappers and grunts are known to swim among or near mangrove root structures because they provide shelter and shade (Cocheret de la Morinière *et al.* 2004; Nagelkerken *et al.* 2010). Barracuda use mangrove roots for their ambush hunting and piscivorous snappers use mangrove habitats for feeding (Verweij *et al.* 2006a; Verweij *et al.* 2006b). In addition, the function of mangrove habitats is also regionally different;

Caribbean mangroves harbour high density of juvenile fishes with high species richness and serve as important nursery habitats for teleosts, while Indo-Pacific mangroves are used by fewer species as nurseries due to larger tidal amplitude (Igulu *et al.* 2014). For megafauna, such as sea turtles, dolphins, dugongs, crocodiles and elasmobranchs, a recent study suggested that coastal wetland habitats are important in supporting and sustaining their populations (Sievers *et al.* 2019). Compared to teleost taxa, however, our understanding of the importance of mangroves to megafauna is limited and there is a knowledge gap in the functions of mangrove habitats to these groups.

A growing number of studies have addressed how elasmobranchs utilise nearshore habitats (Knip *et al.* 2010; Speed *et al.* 2011; Leurs *et al.* 2023), yet little research has primarily focused on the function of mangrove habitats for elasmobranchs and the association of elasmobranchs with mangroves remains understudied and undervalued (Sievers *et al.* 2019). As such, our current understanding of mangrove use by elasmobranchs is supported by relatively few studies that have considered the importance of mangroves (Guttridge *et al.* 2012; Escalle *et al.* 2015; Hussey *et al.* 2017; Kanno *et al.* 2019). According to some previous studies, mangroves provide essential services to some elasmobranch species, including predator refuge and possible feeding habitats (Simpfendorfer *et al.* 2010; Guttridge *et al.* 2012; Kanno *et al.* 2019). The use of mangroves appears to vary by species, age class, season and regions (e.g. White *et al.* 2014; Escalle *et al.* 2015), but the range of studied species and the types of mangroves (shape of mangrove forests, marine, estuarine or freshwater, tidal effect etc.) are limited. Consequently, at present, the functions of mangrove habitats have been extrapolated based on the data from a few well-studied species and regions, and there is a need to increase the variety of species and systems examined.

Loss of mangrove forests has occurred globally through coastal development for activities such as aquaculture, agriculture, infrastructure and tourism (Faridah-Hanum *et al.* 2014; Richards and Friess 2016; Goldberg *et al.* 2020). Over the past 30 years, more than one-third of mangrove extent has been lost worldwide (Valiela *et al.* 2001; Alongi 2002; Hamilton and Casey 2016). In particular, Asian mangrove cover has experienced the largest net loss, with approximately 1.9 million ha (25% of the 1980 extent) of mangroves having disappeared between 1980 and 2005, followed by North and Central America with 0.7 million ha loss (23% of the 1980 extent) (FAO 2007). More recent estimates show that more than 50% of mangroves have been lost in Southeast Asian regions (including in Indonesia, Malaysia and Philippines) that are home to the highest diversity of mangrove species (Ellison 2014). Though the rate of loss has slowed down for the last two decades (FAO 2023), mangrove loss is ongoing globally at the rate of 0.16 % area lost per year and more severe in some regions despite their ecological significance (Friess *et al.* 2019). In addition to deforestation activities, climate change is most likely exacerbating the status of global mangrove covers via sea level rise and ocean acidification (Lovelock *et al.* 2015; Walden *et al.* 2019). Loss of mangroves is causing loss and degradation of habitats and negatively affecting species distribution, biodiversity, ecological functions and habitat connectivity between mangrove forests and adjacent systems (Walters *et al.* 2008; Malik *et al.* 2015; Gillis *et al.* 2017). Degraded mangrove habitats are estimated to have suffered from a loss of 20% benthic meiofaunal biodiversity and an 80% reduction in decomposition rates mediated by microbial cycles (Carugati *et al.* 2018). Such significant loss of ecological functions and benthic faunal communities at the base of the mangrove food webs can cause negative impacts on mangrove productivity, resulting in effects on organisms at higher trophic levels due to loss of habitat and dietary resources (Duke *et al.* 2007; Carugati *et al.* 2018). Despite the current vulnerable status of mangroves, it remains unclear how mangrove loss is affecting species that depend on mangrove habitats (Upadhyay *et al.* 2002; Wilson *et al.* 2010).

In one of the only studies related to elasmobranch use of mangroves, Jennings *et al.* (2008) found that a reduction in survival of lemon sharks (*Negaprion brevirostris*) was correlated with the loss of mangroves and other essential habitats due to infrastructure development. Degradation of mangrove habitats can cause an increase in species' exposure to predators and a decline in prey species (Jennings *et al.* 2008; Curtis *et al.* 2013), change in genetic diversity and a reduction in juvenile mortality (DiBattista *et al.* 2011). Given the global declining status of mangrove habitats, the relationship and the critical ecological processes between mangroves and elasmobranchs needs to be better understood. Consideration of the mangrove-elasmobranch association is particularly crucial because species conservation management is now shifting towards habitat-based efforts as recommended by Red List assessments of the IUCN (Rodrigues *et al.* 2006). Better understanding of habitat association of elasmobranchs will be effective in identifying ways to improve conservation management not only for elasmobranch species but also for mangrove forests that are under threat of deforestation as elasmobranchs and mangrove systems interplay each other via critical ecological processes. To predict how mangrove loss is affecting elasmobranch populations, improved knowledge of mangrove use by elasmobranchs and function of mangrove habitat for elasmobranchs is urgently required.

The present research aimed to reveal how elasmobranchs use mangrove habitats and define the functional roles and importance of mangrove habitats to elasmobranchs. For this aim, this thesis was focused on investigating the links between mangrove habitats and certain elasmobranch species, with particular emphasis on how elasmobranchs use fringing mangrove habitats in an intertidal bay. To identify the habitat functions of mangroves, detailed study inside mangroves was necessary and this PhD research project was designed to observe fine-scale association between mangrove habitats and elasmobranch species in an intertidal clear-water mangrove system. To set the scene for this research, CHAPTER 2 reviewed the current knowledge of the relationship between mangroves and elasmobranchs. This literature review work identified a number of research questions that could be the focus of future research. CHAPTER 3 looked at life history of a data deficient species that are known to have a close association with mangrove habitats. Life history characteristics of graceful sharks *Carcharhinus amblyrhynchoides* were investigated and interactions between their use of mangrove habitats and life history were considered. CHAPTER 4 examined the efficacy of acoustic telemetry in structurally complex, shallow water mangrove habitats to test if the acoustic telemetry could be used for elasmobranch tracking in mangrove habtiats. To the best of my knowledge, acoustic receivers and transmitters have never been used inside mangrove habitats presumably due to the assumption that acoustic signal would not transmit and be received properly by acoustic telemetry equipment. CHAPTER 4 included range test and receiver performance analysis, followed by animal application tests. This study found that acoustic telemetry inside mangrove habitats can be used for animal tracking. Then, CHAPTER 5 applied passive acoustic telemetry monitoring techniques to juvenile sharks and stingrays to investigate their daily and seasonal patterns of movement and use of an intertidal mangrove system. The differences and similarities in mangrove use by co-occurring elasmobranch species were examined and discussed in CHAPTER 5. Finally, CHAPTER 6 discussed how this PhD research findings add to previous knowledge on mangrove-elasmobranch association and suggested potential applications of the findings from this research and future directions for better understandings of the relationship between mangroves and elasmobranch populations.

CHAPTER 2

Mangrove use by sharks and rays: A review

2.1 Introduction

Mangroves are among the most productive components of intertidal zones, rivers and estuaries of the tropics and subtropics (Kathiresan and Bingham 2001). In the strictest sense, the term mangroves refers to both mangrove plants and the areas dominated by mangrove trees and shrubs (Spalding *et al.* 2010). They occur as narrow fringes along shorelines, estuaries and rivers, or as broad forests covering wide areas of deltas or estuaries (Spalding *et al.* 2010). Mangroves are characterised by unique combinations of structural complexity and biological productivity. Their roots and trunks offer physical structure, which aid in trapping sediments (Furukawa and Wolanski 1996; Chen *et al.* 2018), dampening coastal erosion (Mazda *et al.* 2007) and offering inhabitants shelter from extreme hydrodynamic events (e.g. tsunamis, cyclones) (Dahdouh-Guebas *et al.* 2005; Alongi 2008). Mangroves are highly productive ecosystems, with their primary production equal to that of tropical forests. This productivity is mediated by above- and below-ground biomass, such as mangrove trees (e.g. leaves, seedlings) and algae colonising roots and covering the forest floor (Robertson *et al.* 1992; Alongi 2014). Mangrove-derived nutrients then flow through coastal food webs via water movement (i.e. tide, current) or active animal movement and are used and recycled inside and outside mangrove systems (Adame and Lovelock 2010; Gillis *et al.* 2014).

As mangrove habitats occur at the interface between marine, estuarine and freshwater areas, both biotic and abiotic factors undergo large changes (Knip *et al.* 2010). In mangroves, environmental factors, such as water depth, temperature, salinity, turbidity, wave intensity and dissolved oxygen level are constantly changing at tidal, daily and seasonal time scales (Lam *et al.* 2005). Such fluctuations in environmental factors ultimately determine a pattern in the accessibility of mangrove habitats on a daily or seasonal basis and how useable it is for associated organisms (Bradley *et al.* 2020). Thus, there is no such thing as a “general” or “typical” mangrove habitat and so their functions must be considered carefully and account for local context (Chittaro *et al.* 2005; Bradley *et al.* 2020).

Mangroves provide important habitats to an array of terrestrial and aquatic organisms, including economically and ecologically important species (Nagelkerken *et al.* 2008, Luther and Greenberg 2009, Rog *et al.* 2017); offering inhabiting species shelter, breeding and feeding grounds, and nesting sites (Nagelkerken *et al.* 2008). A wide range of micro- and macro- organisms (e.g. barnacles, tunicates, sponges, molluscs and crustaceans) are found in mangrove trees, roots and sediments, and many of those are the base of mangrove food webs that support mangrove ecosystems (MacDonald and Weis 2013). Mangrove habitats are also used by teleosts and other megafauna, including sea turtles, dolphins, dugongs, crocodiles and sharks and rays (elasmobranchs) (Sievers *et al.* 2019). Thus, mangroves host a high diversity of species of bacteria, fungi, plants and animals, and they form a complex ecosystem as a whole, supporting and sustaining populations of a variety of organisms (Nagelkerken *et al.* 2008; Spalding *et al.* 2010). Despite these important roles, mangroves have been lost at alarming rates over the past century (Polidoro *et al.* 2010; Spalding *et al.* 2010). Between 1980 and 2005, more than one-third of mangrove areas were lost globally (FAO 2007). Although the most recent rate of deforestation has dropped to 3.4 % between 1996 and 2020, the loss of mangrove cover is ongoing globally at 0.16 % area lost per year and more severe in some regions (Friess *et al.* 2019). For example, in Southeast Asia, Central America and the Caribbean, loss is up to 0.7 % area lost per year (Hamilton and Casey 2016; Bunting *et al.* 2022). Major threats to mangroves include coastal development for human activities, such as aquaculture, agriculture, infrastructure and tourism (Richards and Friess 2016; Friess *et al.* 2019; Goldberg *et al.* 2020), and climate change, particularly ocean warming and sea level rise (Lovelock *et al.* 2015; Walden *et al.* 2019). The loss of mangroves affects those organisms that use and benefit from them (e.g. Shinnaka *et al.* 2007, Carugati *et al.* 2018), and the loss of biodiversity is ultimately negatively affecting ecological functions in coastal systems (Carugati *et al.* 2018).

The importance and function of mangrove habitats from coastal systems have received growing attention with increasing concerns for global mangrove loss. For example, the value of mangrove habitats and associated coastal systems for teleost fishes has been intensively studied for the last 50 years and findings have been widely reviewed (e.g. Faunce and Serafy 2006; Nagelkerken *et al.* 2008; Lee *et al.* 2014; Whitfield 2017). For elasmobranchs, there are studies that have examined the importance and function of nearshore or intertidal habitats where mangroves are present (e.g. Knip *et al.* 2010, Leurs *et al.* 2023). Yet, compared to teleosts, fewer studies have been conducted to focus on the importance of mangroves, mangrove habitat and associated coastal systems. At the very least, there is no review available on the value, function and role of mangroves and associated coastal systems to elasmobranchs.

Understanding the relationship between elasmobranchs and mangroves is of growing importance because coastal elasmobranchs are increasingly threatened with extinction. More than one-third of elasmobranchs are now threatened with extinction, and more than 50 % of those threatened species inhabit coastal habitats (Dulvy *et al.* 2021). Habitat loss and degradation is one of the major threats for species, and ongoing degradation of coastal vegetated habitat, including mangroves, can negatively affect coastal elasmobranch populations, such as lowering the survival rate of juvenile sharks (e.g. Jennings *et al.* 2008; Dulvy *et al.* 2021). Therefore, a better understanding of the value and importance of mangroves for this group is urgently required to predict how mangrove loss and alteration of mangrove ecosystem functions will affect elasmobranch populations and their recovery potential, and to help guide habitat-based conservation processes both for mangrove habitats and coastal elasmobranch populations.

The objectives of this work were to: (1) describe the current understanding of the relationship between elasmobranchs and mangroves, (2) identify the important functions of mangrove habitats and associated coastal systems for elasmobranch species, and (3) identify a series of key research questions that will help improve knowledge on the importance of mangroves, mangrove habitats and associated coastal systems to elasmobranch populations. For the purpose, this review specifically used literature where research has been conducted to examine the importance and functional role of mangroves towards the studied species and included research conducted directly inside mangroves (mangrove habitats) and in associated coastal systems.

2.2 Literature review methods

Research articles that discussed the relationships between mangroves and elasmobranch species were reviewed; for example, direct use of mangrove habitat (e.g. rays resting among the root structures), occurrence in mangrove habitats or associated coastal systems (e.g. juveniles showing habitat preference and spending their first several years in coastal systems that include mangrove habitat) or evidence of direct or indirect trophic linkage (e.g. species consuming mangrove-derived carbon sources). Conversely, this review did not include studies that were merely conducted in coastal systems and did not discuss the value and/or use of associated mangrove habitat for studied species.

Literature searches were conducted using Google Scholar and Web of Science with the search string using a combination of terms “mangrove*”, “shark*”, “ray*”, “elasmobranch*” and “batoid*”. After the search, articles were carefully read and excluded from the list when search terms were used in a different context, such as *mangroves* in *Shark* River or when the study merely described the presence of mangroves but did not discuss their importance or functional role to the studied elasmobranch species. The reference lists of searched articles were also examined and added to the review if relevant. After the literature search, each article was examined and checked if the research discussed or mentioned the importance or the roles of mangroves for the studied elasmobranch species. This process was performed to differentiate studies that merely described the presence of mangroves in a study site from studies that actually focused on the benefits/roles of mangrove presence.

2.3 Occurrence of elasmobranchs in mangrove systems

Total 65 papers were identified that recorded shark or ray species occurring in mangrove habitats or associated coastal systems and ascertained the relationship between mangroves and species i.e. value, use and linkage (Appendix 1). While research on mangroves has occurred globally within their distribution, research on the use of mangrove habitat and associated coastal systems by elasmobranchs is more geographically limited and biased. Of the 65 papers identified, research was most commonly conducted in The Bahamas (18), Florida, US (16) and Queensland, Australia (14) (**Fig. 2.1**). As some studies conducted research on multiple species and one study was conducted in multiple locations, a sum of total species and locations studied was 100. Unfortunately, there is little overlap between well-studied areas and the regions that have suffered from large net loss of mangroves including Asia, Africa and North (outside of Florida), Central and South America (FAO 2007; Richards and Friess 2016; Goldberg *et al.* 2020), and where elasmobranch populations are most threatened, including the Indo-West Pacific around Southeast Asia, South America and East and West Africa (Dulvy *et al.* 2021). Research is urgently needed in those regions to better understand how mangrove loss is potentially affecting elasmobranch populations.

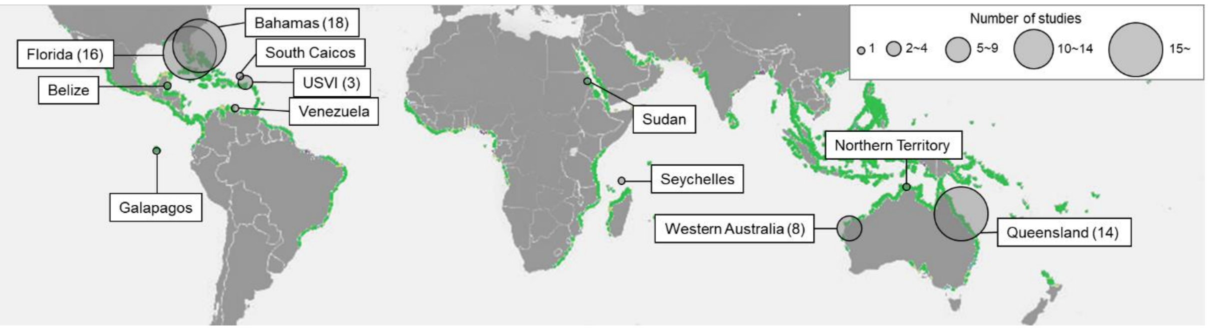


Fig. 2.1 Map of the studied areas where research on the relationships between mangroves and elasmobranchs has been conducted. The data only include studies that discussed the relationship between mangroves and species i.e. the studies that merely mentioned the presence of mangroves in the study site but did not discuss the relationship were not counted. Green dots indicate distribution of mangroves. Mangrove distribution map was sourced from Mapping Ocean Wealth Explorer (https://maps.oceanwealth.org/mangrove-restoration/).

Research on the relationships between elasmobranchs and mangrove systems has been conducted for 28 species, representing 13 genera and 7 families (sharks: 18 species, 6 genera and 3 families; rays: 10 species, 7 genera and 4 families) (**Fig. 2.2**). Sixty-seven of the 100 species-locations studied were restricted to two groups: 39 studies of requiem sharks (family Carcharhinidae) and 20 of sawfishes (family Pristidae). Whether this taxonomic representation is the result of bias in research studies (e.g. size, commercial value, conservation status, ease of study) or a reflection of the groups that occur commonly in coastal tropical areas and as such are most likely to have the opportunity to use mangrove systems, is currently unclear. Among those well-studied species, the great focus on sawfishes is likely due to their conservation status. A small number of species within the three most commonly reported families account for much of the research available (**Fig. 2.2**). Amongst sharks, the lemon shark *Negaprion brevirostris* is the most studied species (**Fig. 2.3(a)**), with multiple studies also on common blacktip *Carcharhinus limbatus*, bull *C. leucas*, blacktip reef *C. melanopterus* and nervous sharks *C. cautus*. Lemon sharks have been studied for more than 40 years in Bimini, The Bahamas and nearly 2/3 of all the studies found in this review are from this region. Smalltooth sawfish *Pristis pectinata* is the most commonly studied ray species, and two other sawfish species have also been studied (*P. clavata* and *P. zijsron*). An increasing number of studies have revealed a close relationship between sawfishes and mangroves, with conservation concern for this family increasing research needs and interests (Dulvy *et al.* 2016). Other commonly studied rays include giant guitarfish *Glaucostegus typus*, mangrove whipray *Urogymnus granulatus* and cowtail ray *Pastinachus ater* (**Fig. 2.3(b)**-**(d)**).

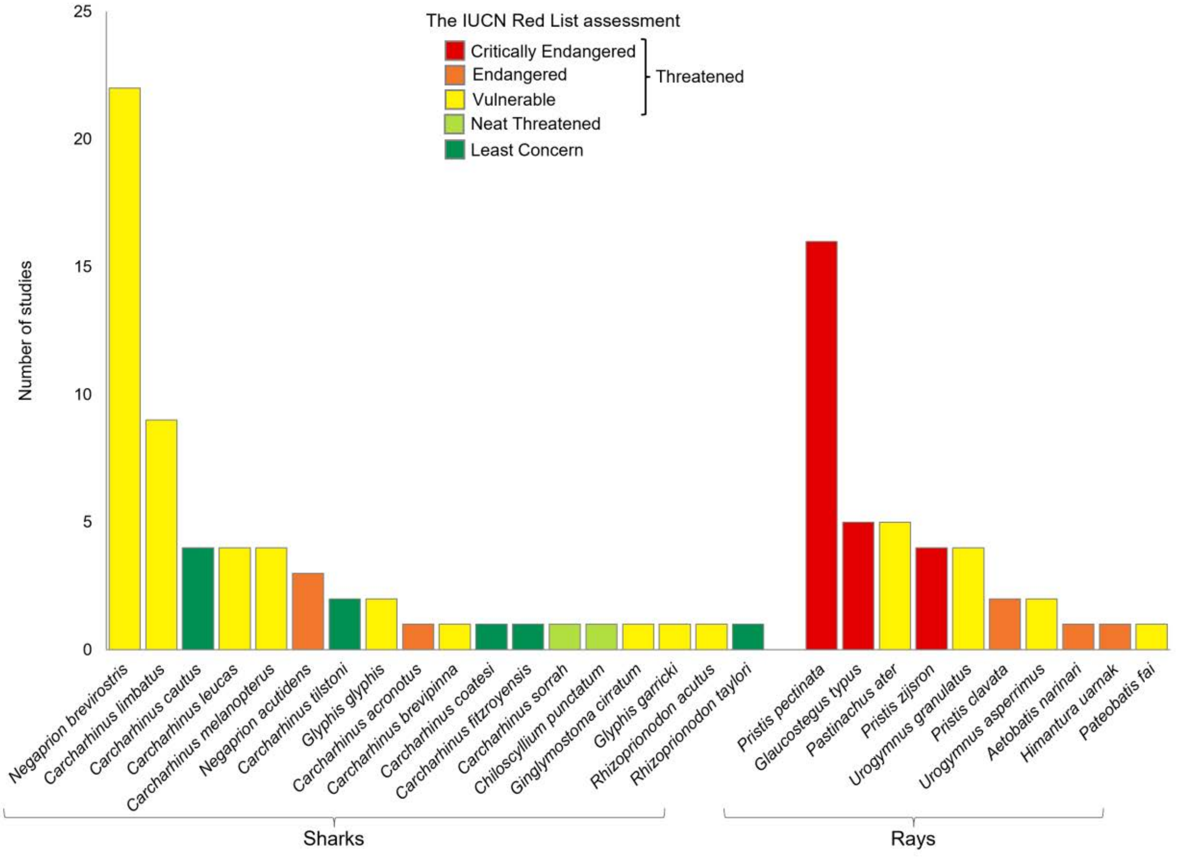


Fig. 2.2 Number of research articles on the relationships between mangroves and elasmobranchs for each species.

Fig. 2.3 Shark and ray species swimming and resting among the mangrove roots (a) lemon shark *Negaprion brevirostris*, (b) cowtail ray *Pastinachus ater*, (c) juvenile mangrove whipray *Urogymnus granulatus* and (d) sub-adult mangrove whipray. Photo credits: (a) Baylie Fadool and Bimini Biological Field Station Foundation; (b), (c) & (d) Colin Simpfendorfer.

One of the challenges in interpreting studies on elasmobranchs and mangrove habitats is that many previous studies have not clearly demonstrated how closely species were associated with mangrove habitat or associated coastal systems. For example, Simpfendorfer and Milward (1993) identified six species of shark from Cleveland Bay, Australia, from fishing surveys and noted that they occurred close to mangrove habitats (i.e. in a mangrove fringed bay), but the study did not demonstrate direct use of mangrove habitat by those species. As other examples, White *et al.* (2014) and Pikitch *et al.* (2005) found the habitat preference of juvenile sharks and rays to coastal systems, but how those species are interacting with mangrove habitats within these systems or if they benefit from the presence of mangroves is unknown. In contrast, Davy *et al.* (2015) and George *et al.* (2019) using acoustic telemetry at Orpheus Island, Australia, reported specific use of mangrove habitat (i.e. inside the mangrove root habitat) and associated coastal habitats, by mangrove whiprays and blacktip reef sharks that were repeatedly resting under or swimming within the root structure (**Fig. 2.3**). Newman *et al.* (2010) is another example of investigating a detailed role of mangrove habitat and associated coastal system, finding overlap between lemon shark diet and mangrove communities (e.g. the community composed of mangroves and mangrove-associated organisms, including micro-organisms, plants and animals, Kathiresan and Bingham 2001), suggesting sharks relied on the mangrove community for their diet. This level of detail is what is needed from more studies to closely assess the functional role of mangroves to elasmobranchs. This is not limited to direct habitat use by the occurrence of species but also indirect benefits from the mangrove-derived productions. Our understanding of how important mangroves are for this group is limited due to a lack of research on how closely shark and ray species are associated with mangrove habitats.

The majority (44 out of 65) studies on sharks and rays associated with mangrove habitats focused on juveniles, often identifying mangrove habitat or associated coastal systems, as nursery areas (see 2.4.3. nursery area section for more on this topic). The preponderance of studies on juveniles may be because for many coastal species, the youngest animals are found in the shallowest waters, and so would be more likely to be associated with coastal systems where mangrove trees can survive. However, adult individuals of some species are known to occur adjacent to mangrove habitats and may gain benefits from mangrove ecosystems (e.g. blatcktip reef sharks Chin *et al.* 2016; nervous sharks Escalle *et al.* 2015; spottail sharks *C. sorrah* Knip *et al.* 2012; freshwater sawfish *P. pristis* Morgan *et al.* 2015). Further research focused on adults associated with mangrove habitats or associated coastal systems will help resolve the reasons for this bias in studies and better elucidate the importance of mangrove habitats for adult elasmobranchs.

The conservation status of most species of elasmobranch associated with mangrove habitats and associated coastal systems is of concern. Twenty-one of 28 species from the literature search are in a threatened category based on recent International Union for Conservation of Nature (IUCN) Red List assessments: 13 Vulnerable, 5 Endangered and 3 Critically Endangered (**Fig. 2.2**). The only species not in a threatened category were four carcharhinids that occur only in northern Australia and southern Papua New Guinea. All ray species found in this review are categorised as Threatened. This result is not surprising given that coastal elasmobranch species are the most threatened elasmobranch, and are focused by such ecological research (Dulvy *et al.* 2021). Further research to understand the level of association with, and benefits derived from mangroves, will benefit conservation efforts for these species. One successful example of where research is informing conservation of a threatened elasmobranch species is found in the work on sawfish in US waters (e.g. Norton *et al.* 2012; Dulvy *et al.* 2016; Brame *et al.* 2019). This work is underpinning increased conservation efforts by identifying their critical habitat and implementing monitoring.

2.4 Functions of mangroves for elasmobranch species

Mangroves have been documented to provide a broad range of ecosystem goods and services, in part because they occur at the junction of the marine and terrestrial realms, have high primary productivity, and complex trunk and root structures. These functions include providing habitat for both terrestrial and aquatic organisms, refuge from adverse conditions, a source of primary productivity and areas for feeding, mating and birthing, improving water quality, reducing coastal erosion and mitigating storm impacts on coastal systems (Alongi 2008, Nagelkerken *et al.* 2008, Lee *et al.* 2014). Here, this review considers only those functions that have been identified, or hypothesised, to be relevant for elasmobranchs.

2.4.1 Physical shelter and refuge from predation

Densely growing mangrove trees offer effective shelter from potential predators where organisms can hide and rest between or under the complex structures formed by the trunks and roots (e.g. Cocheret de la Morinière *et al.* 2004; Mumby 2006). This function has been demonstrated for a number of shark and ray species using at least two different approaches. Firstly, experimental studies have been conducted to understand predation risk and habitat use in a controlled setting. For example, Stump *et al.* (2017) demonstrated that juvenile lemon sharks (~60cm precaudal length [PCL]) tended to swim close to artificial mangrove units when a large potential predator (a 116 cm PCL lemon shark) was present, suggesting the importance of root-like structures for their anti-predator behaviour. The second line of evidence is direct observation using either video or photos (e.g. Davy *et al.* 2015; Kanno *et al.* 2019), or telemetry (e.g. George *et al.* 2019; Martins *et al.* 2020a; Martins *et al.* 2020b). For example, Kanno *et al.* (2019) used video cameras mounted in mangrove trees to demonstrate that small mangrove whiprays used mangrove root habitats on high tides while large sharks were excluded. Martins *et al.* (2020ab) confirmed this behaviour using satellite-linked data loggers and acoustic telemetry. Based on field observations, a range of species are hypothesised to display refuging behaviour in structurally complex mangroves, such as smalltooth sawfish (Simpfendorfer *et al.* 2010; Poulakis *et al.* 2011; Hollensead *et al.* 2018; Lear *et al.* 2019), dwarf sawfish (Stevens *et al.* 2008), mangrove whiprays, cowtail rays (Kanno *et al.* 2019, Martins *et al.* 2020b) and blacktip reef sharks (George *et al.* 2019). Additionally, turbid water in mangrove habitats is thought to reduce the ability of predators to locate prey, decreasing predation risk for inhabitants (Cerutti-Pereyra *et al.* 2014), but this is yet to be specifically tested.

The ability of elasmobranchs to use mangrove habitat as a refuge from predation is likely to be a function of a number of physical features of the habitat. The level of tidal inundation is one important factor since habitats can only be accessed when there is sufficient water present (Davy *et al.* 2015). Given the nature of tides, greater access to the habitat would be available during spring tides compared to neap tides. In fact, depending on the amount of tidal variation, there may be some periods during neap tides when no access to mangroves is available. In some microtidal systems such as in parts of the Caribbean, there is near continuous access to mangrove habitat, albeit a very shallow water (Sheaves 2005; Krumme 2009). A second physical characteristic that affects the level of refuge is the complexity of mangrove habitat. This is a function of at least two factors: the density of trees and the form of their root structure. Across the full range of mangrove species (73 species and hybrids, Spalding *et al.* 2010), there are many root structures, from simple straight trunks and pneumatophores and knee roots (e.g. *Avecinnia, Bruggeria*), to moderately complex buttress roots (e.g. *Heritiera*), to highly complex prop roots (e.g. *Rhizophora*) (Ewel *et al.* 1998). Hollensead *et al.* (2018) demonstrated using acoustic tracking that juvenile smalltooth sawfish were more commonly found in areas with higher prop root density, supporting the hypothesis that more complex habitats are likely to provide greater refuge.

Characteristics of the elasmobranch species also are important for how mangrove habitat is used as a refuge. For example, body size is one of the characteristics that can affect mangrove refuge use. The complexity of mangrove habitat, especially those composed of mangrove species that have dense prop roots, means that smaller sized individuals will likely have greater access and manoeuvrability within mangrove habitat and so be more likely to take advantage of it as a refuge. This hypothesis is supported by research showing that most species confirmed to occur within mangrove habitat are often newborn or small juveniles, including lemon sharks (e.g. Morrissey and Gruber 1993a), blacktip reef sharks (e.g. George *et al.* 2019) and mangrove whiprays (e.g. Davy et al 2015). However, there are some reports of larger juveniles and even adults refuging within mangrove habitat, including adult dwarf sawfish (Stevens *et al.* 2008) and mangrove whiprays (C. Simpfendorfer unpubl. data) (Fig. 2.3(d)). In the case of dwarf sawfish, large potential predators (e.g. great hammerheads *Sphyrna mokarran*, tiger sharks *Galeocerdo cuvier* and estuarine crocodiles *Crocodylus porosus*) were observed in the area (Stevens *et al.* 2008) suggesting that the refuge function can still be important even for larger individuals. Additionally, body shape is also likely to play a role in the successful use of mangrove habitat as a refuge from predation. Dorso-ventrally flattened rays, for example, would be able to gain access to mangrove habitat on lower tidal heights than deeper bodied species such as sharks, allowing them to remain in shallow water longer, as their water depth requirements are lower. Respiratory mode may be another characteristic of species that allow for the use of mangrove habitat as a refuge. Species that can rest on the bottom and use buccal pumping and spiracles to enable water flow over their gills should be able to use the most complex of mangrove habitats, including resting under and among roots and trunks (Fig. 2.3). This type of behaviour is regularly observed with mangrove whiprays that spend long periods resting in complex structure (Davy *et al.* 2015). Such concealment would have significantly greater benefit for such species than for ram ventilating species that must continue to swim and manoeuvre within complex habitats.

To date, few studies have considered the importance of biological and physical features of elasmobranchs to the level of refuge from predation that elasmobranchs generate from mangrove habitats (e.g. Stump *et al.* 2017; Kanno *et al.* 2019). Future research that investigates those characteristics will enhance our understanding of the protective role that mangrove habitats play for elasmobranchs.

2.4.2 Feeding grounds and food hotspots

Due to their high primary productivity, mangrove communities are thought to be a good food source to a wide range of organisms, including crustaceans (Wassenberg and Hill 1993) and teleosts (Nagelkerken and van der Velde 2004a). The importance of mangrove communities for teleost feeding is well studied, and accordingly, both mangrove residents and migrants from adjacent habitats feed in mangrove habitats (e.g. Nagelkerken *et al.* 2000a; Nagelkerken and van der Velde 2004a; Nagelkerken and van der Velde 2004b; Verweij *et al.* 2006a; Verweij *et al.* 2006b; Nanjo *et al.* 2008). Mangrove habitats attract a variety of invertebrates and vertebrates partly because of such substantial feeding opportunities, and thus, are considered to host many potential prey items for some elasmobranchs. Newman *et al.* (2010) is one of the only studies that directly examined stomach contents of a shark and faunal communities in a mangrove habitat where the sharks occur. They found a high overlap between the diet of juvenile lemon sharks and the faunal communities in the mangrove habitats in Bimini, The Bahamas. Recently, Kanno *et al.* (2019) conducted stationary video monitoring using above water cameras and observed stingray feeding behaviour among mangrove roots multiple times, which may be the first direct observation of an elasmobranch species feeding directly in mangrove habitats.

Although direct observation of feeding activity by elasmobranchs is scarce, an indirect approach is to compare mangrove-derived carbon stable isotope signatures and elasmobranch diets. For example, Hussey *et al.* (2017) conducted active acoustic telemetry tracking and stable isotope analysis (carbon and nitrogen isotopes) on juvenile lemon sharks in Bimini to assess the foraging locations of individuals within the mangrove and adjacent seagrass habitats. Their results highlighted that individuals with slow growth rates and small body size predominantly fed on prey from the sheltered mangrove habitats rather than more open seagrass beds. Shipley *et al.* (2019) conducted multi-tissue stable isotope study in Florida Bay, USA to investigate whether prey resources of coastal shark species were derived from mangrove or coastal neritic (seagrass and/or coral reef) ecosystems. Accordingly, at least for the short-term (2 to 3 months), all shark species tested obtained prey with carbon signatures originating from mangrove primary production, but over the long-term (6 to 12 months), the degree of contribution of mangroves- and neritic ecosystem derived food resources differed depending on species, possibly due to different lifestyle and residency patterns. These studies demonstrate that species do not have to physically occur within mangrove habitats to derive benefits from mangrove productivity. However, a recent study has found that this trophic linkage is not simple and differs between species or the local nutrition availability. Martins *et al.* (2022) showed that two species of stingray that commonly occur in mangrove habitats (mangrove whipray and cowtail ray) had carbon isotope signatures indicating they fed from food webs based on algal productivity in adjacent habitats. These results indicate that just because a species occurs in a mangrove habitat, it does not necessarily derive significant nutrition from food webs based on mangrove primary productivity.

From the reviewed literature, mangrove communities can play an important role in providing food resources to some elasmobranch species at least indirectly and possibly offer physical feeding grounds, but it may be context-dependent. Overall, previous findings are limited and strongly biased towards a small number of well-studied locations (e.g. Bimini, The Bahamas, and Orpheus Island, Australia) and study species (e.g. lemon shark, mangrove whipray). Some mangrove habitats, particularly those with dense prop roots, may be structurally too complex to successfully hunt, especially for those species that consume highly mobile prey (e.g. Newman *et al.* 2010; Lear *et al.* 2019). Thus, the common assumption that mangroves provide feeding opportunity to elasmobranch species remains to be fully tested. Further research is required for various species to confirm that mangrove habitats provide (or do not provide) food resources to elasmobranchs directly or indirectly.

2.4.3 Nurseries

One of the most commonly assigned functions of mangrove habitats and associated coastal systems is as nursery areas, not only for elasmobranchs (Heupel *et al.* 2018) but also teleosts (Nagelkerken *et al.* 2000b; Nagelkerken 2009) and crustaceans (Primavera 1998). For elasmobranchs, this review identified 28 research articles that met all three nursery criteria proposed by Heupel *et al.* (2007) demonstrating mangrove habitats are important nursery areas for at least 22 species (Table 2.1). The use of coastal systems, and especially mangrove habitat within these systems, as nursery areas by elasmobranchs likely occurs because they provide an abundance of food and protection from predators (Heupel *et al.* 2007). As identified in the previous sections, both of these are features of mangrove habitat that are used by juvenile elasmobranchs.

Table 2.1 A list of species known to use mangrove systems as a nursery area. Literature cited as a reference in this table is comprehensive list of research articles that meet all three nursery criteria proposed by Heupel *et al.* (2007). Abbreviations for the IUCN Red List status: Least Concern (LC), Vulnerable (VU), Endangered (EN) and Critically Endangered (EN).

Species	IUCN Red List status	Location	Mangrove systems	Reference

Sharks	*Carcharhinus coatesi*	LC	Queensland, Australia	Coastal fringing mangroves	Simpfendorfer and Milward (1993)
	Carcharhinus fitzroyensis	LC	Queensland, Australia	Coastal fringing mangroves	Simpfendorfer and Milward (1993)
	Carcharhinus leucas	VU	Florida, USA	Estuarine and riverine mangroves	Simpfendorfer *et al.* (2005) Wiley and Simpfendorfer (2007) Heupel and Simpfendorfer (2008) Heupel *et al.* (2010) Curtis *et al.* (2011)
	Carcharhinus limbatus	VU	United States Virgin Islands, USA	Coastal fringing mangroves	DeAngelis *et al.* (2008) Legare *et al.* (2015)
			Santa Cruz Island, Galapagos	Coastal fringing mangroves	Llerena *et al.* (2015)
			Queensland, Australia	Coastal fringing mangroves	Simpfendorfer and Milward (1993)
	Carcharhinus melanopterus	VU	Queensland, Australia	Coastal fringing mangroves	Chin *et al.* (2013c)
	Carcharhinus tilstoni	LC	Queensland, Australia	Coastal fringing mangroves	Simpfendorfer and Milward (1993)
	Ginglymostoma cirratum	VU	Glover's Rees, Belize	Coastal fringing mangroves	Pikitch *et al.* (2005)
	Glyphis garricki	VU	Western Australia	Estuarine and riverine mangroves	Morgan *et al.* (2011a)
	Glyphis glyphis	VU	Western Australia and Northern Territory, Australia	Estuarine and riverine mangroves	Pillans *et al.* (2009)
			Queensland, Australia	Riverine mangroves	Lyon *et al.* (2017)
	Negaprion acutidens	EN	Western Australia	Coastal fringing mangroves	Oh *et al.* (2017)
	Negaprion brevirostis	VU	Bimini, Bahamas	Coastal mangroves	Morrissey and Gruber (1993)

					Feldheim *et al.* (2002) Chapman *et al.* (2009) Guttridge *et al.* (2012)
			United States Virgin Islands, USA	Coastal fringing mangroves	DeAngelis *et al.* (2008) Legare *et al.* (2015)
	Rhizoprionodon acutus	VU	Queensland, Australia	Coastal fringing mangroves	Simpfendorfer and Milward (1993)
	Rhizoprionodon taylori	LC	Queensland, Australia	Coastal fringing mangroves	Simpfendorfer and Milward (1993)
Rays	*Glaucostegus typus*	CR	Western Australia	Fringing mangroves	Cerutti-Pereyra *et al.* (2014)
	Himantura uarnak	EN	Western Australia	Fringing mangroves	Cerutti-Pereyra *et al.* (2014)
	Pastinachus ater	VU	Western Australia	Fringing mangroves	Cerutti-Pereyra *et al.* (2014)
			Queensland, Australia	Fringing mangroves	Davy *et al.* (2015)
	Pristis clavata	EN	Western Australia	Estuarine and riverine mangroves	Morgan *et al.* (2011)
	Pristis pectinata	CR	Florida, USA	Coastal, estuarine and riverine mangroves	Wiley and Simpfendorfer (2007) Simpfendorfer *et al.* (2010) Poulakis *et al.* (2011) Norton *et al.* (2012) Poulakis *et al.* (2013) Carlson *et al.* (2014)
	Pristis pristis	CR	Western Australia	Estuarine and riverine mangroves	Whitty *et al.* (2008)

Pristis zijsron	CR	Western Australia	Estuarine and riverine mangroves	Morgan *et al.* (2011) Morgan *et al.* (2015)
		Red Sea, Sudan	Fringing mangroves?	Elhassan (2018)
Urogymnus asperrimus	VU	Western Australia	Fringing mangroves	Cerutti-Pereyra *et al.* (2014)
Urogymnus granulatus	VU	Queensland, Australia	Fringing mangroves	Davy *et al.* (2015)

Neonates and small juveniles (the age classes that occupy nursery areas) of some elasmobranch species are regularly observed within fringing, riverine and dwarf mangroves at many locations; and there is a consensus that habitats in mangrove systems are often used as pupping grounds or nursery areas (e.g. Heupel *et al.* 2018). Although parturition has rarely been directly observed, anecdotal evidence suggests that some species give birth in mangroves habitats or associated coastal systems, including lemon sharks (Gruber *et al.* 2001; Feldheim *et al.* 2002; DeAngelis *et al.* 2008; Henderson *et al.* 2010), sicklefin lemon sharks *N. acutidens* (Oh *et al.* 2017), blacktip reef sharks (Chin *et al.* 2013, Oh *et al.* 2017), nurse sharks *G. cirratum* (Pikitch *et al.* 2005), smalltooth sawfish *P. pectinata* (Poulakis *et al.* 2016), giant shovelnose rays (White *et al.* 2014) and southern stingrays *Hypanus americanus* (Pikitch *et al.* 2005). Lemon sharks in Bimini, The Bahamas, have been well studied using long-term tagging and genetic methods and revealed mature females return to their natal nursery area associated with mangrove habitats to give birth (known as natal philopatry) (Feldheim *et al.* 2014). Similarly, pregnant female smalltooth sawfish show philopatric movement to mangrove-lined nearshore nurseries in mangrove-fringed estuarine systems for parturition (Poulakis *et al.* 2016). After pupping, neonates tend to remain in their natal areas for an extended period, suggesting the importance of those habitats for juvenile survival as potential nursery grounds (Gruber *et al.* 2001; Chapman *et al.* 2009).

Mangrove associated nursery sites have often been considered to be used by juvenile individuals for their first 2 to 3 years (Gruber *et al.* 1988; Morrissey and Gruber 1993a); however, the duration of nursery dependence varies by species and is not well examined. Chapman *et al.* (2009) is the exception, testing the question of how long individuals stay within nurseries. They found that more than half of up to 6-year-old lemon sharks still remained in the same nursery area. Similarly, Morgan *et al.* (2011) and Morgan *et al.* (2015) revealed that freshwater sawfish stayed in nursery sites in tidal mangrove creeks for 3 to 4 years and thus the nursery areas are critical for freshwater sawfish early life-history stages from neonates to sub-adults. These findings suggest that mangrove habitats and associated coastal systems can act as a nursery longer than previously expected, not only small-sized individuals (e.g. neonates) but also relatively large-sized individuals (e.g. 5-6 years old, possible sub-adults).

The use of mangrove habitats and associated coastal systems as nursery areas by elasmobranchs is relatively well documented in research publications and has demonstrated that they can play an important role in supporting species at their most vulnerable life stage. It must be noted, however, that most of these previous studies were conducted in estuarine or coastal areas fringed by mangroves rather than directly in mangrove habitats, and thus have not investigated the direct association between mangrove habitats and elasmobranchs. Thus, if the presence of mangrove habitats actually benefits elasmobranchs, or whether it is a coincidence based on preference for similar physical environments (e.g. shallow, low salinity areas) is unknown for many species, but should be tested with further research. Furthermore, fish-mangrove research has now come to the consensus that nursery function is context-dependent and not equivalent between mangrove habitats and associated coastal systems in different locations (e.g. Igulu *et al.* 2014) and the function for elasmobranchs may also be variable depending on context and environmental factors specific to a location.

2.4.4 Thermal refuge

The shallow waters in which mangrove habitats occur can rapidly heat during sunny days and reach temperatures that approach or even exceed those which inhabitants can tolerate (Higgins 2018). Such temperatures can have physiological costs to sharks and rays even if they do not reach critical levels (Bouyoucos *et al.* 2018). Mangrove branches and leaves create shade that lowers water temperatures relative to surrounding open areas and in doing so may provide a thermal refuge to inhabitants (Cocheret de la Morinière *et al.* 2004; Davy *et al.* 2015). In the reviewed literature, there are few studies that have tested if elasmobranchs use mangroves as thermal refuge. A recent physiological study found that juvenile mangrove whiprays selected cooler water during the hottest periods of the day to avoid the extreme temperature range, including by inhabiting mangrove habitat (Higgins 2018). While warm water appears to assist effective digestion and food intake of juvenile mangrove whiprays (Tenzing 2014), a cooler water refuge, such as mangrove shade, may also be beneficial to inhabitants particularly when water temperature in sunny areas approaches or exceeds critical thermal maxima (e.g. Cocheret de la Morinière *et al.* 2004; Davy *et al.* 2015; Higgins 2018). Further research into this potential benefit of mangrove habitat is needed before it can be conclusively shown to benefit any species of elasmobranchs.

2.5 Function of elasmobranchs for mangroves and associated coastal systems

Elasmobranch species play various important ecological roles, such as prey population control, energy vectors and bioturbation (physical and ecological engineering) in habitats, including seagrass beds, sandflats and coral reefs (e.g. O'Shea *et al.* 2012; Heupel *et al.* 2014; Roff *et al.* 2016; Leurs *et al.* 2023). The ecological roles of elasmobranchs in mangrove habitats are also likely important, although there is limited research that has specifically investigated their functional roles. As highly mobile predators, elasmobranchs have possible ecological functions, specifically in linking mangrove habitats with the adjacent habitats, including translocating nutrients by their movement. Here, this review gathered information on activities of elasmobranch species that may contribute to the ecological function of mangrove ecosystems.

Active migration of animals between mangrove habitats and adjacent habitats is known to translocate biomass, nutrients and minerals to the other systems, resulting in resource links between habitats (e.g. Kneib 2000). Many elasmobranch species exhibit migration between mangrove and adjacent habitats due to tidal fluctuations (e.g. Stevens *et al.* 2008; Guttridge *et al.* 2012; Davy *et al.* 2015; George *et al.* 2019) and ontogenetic change in biological and ecological needs (Simpfendorfer and Wiley 2005; Whitty *et al.* 2009; Knip *et al.* 2011; Werry *et al.* 2011; Poulakis *et al.* 2013; Carlson *et al.* 2014; White *et al.* 2014; Davy *et al.* 2015). Given the large individual biomass and high mobility of elasmobranch species, their contribution to trophic linkage between different coastal systems is potentially significant (e.g. Shipley *et al.* 2023). Although this has not been quantitatively investigated.

In addition to their movement of nutrients between coastal habitats, feeding activities of sharks result in consumptive and non-consumptive effects on prey species (Ritchie and Johnson 2009). Fear effects, for example, cause the behavioral change of prey species, such as small teleosts and rays refuging in mangrove habitats. Bottom feeding by ray species, alternatively, causes bioturbation that creates, shapes and modifies the physical and biological properties of the habitat, altering microbial loops in the system and ultimately contributing to restructuring food webs and energy and nutrient transfer (O'Shea *et al.* 2012). Thus, elasmobranchs' feeding and predation activities influence community structure and function. Furthermore, elasmobranchs using mangrove habitats may also supply nutrients through excretion and egestion (Allgeier *et al.* 2013; Allgeier *et al.* 2017). Such consumer-mediated nutrient supply can enhance primary production in nutrient-limited ecosystems and consequently influence ecosystem function (Allgeier *et al.* 2013). However, this has not been examined for elasmobranchs in mangrove habitats but has been demonstrated in coral reef habitats (Williams *et al.* 2018).

2.6 Knowledge gaps and future direction related to use of mangrove habitat by elasmobranchs

This review of the available literature indicates that many gaps remain in our knowledge of the relationship between mangrove systems and elasmobranchs. Below this review work identify 8 key questions that need to be addressed and investigated to improve our understanding of this relationship. Data resulting from the suggested research can ultimately inform management and conservation decisions of elasmobranchs, and mangrove habitats and associated systems.

What is the full range of elasmobranch biodiversity that benefits from mangrove habitat?

Research on elasmobranchs that benefit from mangrove habitats currently shows bias toward a small number of species within a limited number of families and in a limited number of geographic locations. Research across more species that potentially utilise and benefit from mangrove and associated coastal habitats is required to understand the extent of benefits that the systems provide. Particularly, given the common occurrence of ray species in shallow nearshore areas and their ecological and economic importance (e.g. Pierce *et al.* 2009; O'Shea *et al.* 2012; Cerutti-Pereyra *et al.* 2014; Barría *et al.* 2015; Haas *et al.* 2017), greater focus on rays in future research would be beneficial. Data resulting from this type of research can be important to elasmobranch conservation efforts as it will assist in understanding the importance of mangrove habitats across a greater number of species in more geographic locations. Further information on threatened or rare species can be gained that will help understand the role of mangrove loss may play as a threat to various elasmobranch species. Research focused in areas where mangroves and elasmobranchs are most threatened, such as Southeast Asia, West and East Africa and South America will be valuable.

How does the mangrove-elasmobranch relationship change with mangrove habitat context?

To date, published research has focused on a small number of systems in a limited range of mangrove contexts (e.g. red mangroves (*Rhizophora*) and clear water adjacent to coral reefs in marine nearshore systems) and thus our current understanding of other mangrove contexts remains poor. For example, it is largely unknown how estuarine and riverine mangroves are used by euryhaline species. Given the unique life history and habitat use of euryhaline species, it would be beneficial for their conservation as mangrove loss may be critical for this group due to their limited and often fragmented distribution (Grant *et al.* 2019). Ecology and interactions of euryhaline species with mangroves are understudied. Future research should focus on a broader range of contexts (e.g. tidal regimes, time of day, turbidity level, mangrove species, geomorphologies, seasons) to better document how these factors affect the relationship between mangrove habitat and elasmobranchs.

What is the behaviour of elasmobranchs within mangrove habitats?

There is limited information available on the behaviour (i.e. feeding, interacting with other species, resting, refuging etc.) of elasmobranchs inside mangrove habitat. This lack of information is mainly because mangrove habitats can be difficult systems to conduct research in due to the complexity of habitats, soft sediments, intermittent inundation and presence of dangerous animals (e.g. crocodiles); and high turbidity of water in many coastal mangrove systems makes direct observation and photography/video difficult to impossible. As a result, limited data is available on what species are doing in mangrove habitats, and where it is available comes mostly from mangroves in clearer water (e.g. Bimini, The Bahamas and Orpheus Island, Australia). Added to this, the habitat complexity makes traditional methods such as fishing and telemetry challenging. Developing techniques to study elasmobranch behaviour in turbid water mangrove habitats will be important in understanding if there are differences with clear water habitats, and what those differences are. Recent advancement in imaging sonar may help reveal the distribution, size and behaviour of species inside mangroves even in low visibility conditions or at night (e.g. Frias-Torres and Luo 2009). This would provide knowledge on how elasmobranch species are using mangrove habitats during the day and at night in clear or turbid water.

How important is mangrove primary production that flows through coastal food webs to elasmobranchs?

There is limited information available on how important mangrove derived carbon is for elasmobranchs, and the evidence that exists is somewhat contradictory (e.g. Shipley *et al.* 2019, Martins *et al.* 2022). The presence of mangroves may be important to elasmobranch species that are physically absent from mangrove habitats because mangroves potentially provide food resources indirectly to species living away from mangrove habitats. Conversely, the loss of mangroves may affect populations that have no direct or clear association with the mangrove habitat. Studies that track the flow of carbon derived from mangrove primary production (e.g. using carbon stable isotope studies) over a range of spatial and temporal scales will help answer this question.

How important are elasmobranchs to habitat connectivity in coastal systems?

Given the mobility of elasmobranchs and their high individual mass compared to other taxa that occur in mangrove habitats, it is hypothesised that they may contribute significantly to translocation of mangrove-derived production. Work to quantify this by examining the role of elasmobranchs in mangrove food webs in conjunction with movement studies will address this question. The role of elasmobranchs in habitat connectivity will be helpful to consider the spatial scale of conservation measures, based on essential ecological processes (e.g. migration, energy transfer and nutrient translocation), which for example have been well studied in coral reef systems (McCauley *et al.* 2012; Espinoza *et al.* 2015; Martín *et al.* 2020). Additionally, such knowledge is important to predict possible effects on habitat connectivity by loss of elasmobranchs species from coastal systems.

What are the physiological benefits of occurring in mangrove habitats?

Preliminary research (e.g. Davy *et al.* 2015; Higgins 2018) suggests that elasmobranchs may derive some physiological benefit from occurring inside mangrove habitats and taking advantage of temperature differences as part of a behavioural thermoregulation strategy. Mangrove-occurring individuals may use mangrove habitats to adopt hunt warm-rest cool or hunt cool-rest warm strategies by shuttling inside and outside mangrove habitats where water temperature is different (e.g. Di Santo and Bennett 2011). Alternatively, species may use the inside mangrove habitats to avoid heat stress by resting under the shade when water temperature is excessively high (e.g. Bouyoucos *et al.* 2018). This hypothesis requires further investigation using a range of experimental and field studies. If there are physiological benefits from using mangrove habitats, then this work would provide information on the costs that the loss of mangroves would have on elasmobranch populations, especially those species with elevated risk of extinction.

What are the consequences of mangrove loss to elasmobranch populations?

Given the substantial loss of mangroves and the demonstrated roles that they play for elasmobranchs, it is likely that there are significant consequences of mangrove loss to elasmobranch populations. Loss and degradation of habitats are one of the major threats to coastal elasmobranchs (Dulvy *et al.* 2021) and to our knowledge, Jennings *et al.* (2008) is the only study that has investigated the impact of loss of mangrove habitats on survival rate of local populations of an elasmobranch. The impacts of habitat loss and degradation can be broad, such as reducing the quantity and quality of food, losing the key habitat for the early life stages of species (i.e. breeding or nursery habitats), reducing habitat connectivity (Sievers *et al.* 2019), and affecting life history parameters (e.g. survival, growth, reproduction). There is a positive correlation between mangrove cover and teleost species diversity, and population decline of teleosts was attributed to the loss of mangrove habitats and connectivity due to loss of refuging or spawning habitats and reduction in survival and recruitment rates (e.g. Grol *et al.* 2011; Tran and Fischer 2017). A recent study found that degradation of mangrove habitats significantly affected biodiversity of meiofauna, resulting in collapse of ecosystem functions due to the loss of the basis of food webs (e.g. production and storage of organic matter, primary production) (Carugati *et al.* 2018). This alteration of the food web can cause bottom-up impact on animals at higher trophic level.

How do elasmobranchs respond to mangrove restoration?

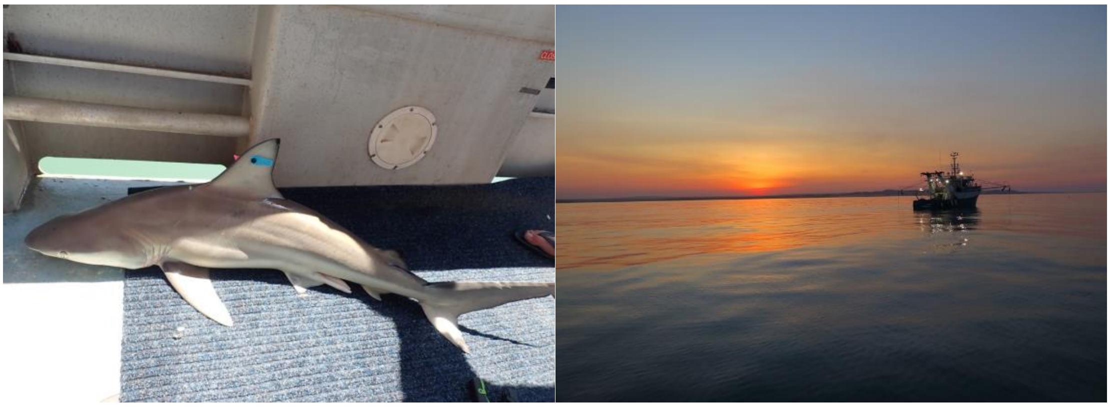
With the recognition that mangrove loss is detrimental to coastal systems, there has been significant action to restore mangroves (e.g. Ellison 2000; Bosire *et al.* 2008). As these restoration activities occur it will be important to monitor how elasmobranchs use these habitats compared to natural habitats. One study from Florida showed that nurse sharks started using restored mangrove areas 15 years after initial replanting (Enchelmaier *et al.* 2020). This observation suggests that time lags may be long between restoration and the recovery of functions for elasmobranchs, but further investigation is required.

2.7 Conclusion

This review demonstrates, based on a review of the literature, that there are important relationships between elasmobranchs and mangroves. However, this understanding is fragmented and available for few species in limited geographic regions. Future research should aim to address key questions that will improve our understanding of both the functions that mangrove habitats provide to elasmobranchs, as well as what benefits elasmobranchs can provide to mangrove habitats. Global mangrove deforestation is causing degradation of habitat availability and quality, which is negatively affecting global coastal communities, and elasmobranch species that are closely associated with mangrove habitats most likely suffer from a loss of essential ecological services and functions of mangrove habitat and associated coastal systems. Due to the nature of ecological connectivity, the impacts of mangrove loss could be broad and complex. Conversely, the conservation of mangroves can provide substantial benefits, such as bottom-up trophic well-being and biodiversity support. Elasmobranchs are playing an important role in coastal systems, including mangrove habitats, and their roles can be integral for ecological function not only in these systems but also wider coastal systems. Knowledge of the value of mangrove habitats and elasmobranch-mangrove relationships will be integral to ultimately understand such complex coastal connectivity and ecological functions.

CHAPTER 3

Age and growth of the graceful shark *Carcharhinus amblyrhynchoides* from the Kimberley Region, Western Australia



3.1 Introduction

Understanding the life history of a species is an important step for assessment of its population status and extinction risk. Species-specific data on ages, growth characteristics, maturation processes and longevity are fundamental to determine the vulnerability of species to exploitation (Cailliet 2015). For example, if accurate and precise age estimates are available, the relationship between length (or weight) and age can be assessed. Then growth models can be applied to the age-at-length data and growth parameters (e.g. length at birth, maximum length and growth completion coefficient) can be estimated using a model fitting approach. These parameters of the growth equation are indicators of population productivity, natural mortality and other important metrics for developing reliable fisheries management and conservation strategies (Goldman *et al.* 2012). Such life history studies of elasmobranchs have been a challenging task due to their highly mobile nature, difficulty of sampling and fewer calcified structures compared to those widely used for bony fish studies. Nevertheless, age and growth characteristics of elasmobranch species have been used to study species that are commercially important or that are common, and used to improve fisheries management. However, most shark and ray species have not been aged reliably (Cailliet 2015; Harry 2017). Thus, most species are still data deficient and understanding their basic life history is urgently required so that their population status and trend and extinction risk can be assessed.

The graceful shark *Carcharhinus amblyrhynchoides* (Whitley 1934), a medium-sized shark species, is one of those data deficient species possibly because it is difficult to identify and fragmented distribution. This species occurs in the Indo-West Pacific, from northern Australia to Somalia, though distribution records are not continuous (Simpfendorfer *et al.* 2021). The species lives in nearshore water up to 50 m deep, and is often associated with mangrove habitats (Stevens and McLoughlin 1991; Simpfendorfer *et al.* 2021). Although the biology and ecology of this species are poorly known, they are thought to have similar characteristics (e.g. productivity, longevity and growth characteristics) to other medium-sized coastal *Carcharhinus* species such as common blacktip *C. limbatus*, Australian blacktip *C. tilstoni* and pigeye sharks *C. amboinensis*. In fact, this species is often misidentified as those species due to genetic and morphological similarity (Morgan *et al.* 2011b; Tillett *et al.* 2012). This identification issue makes it more difficult to assess the catch data and study its biology and ecology.

The age and growth characteristics of graceful sharks have not been studied and there is no information on the growth pattern for this species. The size at birth and maximum size data are recorded based on fishing data (Stevens and McLoughlin 1991; White 2007). The other life history traits, such as growth coefficient, maturity and longevity are unknown, and population size, structure or trend are not examined within Australia (Simpfendorfer *et al.* 2019) or any other countries and regions. In Australian waters, graceful sharks are not targeted by fisheries and mainly taken as by-catch. The take in fisheries is well managed in Australian waters, and the species is assessed as Least Concern nationally based on the International Union for Conservation of Nature (IUCN) Red List Categories and Criteria (Kyne *et al.* 2021); however, its global population is assessed Vulnerable because of possible population declines and ongoing heavy fishing pressure through much of its distribution (Simpfendorfer *et al.* 2021). Given their occurrence in coastal zones, particularly in mangrove habitats, loss and degradation of habitat is also possibly a significant risk to graceful shark populations. Indeed, more than one-third of elasmobranchs are threatened with extinction with a half of them living in coastal habitats, and loss and degradation of coastal habitat is one of the important threats for elasmobranchs (Dulvy *et al.* 2021). To help understand population status and potential vulnerability of this species, life history data are urgently required. Given the population status, Australian waters provide a good opportunity to obtain samples for studying the life history of graceful sharks and the data could be used for the species management and conservation in the more threatened parts of its range.

The objectives of this study were to obtain age-at-length data of graceful sharks from the Kimberley Region, Western Australia, and to estimate growth parameters by growth model fitting. The present study then compared those growth parameters to genetically and morphologically similar *Carcharhinus* species.

3.2 Materials and methods

3.2.1 Sample collection and species identification

Samples were collected between May 2017 and November 2020 through the dry season (May to November) from the Kimberley Region in northern Western Australia (**Fig. 3.1**). Samples were obtained from fishery-independent and fishery-dependent sampling undertaken in intertidal areas in the region. Animals were caught mainly with gillnets with mesh sizes 2-8 inches stretch for fishery-independent and 6-inch stretch for fishery-dependent sampling. Fishery-independent longline was occasionally employed, using gangions made of 1 m of nylon cord and 1 m of 1.5-mm wire leader. Approximately 20 hooks total of size 3/0 and 1/O Mustad tuna circle hooks were used per longline and baited with mullet cut into different size depending on the hook size.

Captured animals were individually sized and sexed. For measurement, folk length (FL) and total length (TL) were obtained. All measurements were conducted using straight-line methods, as described in Francis (2006). Some specimens did not have TL data and one specimen was missing FL data; for those individuals, TL (or FL) was calculated using the equation *TL* (cm) = 1.2463 * *FL* (cm) + 0.5894 based on available *FL-TL* data from all fishing data from the region (**Fig. 3.2**). Maturity status was determined by examining umbilical scar condition, clasper calcification or uterus conditions. The maturity was determined according to the criteria adopted from Walker (2007) and modified by Harry et al. (2019) (**Table 3.1**). A section of three to five vertebrae was sampled from the cervical region of each vertebral column between the pectoral and the first dorsal fins for age determination. Vertebrae removed were frozen until processed.

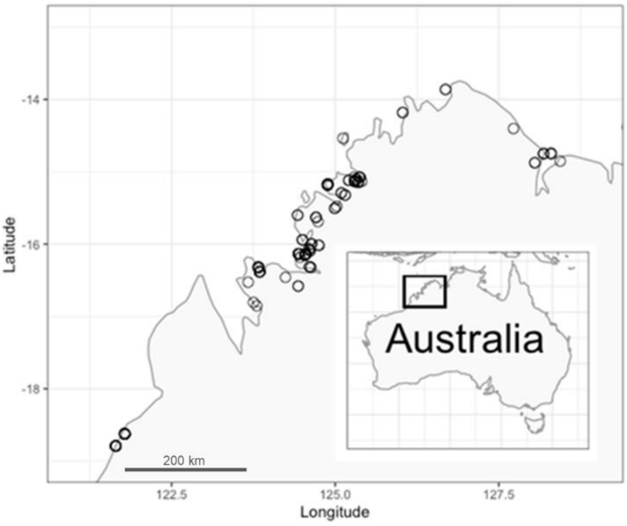


Fig. 3.1 Sampling locations for the study in the Kimberley Region, Western Australia.

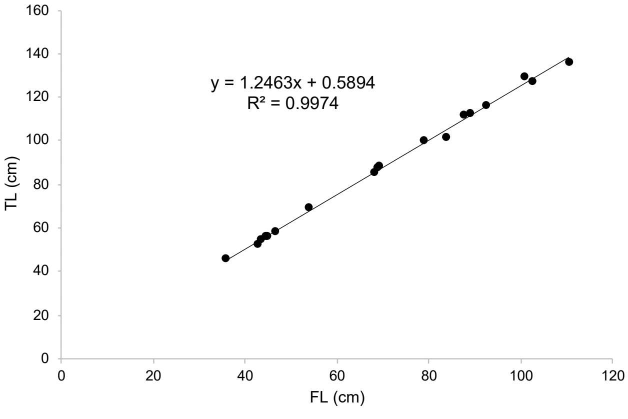


Fig. 3.2 Fork length-total length relationship of graceful sharks from the Kimberley Region.

Table 3.1 Indices for staging reproductive condition adopted from Walker (2007) and modified by Harry *et al.* (2019).

Organ	Index	Description	Maturity assumption
Female Uterus	U = 1	Uniformly thin tubular structure	Immature
	U = 2	Thin tubular structure partly enlarged posteriorly	Immature
	U = 3	Uniformly enlarged tubular structure	Mature
	U = 4	In utero eggs present without macroscopically visible embryos present	Mature
	U = 5	In utero embryos macroscopically visible	Mature
	U = 6	Enlarged tubular structure distended	Mature
Male Clasper	C = 1	Pilable with no calcification	Immature
	C = 2	Partly calcified	Immature
	C = 3	Rigid and fully calcified	Mature

3.2.2 Vertebral processing and age estimation

In the laboratory, frozen vertebral samples were thawed, cleaned to remove connective tissue and muscle and separated into individual centra using a scalpel. The centra were soaked in 5% bleach for 30 minutes to remove remaining soft tissue and then dried in the oven overnight at 60 C°.

One centrum from each individual was randomly selected from the dried samples for ageing. A sagittal section was taken by cutting through the centre of the centrum focus using a low-speed saw with double diamond-tipped blades (Beuhler, Lake Bluff, IL, USA). The thickness of the section was between 0.4 mm and 0.6 mm. Then, the section was fixed to a microscope slide with Crystal Bond adhesive (SPI supplies, PA, USA) for viewing.

The sectioned vertebral centra were examined under a binocular dissecting microscope (SZX9, Olympus, Tokyo, Japan) with transmitted light (LG-PS2, Olympus, Tokyo, Japan). The age estimation process (hereafter, ageing) was achieved by identifying and counting a pair of opaque and translucent bands in the corpus calcareum from the birth mark to the last pair observed at the outer edge of the section. The birth mark, which was counted as age 0, was identified by a change of angle, or a small bulge of the inner margin of the corpus calcareum (**Fig. 3.3**). Then, an outer opaque band was identified, and the increment was counted one by one (1, 2, … as followed) by assuming that the band pair was formed annually. The annual deposition of band pairs in species of the genus *Carcharhinus*, including close relatives of graceful sharks, has been regularly reported (e.g. Davenport and Stevens 1988; Simpfendorfer *et al.* 2002b; Joung *et al.* 2022), although age validation of this species has not been established. If there was no band after the birth mark, the age of the specimen was estimated as 0.

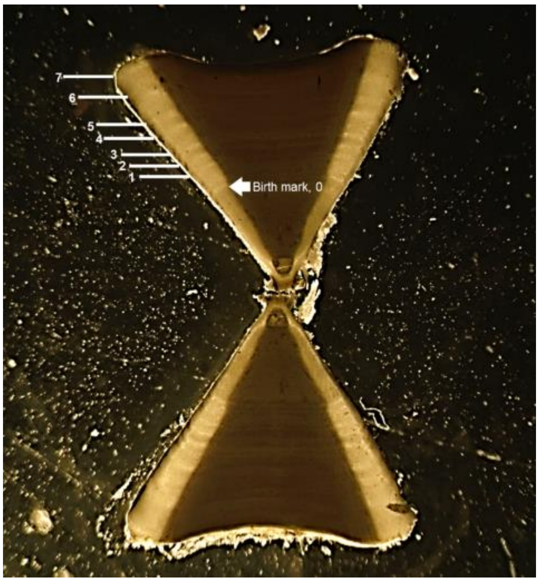


Fig. 3.3 Vertebral section of the graceful shark. A white arrow indicates the birth mark and white lines indicate translucent bands.

Ageing was conducted by three independent readers. Reader 1 conducted two independent practice reads, followed by two independent final reads. The second final read was conducted at least a week after the first read. Reader 2, as an experienced reader, performed ageing once independently. Once ageing was completed by both Readers 1 and 2, the results were compared and a consensus age was determined to obtain final age estimation using the following process: if the difference between Reader 1 and 2 was less than or equal to 2 years, the consensus read was determined based on the result of Reader 2; if the difference was greater than 3, Reader 3 (experienced reader) performed their independent read, and then the consensus age was determined based on the comparison between the counts of Readers 1, 2 and 3. All counts were performed by the three readers without any prior information of TL and sex of the individuals.

3.2.3 Precision and bias

To assess the precision and bias of ageing by readers, percent reader agreement between readers (PA), PA plus or minus one year (PA ± 1), average percent error (APE) and the coefficients of variation (CV) were calculated based on Beamish and Fournier (1981) and Chang (1982) to compare the precision of age determinations between readers. PA, which was calculated as the number of agreed divided by the number of read, was used to assess the precision between Reader 1 and 2. APE is an index of the precision of age determinations dependent on the age of the species (Beamish and Fournier 1981). CV was calculated to test the reproducibility of age estimations between readers

(Chang 1982). Additionally, Bowker's test of symmetry was conducted to assess the two readers' biases (Evans and Hoenig 1998).

3.2.4 Growth modelling and analysis

Growth parameters for graceful sharks were estimated by fitting the candidate models to length-at-age data. Total length (cm) was used for analysis in this study. The three candidate models were the most commonly used growth models for elasmobranch species: von Bertalanffy growth function, Gompertz function and logistic function (**Table 3.2**).

Table 3.2 Candidate growth models and equations.

Model	Equation	Reference
von Bertalanffy (VB)	$L_t = L_0 + (L_\infty - L_0)(1 - \exp(-kt))$	von Bertalanffy (1938)
Gompertz (Gom)	$L_t = L_0 e \ln(\frac{L_\infty}{L_0})(1 - e^{-gt})$	Ricker (1975)
Logistic (Log)	$L_t = \frac{L_\infty - L_0(\exp(gt))}{L_\infty + L_0(\exp(gt - 1))}$	Ricker (1979)
L_t : length at age t, L_0: length at birth, L_∞: asymptotic length, k: growth coefficients for VB, g: growth-completion coefficients for Gom and Log		

Individual models were fit using the 'AquaticLifeHistory' package (Smart 2019) in the R program environment (R Core Team 2022). Model fitting was performed for all individuals (both sexes combined), and female and male separately. Growth parameters, including length at birth L_0, asymptotic length L_∞ and growth completion coefficients (k, g_{Gom} and g_{Log} for VBGF, Gompertz and Logistic functions respectively) were estimated. To identify the best fit model among the three candidate models, performance of models relative to each other was evaluated based on AIC_C (Akaike information criterion for small sample sizes) (Smart *et al.* 2016). The best model was the one with the lowest AIC_C value (minimum AIC_C). To evaluate the strength of support for each model, AIC_C differences (ΔAIC) between the minimum AIC_C value and AIC_C values were calculated for each model to rank the three candidate models. Then, to estimate the likelihood of each model, Akaike weights (w_i) were calculated (Burnham and Anderson 2001):

$$w_i = \frac{\exp(-\Delta \mathrm{AIC}_i/2)}{\sum_{r=1}^{R} \exp(-\Delta \mathrm{AIC}_r/2)}$$

Where ΔAIC_i is the AIC difference of model i, and ΔAIC_r is the AIC difference of model r ($r = 1, 2, ..., R$). If the difference of ΔAIC values was within 2 between the models, those models were both likely and the best model was not chosen with confidence.

3.2.5 Maturity

Maturity status was plotted against estimated age and total length respectively. Logistic curves were fitted to the data using a general linear model with binomial function to estimate age-at-50% maturity (a_{50}) and length-at-50% maturity (l_{50}). Due to small sample size, the data of both sexes combined was analysed for maturity assessment.

3.3 Results

A total of 45 vertebrae from graceful sharks were aged, consisting of 30 females (mean TL = 94.3 cm) and 15 males (mean TL = 84.9 cm) (**Fig. 3.3**). The youngest female and male were both age 0 and were 52.6 cm TL and 45.6 cm TL, respectively. The oldest female and male were both age 18 and were 136.2 cm TL and 121.2 cm TL, respectively. The results from the between-reader agreement and precision test were assessed and Reader 1 tended to overestimate the age for the specimens between 7 and 16 years old and the matrix of reading result was not symmetric (**Fig. 3.4**), indicating that the reading bias was present.

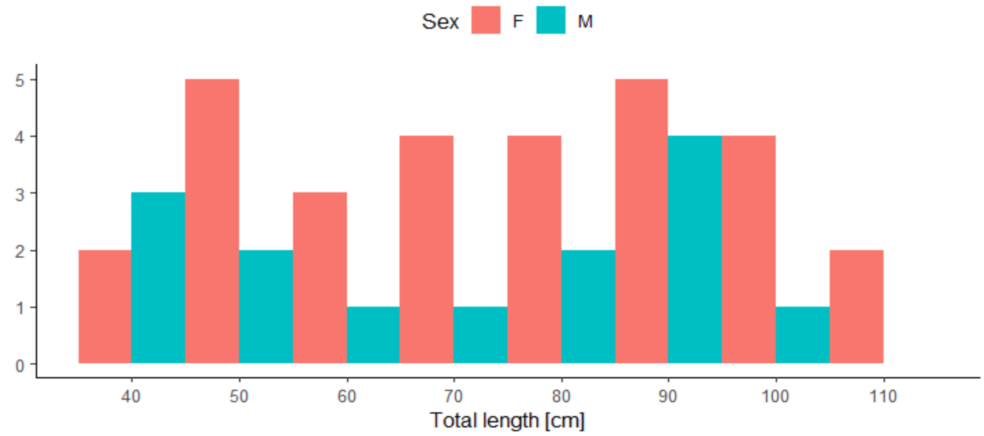


Fig. 3.3 Length-frequency distribution of samples used in the study.

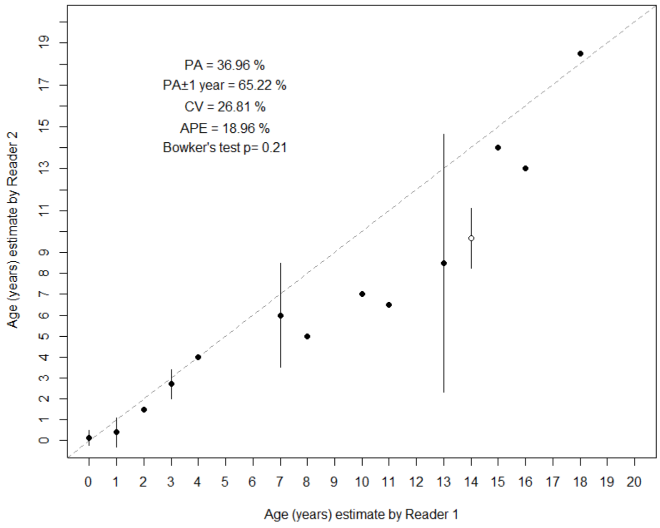


Fig. 3.4 Reader's reading bias test. Abbreviations of indices: percent reader agreement between readers (PA), PA plus or minus one year (PA ± 1), the coefficients of variation (CV) and average percent error (APE).

The best fit model for the combined sexes was the logistic model, which had strong support ($w_i = 0.85$) (**Table 3.3**). For females, the logistic model was the best fit with relatively strong support ($w_i = 0.73$) (**Table 3.3**). For males, the logistic model had the highest support ($w_i = 0.52$) although the Gompertz model had some degree of support ($w_i = 0.31$, ΔAIC = 1.01) (**Table 3.3**). Both females and males displayed asymptotic growth, where growth slows down after 5 to 7 years and it then reaches a plateau (**Fig. 3.6**).

Final growth parameters were estimated based on the best fit model (**Table 3.4**). Estimated length at birth (L_0) of graceful sharks was 52-55 cm TL, which was slightly larger than the smallest size of 0-year-old individuals (45.6 cm TL). Therefore, the species may be born at 45~55 cm TL in this region. Females may be born smaller than males, and females grow slower than males (**Fig. 3.5**). Asymptotic length was 132.7 cm TL for female and 119.5 cm TL for male. For males, although growth coefficients demonstrated somewhat different values between Logistic and Gompertz functions, length at birth and asymptotic length were similar between the two models.

Estimated age at maturity (a_{50}) was 7 years and length at maturity (l_{50}) was estimated to be 107 cm TL (**Fig. 3.6**).

Table 3.3 Akaike weights (w_i) analysis results for growth model fitting. Results in bold represents the best fit model for each data category.

Data	Model	Number of parameters	AIC_C	ΔAIC	w_i
Both sexes	VB	3	304.85	9.02	0.01
	Gom	3	299.41	3.58	0.14
	Log	**3**	**295.83**	**0**	**0.85**
Females	VB	3	201.03	6.68	0.03
	Gom	3	196.55	2.2	0.24
	Log	**3**	**194.35**	**0**	**0.73**
Males	VB	3	106.42	2.27	0.17
	Gom	3	105.16	1.01	0.31
	Log	**3**	**104.15**	**0**	**0.52**

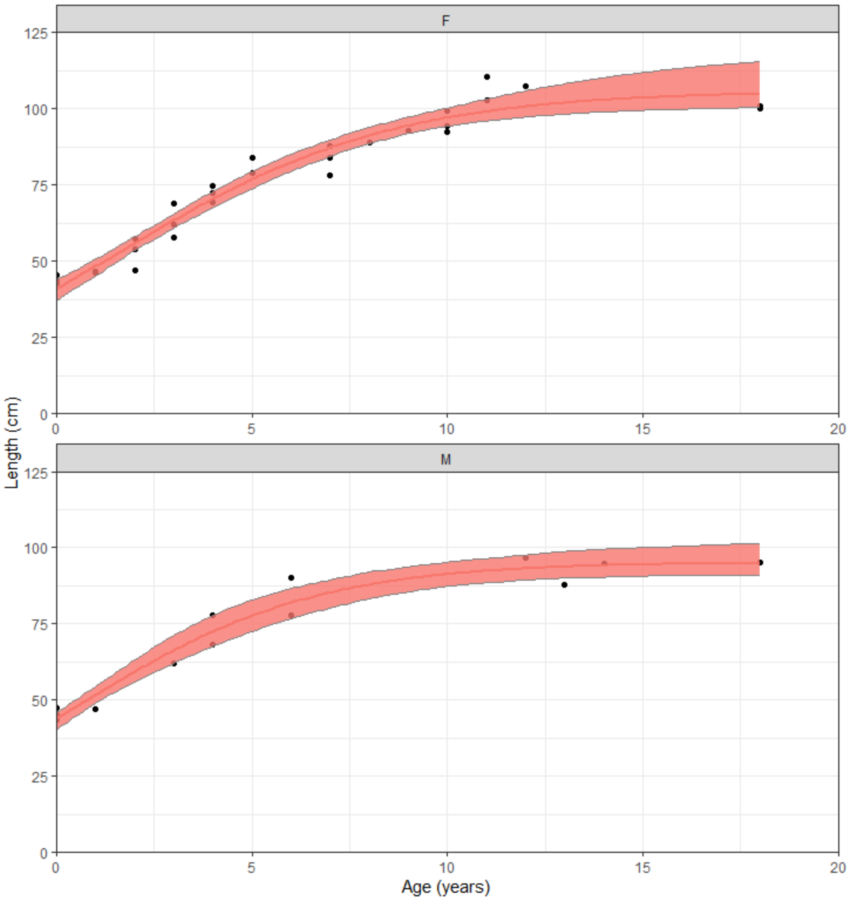


Fig. 3.5 Length-at-age of graceful sharks fitted with logistic growth function curve for female (F) and males (M). Length data represents total length (cm).

Table 3.4 Growth parameter estimation of the best fit models for graceful sharks. L_0 and L_∞ estimates are in total length (cm).

Data	Model	L_0	L_∞	Growth completion coefficients
Both sexes	Logistic	52.2	127.3	g_{Log} = 0.31
Females	Logistic	51.8	132.7	g_{Log} = 0.28
Males	Logistic	53.4	119.5	g_{Log} = 0.34
Males	Gompertz	53.3	120.7	g_{Gom} = 0.27

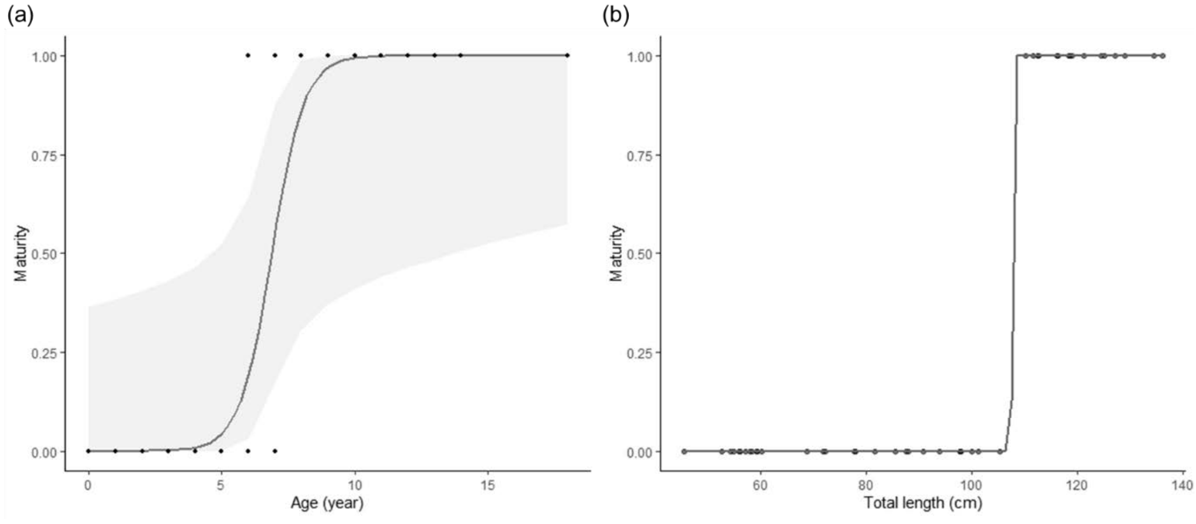


Fig. 3.6 Maturity at age and length of graceful sharks. Logistic regression models with 95% confidence intervals (shaded area) used to estimate (a) age and (b) length at 50% maturity.

3.4 Discussion

The present study reported growth information on graceful sharks based on length-at-age data from vertebrae. The results confirmed that graceful sharks are a medium sized species with average to slow growth compared to biologically and ecologically similar species (**Table 3.5**). Size at birth was estimated to be 54.5 ± 1.5 cm TL, similar to that observed in wild-caught individuals (50-60 cm TL, Last and Stevens 2009). The results suggest that males are born slightly larger, but females attain larger body size and overall grow slower than males. Asymptotic length was smaller than the reported maximum length of this species; L_∞ was 132.7 cm TL for females and 119.5 cm TL for males in this study whereas the largest individual known was a 178.3 cm TL female from Indonesia (White 2007) and the second largest was a 166.5 cm TL female from the Gulf of Thailand (Garrick 1982). The body size of the Kimberley population of graceful sharks may be small compared to the maximum size known for this species from other locations. In the Kimberley Region, individuals up to 130 cm TL have been caught several times and individuals >130 cm TL are rare (A. Harry unpubl. data) while maximum size of specimen in this study was 136 cm TL (estimated age = 11). Life history and growth parameters are known to differ between populations (e.g. Harry *et al.* 2019) and this may support the hypothesis that the body size of graceful sharks of the Kimberley population is relatively small. Alternatively, the relatively small L_∞ for the Kimberley population might be explained by underestimation due to small sample size of large sized, mature individuals.

Based on estimates of growth parameters, graceful sharks' growth from the Kimberley population is most similar to spottail sharks *Carcharhinus sorrah* from Australian waters (Table 3.5). They have similar birth and asymptotic sizes, but the growth completion coefficient is much smaller in graceful sharks*,* with this parameter more similar to that of common blacktip sharks *C. limbatus* when comparing growth completion coefficient with the same model (**Table 3.5**, Harry *et al.* 2013; Harry *et al.* 2019). There appear to be two distinct groups of inshore *Carcharhinus* spp. that co-occur with graceful sharks*:* (1) relatively fast growth, medium sized (including spottail sharks and Australian blacktip sharks *C. tilstoni*) and (2) slow growth, large sized (including common blacktip sharks and pigeye sharks *C. amboinensis*). Given that the body size of graceful sharks is similar to the former group, but the growth completion coefficient is similar to that of the latter group, graceful sharks do not fit in either group, being medium sized with slower growth. The graceful shark is often misidentified as common blacktip, Australian blacktip and pigeye sharks (Morgan *et al.* 2011; Tillett *et al.* 2012). Interestingly, their body size is different, but those three may be similarly slow growth species.

Maturity data also indicated graceful sharks have relatively slow growth to sexual maturity. Based on the present data, estimated age at 50% maturity of graceful sharks from the Kimberly Region is 7 years and length at 50% maturity is approximately 107 cm TL. This maturity data is consistent with fishing-based data (sexually mature at a size of 110 to 115 cm TL, Stevens and McLoughlin 1991). These values are in contrast to spottail sharks that have similar L_∞ and L_0, but they reach maturity at 2.3-2.4 years, and the growth to maturity of graceful sharks is even slower than the slightly larger species Australian blacktip sharks (maturity at 5.2-6.1 years) (Harry *et al.* 2013). These observations further support the medium sized, slow growth characteristics of graceful sharks in contrast to previous assumption of similarity to small-seized, fast growth *Carcharhinus* group. Maturity data for graceful sharks is reported for the first time in this study, and the data indicates the different aspects of growth of graceful sharks that are not identifiable in growth modelling by itself. Here, the data clearly demonstrate that graceful shark's life history traits are fundamentally different from closely related species and even though growth parameters are similar, age at maturity can be strikingly different. Thus, vulnerability to exploitation is different between those species and therefore, population status and management should be tailored for each species. The species-specific life history data gathered in this study may prove useful for improving management of this species.

The data in this study may need to be interpreted with caution due to possible size- and sex-based sampling bias. Although the samples included old age classes (10-18 years old), samples older than 10 years old were scarce and therefore, L_∞ was possibly underestimated and growth completion coefficient was overestimated. This size distribution may be related to gear selectivity (Thorson and Simpfendorfer 2009) or size-based differences in distribution. However, relatively large sized specimens (120-130 cm TL) have been caught in the area by the same fishing methods in similar inshore areas (A. Harry unpubl. data). Gear selectivity was an unlikely factor because a range of mesh sizes was used. One possible explanation of a small sample size of large individuals is the size-based difference in distribution, although this has not been investigated nor reported from the region. Furthermore, overall sample size (n = 45) is not large and particularly male sample size (n = 15) was small, and this could be the reason why both Logistic and Gompertz growth functions had relatively strong support for males and one model could not be selected as best. Nonetheless, because the samples included substantial numbers of juvenile length classes and several mature and possibly some older individuals, the present parameters for both sexes are biologically realistic (see Smart *et al.* 2013).

This study was conducted based on the assumption that a growth-band pair is formed at approximately one-year intervals. Annual band deposition has been observed in biologically similar species such as spottail and Australian blacktip sharks (Davenport and Stevens 1988). Age validation for graceful sharks has not been conducted, and further research is required to validate age estimates and thus growth parameter estimates (Cailliet *et al.* 2006). As several studies have warned, age underestimation is common in elasmobranch studies (e.g. Harry 2018; Francis *et al.* 2007). Specifically, age is underestimated in larger and older individuals because growth bands become small and unresolvable as individuals get older or growth bands simply may not be formed temporally or permanently at some point of growth (Chin *et al.* 2013b; Natanson *et al.* 2018). Francis *et al.* (2007) pointed out that age underestimation can affect growth modelling especially when sample size is small, and this underestimation could result in inaccurate estimates of growth parameters. The present data included some of the oldest estimated ages for graceful sharks (18 years) and this is older than their predicted longevity based on data from sister taxa (11 years, Simpfendorfer *et al.* 2019) and tag recapture study (recaptured after 8.8 years, Stevens *et al.* 2000). Therefore, age underestimation may have little or negligible effect in this study. However, it is not possible to prove if age underestimation occurred in larger, mature individuals in this study and as a consequence, the longevity and growth completion coefficient may be biased (e.g. Natanson *et al.* 2018). Future research should focus on age validation of graceful sharks and test if the assumption of one-year cycle of growth band formation is correct.

One possible hypothesis for the question of why graceful sharks from the Kimberley Region grow more slowly compared to related and similar-sized species worth future consideration is that growth rate reduction in low oxygen environments. Mangrove habitats, where this species spends much of its time, especially as juveniles, are known to regularly experience low dissolved oxygen (DO) levels (Altieri *et al.* 2021). In some places, diel fluctuations of DO in mangroves are extreme, ranging from near anoxic to hyperoxic over the course of a day (e.g. Gedan *et al.* 2017). Such low oxygen availability may restrict growth of species that spend a considerable amount of time in hypoxic mangrove habitats as one of the adaptation mechanisms to hypoxia is reduction in metabolic rate (Bickler and Buck 2007). While reduced growth in low oxygen mangrove areas has not been demonstrated in sharks or rays to date, it has been reported in teleosts (e.g. Pérez-Domínguez *et al.* 2006; Stierhoff *et al.* 2006) and the negative effects of low oxygen level on elasmobranch's embryo survival rate has been observed under the laboratory experiment condition (Musa et al. 2020). Further investigation of whether oxygen limitation has consequences for the growth of sharks or rays that regularly occur in mangrove habitats is needed to better understand the consequences of the use of this habitat. However, if there are, it suggests that these costs are outweighed by the benefits species derive from using mangrove habitats (e.g. increased food availability, refuge from predation, etc).

In conclusion, the present study provided the first data on ages and growth parameter estimates of graceful sharks. This species from the Kimberley Region appears to attain smaller size than the maximum size reported from the other regions. This study revealed their later maturity than other similar *Carcharhinus* species and relatively slow growth. This growth data will provide improved information for population management particularly outside of Australian waters because the global population status of this species is assessed as a Vulnerable by IUCN Red List. Currently, there is little information available on the ecology of graceful sharks other than their close association with inshore habitats. This growth information indicates possible susceptibility of this population to exploitation due to slow maturity and possible longevity as well as a potential risk of degradation of coastal habitat. Their life history trait reveals their potential vulnerability and emphasises research needs for graceful sharks.

Table 3.5 Comparison of life history parameters from growth modelling to ecologically similar species of *Carcharhinus*. Estimated parameters of growth completion coefficient are calculated based on its best fit model. L_0 and L_∞ estimates are in total length (cm).

Species	Location	Sex	Model	L_0 (TL)	L_∞ (TL)	Growth completion coefficient	Reference
C. amblyrhynchoides	Kimberley, WA	F	**Log**	**51.8**	**132.7**	**0.28**	This study
		M	**Log**	**53.4**	**119.5**	**0.34**	
		F	VB	49.4	142.0	0.14	
		M	VB	53.2	122.8	0.20	
		F	Gom	50.5	135.9	0.21	
		M	Gom	53.3	120.7	0.27	
C. tilstoni	Coral Sea, QLD	F	VB	63.1	218.2	0.15	Harry *et al.* 2013
		M	VB	61.6	169.8	0.09	
	Arafura Sea, NT	F	VB	59.7	181.4	0.19	Davenport and Stevens 1988
		M	VB	59.3	156.8	0.25	
C. sorrah	Coral Sea, QLD	F	VB	55.3	126.6	0.34	Harry *et al.* 2013
		M	Log	49.5	105.6	0.63	
	Arafura Sea, NT	F	VB	59	123.9	0.34	Davenport and Stevens 1988
		M	VB	49.6	98.4	1.17	
	Taiwan Strait	F	Gom		158.6	0.23	Joung *et al.* 2022
		M	VB		170.2	0.14	
C. limbatus	NSW	F	VB	72.8	263.6	0.14	Harry *et al.* 2019
		M	VB		241.9	0.16	
C. amboinensis	NT	F	Gom		267.2	0.15	Tillett *et al.* 2011
		M	Gom*		254	0.16	

* two-parameter Gompertz growth function (Mollet *et al.* 2002)

CHAPTER 4

The performance and detection range of acoustic receivers in mangrove habitats

4.1 Introduction

Acoustic telemetry is a useful tool to study the spatial ecology of aquatic animals (Hussey *et al.* 2015). Passive acoustic monitoring, in particular, can be used to provide detailed insights into the habitat use and movement patterns of animals by remotely monitoring their presence in a given area over relatively long time frames (months to years) with reasonably low labour cost (Heupel *et al.* 2006). Advances in telemetry technology have not only lowered the financial cost of acoustic receivers and transmitters but also offered more variety in equipment in terms of size, battery life, additional sensors (e.g. pressure, temperature and acceleration) and communication ability between equipment and users (Donaldson *et al.* 2014; Hussey *et al.* 2015). Along with technological improvements, improvements in spatial analysis methods (Whoriskey *et al.* 2019) have enabled new insights into the relationship between aquatic animals and their habitats (Papastamatiou *et al.* 2013; Espinoza *et al.* 2021).

As acoustic monitoring uses acoustic signals, this method can only be used where the acoustic signal from the transmitter can reasonably travel through the environment and be detected by a receiver. Transmissions from acoustic transmitters are subject to a range of factors that could alter their ability to be detected by a receiver. These include attenuation (e.g. signal is absorbed by particles or organisms in the water), reflection (e.g. signal hits hard objects in the water) and refraction (e.g. signal hits a boundary, such as thermocline and changes travel direction) (Heupel *et al.* 2006). In addition, other environmental noise at a similar frequency can interfere with detection resulting in the code from the transmitter being misunderstood or missed by the receiver (Simpfendorfer *et al.* 2015). Thus, the detection performance of receivers is affected by physical (e.g. wave action, rain, wind, topography), biological (e.g. biological noise, animal movement, algal blooms) and anthropogenic (boat and other human activity noise) factors (Heupel *et al.* 2006; Cooke *et al.* 2013). Hence, the effectiveness of telemetry research depends on the system in which the experiment is conducted and the equipment configuration. As a result, understanding detection range and receiver performance before conducting animal monitoring is essential to accurately interpret the collected data (Kessel *et al.* 2014).

Acoustic monitoring has been commonly deployed to investigate movement patterns of animals that have relatively high fidelity to the study site in relatively deep, physically open habitats, such as large rivers, lakes, and open water marine systems (e.g. Hanson *et al.* 2007; Heupel and Simpfendorfer 2008, 2015) because these systems often have few impediments to detecting transmitter signals and make interpretation of results straightforward. Environments in which signal transmission is regularly impeded, such as in nearshore, shallow, vegetated or coral reef systems, have a sampling difficulty for an acoustic telemetry study because of the challenges in designing methods that allow the collection of useful data. For example, the detection range of acoustic receivers in shallow coral reef environments that have complex topography was smaller than that in open water habitats due to the complex topography and inherently noisy environment of the reef (e.g. Welsh *et al.* 2012; Cagua *et al.* 2013). The presence of vegetation also negatively affects receiver performance by blocking and attenuating signals, resulting in low detection probability and small detection range. For example, Swadling *et al.* (2020) compared detection efficiency of acoustic receivers between transmitters positioned above and among a seagrass canopy and found significant reduction in detection range when the transmitter sat among the canopy (from 90 m to 45 m). Similarly, (Weinz *et al.* 2021) conducted range testing of acoustic receivers in seasonally submerged vegetated habitats in a freshwater system and reported substantial differences in detection range (from nearly 200 m when vegetation coverage was low to less than 10 m when the coverage was high). Thus, environmental conditions, such as biological noise, shallow water and vegetation density can be a challenge for acoustic telemetry and if these factors are not incorporated into animal tracking studies, the data can be misinterpreted, leading to a misunderstanding movement.

Nearshore vegetated habitats are important to aquatic animals due to their productivity and the ecological services they provide (i.e. food, nursery and shelter) (Sievers *et al.* 2019). Mangroves are one of the most productive systems in tropical and subtropical areas and a variety of animals, including invertebrates, teleosts, elasmobranchs, amphibians, reptiles, birds and mammals are dependent on mangrove habitats (Nagelkerken *et al.* 2008; Rog *et al.* 2017). Despite their significance to coastal ecosystems, mangroves are currently under pressure of deforestation globally (Goldberg *et al.* 2020; FAO 2023). Knowledge of the relationship between mangrove systems and the animals that use them is critical to predict how coastal communities respond to the loss of mangrove systems. For acoustic telemetry, however, mangrove systems are challenging environments to operate in mainly due to shallow water depth that changes rapidly with tidal fluctuations, physical complexity from submerged trunks and roots (e.g. Swadling *et al.* 2020) and turbidity (e.g. Cooke *et al.* 2013). As a result, there have been no long-term acoustic telemetry studies conducted within mangrove habitats (i.e. within mangrove forests).

Studies in other nearshore vegetated ecosystems, however, may provide insights to guide studies in mangroves. Recently, detection performance of active and passive acoustic telemetry has been tested in wetland environments with submerged aquatic vegetation in lakes and found that acoustic transmitters can be used successfully in vegetated shallow water environments (Swadling *et al.* 2020; Weinz *et al.* 2021; Thiemer *et al.* 2022). They collected range testing data showing temporal variability in detection range due to submerged vegetation, and based on the data, Matley et al. (2022) accurately interpreted the spatial ecology of yellow perch *Perca flavescens*. Their study highlighted that accurate interpretation of results is possible within acoustically challenging environments with appropriate testing.

The aim of this study was to determine if acoustic monitoring in dense mangrove habitats could yield useful ecological data on how elasmobranchs, and potentially other taxa, use this habitat. The objectives for this study were: (1) to test the detectability of acoustic transmitters in structurally complex mangrove habitats by examining detection range and how it varies with diel period, tidal height and habitats, (2) to examine receiver performance in mangrove habitat and compare it to non-mangrove habitats, and (3) to demonstrate whether acoustic monitoring can be used to track the movements of animals in mangrove habitats by examining the movement of sharks and stingrays known to enter mangrove habitat (e.g. George *et al.* 2019; Martins *et al.* 2020b).

4.2 Methods

4.2.1 Study area

The study was conducted in Pioneer Bay, Orpheus Island, 17 km offshore of the coast of northeast Queensland, Australia (**Fig. 4.1**). The bay has both fringing (i.e. mangroves growing along the coast) and patchy (i.e. mangroves growing sparsely with a space each other rather than densely) mangrove areas with a reef flat extending approximately 400 m from the shoreline to the reef crest with patchy coral rubble areas. There are four distinct mangrove stands in the bay which vary in their width and shape; two small mangrove stands forming isolated patches at the sandy beach and two fringing mangroves occur along the north and south shorelines. The south fringing mangroves are longer and wider than the north fringing mangroves, reaching a width of ~85 meters from the shoreline. Mangrove stands are predominantly composed of red mangroves *Rhizophora stylosa,* mixed with grey *Avicennia marina* and myrtle mangroves *Osbornia octodonta*. The mangroves in the study area are evergreen and the extensive arching prop roots make structurally complex habitats in mangrove areas.

The main substrate in the mangrove areas is a soft sand-mud mixture and some sections have rocky substrate, especially at the far end of both the south and north fringing mangroves. The reef flat and two small mangrove stands in the middle of the bay are covered throughout with soft mud and sand. In the reef flat away from the shoreline mangroves, there are patchy corals and algal dominated coral rubble in proximity to the reef crest. The tidal range is ~4 m and semidiurnal, and mangrove areas are normally flooded at high tide and completely exposed at low tide. The reef flat is exposed occasionally at very low tide (when predicted tidal height is <70~80 cm).

4.2.2 Field methods

Receiver deployment

An array of 38 acoustic receivers (VR2W; Vemco Ltd., Canada) was installed in Pioneer Bay in October 2020 and removed in December 2021. Four receivers were located at the edge of the reef crest, three in the middle section of the reef flat and 31 were located either along the mangrove edge or inside mangrove stands (**Fig. 4.1**). The array was designed to examine the performance of receivers deployed inside mangroves to track the movements of sharks and rays. For this purpose, the habitat type of receiver location was categorised into the four zones (hereafter the zones): (1) reef flat, (2) mangrove edge, within 2 m of the seaward edge of the mangrove root system, (3) mangrove middle, midway between mangrove edge and mangrove rear receivers where there was sufficient space and (4) mangrove rear, within 10 m of the landward edge of the mangrove stand and at least 25 m away from the shore line. Within mangrove stands distances between receivers were less than 20 m.

Prior to deployment approximate locations of receivers was planned, but final locations were determined in the field, with deployment occurring in more open areas within the mangrove root complex whenever possible. Receivers were deployed at each designated location by driving a 45-cm star picket into the substrate and a hole was dug next to the picket (the hole size was approximately 10-cm diameter, approximately 25 cm deep). A receiver was placed in the hole and cable tied to the picket. The hole was refilled with at least the top 5cm of the receiver above the substrate (**Fig. 4.2**). Receivers were deployed in this way to enable transmitter detection at the lowest possible water levels and thus maximise detection times during each tidal cycle.

Data were downloaded from all receivers in December 2020, May 2021 and December 2021 (on removal). Five receivers malfunctioned and were replaced with new receivers. The data were combined with the old and replaced receiver data from the replacement dates. Those five receivers were on the mangrove edge zone and away from the transmitters and therefore, receiver replacement would not significantly affect the range testing data.

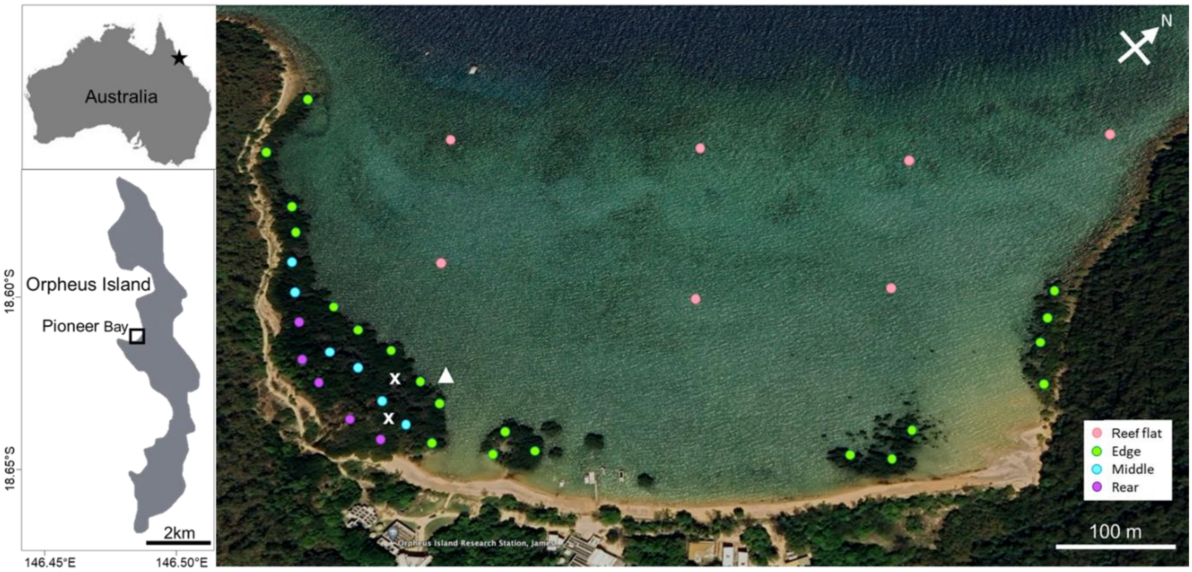


Fig. 4.1 Maps of study site and receiver deployment. Circle indicates receiver (different zones in different colours: pink = zone 1: reef flat, green = zone 2: mangrove edge, blue = zone 3: mangrove middle and purple = zone 4: mangrove rear); ▲ and x are one-month and two-day transmitter positions, respectively.

Fig. 4.2 Receivers deployed among mangrove roots.

Deployment of transmitters for range testing

One transmitter (V13AP, Vemco) was attached to a solitary mangrove tree just seaward of the southern mangrove stand for one-month. This test was designed to simulate how transmissions from transmitters on animals swimming seaward of the mangrove edge would be detected by the different types of receivers (edge, middle, rear). This testing is called hereafter *outside mangrove test* as the test transmitter was placed outside of mangrove habitats. In addition, two transmitters (V13AP, Vemco) were attached to prop roots within the southern mangrove stand for two days, one between edge and middle receivers and one between middle and rear receivers. Each transmitter was placed in a small net bag and the bag was tied to the root or trunk of the tree about 25 cm above the substrate. The two-day test transmitters were used to test receiver performance inside mangrove habitats i.e.

among the mangrove trees. This latter testing is called hereafter *inside mangrove test*. All transmitters were recovered after the study. All test transmitters had pressure and acceleration sensors (hence, there were two consecutive ID numbers for each transmitter; one for each sensor). Deployed test transmitters were submerged in water at high tide and completely exposed at low tide.

4.2.3 Data analysis

Detection range

To test the detection range of acoustic receivers in the mangrove system, detection probability (%D) was calculated as the number of detections recorded by each receiver divided by the total possible codes sent from the transmitter during the test period. The total possible number of coded transmissions by one transmitter (with two independent sensors) was calculated based on: (i) the interval of signal made by one transmitter, and (ii) the time period both the transmitter and receiver were underwater. This later requirement occurred because of the cyclical inundation of the mangroves. The mean transmission rate of transmitters was 120 seconds with transmissions alternating between the different sensors (pressure or acceleration). Thus, if only data from one sensor was used in analysis, then the ping frequency was 240 seconds. Next, the time period transmission could be set and received was calculated based on tidal cycle data. The tidal height at which transmitters and receivers were both submerged was determined by comparing the timing of detections with depth indicated as 0 m by the transmitter depth sensor and local tide charts. Based on 186 data points with 0 m depth the average minimum tidal height at which detections were first made was approximately 2.0 m. Finally, the total possible number of transmissions made was calculated by multiplying the transmission frequency by the amount of time tidal height exceeded 2.0 m. For the outside test transmitter, for example, the transmission interval for one transmitter (includes two sensors) was 120 sec and the total time of the local tidal height >2m was 375 hours (125 hours for day and 250 hours for night). Therefore, the total possible number of transmissions was 11250 (375 x 60/2 transmissions). %D was calculated for both outside and inside mangrove tests separately.

To determine the detection range of at least 50% of detections, distances between the transmitters and each receiver were calculated and plotted against %D. The data from outside and inside mangrove tests were plotted separately to examine if the detection range is different when the transmitter was inside mangrove habitats or outside mangroves. The relationship between %D and distance was plotted separately for each receiver zone (i.e. reef flat, edge, middle and rear). A binomial curve was fitted to distance-detection probability data using a general linear model. Additionally, a generalised linear mixed model (GLMM) was used to examine if %D was affected by (1) distance between receiver and transmitter, (2) the zone and (3) day or night shift. Individual receiver was incorporated into the model as a random factor. The model selection was conducted outside and inside mangrove tests separately. Day and night was determined based on local sunset/sunrise times. The full model (%D ~ Distance + Zone + Day or Night + (1|Receiver)) was fitted using the '*lme4*' package (Bates *et al.* 2015) in the R program environment (R Core Team 2022). The '*MuMIn*' package (Bartoń 2023) was used to evaluate all combinations of parameters to determine best fit model that best explained the data. The best fit model was selected based on Akaike Information criterion (AIC) model evaluation and analysis of deviance test (type II Wald chi-square tests) was used to test which factor(s) was statistically significant.

To examine if water depth affected the number of detections made, detection per depth was analysed using a chi-square test. To do this, total hours when tidal height was >2m during the outside mangrove test were calculated based on hourly tide chart. Second, estimated water depth was calculated for each detection using the pressure sensor data. Third, both tidal height and estimated water depth data were then categorised into the depth bins (15 cm) separately. This step enabled the calculation of the frequencies of tidal height occurrence and frequency of detections at the given depth. Finally, those two frequency data were tested for independence using a chi-square test to examine if detection was made equally throughout the water depth >2m or more (or less) detection was made at particular water depth.

Event data

Event data was collected from the entire study period from Dec 2020-Dec 2021 and included all tags deployed during the study. The system used in this study had a coding scheme where each code sends eight (V13) or ten pulses (V13AP) to transmit data (the number of pulses is different in different transmitter type). The transmitter information sent using this eight- or ten-pulse code is composed of the three sections. The first section, called the synchronisation interval, is the time between the first two pulses. This value is so tightly defined that it is rarely replicated by environmental noise, allowing the receiver to identify it as transmission from a transmitter amongst other similar noises in the environment. The second section is the unique identification number of the transmitter. The third section is a checksum that is used to validate the code. The code detection is discarded if the checksum is invalid. The number of valid codes, pulses detected and codes rejected are stored in the receiver, along with the number of pulses detected. Those data can be used to calculate code detection efficiency (CDE) and rejection coefficient (RC) as demonstrated by Simpfendorfer *et al.* (2008). CDE and RC were calculated by the following formula:

$$CDE = D/S$$

$$RC = C/S$$

Where D is the number of valid detections, S is the number of valid synchronisation intervals (as an estimate of the number of codes transmitted) and C is the number of codes rejected because of invalid checksum. CDE is the proportion of detection and transmitted codes, and if CDE =1, the receiver detects 100% of codes transmitted. RC is the proportion of codes rejected and the number of codes transmitted, and low RC value (close to 0) indicates low frequency of invalid checksum and that the receiver detects transmission well.

The stored data were also used to estimate noise quotient (NQ) as described by Simpfendorfer *et al.* (2008) as follows:

$$NQ = P - (S * cl)$$

Where P is the number of pulses detected, and cl is the number of pulses used for one valid code; since some transmitters used 8-pulse code and others used 10, here we used the midpoint of cl = 9. Essentially, if there is a significant amount of environmental noise that can be detected by the receivers as a pulse, the data would show more pulses than could possibly be transmitted by a transmitter. Positive NQ values indicate more environmental noise because this means that there are more pulse-like noises in the environment that are detected by the receiver.

CDE and RC data were stored daily while NQ was stored both hourly and daily. Daily CDE, RC and NQ were compared between the four receiver zones using a linear mixed-effect model with individual receiver as a random factor with analysis of deviance test and post-hoc Tukey's HSD was conducted to assess if receiver performance was different among the zones. Additionally, hourly NQ was compared between the zones and time of the day using a linear mixed-effect model with individual receiver as a random factor. Analysis of deviance chi-square test was then conducted to examine if NQ values had a different trend throughout the day between the zones. For these analyses, CDE, RC and NQ values were log-transformed prior further analysis.

4.2.4 Animal tracking test

To examine if the acoustic receivers in mangroves could be used for animal tracking, tagged sharks and rays were released into the study area. Sharks and stingrays were caught by a seine-netting or rod-and-reel fishing, their size measured and their sex and maturity state (juvenile or sub-adult) recorded. A transmitter (V13 or V13AP; Vemco Ltd., Canada) was surgically implanted in the abdominal cavity.

The animal was placed in a container filled with water taken directly from the study site to ensure ambient conditions were maintained. Once the individual was immobilised, an approximately 2-cm incision was made in the abdomen with a sterile scalpel, the transmitter was inserted and pushed cranially until it was completely within the abdominal cavity. Finally, the incision was closed using surgical sutures. After checking the health condition of the animal and safety of the environment, the animal was released. The whole procedure took less than 5 minutes. Two animals, one blacktip reef shark *Carcharhinus melanopterus* (Quoy and Gaimard 1824) and one mangrove whipray *Urogymnus granulatus* (Macleay 1883) were caught and tagged for the trial. All animal capture and surgery techniques were consistent with Animal Ethics approval from James Cook University A2672.

Detection data downloaded from the receiver array were used to estimate animal position using the mean-position algorithm described by Simpfendorfer *et al.* (2002a). Time step for position averaging was 15 minutes. The positions of two selected individuals were mapped to display locations and examine if they were detected within mangrove stands.

4.3 Results

4.3.1 Range test

Outside mangrove range test

Detection probability (%D) increased as the distance between transmitter and receiver decreased (**Fig. 4.3**). The receiver located closest to the test transmitter had the highest value of %D (94.0%). The detection range of at least 50% of detections was up to 120 m (**Fig. 4.3**). This is the flat receiver located 120 m away from the transmitter that recorded more than 50% of detection. Other than four receivers that were located either There was no major physical obstruction between the transmitter and the receiver. The other receivers, especially located in the middle and rear zones had few or no detections even when the range was less than 50 m. These results were backed up by GLMM demonstrating that distance and the zone had no significant effect on %D (**Table 4.1**, **Fig. 4.4**). However, day or night significantly affected %D and %D was higher at night than during the day (**Fig. 4.4**).

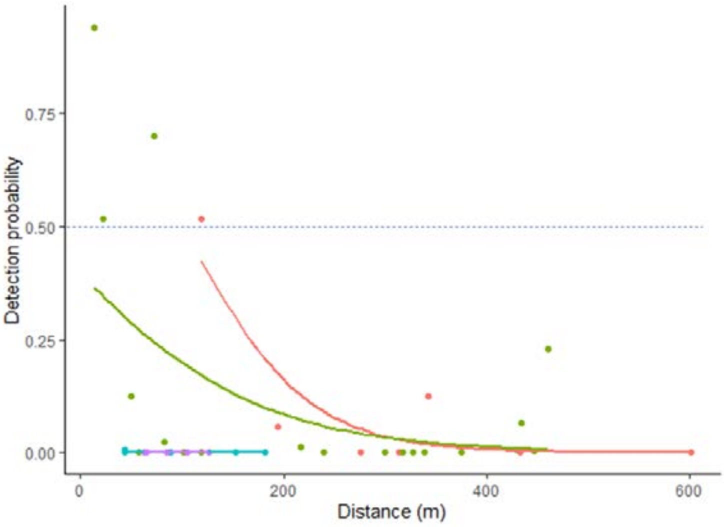


Fig. 4.3 Detection probability of the four zones for the outside mangrove test. Dotted line indicates 50% of detection probability.

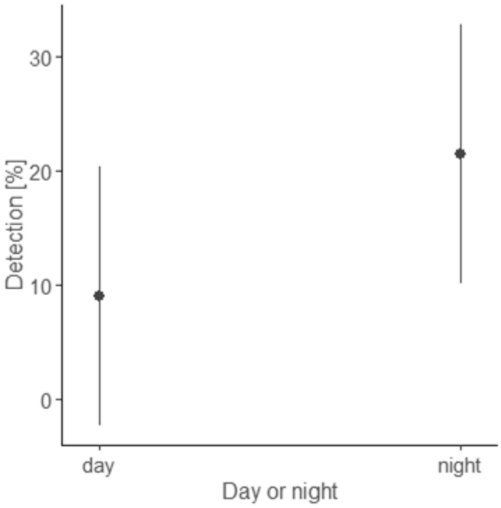


Fig. 4.4 Predicted detection probability between day and night for the outside mangrove test.

Table 4.1 Analysis of deviance table for the outside range test analysis.

Best model: %D ~ Day or night + (1 | Receiver)			
	Chi-square	df	p-value
Day or night	11.801	1	p<0.001
Distance	0.274	1	0.6007
Zone	1.3576	2	0.5072

Frequency of tidal height at Lucinda and frequency of detection at estimated water depth are not independent (Chi-square test: X^2 = 143, df = 132, p-value = 0.242) (**Fig. 4.5**). Between 200cm and 320cm depth, detection was made equally throughout the water depth >2m.

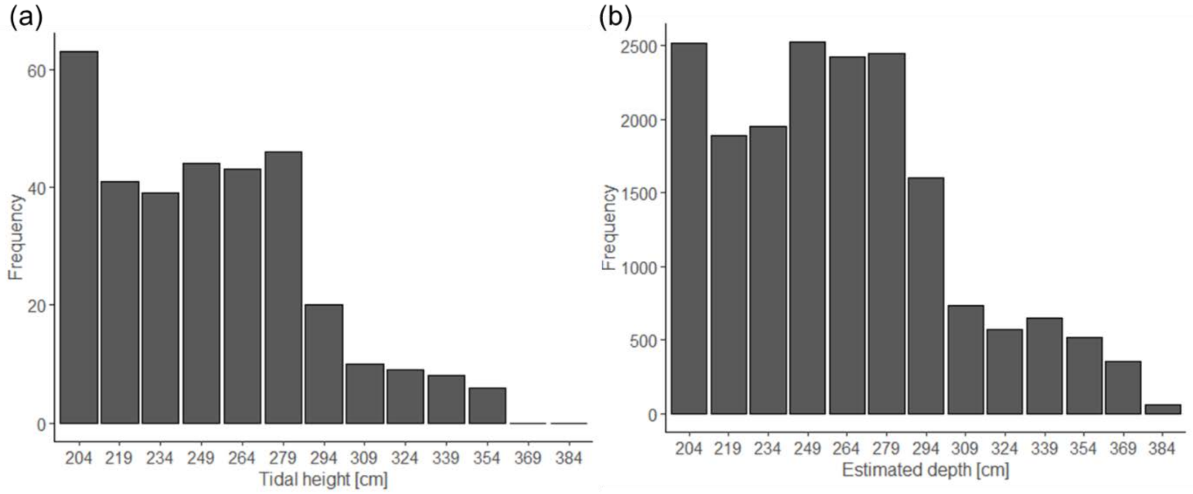


Fig. 4.5 Frequencies of (a) tidal height at Lucinda and (b) detections at estimated depth.

Inside mangrove range test

Detections were recorded by the six receivers located closest to the transmitters, while all other receivers had no detections (**Fig.4.6**). The receivers adjacent to the transmitters (<20 m) had 40 to 45% detection probability (%D) and the detection range was approximately 15 m (**Fig. 4.6**). Receivers located >20 m from the transmitters had very few or no detections. Detection probability was significantly affected by distance and day or night but not by the zone (**Table 4.2, Fig.4.7**). %D was higher when the distance was smaller and during the day than at night inside mangroves (**Fig. 4.7**).

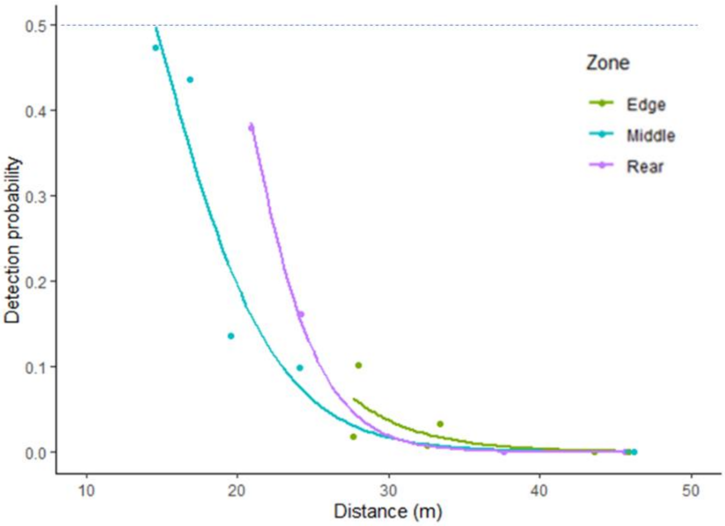


Fig. 4.6 Detection probability of the different zones for the inside mangrove test. Dotted line indicates 50% of detection probability. No detection was made by the flat receivers.

Table 4.2 Analysis of deviance table for the inside range test analysis.

Best model : %D ~ Day or night + Distance + Zone + (1 | Receiver)

	Chi-square	df	p-value
Day or night	13.9686	1	$p<0.001$
Distance	14.0604	1	$p<0.001$
Zone	2.4405	2	0.2952

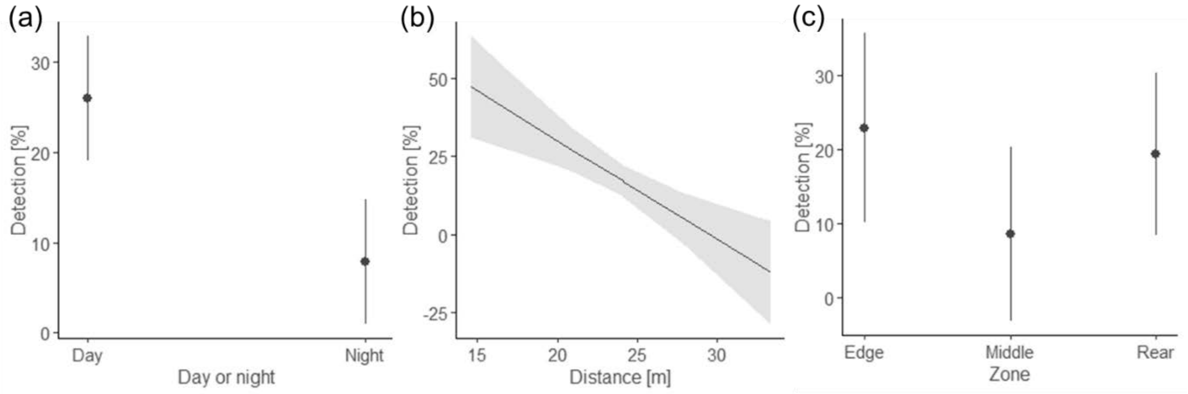


Fig. 4.7 Predicted detection probability (a) between day and night, (b) distance and (c) zones for the inside mangrove test.

4.3.2 Receiver event data

The daily event data results differed between inside (middle and rear) and outside (reef flat and edge) mangrove receivers (**Fig. 4.8(a)**-**(c)**). Overall, inside mangrove zones showed low rejection rates and reasonably high code detection efficiency, while the outside mangrove zones showed greater noise, low rejection rates and lower code detection efficiency.

Daily code detection efficiency (CDE) was significantly different between the mangrove rear and the other three zones, where overall CDE was lower in the rear mangrove zones than the other three zones (Analysis of deviance type II Wald chi-square test: X^2 = 18.727, df = 3, $p<0.001$) (**Fig. 4.8(a), Fig. 4.9(a)**). Daily rejection coefficient (RC) was low in the all four zones and less than 2.5% of codes were rejected due to invalid checksums (**Fig. 4.8(a)**). This indicates that there were very few transmitter collisions throughout the study. RC was significantly different among the zones, but the effect was small (Analysis of deviance test: X^2 = 8.4106, df = 3, p=0.038) (**Fig. 4.9(b)**). RC was lower in the mangrove rear than the other three (**Fig. 4.9(b)**). Daily noise quotient (NQ) values were significantly different among the four zones (**Table 4.3, Fig. 4.8(c)**). Daily NQ was the highest in the reef flat zone, followed by the edge and the middle, and was the lowest in the mangrove rear zone (Analysis of deviance test: X^2 = 98.835, df = 3, $p<0.001$) (**Fig. 4.9(c)**).

Hourly NQ data showed two distinct patterns (**Fig. 4.8(d)**, log transformed), where the noise at the reef flat and edge mangrove zone declined from 12pm to 5pm before gradually increasing again, while the inside mangrove zone increased around 5am and declined around midday. There was a significant interaction effect between hour and the zone on hourly NQ (**Table 4.3**) and hourly NQ was overall highest at the reef flat, low in the middle and rear zones, both fluctuating similarly throughout the day (**Fig. 4.9(c)**). Hourly NQ values in the mangrove edge moved between the reef flat and the middle and rear mangrove zones (**Fig. 4.9(c)**). The data inside mangroves (middle and rear) needs to be treated with caution as the sample size was small, and few detections were made by close receivers as stated above.

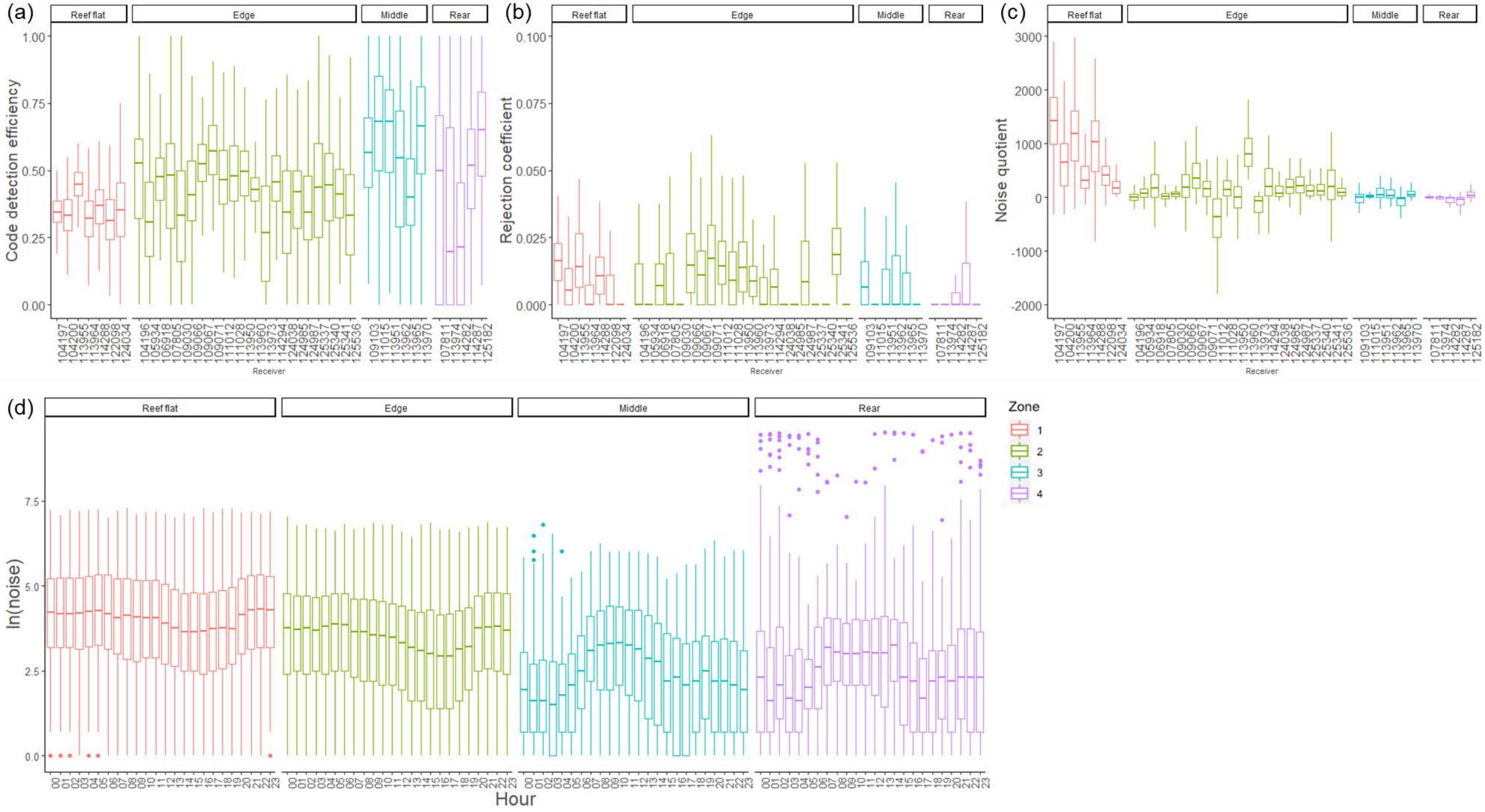


Fig. 4.8 Results of receiver performance. (a) daily rejection coefficient, (b) daily code detection efficiency, (c) daily noise quotient by receivers and (d) hourly noise quotient (log-transformed). (a), (b) and (c) are presented by different receivers. (d) demonstrates noise quotient by time of the day.

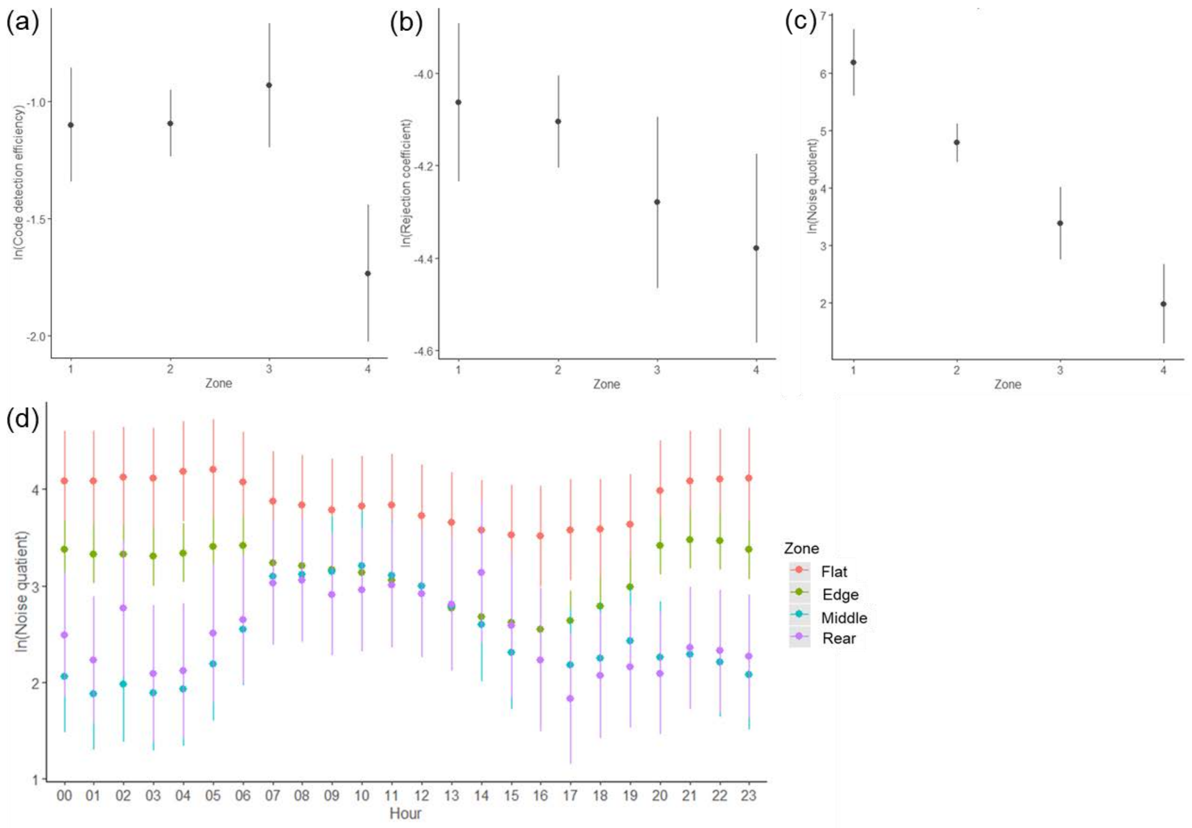


Fig. 4.9 Predicted values of (a) daily rejection coefficient, (b) daily code detection efficiency, (c) daily noise quotient by receivers and (d) hourly noise quotient based on linear mixed-effect models. Values are log-transformed for analysis.

Table 4.3 Analysis of deviance test results for hourly noise quotient.

	Chi-square	df	p-value
Zone	17.046	3	p<0.001
Hour	3429.848	23	p<0.001
Zone * Hour	2021.06	69	**p<0.001**

4.3.3 Animal application

The acoustic receivers at the reef flat, edge, middle and rear mangrove zones successfully detected tagged animals. The trajectories of a juvenile shark (blacktip reef shark, 671 mm total length, female) and juvenile stingray (mangrove whipray, 325 mm disc width, male) demonstrated that both were detected by the middle and rear receivers at the south mangrove stand (timestep = 15 minutes, one day for a shark and four consecutive days for a stingray) (**Fig. 4.10(a)**-**(d)**). The shark roamed over the reef flat, repeatedly swimming near the south mangrove edge and occasionally visiting middle and rear mangrove areas (**Fig. 4.10(a)** and **(b)**). Examination of the timing of these events showed that the use of the middle and rear mangrove areas occurred during the high tide periods of the presented days. The trajectory of a juvenile stingray demonstrated frequent use of rear mangrove zones (**Fig. 4.10(c)** and **(d)**).

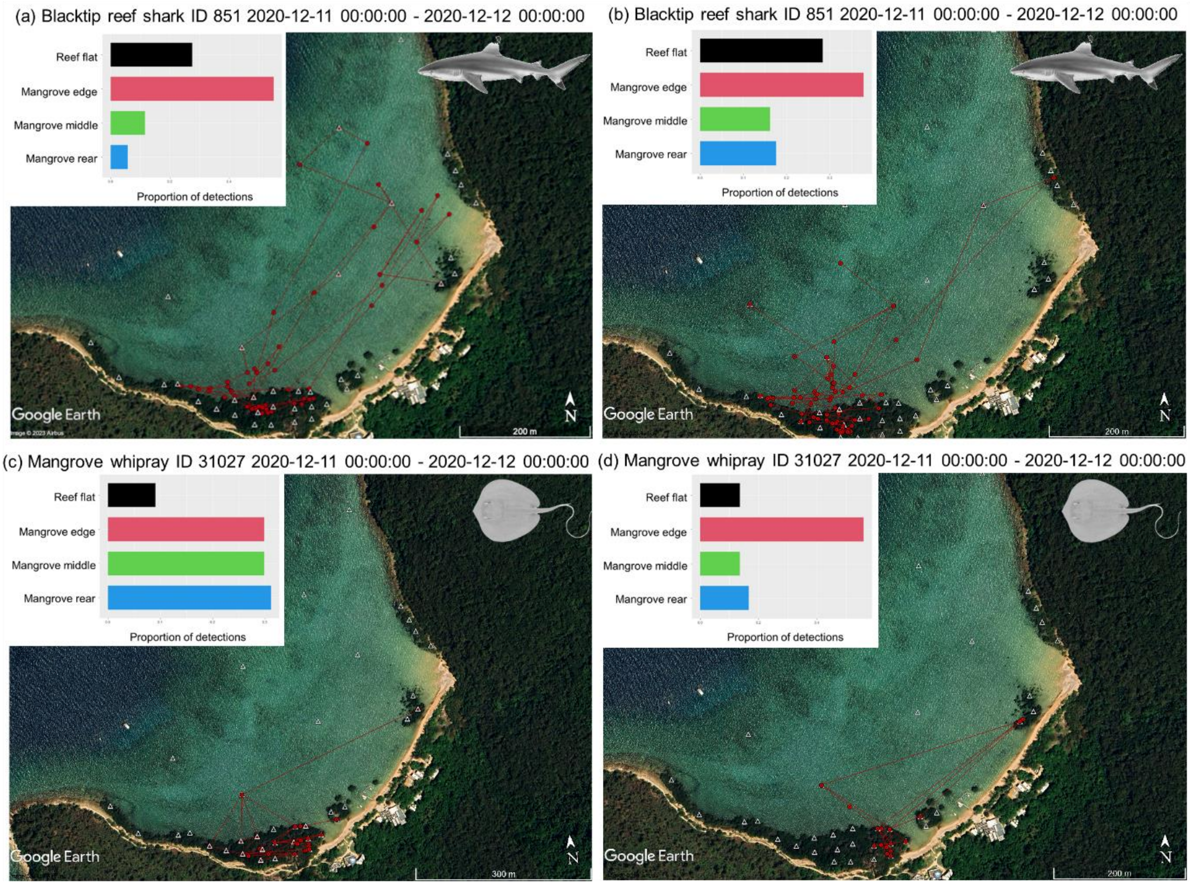


Fig. 4.10 Trajectories of tagged animal movement and bar graphs of the proportion of detections in the four different zones. Blacktip reef shark (ID 851) (a) from 11th to 12th of December 2020 and (b) from 11th to 12th of January 2021. Mangrove whipray (ID 31027) (c) from 10th to 14th of January 2021 and (d) from 1st to 5th of January 2021. △ represents acoustic receivers.

4.4 Discussion

This study demonstrated that acoustic receivers can be used for tracking animals where dense mangrove roots are present. As expected, dense mangrove roots and trunks blocked signal transmission (e.g. Claisse *et al.* 2011; Thiemer *et al.* 2022), resulting in only very short detection ranges for receivers deployed within the mangrove habitat. Receivers only logged at least 50% of detections from a transmitter when it was located within 20 m. When the distance between the transmitter and the receiver was more than 20 m in mangrove habitat, detections were rare. While detection ranges in the mangrove habitat were small, placement of receivers in a dense array (mean distance between adjacent receivers = 19.1 m) enabled the reception of many transmissions from transmitters and thus facilitated the tracking of animals inside the mangrove habitat. Very local detection as in this situation is an advantage for animal tracking because if the transmission from the tagged animal was detected there is a high probability it was present within a small area, and hence its location is known with a relatively high level of accuracy.

The detection range of acoustic receivers is expected to be small in topographically complex environments, such as vegetated and coral reef habitat. As expected, the detection range inside mangrove habitats in this study (i.e. ~20 m) is comparable to those reported from shallow seagrass, macrophytes and coral reef environments (**Table 4.4).** For example, Swadling *et al.* (2020) tested detection probability and detection range among the seagrass canopy and found that detection rage was up to 40 m. Similarly, Weinz *et al.* (2021) and Thiemer *et al.* (2022) conducted range testing in two macrophyte habitats and detection range was less than 8 m and 20 m, respectively. Welsh *et al.* (2012) conducted acoustic receiver performance tests in a shallow (~5m deep) coral reef at the same bay at Orpheus Island (a little farther offshore) and reported the detection range was as low as 60 m. Such small detection ranges are caused by low detection probability, and there are several possible factors that could lead to poor detection probability in mangrove habitats. First, signal blockage by physical structure was likely a major factor affecting detection probability as there were many obstacles (i.e. mangrove trees) between the transmitter and most receivers (Selby *et al.* 2016; Weinz *et al.* 2021). Second, water depth is an important factor for conducting acoustic telemetry; in very shallow water, acoustic signals do not travel far, resulting in low performance (Claisse *et al.* 2011; Cooke *et al.* 2013). Threshold water depth that acoustic signals travelled and were detected properly varies in the study site, and this study demonstrated that when tidal height was greater than 2 m and mangrove habitats were flooded, the detection probability was not affected by tidal height. Finally, reef environments are known to be quite noisy and environmental noise can interfere with the detection ability of acoustic receivers (e.g. Welsh *et al.* 2012) and hence, the proximity to the reef environments in this study may have affected acoustic receiver performance in the adjacent mangrove systems. It may also be possible that the mangrove habitat is noisy, but this has rarely been tested. Results of the NQ analysis suggest that the mangrove habitat was less noisy than the reef flat habitat, but further research is needed to understand the noise environment within mangrove habitats.

Table 4.4 Comparison of detection range between shallow structurally complex habitats.

Reference	Habitat type	Transmitter placement condition	Detection range
Swadling *et al.* 2020	Seagrasses	Above seagrass canopy	85 m
		Within seagrass canopy	40 m
Weinz *et al.* 2021	Macrophytes	Highest SAV density	7.85 ± 1.98 m
		Lowest SAV* density	196.08 ± 51.89 m
Thiemer *et al.* 2022	Macrophytes		17.26 ± 0.74 m
This study	Mangroves	Inside mangroves	20 m
	Reef flat	Outside of mangroves	100 m
Claisse *et al.* 2011	Coral reefs	5-10 m deep	30 m
		10-15 m deep	40 m
		15-20 m deep	50 m
Welsh *et al.* 2012	Coral reefs	<5 m deep	60 m

*SAV = submerged aquatic vegetation

In mangrove edge and reef flat (i.e. outside mangroves) habitats, the detection range was up to 120 m when there were no obstacles between the transmitter and the receivers. One receiver located 120 m away from the transmitter in the reef flat zone had a detection probability greater than 50% during the one-month test where the transmitter was located on the edge of the mangrove habitat. There were no major obstacles between this receiver and the transmitter, resulting in exceptionally high detection probability in the reef flat zone. Other than this receiver, detection was not made even when the distance was less than 100 m because thick mangroves were present between the receiver and the transmitter, and the transmission was blocked as such. In dense mangrove habitats, the distribution of vegetation (or any kinds of obstacles in the study area) influences the detection range more than distance between transmitter and receiver does. In some contexts, the density of vegetation and the structural complexity of habitat may matter more than distance. Additionally, shallow water depth and topography of the reef flat might affect detection efficiency (e.g. Cagua *et al.* 2013). The detection range in this study for both inside and outside mangrove habitats was much smaller than that in open water or estuarine river systems e.g. ~450m in an estuarine river system in Simpfendorfer *et al.* (2008), ~650m in open water in Huveneers *et al.* (2016) and ~950m at an offshore reef atoll Meyer *et al.* (2010). These findings suggest that detection range is fundamentally different depending on environmental factors, such as topography, habitat type and water depth, and therefore, the range test prior to the animal tracking is essential to interpret the tracking and monitoring data (e.g. Matley *et al.* 2022).

Detection probability during testing differed between day and night. In the present study, outside and inside mangrove tests showed the opposite pattern between day and night. In the outside experiment, detection probability was higher at night than daytime, whilst in the inside experiment it was higher during the day. Diel patterns in detection probability have been observed by several studies. For example, some studies have reported that detection frequency drops with the onset of sunset and stayed low at night until increasing at sunrise (e.g. Payne *et al.* 2010; Stocks *et al.* 2014) and attributed this pattern to an increase in biological noise at night that interfered with signal transmission and detection. In contrast, Welsh *et al.* (2012) found no diel pattern in detection probability in the coral reef environment in Pioneer Bay. Although our field study could not identify the potential causes of this diel pattern in detection, one possible explanation is the difference in daily fluctuation in environmental and biological noise (background noise) between reef flat and mangrove habitats due to physical context (e.g. open vs sheltered) and biological differences (e.g. faunal composition). Importantly, the comparison between the inside and outside tests should be treated with caution because of the difference in study durations (2-day vs 1-month) and the number of detections (much fewer detections inside mangroves than outside).

The performance metrics of acoustic receivers were tested for the first time in a mangrove habitat and were characterised by low background noise and low rejection rates (i.e. middle and rear mangrove zones). In this study, less than 2.5% of codes were rejected due to invalid checksum, indicating that there were very few transmitter collisions (e.g. Simpfendorfer *et al.* 2008). Noise analysis results suggest that inside mangroves (i.e. the back and middle zones) were less noisy habitat than outside mangroves (i.e. the reef flat and mangrove edge zones). Noise in the reef flat zone was especially high compared to the other zones., which is not surprising as the coral reef environment is very noisy (Welsh *et al.* 2012); and as such, total number of detections was most likely to be lower than the synch codes transmitted by the transmitter due to noise, resulting in low code detection efficiency. Inside mangrove zones, in contrast, was less noisy and showed higher code detection efficiency than that from the reef flat and mangrove edge receivers. Lack of noise in mangrove zones possibly occurs because mangrove trees block noise from the outside, such as wind, rain (Gjelland *et al.* 2013) and waves (Stocks *et al.* 2014) and therefore the water surface was calmer inside mangroves, and additionally, the mangrove habitats were located away from the noisy reefs. Thus, the results of receiver performance metrics support the use of acoustic receivers in mangrove habitats. As this experiment demonstrated, codes sent from the transmitter were detected with high code detection efficiency, low rejection rates, less noise and virtually no signal collision inside mangrove habitats as long as the transmitter was nearby.

Diel variation in the degree of noise was found to be different inside and outside mangrove habitats. At the outside mangrove zone, noise was relatively higher throughout the day except late afternoon and evening (between 2pm and 8pm) when the level of noise dropped. This is somewhat contradictory with the findings by Payne *et al.* (2010) and Radford *et al.* (2008) that biological noise increased at night in reef environments. Inside mangroves, the level of noise increased in the morning after sunrise until midday and then dropped and stayed low outside of those hours. It is difficult to explain why we observed this pattern in noise inside and outside mangroves in the current study, but there was likely to be unknown factor(s) causing the daily noise pattern. Patterns in diel noise difference are likely to vary significantly between systems (reef vs non-reef) and possible causes of this diel pattern in noise could be animal activity and surface water movement. (Payne *et al.* 2010; Gjelland and Hedger 2013). Future research should examine the source of background noise inside mangroves to examine what possibly effect it may play in acoustic receiver performance.

The range testing data from the inside mangrove test need to be treated with caution because of a short duration of range testing 2 days. Although the data demonstrated general pattern of small detection range inside mangroves, future research with longer duration (at least 2 weeks) would be beneficial to assess more detailed information. In addition, receiver deployment method is known to affect receiver performance (Heupel *et al.* 2006; Huveneers *et al.* 2016). Although this needs future research in mangrove habitats, this study demonstrated the effectiveness of the deployment method we used because some receivers recorded more than 90% of signals that arrived at the receiver and previous research has been successfully conducted using the same deployment method (Schlaff 2020). Biofouling on the receiver, which is another major factor that negatively affects the receiver performance (Heupel *et al.* 2008), had negligible effects in this study because biofouling was minimal. Lack of biofouling may have been in part because of the regular drying of receivers at low tide which would have reduced the ability of fouling organisms to survive.

The results of animal tracking demonstrated that the receiver array was able to track tagged sharks and rays when they were present in areas well inside mangrove habitat, including in very shallow areas located in dense mangroves. Based on range test results, the detections by middle and rear receivers indicated the presence of individuals nearby (likely within 20 m), confirming that tagged sharks and rays were regularly roaming near the rear and middle receivers. Although the use of mangrove root habitat by stingrays and blacktip reef sharks in the study area was previously observed by active acoustic tracking (George *et al.* 2019; Martins *et al.* 2020b), passive monitoring (Davy *et al.* 2015) and video observation (Kanno *et al.* 2019), the present study revealed these species move farther into the dense mangrove areas and away from the edge habitat than previously thought. The use of thick mangrove habitats by sharks is somewhat surprising because free-ranging sharks were thought to avoid dense mangrove habitats to avoid stranding in shallow water and getting stuck in mangrove structures (e.g. Davy *et al.* 2015). In fact, one tagged shark got caught in mangrove roots at low tide in our study area (and released by our research team; S. Kanno pers. obs.). These field experiments and observations suggest that although there is a risk of swimming into dense mangrove habitats, these species use them presumably for some benefit and there is a trade-off between predation risk, stranding risk and possibly feeding opportunities (e.g. Leurs *et al.* 2023).

The trajectory of the tagged shark shows that this individual was repeatedly detected along the edge receivers at the south mangrove stands. This finding further supports their repetitive movement and habitat preference, found in the same study site by active tracking (George *et al.* 2019). Furthermore, the stingray did not move extensively inside the mangrove habitat compared to the shark, but rather, stayed near the rear mangrove zones for a prolonged period during high tide. These movements are consistent with observations from a video study in this bay, where juvenile stingrays were observed resting sometimes for up to 20 mins inside mangrove habitats on high tide (Kanno *et al.* 2019). For the shark, the proportion of detections was generally higher at the reef flat and edge habitats than middle and rear mangrove habitats, presumably due to limited accessibility of mangrove habitats during high tide. The stingray was, in contrast, detected less in the reef flat zone likely because their flattened body shape allows mangrove whiprays to remain in very shallow water (less than 20 cm) at lower tidal levels and move much less than blacktip reef sharks (Davy *et al.* 2015; George *et al.* 2019; Martins *et al.* 2020b) and so are rarely detected by reef flat receivers. Thus, acoustic receivers deployed in the different zones in mangrove habitats were able to reveal differences in the use of mangrove habitats between juvenile sharks and stingrays.

Importantly, acoustic receivers and transmitters were successfully used for monitoring the movements of sharks and rays within mangrove habitats in this study. Conducting the range test prior to the animal application allowed us to examine if the design of a receiver array in the mangrove system was appropriate and demonstrated a very localised detection range inside mangrove habitats. The receiver performance metrics identified row rejection rates and environmental noise, resulting that the acoustic receivers and transmitters functioned appropriately within a mangrove habitat as long as the short detection range was taken into account in the array design. Those test results gave strong support for how to interpret the data obtained from the animal tracking in mangrove habitats, and as such, the animal application test revealed the holistic movement of individuals within mangrove habitats. Future research using acoustic telemetry will be able to reveal more detailed habitat use and movement pattern of aquatic animals, such as elasmobranchs, in mangrove habitats and help inform the significance of the presence of mangrove habitats for nearshore species.

CHAPTER 5

Mangrove use by juvenile sharks and rays

5.1 Introduction

Mangroves are one of the most productive components of tropical nearshore systems, characterised by high productivity, efficient nutrient recycling and physical structures (Alongi 2014). Mangroves offer essential habitats to a wide range of both terrestrial and aquatic organisms. Structurally complex roots and trunks of mangroves provide physical shelter while their high productivity and biomass offer food resources to inhabitants. Mangrove habitats also serve as nursery grounds because the services mangroves provide enhance species' survivability and fitness (Nagelkerken *et al.* 2000b; Nagelkerken *et al.* 2015). The importance of mangrove habitats is well recognised, and their functional roles are well studied for some taxa, such as invertebrates and teleosts (Nagelkerken *et al.* 2008; Lee *et al.* 2014). For example, some teleost species are known to use mangrove root structures because structures offer shelter and shade (Cocheret de la Morinière *et al.* 2004; Nagelkerken *et al.* 2010). Piscivorous fish use mangrove habitats during daytime for feeding while other species stay in mangroves during the day and move to adjacent seagrass habitats at night for feeding (Nagelkerken *et al.* 2000a; Verweij *et al.* 2006a; Verweij *et al.* 2006b). Some fish species spend early life stages in mangrove habitats, and some may migrate to the coral reefs when they mature (Nakamura *et al.* 2008; Jones *et al.* 2010). Therefore, mangrove habitats provide essential nursery functions and support high abundance and species richness of reef fish populations in the adjacent coral reefs (Nagelkerken *et al.* 2012; Nagelkerken *et al.* 2015; Nagelkerken *et al.* 2017). Thus, habitat association of teleost species with mangroves have been well understood both for short-term (daily) and long-term (seasonal, ontogenetic) use (Faunce and Serafy 2006; Whitfield 2017).

Associations between mangroves and megafauna, including elasmobranchs, have only recently begun to receive research attention (e.g. Sievers *et al.* 2019). Additionally, sampling is often logistically difficult inside mangroves due to complex structures, occurrence of dangerous animals, low water visibility and tides. As a consequence, how elasmobranchs use mangrove habitats (e.g. detailed movement pattern and behaviour inside mangroves) is largely unstudied. Although refuge, feeding and nursery functions are often hypothesised for elasmobranch populations, these hypothesis need more study to determine if they are true and if so, which species benefit and what type of mangroves (e.g. species, location) provide those functions (see Newman *et al.* 2009; Stump *et al.* 2017). Thus, the function of mangrove habitats for elasmobranchs is poorly understood and likely undervalued. Knowledge on how elasmobranchs use mangrove habitats is urgently required as mangroves are disappearing globally mainly due to human activities (Thomas *et al.* 2017; Goldberg *et al.* 2020), and loss and degradation of habitats due to mangrove deforestation is negatively affecting elasmobranch populations (Jennings *et al.* 2008; Dulvy *et al.* 2021).

Detailed movement patterns and habitat use in mangrove habitats are a starting point to understand associations between elasmobranchs and mangrove habitats. The differentiation between elasmobranch use of mangrove habitats (i.e. within mangrove stands) and mangrove systems (i.e. habitats in proximity to mangrove habitat – see CHAPTER 2 for details) is particularly important because if species do not use mangrove habitats and there is no direct interaction between mangroves and species, it is not possible to describe if mangrove presence actually benefits species or if species would use the habitat without mangroves.

Due to the daily or seasonal change in environments in the coastal systems where mangroves grow, species must cope with cyclical changes in habitat availability and environmental factors, such as water temperature, wind, salinity and water depth (Knip *et al.* 2010). Recent research efforts revealed the fine-scale movement patterns of juvenile sharks and stingrays within an intertidal mangrove system in Orpheus Island, Australia (Davy *et al.* 2015; George *et al.* 2019; Kanno *et al.* 2019; Martins *et al.* 2020ab). For example, juvenile mangrove whiprays *Urogymnus granulatus* show strong affinity to mangrove habitats, and as the mangrove habitats is cyclically exposed and flooded with tide, their movements are known to be influenced by the local tidal cycle (Davy *et al.* 2015; Martins *et al.* 2020ab). This species is observed resting among the root structure when the mangrove habitats are flooded, suggesting that they use mangrove habitats as a predation refuge when it is available (Davy *et al.* 2015; Kanno *et al.* 2019; Martins *et al.* 2020b). Similarly, juvenile blacktip reef sharks *Carcharhinus melanopterus* are also known to use dense mangrove habitats when it is accessible to them during incoming tidal phases to reduce predation risk (George *et al.* 2019). Thus, at least during daytime hours, some juvenile shark and stingray species preferably use mangrove habitats for refuging, and their movement patterns and habitat use within mangrove habitats are largely driven by tidal cycles in an intertidal mangrove system. However, these studies have not provided long-term detailed observations of the use of mangrove habitats that would provide a better understanding of the patterns of mangrove habitat use.

Identifying behavioural patterns of animals in mangrove habitats provides important information of how and why animals use the habitat. Safety from potential predators may be of importance especially for juveniles, and some behavioural patterns are inferred to be means of predator avoidance. For example, George *et al.* (2019) found lap-like movement of blacktip reef sharks in mangrove habitats that enabled them to remain within mangrove stands during high tide. During high tide, juvenile sharks appear to repeatedly use the same locations or with similar movement paths that have provided safety from predation (Morrissey and Gruber 1993; Guttridge *et al.* 2012). Similarly, some ray species are known to return to the same refuging location during high tides (Stevens *et al.* 2008; Davy *et al.* 2015). Additionally, aggregation behaviour may be used as a predator avoidance strategy by juvenile individuals possibly because it dilutes the risk of predation or provides early predator warning (Klimley 1993; Heupel and Simpfendorfer 2005; Dill and Semeniuk 2005). Alternatively, species may aggregate as a response to changes, time of day, food availability or social drivers, and daily or seasonal patterns (McInturf *et al.* 2023). Though data is scarce, feeding or refuging behaviours have been observed in specific habitats (Simpfendorfer *et al.* 2010; Davy *et al.* 2015; Kanno *et al.* 2019) and behavioural patterns could infer the potential drivers of habitat use and functional roles of habitats that animals use.

The present study aimed to further extend the study duration of elasmobranchs in mangrove habitats by using passive acoustic telemetry to investigate diel and seasonal movement patterns and habitat use of juvenile sharks and stingrays within a mangrove habitat in Pioneer Bay, Orpheus Island. The bay has clear-water mangrove habitats that are routinely flooded and exposed with the semidiurnal tidal cycle. To examine if individuals used mangrove habitats, acoustic receivers were positioned inside mangroves among the root and trunk structures. Prior range testing revealed these receivers have small detection ranges, low environmental noise and high detection efficiency (see CHAPTER 4). Blacktip reef sharks, juvenile mangrove whiprays and juvenile cowtail stingrays *Pastinachus ater* (Macleay 1883) show high residency in the bay and are generally observed near, and at times in, mangrove habitats (Davy *et al.* 2015; George *et al.* 2019; Martins *et al.* 2020ab). Blacktip reef sharks are one of the most common sharks found on coral reefs in the Indo-Pacific region (Last and Stevens 2009). Their close association with mangroves has been reported from the local area around the study site (Chin *et al.* 2013a; George *et al.* 2019; Schlaff *et al.* 2020). Mangrove whiprays are inshore species, known to reside mainly in mangroves and estuaries (Last *et al.* 2016) and cowtail stingrays are demersal stingray species living mainly in inshore waters (Sherman *et al.* 2020). For both stingray species, juveniles are seen in the study site, but newborns are never sighted so they may be born elsewhere or remain cryptic.

Although Australian populations of both stingray species are not threatened with extinction (Kyne *et al.* 2021), global populations for both species are assessed as Vulnerable by the International Union of Conservation of Nature (IUCN) (Manjaji Matsumoto *et al.* 2020; Sherman *et al.* 2020). Given their population status, loss of mangrove habitats may have a critical impact because these species may spend some of their most vulnerable life stage in mangrove habitats. Therefore, research is urgently required to investigate how these species use mangrove habitats and what functions mangroves may play. The research objectives of this study were to investigate short-term (daily, tidal) and long-term (seasonal, annual) habitat use patterns of juvenile blacktip reef sharks, mangrove whiprays and cowtail stingrays within intertidal mangrove habitats and surrounding coastal systems (e.g. reef flat, coral reef) and assess behaviours of those species in the mangrove habitat. Specifically, this study examined (1) if mangrove use by each species was influenced by time of the day, season and tides, (2) whether individuals returned to the same or close locations on subsequent high tides, (3) if there was a pattern in the occurrence of aggregation behaviour by juvenile mangrove whiprays and (4) if the tortuosity of the movement paths of blacktip reef sharks differed with time of the day, season, tides and body size. The outcome of this study will help us understand the function(s) of the mangrove habitat for these species.

5.2 Methods

5.2.1 Study area

This study was conducted in Pioneer Bay, Orpheus Island in northeast Queensland, Australia. Further details of the study site are described in CHAPTER 4.

5.2.2 Study species

The study species were blacktip reef shark *Carcharhinus melanopterus* (family Carcharhinidae), mangrove whipray *Urogymnus granulatus* (family Dasyatidae) and cowtail stingray *Pastinachus ater* (family Dasyatidae). In Australian waters, the blacktip reef shark is born at about 50 cm TL, and it reaches 140 cm in length, with maturity between 95 cm and 110 cm TL (Last and Stevens 2009). Adult individuals are regularly seen in the study site although their home range extends beyond the Pioneer Bay area (Schlaff *et al.* 2020). In the study region, this species parturition occurs in November-December and neonates are observed in the bay. Mangrove whiprays are born at 14 cm DW and males mature at 55-65 cm DW (Last *et al.* 2016). Maximum disc width is around 140 cm (Last *et al.* 2016). The size commonly seen in the study site is between 35 cm DW and 70 cm DW (S. Kanno pers.obs.). Cowtail stingrays are born at 18 cm DW, and they attain approximately 200 cm DW (Last *et al.* 2016). The body size seen in the study site is usually no smaller than 35 cm DW and up to 80-90 cm DW. Both stingrays are common in the nearshore habitats in this study site and individuals inhabiting the intertidal area in the bay are presumably all juveniles. Newborn size has never been observed and birth location or timing of reproduction is unknown for both species around this study site.

5.2.3 Field methods

Receiver deployment

To monitor the movement of tagged sharks and rays for at least one year, passive acoustic telemetry was used. The receiver deployment details were described in CHAPTER 4. A transmission from the implanted transmitter was detected and recorded by the acoustic receiver(s) when the tagged animal was swimming close to the receiver.

Receiver location was categorised into four zones: reef flat (zone 1), mangrove edge (zone 2), rear mangroves up to 80 m from the mangrove edge (zone 4) and the middle between the edge and rear (zone 3) (**Fig. 5.1**). The data was stored in each receiver and downloaded in May 2021 and in December 2021. Based on the range test results (see CHAPTER 4), approximate detection range is 20 m inside mangroves (i.e. the receivers located in the mangrove middle and rear) and up to 100 m in the reef flat area (reef flat and mangrove edge receivers). The receiver array was designed to estimate the position of tagged animals within the bay including reef flat, but not beyond the reef crest.

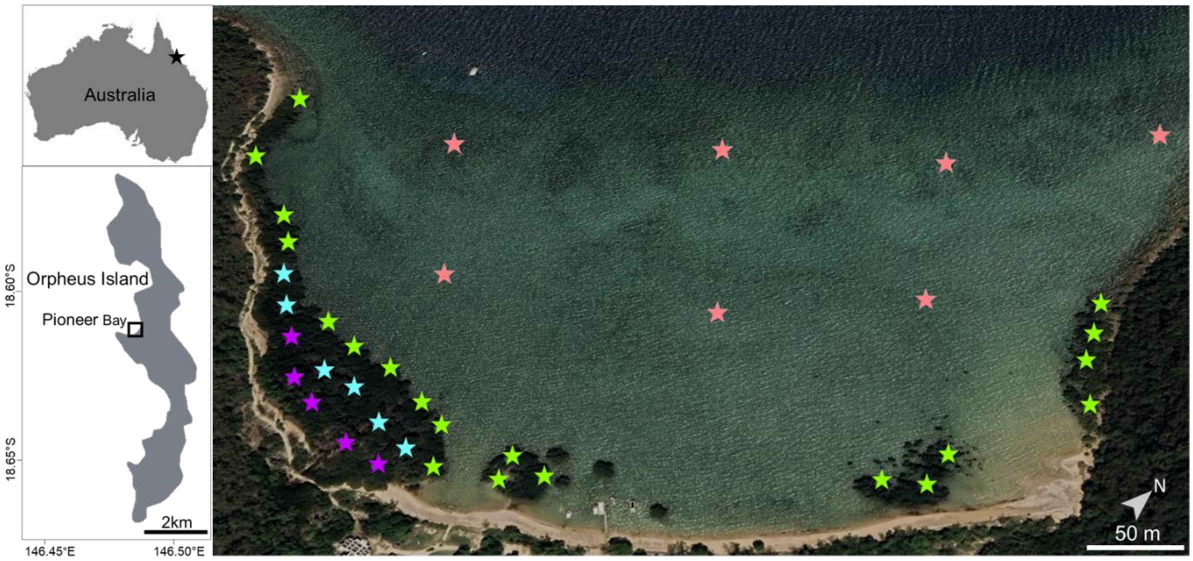


Fig. 5.1 Maps of study site and receiver deployment. Star indicates receiver (different zones in different colours: pink = zone 1: reef flat, green = zone 2: mangrove edge, blue = zone 3: mangrove middle and purple = zone 4: mangrove rear).

Animal handling and tagging

Study species were captured by rod-and-reel fishing and seine-netting. For line fishing, pilchards and squids were used as baits. The seine net used in this study was 30 m long and stretched mesh size was 1 cm. Each individual was measured, and the sex and maturity status (based on umbilical scar condition, body size and clasper calcification if available) were recorded. For body size data, total length (TL) or disc width (DW) were measured for sharks and stingrays, respectively. After measurement, each individual was tagged with an individually numbered tag (Roto tags for sharks on first dorsal fin and spiracle tags for stingrays). Individuals were then surgically implanted with V13, V13P (equipped with pressure sensor) or V13AP (equipped with accelerometer and pressure sensor) transmitters (Vemco Ltd., Canada). The detailed surgery procedure was described in CHAPTER 4. The surgery procedure took between 3 and 6 mins. After suturing, the tagged individual was released and its release condition was noted on a 5-stage assessment scale (1 good, 2 fair, 3 poor, 4 very poor and 5 dead). Generally, release condition was between 1 and 3. No individuals were recorded as dead when released in this study. Transmitter battery life listed by the manufacturer was 1117 days for V13, 596 days for V13P and 334 days for V13AP. All animal capture and surgery techniques were consistent with Animal Ethics approval from James Cook University A2672. This research was conducted under research permits from Queensland Department of Agriculture, Fisheries and Forestry (187250 and 208733) and the Great Barrier Reef Marine Park Authority (G15/37987.1 and G10/33240.1).

5.2.4 Data analysis

Mangrove use

To test if the mangrove use by each study species was affected by environmental factors, the presence of each species in zone 3 and 4 (= mangrove habitats) was calculated and analysed using a generalised linear mixed model (GLMM) framework with a binomial link function. Since mangrove habitats are only available to species, and as such transmission detections can only be made, when mangrove habitats are flooded, the data for analysis on mangrove habitat use was extracted when tidal height was more than 200 cm. This threshold tidal height was determined from the range test results (see CHAPTER 4).

The mean position of individuals was estimated every 30 minutes (timestep = 30 min.) for the periods when tide height was >200 cm using the mean position algorithm described by Simpfendorfer *et al.* (2002). The presence of individuals inside mangroves at a given 30-minute window was determined when it was detected by receiver(s) in zones 3 or 4. Individual was determined to be absent from mangrove habitats when detections during a 30-minute period did not occur on zone 3 or 4 receivers. The dataset for each individual ended at the last detection.

For GLMM construction, the response variable was presence/absence in mangrove habitats (binary response) and individual was incorporated as a random factor. The following environmental factors were sampled throughout the acoustic monitoring period and included in the models as explanatory variables: time of the day (hour), year-month (to enable the same month in different years to be differentiated), tidal stage (Top – 1 hour either side of high tide, Bottom – 1 hour either side of low tide, Rising – the period between the end of Bottom and beginning of Top, Falling – the period between the end of Top and the beginning of Bottom), tidal height and the proportion of the tidal height to the maximum tidal height during the study period in five categories (from 50% to 100%, hereafter, tidal magnitude). More specifically, the tidal magnitude is the maximum tidal height for an individual tidal cycle divided by the maximum tidal height during the study period (= 376 cm) and then was categorised into the five levels by increments of 10% (category 50, 60, 70, 80, 90 and 100%). For instance, if the maximum tidal height for a given tidal cycle was 200 cm, the tidal height was 200/376 x 100 = 53% of maximum tidal height and thus, the tidal magnitude was 50%. Additionally, body size was incorporated into the analysis only for sharks, as body size variation was relatively small between individual stingrays. For cowtail stingray analyses, the categorical factors of day or night was included in the model instead of time of the day because of small sample size. Day or night was determined based on local sunrise and sunset time. The full model was fitted using the '*lme4*' package (Bates *et al.* 2015) in the R program environment (R Core Team 2022). The '*MuMIn*' package (Bartoń 2023) was used to evaluate all combinations of parameters to determine the best fit model. The best fit model was selected based on Akaike Information criterion (AIC) model evaluation. If the difference of ΔAIC values between the best and the second-best models was less than 2, this indicates those two models had statistical support.

Reuse of high tide locations

Mangrove habitats in the study area are temporarily not available to sharks and rays due to cyclical change in tidal height, and therefore, during low tide the animals move out of the mangrove habitats. This study tested the hypothesis that individuals would come back to the same location in the mangrove habitat on subsequent high tides once mangrove habitats were flooded again and available to the animal. To test this hypothesis, the mean position algorithm was used to calculate the centroid of each individual during high tide (see information on identifying Top tidal stage above) for every tidal cycle and the distance between centroids of each consecutive high tide period calculated. If the distance was small, individuals came back to the same or similar location on the following high tide. The analysis was conducted for all three species.

The distance values were plotted in the histogram and G-test was conducted to test if the distance values were randomly distributed (i.e. occurrence of the distance between the last spot and the current spot at high tide would follow Poison distribution). If the distribution of the distance was not random, further analysis was conducted using a GLMM to assess which environmental factor(s) predicted the distance between consecutive high tide locations. Candidate and sampled environmental factors were time of the day, year-month and tidal magnitude. Body size was also included as a factor for shark's analysis. Individual was treated as a random factor. A model fitting was performed using *lme4* and *MuMIn* packages in the R statistical environment and the models were evaluated based on AIC*c*.

Aggregation

Aggregation of stingrays was commonly observed in the study site and animals were sometimes sampled when aggregating. To examine where and when aggregations occurred and if there is a relationship between the occurrence of aggregations and any environmental factor(s), aggregation analysis was conducted for mangrove whiprays. Nearest neighbour analysis was performed based on Clark and Evans (1954) and aggregation index was calculated following Heupel and Simpfendorfer (2005). First, the mean position of each individual was estimated using the mean position algorithm for every 30 minutes. Then, if 5 or more individuals were detected in the same 30-min period, the distance between the position of individuals of all combinations of pairs of animals was calculated. Next, the nearest neighbour distance r_i was determined and the mean nearest neighbour distance $r\bar{A}$ was calculated:

$$r\bar{A} = \Sigma r_i/n$$

where n is the number of individuals in the same 30-min time frame ($n \geq 5$). When n individuals were present in the study area a, the density of the observed animals is *n/a* and the expected distance to the nearest neighbour $r\bar{E}$ is calculated based on the density of animals in the study area as follows:

$$r\bar{E} = \frac{1}{2}\sqrt{n/a}$$

where a is the area of the Pioneer Bay mangrove area (7000 m^2 based on GIS calculations from aerial photography). Finally, the index of aggregation R was calculated:

$$R = r\bar{A}/r\bar{E}$$

If $R<1$, the population was aggregated. If $R = 1$, the population was randomly distributed and if $R >1$, then the population was uniformly distributed. To test if the value of R was significantly different from 1, the standard normal deviate (z) was calculated by:

$$Z = (r\bar{A} - r\bar{E})/sr$$

Where $sr = 0.26136/\sqrt{n(\frac{n}{a})}$. The value of R is significantly different if $|Z| > 1.96$. If $R<1$ and R is significantly different from 1, the animals detected in that 30-minute time period were considered to be aggregated. If $R \geq 1$ or R is not significantly different from 1, aggregation did not occur. Here, if 4 or fewer animals were detected in a given 30-minute time frame, this study determined this as the animals not being aggregated.

To examine if the occurrence of aggregation behaviour by stingrays was related to environmental factors, a generalised linear model (GLM) was conducted using the *lme4* package. Fixed factors were time of the day, year-month, tidal stage, tidal height and the tidal magnitude. All candidate models were evaluated using the *MuMin* package, and the models ranked based on weighted AIC (AIC*c*). The best fitting model had the lowest AIC*c* value. If the difference of ΔAIC values between the best and the second-best models was less than 2, this indicates those two models had statistical support.

Aggregation sites were mapped to visualise where aggregation occurred within the study area using the '*ggplot2*' package (Wickham 2016). The locations of aggregations were calculating as the centroid of all of the individuals in a 30-minute period that was determined to meet the criterion for aggregation (see above). The locations were then plotted using a density function to illustrate the intensity of aggregation locations.

Straightness of movement paths

The tortuosity of an animal's path is a parameter to assess orientation and searching behaviours (Benhamou 2004). Tortuosity is described as the degree of convolution (or straightness) relative to the path (Claussen *et al.* 1997). In the study site, George *et al.* (2019) observed circling behaviour by blacktip reef sharks inside mangrove habitats using active acoustic tracking. The current study examined the straightness of movement between different tidal stages. The 30-minute position average locations of each individual were segmented into tidal stages during each tidal cycle and the straightness of each of these periods calculated. The straightness index (S) was calculated when at least 4 locations were available in a period. The distance between the first and last points (D) was calculated; and the sum of the distances of temporally adjacent points (i.e. points 1 and 2, 2 and 3, etc) (P) were calculated. Thus, straightness index (S) was calculated as:

$$S = D/P$$

If S is 1, the movement between all points was linear. If S is close to 0, the movement was not straight, but rather tortuous with twists and turns. This analysis was conducted only for blacktip reef sharks as stingrays did not move as much as sharks and often lacked sufficient data to calculate straightness. To examine if there was a pattern in straightness, a GLMM was constructed and fitted using *lme4* and *MuMIn* packages in the R statistical environment. The following environmental factors were incorporated as fixed factors: time of day, year-month, body size, tidal stage and tidal magnitude. All candidate models were evaluated using the package *MuMin* and AIC*c* was used to determine the best fit model. If the difference of ΔAIC values between the best and the second-best models was less than 2, this indicates those two models had statistical support.

5.3 Results

5.3.1 Tagging and detection

A total of 36 animals were captured and tagged in October 2020, December 2020 and May 2021, including 17 blacktip reef sharks (7 females and 10 males), 12 mangrove whiprays (6 females and 6 males) and 7 cowtail stingrays (2 females and 5 males) (**Table 5.1**).

The range of body size of blacktip reef shark individuals was 543 to 1230 mm TL (mean: female = 754.9 ± 68 mm TL, male = 674.6 ± 66 mm TL). Nine individuals (2 females and 7 males) were classified as neonate based on open or partially open umbilical scars (one had an umbilical cord, and one had a fresh scar). Two individuals (one male and one female) were classified as adults based on their body size (1230 mm TL male and 1100 mm TL female) and calcified claspers although the adult male was never detected within the receiver array after tagging; this individual most likely left the bay after release given its good release condition and mature status. The rest of the eight individuals were identified as juveniles. The mean number of days detected was 115.5 ± 61.8 and the longest number of day monitored was 420 days (adult females) (**Table 5.1**, **Fig. 5.2(a)**).

Mangrove whiprays ranged in size from 310 to 410 mm DW (mean: female = 327.2 ± 6 mm DW, male = 332.5 ± 7 mm DW), while cowtail stingrays ranged from 410 to 480 mm DW (mean: female = 445.0 ± 35 mm DW, male = 456.6 ± 12 mm DW). All stingrays were classified as juveniles based on their body size. For mangrove whiprays, the mean number of days detected was 226.2 ± 15.7 and the longest number of days monitored was 364 days and shortest was 29 days (**Table 5.1**, **Fig. 5.2(b)**). One juvenile cowtail stingray (CWT 1) was possibly predated by a 2-m sickle lemon shark *Negaprion acutidens* while the tagged cowtail was resting in the shallow following release. Given the rate of movement and the detection data for this individual, the transmitter was most likely carried by a sicklefin lemon shark rather than a juvenile cowtail stingray. Therefore, this individual was removed from the dataset. For cowtail stingrays, the mean number of days detected was 164.7 ± 51.9 and the longest number of days monitored was 359 days (**Table 5.1**, **Fig. 5.2(c)**).

Table 5.1 Details of all tagged sharks and rays. Size is TL (mm) for sharks and DW (mm) for rays Abbreviations: date tagged (DT), date of last detected (DL) and number of days detected (DD).

ID	Species	TL (mm)	Sex	Status	tag type	DT	DL	DD
BTS 1	*C. melanopterus*	735	F	Juvenile	V13P-1x	11/10/2020	16/10/2020	5
BTS 2	*C. melanopterus*	883	F	Juvenile	V13P-1x	13/10/2020	7/12/2021	420
BTS 3	*C. melanopterus*	543	M	Juvenile	V13P-1x	6/12/2020	12/12/2020	6
BTS 4	*C. melanopterus*	671	F	Juvenile	V13P-1x	7/12/2020	7/12/2021	365
BTS 5	*C. melanopterus*	560	F	Juvenile	V13P-1x	8/12/2020	20/08/2021	255
BTS 6	*C. melanopterus*	713	M	Juvenile	V13AP-1x	9/12/2020	9/12/2020	0
BTS 7	*C. melanopterus*	755	M	Juvenile	V13AP-1x	9/12/2020	15/06/2021	188
BTS 8	*C. melanopterus*	635	F	Juvenile	V13AP-1x	9/12/2020	10/12/2020	1
BTS 9	*C. melanopterus*	615	M	Juvenile	V13AP-1x	9/12/2020	11/12/2020	2
BTS 10	*C. melanopterus*	545	M	Juvenile	V13P-1x	11/12/2020	15/03/2021	94
BTS 11	*C. melanopterus*	565	M	Juvenile	V13AP-1x	11/12/2020	2/02/2021	53
BTS 12	*C. melanopterus*	572	M	Juvenile	V13AP-1x	11/12/2020	20/12/2020	9
BTS 13	*C. melanopterus*	635	M	Juvenile	V13AP-1x	12/12/2020	19/02/2021	69
BTS 14	*C. melanopterus*	573	M	Juvenile	V13AP-1x	12/12/2020	1/06/2021	171
BTS 15	*C. melanopterus*	1100	F	Adult	V13AP-1x	13/12/2020	5/10/2021	296
BTS 16	*C. melanopterus*	700	F	Juvenile	V13AP-1x	14/12/2020	8/05/2021	145
BTS 17	*C. melanopterus*	1230	M	Adult	V13AP-1x	14/12/2020	No detection	0
MWR 1	*U. granulatus*	315	F	Juvenile	V13-1x	11/10/2020	3/08/2021	296
MWR 2	*U. granulatus*	334	F	Juvenile	V13-1x	11/10/2020	5/08/2021	298
MWR 3	*U. granulatus*	325	M	Juvenile	V13-1x	11/10/2020	26/09/2021	350
MWR 4	*U. granulatus*	314	M	Juvenile	V13-1x	12/10/2020	10/11/2020	29
MWR 5	*U. granulatus*	330	F	Juvenile	V13-1x	12/10/2020	10/08/2021	302
MWR 6	*U. granulatus*	350	M	Juvenile	V13-1x	8/12/2020	7/12/2021	364
MWR 7	*U. granulatus*	310	F	Juvenile	V13-1x	8/12/2020	2/10/2021	298
MWR 8	*U. granulatus*	325	M	Juvenile	V13-1x	9/12/2020	7/12/2021	363
MWR 9	*U. granulatus*	325	M	Juvenile	V13-1x	9/12/2020	13/09/2021	278
MWR 10	*U. granulatus*	324	F	Juvenile	?	9/12/2020	7/12/2021	363
MWR 11	*U. granulatus*	350	F	Juvenile	V13-1x	9/12/2020	21/09/2021	286
MWR 12	*U. granulatus*	356	M	Juvenile	V13-1x	9/12/2020	10/05/2021	152
CWT 1	*P. ater*	410	M	Juvenile	V13-1x	12/10/2020	19/10/2020	7
CWT 2	*P. ater*	473	M	Juvenile	V13-1x	12/10/2020	17/08/2021	309
CWT 3	*P. ater*	410	F	Juvenile	V13-1x	9/12/2020	9/12/2020	0
CWT 4	*P. ater*	480	F	Juvenile	V13-1x	12/12/2020	6/12/2021	359
CWT 5	*P. ater*	455	M	Juvenile	V13AP-1x	21/05/2021	27/09/2021	129
CWT 6	*P. ater*	465	M	Juvenile	V13AP-1x	23/05/2021	22/10/2021	152
CWT 7	*P. ater*	480	M	Juvenile	V13AP-1x	23/05/2021	6/12/2021	197

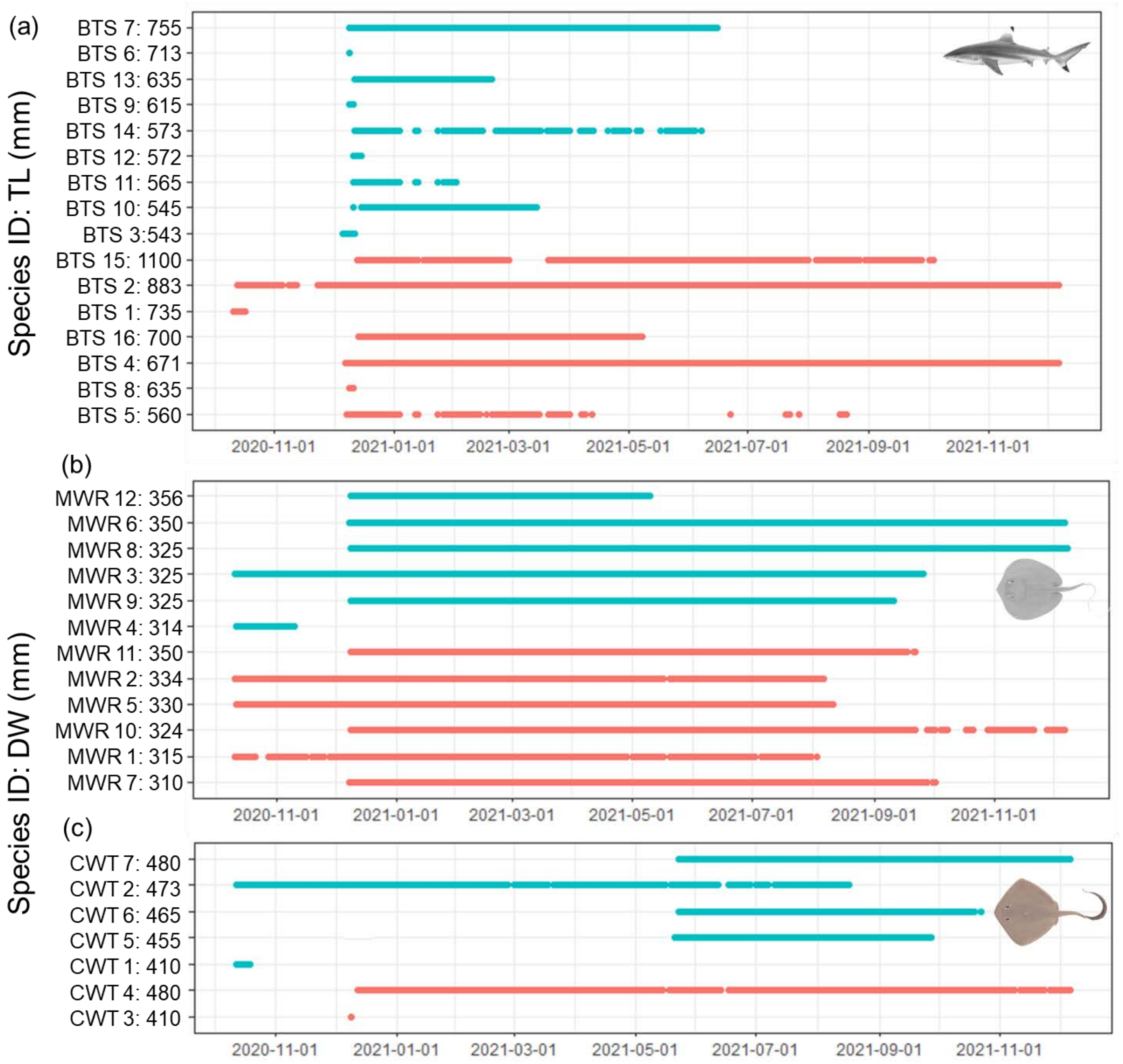


Fig 5.2 Calendar plots of total detections. (a) blacktip reef sharks, (b) mangrove whiprays and (c) cowtail stingrays. Blue is male and pink is female data.

5.3.2 Mangrove use

For blacktip reef sharks, two models had support; one was the full model with hour, year-month, tidal stage, tidal height, tidal magnitude and body size; the other was the full model without the body size term (**Table 5.2, Appendix 2**). The sample size for large individuals was small (only one individual >1m was detected throughout the study period) and this may be the reason for the weak effect of body size. Thus, the effect of body size data needs to be treated with caution. For mangrove whiprays, the full model with hour, year-month, tidal stage, tidal height and tidal magnitude was selected as the best model. For cowtail stingrays, the best model selected was the one with day or night, year-month, tidal height and the tidal magnitude.

Presence of blacktip reef sharks in mangrove habitats was strongly affected by time of the day (**Fig. 5.3(a)**). Sharks occurred inside mangroves during the day but rarely at night. The proportion of time they were detected in mangrove habitat was highest between 7 am and 1pm, fell slightly in the afternoon, before dropping to low levels during the night. Mangrove whiprays occurred most frequently in mangrove habitats at night and around the middle of the day, with relatively small declines in occurrence in the morning and afternoon (**Fig. 5.3(b)**). The similar decline in occurrence in mangroves by blacktip reef sharks and mangrove whiprays in the afternoon suggests that there may be the result of a change in detectability, possibly as a result of changing environmental conditions. Cowtail stingrays occurred inside mangrove habitats more at night than during daytime (**Fig. 5.3(c)**).

Both blacktip reef sharks and mangrove whiprays used mangrove habitats more during late spring and early summer months (**Fig. 5.3(d)** and **(e)**). Their presence inside mangroves increased at the onset of warmer months (September onwards) and decreased around January. Both blacktip reef sharks and mangrove whiprays decreased their presence in mangrove habitats between June and August (**Fig. 5.3(d)** and **(e)**). While this winter decline for blacktip reef sharks is possibly because 14 out of 17 individuals left the bay by the end of August (**Fig. 5.2(a)**), for mangrove whiprays, this winter decline occurred even though 11 out of 12 individuals were present in the area of the receiver array throughout the winter (**Fig. 5.2(b)**). The fact that the higher values in spring occurred in both 2020 and 2021 for mangrove whiprays indicates that the increase in occurrence in mangrove habitat was not the result of a tagging effect and occurs as a result of changing behaviour. Cowtail stingrays had a low affinity to mangrove habitats overall and the occurrence was highest in the months following tagging (October through December 2020) and then decreased towards the winter months (**Fig. 5.3(f)**). Interestingly, cowtail stingrays were not detected inside mangrove habitats between February and March 2021 even though at least two individuals were detected by the other receivers (**Fig. 5.2(c)**) and detected by zone 3 and 4 receivers again from April on.

Tidal stage, tidal magnitude and tidal height had a significant effect on mangrove use for all species (**Fig. 5.3(g)**-**(n)**). Tidal height included in the analysis ranged from 200 and 376 cm and in this range, mangrove use increased with the increase in tidal height. Tidal stage results demonstrated the opposite pattern between blacktip reef sharks and mangrove whiprays; the occurrence of blacktip reef sharks in mangrove habitats was greater at top and falling tides than rising tide (**Fig. 5.3(j)**), whereas that of mangrove whiprays was highest at the rising tide phase, followed by top and falling tide phases (**Fig. 5.3(k)**). For tidal magnitude, blacktip reef sharks showed highest occurrence in mangrove habitats in the 70 – 90 % categories (i.e. when the high tide tidal height was greater than 70% of the maximum tidal height) (**Fig. 5.3(l)**). Mangrove habitat use by mangrove whiprays increased with the tidal magnitude level and was the highest at the 90% category (**Fig. 5.3(m)**). For cowtail stingrays, due to limited detection data, only three tidal magnitude categories were included in the analysis, with the species having the highest occurrence in the 0.8 category (**Fig. 5.3(n)**).

Body size of blacktip reef sharks was included in the best fitting model but was not individually statistically significant. This suggests there may be a tendency that small individuals used mangrove habitats more than large individuals (**Fig. 5.3(o)**), but further investigation is required to confirm this result.

Table 5.2 Analysis of deviance tables for mangrove use analysis.

Blacktip reef sharks			
Best model 1: Presence ~ hour + year-month + magnitude + stage + scale(tideht) + (1 | tag)			
	Chi-square	df	p-value
Hour	1576.129	23	p<0.001
Year-month	363.931	14	p<0.001
Stage	57.259	2	p<0.001
Tidal magnitude	59.56	5	p<0.001
Tidal height	763.179	1	p<0.001
Best model 2: Presence ~ hour + year-month + magnitude + stage + scale(tideht) + scale(size) + (1 | tag)			
	Chi-square	df	p-value
Hour	1576.561	23	p<0.001
Year-month	363.7192	14	p<0.001
Stage	57.2531	2	p<0.001
Tidal magnitude	59.6015	5	p<0.001
Tidal height	763.3	1	p<0.001
Size	0.6456	1	0.4217
Mangrove whipray			
Presence ~ hour + year-month + magnitude + stage + scale(tideht) + (1 | tag)			
	Chi-square	df	p-value
Hour	237.97	23	p<0.001
Year-month	1393.43	14	p<0.001
Stage	208.00	2	p<0.001
Tidal magnitude	397.80	4	p<0.001
Tidal height	1445.69	1	p<0.001
Cowtail stingray			
Best model: Presence ~ daynight + year-month + magnitude + stage + scale(tideht) + (1 | tag)			
	Chi-square	df	p-value
Day or night	31.288	1	p<0.001
Year-month	147.793	11	p<0.001
Tidal magnitude	55.463	2	p<0.001
Tidal height	224.023	1	p<0.001

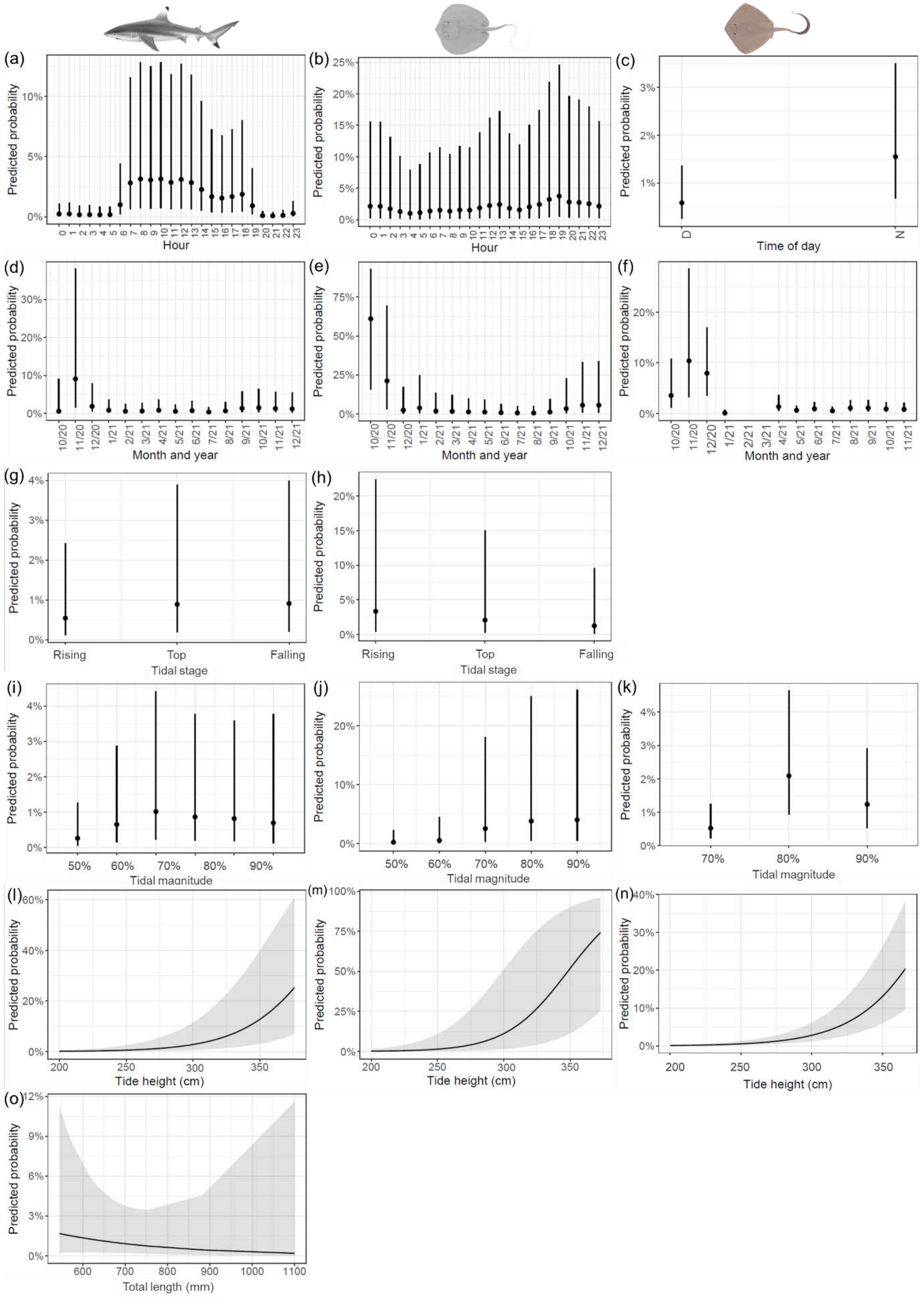


Fig. 5.3 Results of mangrove use analysis. (a) and (b) time of the day, (c) day night, (d)-(f) year-month, (g) and (h) tidal stage, (i)-(k) tidal height, (l)-(n) tidal magnitude and (o) shark body size.

5.3.3 Reuse of high tide locations

Centroid distance between two consecutive high tides was calculated for each species and the distance values compared to a random distribution to determine if individuals returned to the same or similar locations on consecutive high tides (**Fig. 5.4**). The distances between high tide centroids was significantly smaller than would be expected at random (blacktip reef shark: G = 2579.2, df = 14, p<0.01, mangrove whipray: G = 6200.1, df = 10, p<0.01, cowtail stingray: G = 1112.6, df = 10, p<0.01). The mean centroid distance was 184.3±2.5 m (median = 161.82 m) for blacktip reef sharks, 88.0±1.9 m (median = 35.7 m) for mangrove whiprays and 142.4±3.2 m (median = 122.1 m) for cowtail stingrays.

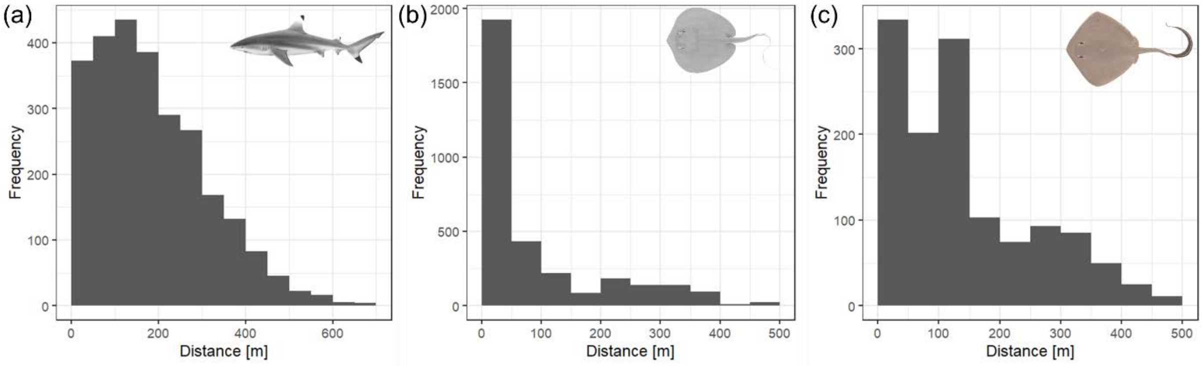


Fig. 5.4 Histogram of centroid distance. (a) blacktip reef sharks, (b) mangrove whiprays and (c) cowtail stingrays.

For all three species, the full model had the strongest support, this model included time of day (hour or day/night), year-month, tidal magnitude, and body size for blacktip reef shark (**Table 5.3, Appendix 3**). Thus, all of these factors were important drivers of the distance between high tide locations on subsequent tides, although overall, the effects of those factors seemed to be limited and weak (**Fig. 5.5**) For blacktip reef sharks, the distance was most commonly between 100 and 200 m from their previous location (**Fig. 5.4(a)**). Blacktip reef sharks demonstrated weak semidiurnal changes in the distance between high tide locations in summer months (**Fig. 5.5(a)**). Interestingly, the distance increased in October and November, which was similar to mangrove use pattern (**Fig 5.5(d)**). The effect of tidal magnitude and body size was limited for blacktip reef sharks, though the distance increased with tidal magnitude ((**Fig. 5.5(g)** and **(j)**). For mangrove whiprays, centroid distances were most frequent between 0 and 50 m indicating that this species generally returned to a location within 50 m of the previous tide (**Fig. 5.4(b)**). Hour, month or tidal magnitude were significant factors on the centroid distance, and there was a slight decline in the distance just after sunrise and in the early afternoon and slight increase in the distance between May and July (**Fig. 5.5(b),(e)** and **(h)**). Cowtail stingrays had two peaks at the distance at 0-50 m and 100-150 m (**Fig 5.4(c)**) and the distance decreased before sunrise and after sunset (**Fig. 5.5(c)**). The distance increased by almost 150% between April and June 2021, but this may be due to tagging effects as three additional individuals were tagged and released in May 2021 (**Fig 5.5(f)**). Tidal magnitude appeared to have a slight effect on the distance between high tide locations for cowtail stingrays, where their distance was greater when the tidal change was small (**Fig. 5.5(i)**).

Table 5.3 Analysis of deviance tables for reuse of high tide location analysis.

Blacktip reef shark			
Best model: distance ~ hour + magnitude + scale(size) + year-month + (1 | tag)			
	Chi-square	df	p-value
Hour	61.1658	23	p<0.001
Year-month	44.6722	14	p<0.001
Magnitude	8.8289	5	0.11609
Size	3.2028	1	0.07351
Mangrove whipray			
Best model: distance ~ hour + magnitude + year-month + (1 | tag)			
	Chi-square	df	p-value
Hour	51.2743	23	p<0.001
Year-month	57.4468	14	p<0.001
Magnitude	9.1612	5	0.102805
Cowtail stingray			
Best model: distance ~ hour + magnitude + year-month + (1 | tag)			
	Chi-square	df	p-value
Hour	94.441	23	p<0.001
Year-month	132.769	14	p<0.001
Magnitude	14.961	5	0.01053

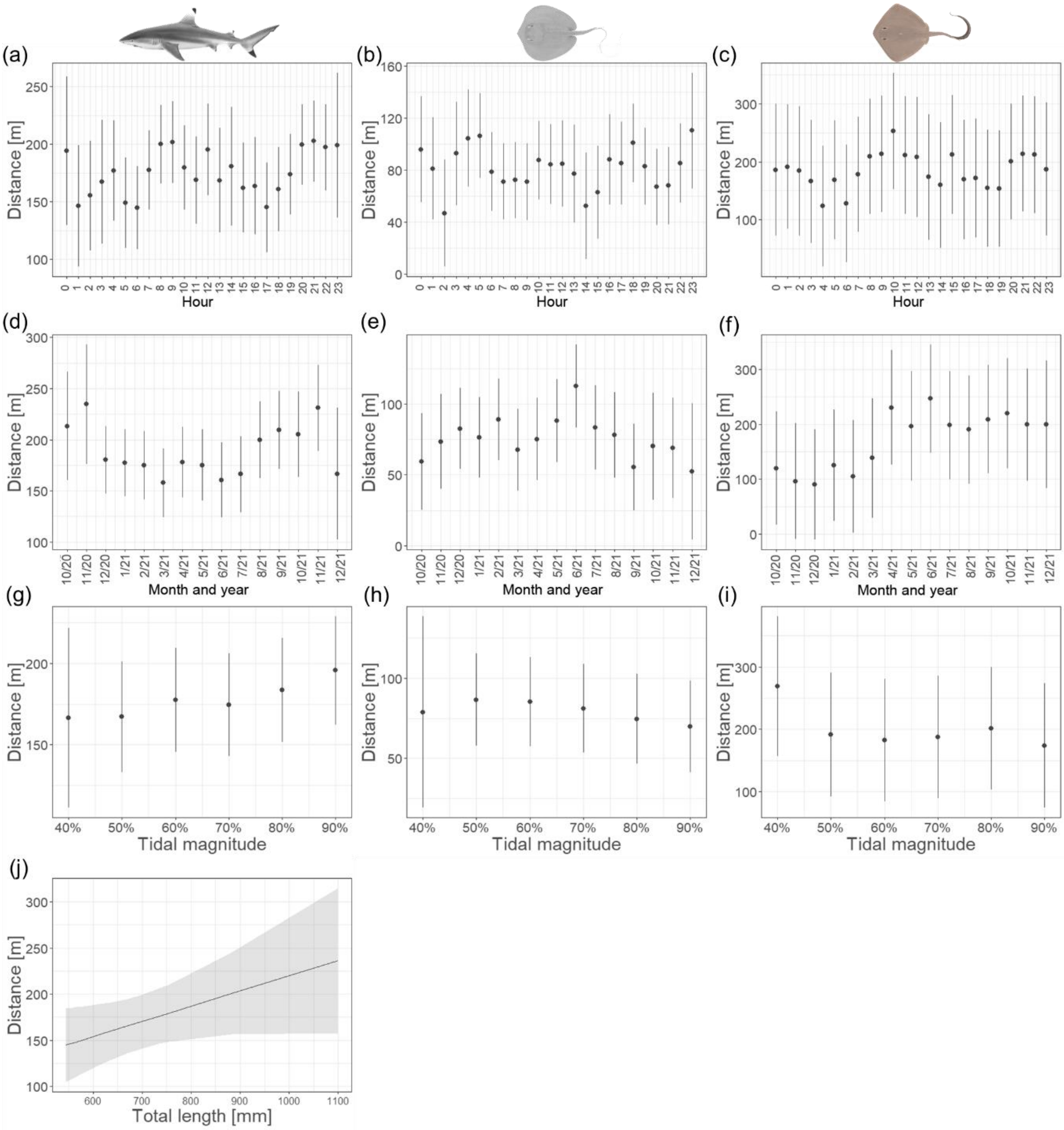


Fig 5.5 Results of reuse of high tide location analysis. (a)-(b) time of the day, (d)-(f) year-month, (g)-(i) tidal magnitude and (j) shark body size.

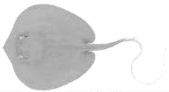
5.3.4 Aggregation of mangrove whiprays

A GLMM was used to identify drivers of aggregation in mangrove whiprays. The best fitting model had year-month, tidal stage, tidal height and tidal magnitude (**Table 5.4**, **Appendix 4**). Year-month had a significant effect on the occurrence of aggregation and more aggregation occurred in December and January, then aggregation declined (**Fig. 5.6(a)**). It is important to note that the occurrence of aggregations was highly dependent on the number of individuals present in the study site as the minimum number of individuals required for aggregation in this study was 5. The overall abundance of mangrove whiprays decreased after August 2021 from 11 individuals present to 3 individuals detected from September 2021 onwards. The decrease in animals within the system may reflect the acute decline in aggregation in August and no data afterwards. Aggregation occurred most during the falling tide, followed by the top of the tide phase (**Fig. 5.6(b)**), and when the tidal magnitude was large (>70 %, i.e. during spring tides) (**Fig. 5.6(c)**). Tidal height also had an effect on aggregation behaviour of mangrove whiprays, where the larger the tidal height became, the less aggregation occurred (**Fig. 5.6(d)**).

There were two frequent aggregation sites, located in the shallowest mangrove habitats, in the south and north mangrove stands (**Fig. 5.7**). mangrove whiprays tended to occur inside mangrove habitats when they aggregated,.

Table 5.4 Analysis of deviance tables for aggregation analysis.

Mangrove whipray			
Best model 1: aggregation ~ year-month + stage + magnitude + scale(tideht)			
	Chi-square	df	p-value
Year-month	488.23	8	p<0.001
Stage	161.76	2	p<0.001
Magnitude	67.34	5	p<0.001
Tidal height	4.36	1	0.03678
Best model 2: aggregation ~ year-month + stage + magnitude			
	Chi-square	df	p-value
Year-month	486.07	8	p<0.001
Stage	188.11	2	p<0.001
Magnitude	78.06	5	p<0.001



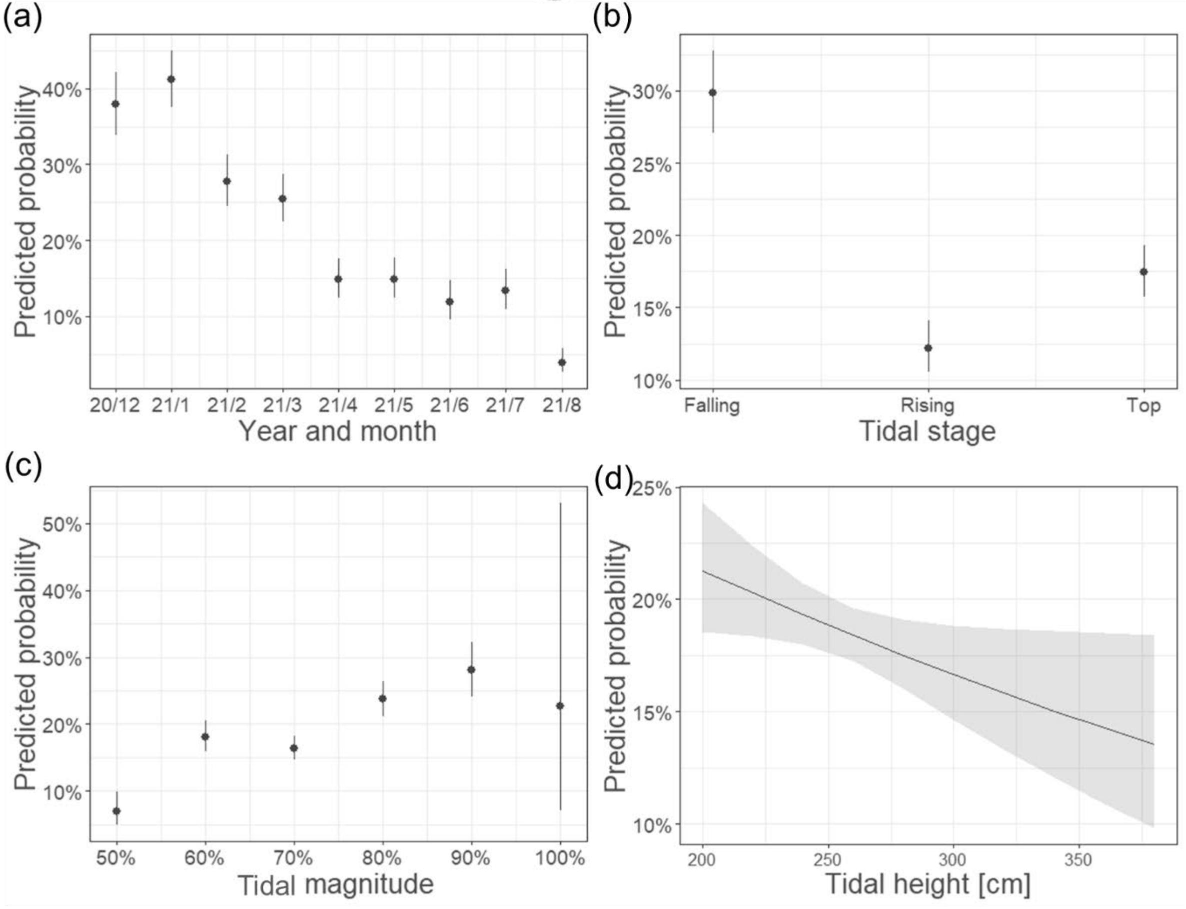


Fig. 5.6 Results of aggregation analysis. (a) year-month, (b) tidal stage, (c) tidal magnitude and (d) tidal height.

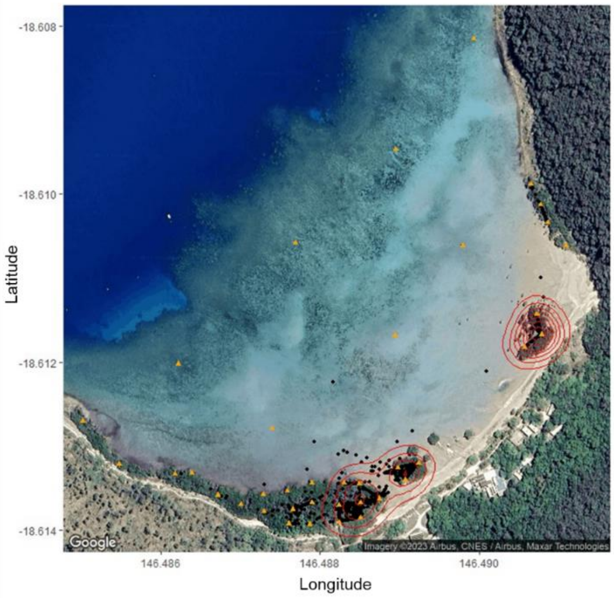


Fig. 5.7 Location of aggregation of juvenile mangrove whiprays. Black dots indicate the mean position of aggregation, red lines indicate the density of frequent aggregation locations and orange triangles indicate the receivers.

5.3.5 Straightness of movement paths of blacktip reef sharks

Two models had support for the pattern in straightness of blacktip reef shark movement paths. The first model had year-month, tidal stage and t tidal magnitude, whereas the second model had those three factors plus body size (**Table 5.5, Appendix 5**). The inclusion of body size in only one of the models suggests that its importance may be relatively small, and further study is required to understand its role in track straightness. Time of the day and sex did not have a significant effect on straightness values.

The movement path of blacktip reef sharks was straighter during the spring and summer months (**Fig. 5.8(a)**). The path was more tortuous between January and August and became straighter from September onwards. There was a difference in the tortuosity between tidal stages, where the movement was straighter at the bottom and rising tide phases than the top and falling tide phases (**Fig. 5.8(b)**). At the top and falling tides, the movement was slightly more tortuous. Tidal magnitude also had an effect on straightness; when the change in tidal height was large on spring tide days (tidal magnitude > 70%), the movement path tended to be straighter (**Fig. 5.8(c)**). As a trend, the larger the body size, the more tortuous the movement path, but the body size effect was minor (**Fig. 5.8(d)**).

Table 5.5 Analysis of deviance tables for straightness analysis.

Blacktip reef shark			
Best model 1: straight ~ year-month + magnitude + stage + (1|tag)			
	Chi-square	df	p-value
Year-month	138.299	14	p<0.001
Stage	62.049	3	p<0.001
Magnitude	61.407	6	p<0.001
Best model 2: straight ~ year-month + magnitude + stage + size + (1|tag)			
	Chi-square	df	p-value
Year-month	136.731	14	p<0.001
Stage	61.292	3	p<0.001
Magnitude	62.455	6	p<0.001
Size	10.14	1	p<0.01

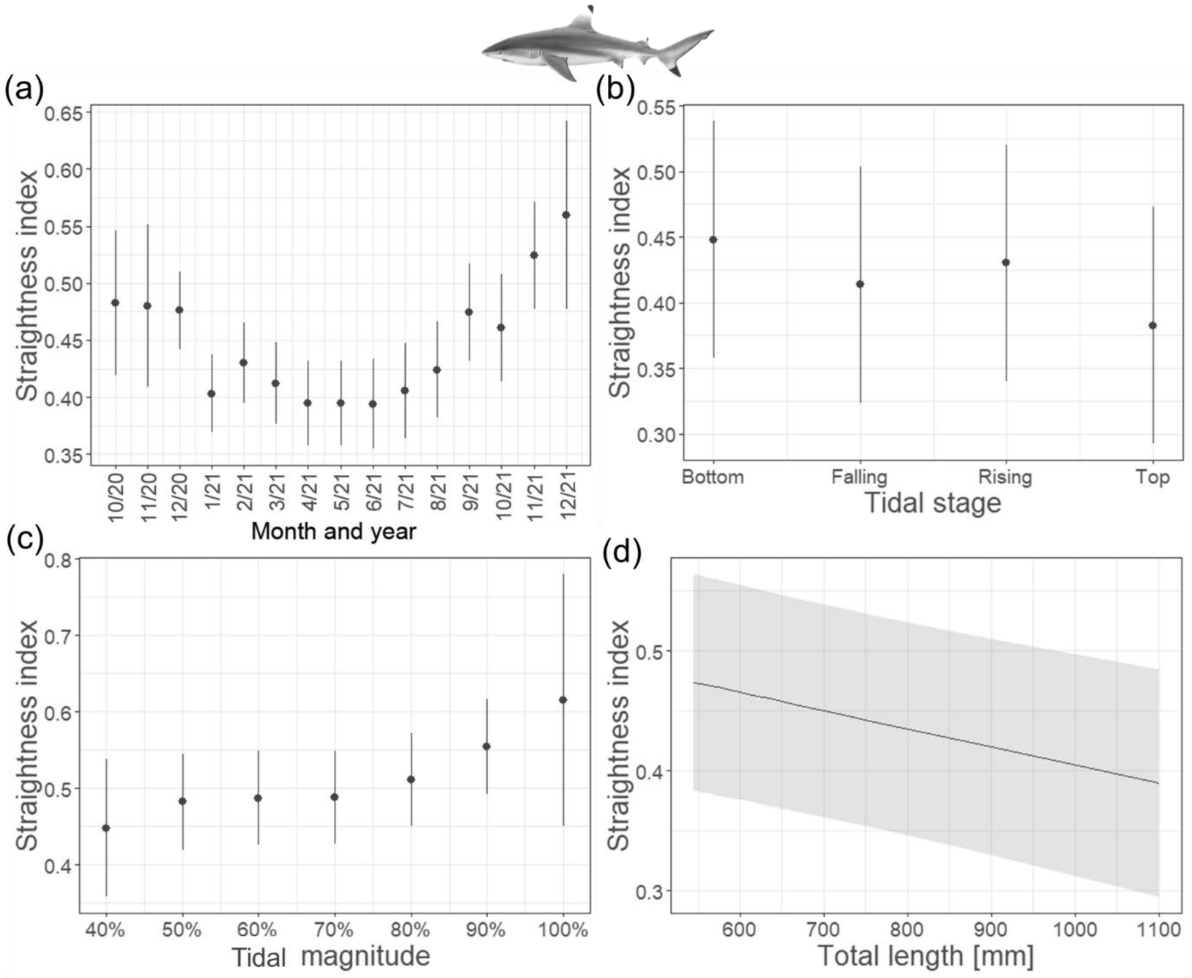


Fig. 5.8 Results of straightness analysis. (a) year-month, (b) tidal stage, (c) tidal magnitude and (d) body size.

5.4 Discussion

This study demonstrated different patterns of intertidal mangrove habitat use among juvenile blacktip reef sharks, mangrove whiprays and cowtail stingrays. Detailed monitoring of their presence inside mangrove habitats revealed daily and seasonal changes in species' habitat use and behaviour. The degree of association with mangroves varied between species and changed over time as lifestyle and ecological needs differ between species, and they were constantly facing fluctuations in biotic and abiotic factors, such as predator presence, water temperature, habitat availability and feeding opportunity (Knip *et al.* 2010). Overall, juvenile blacktip reef sharks and mangrove whiprays showed a close association with mangrove habitats. As the mangrove habitats are cyclically flooded and exposed with the tide, species occurred in mangrove habitats when they were flooded as observed in previous studies in Pioneer Bay (Davy *et al.* 2015; George *et al.* 2019; Martins *et al.* 2020b). In addition to the daily tidal cycle, change in tidal range (i.e. magnitude) had an effect on mangrove use as a large area of mangrove habitats are available during spring tides (tidal magnitude ≥ 0.8) while accessible areas are limited during neap tides. As a result, mangrove use was greater when tidal magnitude was larger because more mangrove areas were available for use. Furthermore, this study successfully monitored species' presence for at least a year and observed high residency of juvenile mangrove whiprays in the bay throughout the year. Female blacktip reef sharks also displayed relatively high residency within the receiver array, and such a sexual difference of residency pattern in blacktip reef sharks is consistent with previous studies in this region (Chin *et al.* 2013a; Schlaff *et al.* 2020).

Even though both species stayed within the study site throughout the year, interestingly, their presence inside mangrove habitats was greater in the spring than any other seasons. Seasonal change in mangrove use was observed with increased use of mangrove habitats in spring months between September and November. This increase was somewhat surprising as mangrove habitats were accessible to animals throughout the year and more than half of tagged mangrove whiprays (7 of 12 individuals) were present within the receiver array in the other months. For sharks, this increase in springtime was observed in two years (2020 and 2021 as some individuals were tagged in October 2020 and others remained until December 2021). Although seasonal change of habitat use in the intertidal habitats is not uncommon for blacktip reef sharks (Papastamatiou *et al.* 2010; Schlaff *et al.* 2020) and stingrays (Cerutti-Pereyra *et al.* 2014; Elston *et al.* 2022a), the evidence of a seasonal shift at a fine-scale (microhabitat level, within a 1 km range) is rare (Vaudo and Heithaus 2012). The reasons why the use of inside mangrove habitats by juvenile blacktip reef sharks and mangrove whiprays increased in spring is unclear, but there are at least two possible factors. One is related to seasonal occurrence of potential predators (Vaudo and Heithaus 2012; Vaudo and Heithaus 2013; Cerutti-Pereyra *et al.* 2014). In Pioneer Bay, November and December are the pupping season of blacktip reef sharks and adult females seasonally visit the nearshore area to give birth around that time (Schlaff *et al.* 2020). Juvenile blacktip reef sharks and mangrove whiprays might use mangrove habitats more frequently as a refuge when potential predators were more abundant in the bay because mangrove habitats are relatively safe from large-sized predators as demonstrated by this and previous studies (Kanno *et al.* 2019). An alternative explanation may be that water temperature is a driving factor for seasonal change in mangrove use. In warmer months, shaded mangrove habitats may serve as a thermal refuge as excessively warm temperature affects the metabolism and stingrays are known to select cooler temperature during the hottest periods of the day (Higgins 2018). However, mangrove use was not highest during the warmest months (December to February), and therefore the thermal refuge hypothesis may not have strong support. Further study is required to test if increased mangrove use in the spring is attributed to water temperature or other factors.

Presence of juvenile sharks and stingrays within mangrove habitats in an intertidal bay, could be underestimated particularly when considering the presence in the entire bay. Although range testing was conducted and the use of acoustic telemetry was confirmed as an appropriate method for tracking the species (see CHAPTER 4), the detection probability is relatively low, and the detection range is very small (up to 20 m inside mangrove habitats) compared to acoustic work in the open water (e.g. minimum 300 m in Heupel and Simpfendorfer 2014; up to 950 m in Meyer *et al.* 2010). The features of intertidal habitats, including shallow water, vegetation and soft substratum may interfere with the acoustic signal transmission (Heupel *et al.* 2006) and it is difficult to have complete coverage of the bay given the receiver array designed for fine-scale monitoring and the presence of physical structures and heterogeneity of the habitat. In addition, due to the fine-scale data sampling design, tag collision was likely to occur at times, and therefore false detections cannot be fully avoided even though receiver performance tests confirmed low rejection rates inside mangroves (see CHAPTER 4). Nonetheless, the array was designed to detect the presence of tagged animals inside mangroves and range tests confirmed that local detection could be successfully made within the range and that receivers positioned within 20 m could cover the mangrove patches in the study site. Range testing also enabled interpretation and use of data; for instance, the threshold tidal height for inside mangrove receivers was 200 cm based on the range test results. Thus, there is high confidence that the data from this study is biologically realistic and can be used to reveal patterns in fine-scale habitat use by juvenile sharks and rays in mangrove habitats for the first time.

Blacktip reef sharks demonstrated diel changes in mangrove habitat use. During the day, sharks occurred inside mangroves regularly. In contrast, at night they rarely were recorded inside mangroves. Mangrove use dramatically dropped around the time of sunset and increased again around sunrise, suggesting a diurnal pattern in the occurrence inside mangrove habitats. Diel change in habitat use and behaviour of reef-associated sharks is reported from other locations, including for blacktip reef (Papastamatiou *et al.* 2009; Papastamatiou *et al.* 2018), sicklefin lemon (Pillans *et al.* 2021), Galapagos *C. galapagensis* (Garla *et al.* 2005), grey reef *C. amblyrhynchos* (Field *et al.* 2010) and scalloped hammerhead sharks *Sphyrna lewini* (Holland *et al.* 1992; Holland *et al.* 1993). Importantly, this study using fine-scale acoustic monitoring revealed juvenile blacktip reef shark avoidance of mangrove habitats at night, which has not previously been reported. The structural complexity of mangroves may make it difficult for blacktip reef sharks to navigate and hunt within the mangrove habitats in the dark. Alternatively, their prey species may be more abundant outside of mangroves as some mangrove-associated fish species are nocturnal and active at night in the adjacent reef flat habitats (e.g. Nagelkerken *et al.* 2000a; Unsworth *et al.* 2007). Such nocturnal foraging behaviour has been seen in other coastal shark species (Garla *et al.* 2005; Legare *et al.* 2018). Papastamatiou *et al.* (2015) reported that hunting of blacktip reef sharks peaked in the early evening because their higher body temperature and better eyesight at low light levels provide advantages over their prey species at that time. The greater presence of mangrove whiprays inside mangroves at night is possibly a predator avoidance response to the shark's nocturnal hunting activity. The presence of mangrove whiprays inside mangroves peaked in the early evening (6pm-7pm), possibly because that is a time window with the highest risk of predation by blacktip reef sharks (Papastamatiou *et al.* 2015). Juvenile blacktip reef sharks presumably did not move far from the array at night, given their high tide returning distance <200m, but they may expand their activity range at night as reported in other species (Holland *et al.* 1992; Holland *et al.* 1993).

Detailed patterns of mangrove whipray aggregation behaviour were revealed for the first time through this analysis. Mangrove whiprays aggregated inside mangroves, especially in the shallowest mangrove habitats. Diel patterns and seasonal change in aggregation behaviour were not apparent in this study unlike Heupel and Simpfendorfer (2005) who reported diurnal aggregation of common blacktip shark *C. limbatus*. Thie lack of a pattern in whiprays may have been due to strong tidal effects in the nearshore habitats and small sample size later in the year, which made aggregations difficult to identify. Rather, aggregation may occur with tidal cycle as the high aggregation timing emerged every 6 hours, with the species aggregated most during the falling tide and least during the rising tide. Given that mangrove whiprays had a high likelihood of returning to a within 50m of high tide location on the next high tide, a possible scenario is: at the rising tide phase, mangrove whiprays individually return to where they were at the last high tide phase. Indeed, they were observed swimming in very shallow water with the tide movement by active tracking (Davy *et al.* 2015) and video surveys (Kanno *et al.* 2019). Once they arrive at their preferred location, they stay inside the mangroves for a prolonged period (sometimes up to 20 mins with no movement, Kanno *et al.* 2019) and start aggregating around the top of the tide phase while seeking and moving to safe locations. Then, when the tide is gradually draining from the mangrove habitat, they need to move towards the edge of the mangroves, especially those with a little more water to enable them to remain in the mangrove habitat as long as possible. Since these safe shallow locations are limited due to heterogeneity of water level caused by topography, individuals are more likely to occur in similar locations, and as a consequence aggregate most during the falling tide phase.

There are possible benefits and costs of stingray aggregation behaviours. Semeniuk and Dill (2005) observed and tested aggregation behaviour of cowtail stingrays and summarised that the benefits include protective spatial arrangement, early warning of predators and coordinated escape while the costs include interference and decreased escape speed. The present data suggest however, mangrove whipray aggregations are more coincidence than strategic activity as a result of occupying safe locations available at the time of a given tidal cycle phase. Cowtail stingrays studied by Semeniuk and Dill (2005) aggregated on the sand flat while mangrove whiprays in this study aggregated in mangrove habitats where physical structure can serve as a shelter. Cowtail stingrays positioned themselves in a rosette formation (“heads-in-tails-out”) to maximise the benefit of early warning and mechanoreceptor function of their tail (Semeniuk and Dill 2005). Mangrove whiprays, on the other hand, usually were positioned among the root structures, trying to squeeze their bodies into the shelter as much as possible, and as such, there was no uniformed formation (Kanno *et al.* 2019; Kanno pers.obs.). Early warnings and the confusion effect (i.e. flee from the predators in a group to confuse predator) are possible benefits for mangrove whiprays but escape costs may exist as they need to navigate through the mangrove structures as well as the other individual(s), and possibly because of that, mangrove whiprays did not aggregate all the time. Thus, mangrove whiprays may get some benefits of predator avoidance by aggregating but those may not outweigh the benefits from refuging among the root structures. Therefore, mangrove whiprays probably aggregate as a result of seeking the safest location available at that time especially when limited mangrove spots are available during falling tides rather than strategically aggregating to gain benefits.

The high tide return distance analysis highlighted that mangrove whiprays often return to within 50 m of their locations on the previous high tides. In Pioneer Bay, a range of 0-100 m is within the same mangrove patch and within a 200 m range is on the same side of the bay (as the distance between the north and south mangrove stands at Pioneer Bay is approximately 400 m). Based on this spatial scale, mangrove whiprays may have specific preferred locations within a particular mangrove patch. High tide distance slightly decreased during warmer months, which is possibly related to higher mangrove use in springtime as individuals may return to their “go-to” location in the specific mangrove patch more often because of their known safety from predators. This evidence further supports the previous findings of the navigational abilities and spatial memory of juvenile elasmobranchs (Edrén and Gruber 2005; Davy *et al.* 2015). Compared to mangrove whiprays, the distribution of blacktip reef shark distance between high tide centroids showed a wider range due to blacktip reef shark's more active nature. Juvenile blacktip reef sharks generally swam back to somewhere between 50 and 200 m from their previous high tide location, suggesting that they also have a preferred side of the bay (George *et al.* 2019). Given the year-round detections of some individuals, the data suggests that juvenile mangrove whiprays and blacktip reef sharks have a strong, fine-scale (less than 1km order) habitat attachment although there is an interspecies difference related to their movement characteristics. This strong site attachment is consistent with previous findings for both species (e.g. Papastamatiou *et al.* 2009; Elston *et al.* 2021), and this study further reveals their fine-scale "location-attachment". Juvenile mangrove whiprays and blacktip reef sharks may have spatial memory over time and repeatedly use the same locations because they may be relatively safe from threats (e.g. predators, adverse conditions) based on their previous experience. For both species, the high tide distance did not change with the tidal magnitude, suggesting that individuals move with the tidal cycle and return close to the previous spot they occupied at every tidal cycle. Adult blacktip reef sharks are known to regularly move outside of the Pioneer Bay (Schlaff *et al.* 2020) and in fact, one blacktip reef shark (adult female, 110 cm TL) that was detected for nearly 300 days was detected by an acoustic receiver located 8 km north from the study array. This shark's movement suggests that adult blacktip reef sharks have a larger home range than juveniles, but they still have a relatively high site fidelity to the area around Pioneer Bay.

Juvenile blacktip reef sharks showed changes in the tortuosity of movement path with tide and season. Detailed observation of straightness of juvenile blacktip reef shark movement paths revealed that sharks swam straighter paths at the bottom and rising tide phases than falling and top tidal phases and were straighter when tidal magnitude was large (around spring tide phase). This change in the tortuosity with the tidal phase is partially consistent with the findings from George *et al.* (2019) who conducted active tracking of juvenile blacktip reef sharks during daytime hours. Their study suggested that juvenile sharks moved with purpose during falling and bottom tidal phases because they were more susceptible to stranding. While at high tide, their movement was rather random, at low speed, and juvenile sharks demonstrated repeated lap-like movements, often within mangrove habitat (George *et al.* 2019). The present study added further details of movement path pattern of this species at both day and night for a year. Given their greater use of mangrove habitats during the day and relatively small high tide returning distance, juvenile blacktip reef sharks, at least during daytime bottom and rising tidal phase, presumably swim in a specific direction (straight paths to a destination) because safe mangrove habitats were not available during those times and transiting open reef flat areas they were at high risk of predation (Benhamou 1992; George *et al.* 2019). During rising tidal phases, sharks may move back to safer locations near mangroves using relatively straight paths, and during top tide phases, circle around mangrove habitats repeatedly to stay close to mangrove shelters. At night, sharks avoid mangrove habitats and the high tide distance slightly increased with more tortuous movement paths, suggesting their behavioural and habitat use change, possibly to allow nocturnal feeding on the reef flat. This hypothesis needs to be tested with detailed movement analysis and possibly acceleration data (to identify feeding bursts). Thus, blacktip reef sharks used both straight and tortuous movement paths, but overall, they stay near the receiver array with high site fidelity as hypothesised by Papastamatiou *et al.* (2009).

Juvenile cowtail stingrays did not show regular use of mangrove habitats in contrast to mangrove whiprays and blacktip reef sharks. Tagged individuals did show site fidelity around the study area, but the small sample size (5 individuals were detected more than a week) made it difficult to detect an overall pattern in their residency. Generally, their mangrove association was low throughout the year. Mangrove use peaked in November 2020 even though only one individual was tagged at that time. It then dropped in January 2021 and no detections occurred inside mangrove habitats between February and April even though two individuals were tagged and detected on the reef flat and mangrove edge. The reason for their absence between those months is unclear. Three additional individuals were tagged in June 2021, but the mangrove use pattern did not change afterwards, suggesting that there is no seasonal pattern in mangrove use by juvenile cowtail stingrays. In the study site, cowtail stingrays were observed occupying the reef flat and mangrove edge areas (Kanno *et al.* 2019; Martins *et al.* 2020a) and their habitat preference for sand and mudflat habitats is also reported from the other regions (O'Shea *et al.* 2012; Vaudo and Heithaus 2013). Preference for sand and mudflat habitats is attributed to high abundance of their preferred prey species such as annelids and polychaetes on the sandflat (Vaudo and Heithaus 2011; O'Shea *et al.* 2013) and the primary driver for their reef flat use is likely feeding opportunities (Vaudo and Heithaus 2013).

Feeding opportunities driving cowtail stingray habitat use is contrary to co-existing mangrove whipray juveniles that rarely occurred reef flat habitat due to high predation risk. The reef flat is an open area with limited opportunity to use structure to avoid co-occurring potential predators, such as adult sharks. Therefore, for their fitness and survival, juvenile cowtail stingrays likely have a well-developed predator avoidance strategy. There are several possible explanations why juvenile cowtail stingrays do not use mangrove refuges. First, juvenile cowtail stingrays may be more powerful than similar-sized mangrove whiprays due to morphological differences; cowtail stingrays have larger pectoral fins and thicker body (Last *et al.* 2016; S. Kanno pers.obs.). Using strong pectoral fins, they adopt a semi-oscillatory swimming mode characterised by powerful and fast swimming. Therefore, cowtail stingrays may be less susceptible to initial attack and be able to flee quickly. Second, they have more active lifestyle, constantly swimming and do not stay at the same place for a prolonged period (Vaudo and Heithaus 2012; Kanno *et al.* 2019). These movements could make it difficult for predators to locate them. Third, cowtail stingrays may strategically adopt aggregation behaviours both with the same species and the other species to reduce predation risk (Semeniuk and Dill 2005, 2006). Finally, cowtail stingrays have their spine near the end of a long tail away from the body while mangrove whiprays have their spine near body. Cowtail stingrays thus have a longer reach with which to strike predators. Food-risk trade-off is inevitable for cowtail stingrays, but because they have different and well-equipped predator avoidance tactics, juvenile cowtail stingrays may be able to focus more on feeding over the reef flat areas where their main prey species are most abundant. This hypothesis still needs to be tested by future research. Nevertheless, two co-occurring stingray species demonstrated contrasting association with mangrove habitats and their use in an intertidal mangrove system.

The movement and habitat use data from this study further supports the hypothesis that a primary driver of mangrove use by juvenile blacktip reef sharks and mangrove whiprays is predator avoidance (e.g. Davy *et al.* 2015; George *et al.* 2019; Martins *et al.* 2020b). Mangrove roots and trunks form a structurally complex habitat and serve as a physical shelter from large-sized predators (Cocheret de la Morinière *et al.* 2004; Mumby 2006). In Pioneer Bay, a video observation found that mangrove habitats are safe from large-sized shark and teleost predators as the predators cannot access the complex mangrove structures (Kanno *et al.* 2019). The preference for sheltered habitat has been shown juvenile lemon sharks *N. brevirostris*, with sharks tending to swim close to the root-like structure when a large potential predator was present nearby (Stump *et al.* 2017), further indicating the importance of root-like structures for juvenile anti-predator behaviour (Guttridge *et al.* 2012; George *et al.* 2019). For rays, particularly, their dorso-ventrally flat body allows them to stay among the root structures in very shallow water (less than 25 cm deep) allowing them to remain separated from predators that cannot access such shallow water; several ray species have been observed refuging under mangrove roots (Stevens *et al.* 2008; Simpfendorfer *et al.* 2010; Poulakis *et al.* 2011; Hollensead *et al.* 2018; Lear *et al.* 2019; Kanno *et al.* 2019; Martins *et al.* 2020b). Daily and seasonal changes in mangrove use may be explained by the presence of predators; when mangroves are available and predators are present, juvenile sharks and rays are more likely to use mangrove habitats (at night for mangrove whiprays when sharks hunt, and springtime when adult sharks are present).

Juvenile sharks and rays did not always use relatively safe mangrove habitats when they were accessible despite its benefits for mitigating predation risk, suggesting that there is a trade-off between predation risk and other ecological or biological need(s), such as feeding and optimal water temperature. In the study site, predation on juvenile stingrays by large-sized sharks occurred in the reef flat (S. Kanno pers. obs.) and predation risk can be high for juvenile sharks and rays in the open reef flat when the water level is high enough for potential predators to access them. Even so, juveniles selected reef flat habitats at certain times for specific reasons. For example, mangrove whiprays and cowtail stingrays were regularly observed feeding on the reef flat where preferred prey, particularly for cowtail stingrays, are abundant (Vaudo and Heithaus 2011). Juvenile lemon sharks are known to adopt a strategy to use either sheltered mangroves or open seagrass beds depending on individual's body size and susceptibility (Hussey *et al.* 2017). The food-risk trade-off is certainly a factor that affects habitat selection particularly for juveniles (e.g. Dhellemmes *et al.* 2020). Alternatively, selection of optimal temperature may be another reason for using areas outside mangrove habitats because stingrays can detect subtle change in water temperature (Vaudo and Heithaus 2013) and behavioural thermoregulation is beneficial particularly for somatic growth of individuals at early life stages (e.g. DiGirolamo *et al.* 2012). Trade-offs such as these can be a driving factor of species' habitat use, growth and fitness, foraging strategies and reproductive output (e.g. Vaudo and Heithaus 2013), and animals' use of multiple habitats indicates the availability of different types of habitats, including mangroves, reef flat and seagrass beds, provide multiple benefits for a wide range of species occurring in shallow water systems.

Mangroves offer protection against predators for small sized inhabitants and juvenile sharks and rays as they learn and use safe mangrove refuges changes in environmental factors (e.g. tide, temperature and presence of predators) as a part of their predation avoidance strategy. This use of mangroves indicates that the presence of mangroves supports the sustainability of local elasmobranch populations by providing refuging habitats for species at their most vulnerable life stage. Conversely, the loss of mangrove habitats may negatively affect the survival rate of juvenile elasmobranchs. Mangroves are disappearing globally with more than one-third lost between 1980 and 2005 (FAO 2007) primarily due to human activities, such as aquaculture, agriculture, infrastructure and tourism (Richards and Friess 2016; Goldberg *et al.* 2020). Additionally, climate change is reducing the health of mangrove habitats, particularly ocean warming and sea level rise (Lovelock *et al.* 2015; Walden *et al.* 2019). Given the important role of mangroves as a refuge for juvenile sharks and rays, ongoing loss of mangrove habitats ultimately affects local population dynamics. Future research should consider the potential effects of mangrove habitat loss for a range of elasmobranch species and as a result, which species are most vulnerable to population decline.

CHAPTER 6

General Discussion

6.1 Importance of mangroves to elasmobranchs and the potential importance of mangrove conservation

Mangroves are not just a plant growing at the interface between land and sea; they are foundation species that play significant roles in coastal systems. This PhD research found that mangroves offer important ecological services to elasmobranch species that occur in coastal ecosystems. Mangrove habitats were used as a predation refuge by juveniles of some shark and ray species (blacktip reef shark *Carcharhinus melanopterus* and mangrove whipray *Urogymnus granulatus*) as the physical structures of mangroves (e.g. prop roots) exclude large sized predators, thus increasing survival (CHAPTER 5). Feeding opportunities are unlikely their main driver for mangrove use (Kanno *et al*. 2019; Martins *et al*. 2022), but predator avoidance is likely a main driver. These findings indicate that the presence of mangroves is critical for some species at their most vulnerable life stage. Yet, the function of mangrove habitats and association with mangroves are species-specific and the different types of mangroves likely offer different functions and benefits, and different shark and ray species have adapted aspects of their biology and ecology to maximise these benefits. Furthermore, there are trade-offs that species must make regarding mangrove use, such as predator avoidance versus foraging needs and growth rate. For example, cowtail stingrays *Pastinachus ater* selected reef flat habitats to feed on their preferred prey while predation risk in this habitat is high relative to that in mangrove habitat. Graceful sharks may gain benefits (e.g. predation refuge) from using mangrove habitats but low oxygen levels within mangrove habitats potentially compromises their growth rate (CHAPTER 3). Thus, the results of the present research demonstrate how four species of sharks and rays have resolved these trade-offs to generate benefits from mangrove habitats.

Conservation of mangrove forests are inarguably important due to ecological services that they offer (Worthington and Spalding 2018; Su *et al.* 2021). Given the demonstrated association between mangroves and elasmobranchs, the presence of healthy mangroves and their ecological functions will benefit elasmobranch species. Therefore, both conservation of existing mangroves, and restoration of lost and degraded mangrove forests, are crucial. Particularly, the areas of high mangrove loss overlap the areas of high levels of threatened coastal elasmobranch species (e.g. Asia, Africa and Central and South America) (Dulvy *et al.* 2021; CHAPTER 2), and those areas need focused efforts on restoration of coastal habitats including mangroves. These efforts will in turn assist conservation efforts for elasmobranch species. For example, bottom-up effects from restored mangroves and ecological functions are one of the benefits. Restored mangrove habitats re-host a variety of teleosts species, and these potentially attract larger fish or sharks (Enchelmaier *et al.* 2020; Kitchingman *et al.* 2022).

Recolonisation of macroinvertebrate communities are potentially important to bottom feeders (e.g. stingrays) (e.g. Van Hieu *et al.* 2020; Basyuni *et al.* 2022). Furthermore, successful mangrove restoration should lead to a recovery of ecological function of mangroves and mangrove-associated species. Enchelmaier *et al.* (2020) found that species composition of teleosts in restored mangrove habitats shifted from taxa that are habitat generalists to taxa that are closely associated with mangrove habitats after 15 years post-replanting. Although the authors considered this mangrove forest may need more time to establish its fish populations and ecosystem function, this community shift is an indicator of increased ecological function and is a key finding that a recovery of ecological functions of mangroves and teleost taxa is possible.

From the other perspective, elasmobranch species play various important ecological roles in the coastal ecosystems, such as population control, energy vectors and bioturbation (physical and ecological engineering) (O'Shea *et al.* 2012; Roff *et al.* 2016), and therefore, the presence of elasmobranch species and their biological activities contribute to healthy ecological functions in mangrove ecosystems. Thus, successful conservation and restoration of mangrove habitats will assist coastal ecosystems, including elasmobranchs, and likewise shark conservation and recovery will benefit mangrove ecosystems. Implementation of marine protected areas (MPAs) is an effective approach to protect marine habitats and organisms residing in these areas. The inclusion of mangrove nurseries is essential for some elasmobranch populations, such as lemon sharks *Negaprion brevirostris*, to support juvenile's fitness potential and survival (van Zinnicq Bergmann *et al.* 2022). Beyond mangroves, MPA design including habitat connectivity between mangroves and coral reefs has positive effects on abundance and species richness of teleost populations and ultimate performance of MPAs as mangroves are important nurseries for reef species (Olds *et al.* 2012; Olds *et al.* 2013). Due to the migratory nature of many elasmobranch species, the inclusion of mangroves in MPAs will most likely benefit species that occur not only occur in mangrove habitats but also in adjacent coastal habitats (e.g. Kot *et al.* 2023).

6.2 Megafauna in vegetated habitats

The importance of vegetated habitats, including mangroves, seagrasses and saltmarshes to megafauna has received growing attention in recent years. Sievers *et al.* (2019) reviewed the literature on associations between coastal vegetated habitats and marine megafauna, including sea turtles, whales, dolphins, otters, minks, seals, crocodiles, alligators, dugongs, manatees and elasmobranchs. Accordingly, at least 174 megafaunal species occur, feed or breed in coastal vegetated habitats and they play important ecological roles for coastal wetlands. However, nearly half of those species are listed as Threatened by the IUCN Red List and loss and degradation of vegetated habitats can have severe impacts on their populations (Sievers *et al.* 2019). The authors stress the importance of inclusion of habitat association into species assessments and therefore, correct identification of habitat association between megafauna and vegetated habitats is crucial. This research provided observations of close association between some coastal elasmobranch species (i.e. blacktip reef sharks and mangrove whiprays) and mangrove habitats. Although Australian populations of those species are not threatened, and Australian mangroves are relatively healthy (FAO 2023), the findings from this study will help guide species assessment and conservation priorities for global populations given that loss and degradation of habitat is the second largest threat to elasmobranch species particularly in coastal areas (e.g. Dulvy *et al.* 2021).

Understandings of how species use vegetated habitats, and how reliant species are on it, are crucial to assess potential impacts of habitat loss and determine the conservation priority for species, but these can be hard to identify. Sievers *et al.* (2019) argued that it is difficult to assess if mangroves provide specific protection and prey resources to species or species would use the habitat as a nursery regardless of mangrove presence. Importantly, the present study provided strong evidence that some mangrove habitats offer specific benefits to shark and ray species. At least in this study, juvenile blacktip reef sharks and mangrove whiprays were shown to actively used mangrove habitats when they are available while cowtail stingrays did not (Kanno *et al.* 2019). Their frequent occurrence in mangrove habitats does not necessarily exclude the possibility that species are attracted to shallow water depth for predator avoidance and indeed, these species have adapted to the local environments without mangroves (e.g. Vaudo and Heithaus 2009; Bouyoucos *et al.* 2020; Elston *et al.* 2021; Elston *et al.* 2022b). Yet, the results presented here demonstrated that when mangrove habitats are available, some elasmobranch species have some degree of association with mangroves and take advantage of them. The observations in this study highlight that some elasmobranch species gain specific benefits from the protections and possible food resources mangrove habitats provide (Kanno *et al.* 2019) while other species use mangroves opportunistically that do not obligate the use of vegetated habitats (Sievers *et al.* 2019). This study suggests that scientific assessment of the specific function of mangrove use is possible, and the presence of mangroves may contribute to sustainability in populations of species by enhancing survival of the most vulnerable life stage.

Although specific ecological roles and contribution of elasmobranchs to ecological functions of mangrove systems has not been thoroughly tested, some elasmobranch species play a significant role in other types of vegetated habitats. For example, tiger sharks *Galeocerdo cuvier* are a top predator in seagrass systems and due to their highly mobile nature, they transport nutrients between coastal and offshore habitats (Ferreira *et al.* 2017). In addition, tiger sharks contribute to maintaining population and abundance of important seagrass glazers, such as dugongs and sea turtles by both consumptive and non-consumptive effects and in turn, mediating the structure and functions of seagrass communities (Heithaus *et al.* 2012). Ultimately, predators including elasmobranchs and the other megafauna in the coastal ecosystems have an important role in carbon cycling due to their indirect effects on herbivores and microbial communities (Atwood *et al.* 2015). Loss of predators is causing cascading effect on carbon storage in vegetated habitats, and it can exacerbate CO_2-level elevation by releasing blue carbon stored for a millennium in vegetated habitats (Atwood *et al.* 2015). Understanding the level of association between vegetated habitats and megafauna is urgently required as it will help guide protection and conservation priorities of both wetland and megafaunal species that are highly threatened due to anthropogenic effects. What is clear is that as the juvenile elasmobranchs that use the mangrove habitats at Orpheus Island grow and leave the system, they transport carbon and other nutrients to other habitats. How significant such a function is yet to be investigated but would be a useful line of research.

6.3 Elasmobranch research in Orpheus Island

The elasmobranch research had been conducted for the last 10 years in Orpheus Island , with a focus in Pioneer Bay. This system includes coral reef, a wide reef flat and fringing mangroves. Focal species for the research have been blacktip reef sharks, mangrove whiprays and cowtail stingrays though more elasmobranch species regularly occur in the bay. During this period, spatial ecology was examined by various methods, such as GPS tag tracking, active acoustic telemetry tracking and passive acoustic telemetry monitoring (Davy *et al.* 2015; George *et al.* 2019; Martins *et al.* 2020ab, Schlaff *et al.* 2020). While those studies provided valuable insights on fine-scale habitats of species, they focused on reef flat habitats rather than mangroves, and for relatively short-periods (daily, tidal cycle, daytime observation); long-term observation was limited. The present PhD research project filled knowledge gaps throughout the full tidal cycle (including nighttime) and seasonal presence and movements of elasmobranch species and revealed how those species use mangrove systems and mangrove habitats for a year. In addition to habitat use, the physiology of stingrays have been studied at Orpheus Island and studies found that while warm water helps effective digestion and food intake for juvenile stingrays (Tenzing 2014), juvenile stingrays avoid the excessively hot water during the hottest periods of the day by selecting cooler water habitats (Higgins 2018). Recently, trophic ecology was examined using stable isotope analysis for both stingray species and found that mangrove-derived carbon was not assimilated into those species despite high residency in the mangrove habitats (Martins *et al.* 2021). Instead, their prey feeds on carbon derived from algae on the reef flat.

What we have learnt from the decade of research at Orpheus Island is that movement and habitat use of juveniles of the three species are largely driven by the tidal cycle as tidal range is 4 m (mesotidal) and the nearshore habitat is cyclically flooded and exposed. Use of shallow water habitats by aquatic animals for predator avoidance is known from numerous studies (e.g. Morrissey and Gruber 1993a; Wetherbee *et al.* 2007) and is likely a main driver for movement and habitat use for three species studied here. During the low tide phase, while mangrove habitats are exposed and not available to them, stingrays stay among shallow coral and rock structures on the reef crest (Davy *et al.* 2015; Martins *et al.* 2020b). Juvenile blacktip reef sharks swim along the reef edge and stay in shallow water (George *et al.* 2019; Schlaff *et al.* 2020). When the tide is flooding toward mangroves, juveniles of all species move with the tide and stay in shallow water as their potential predators have no access to extremely shallow water (<20cm) (Davy *et al.* 2015; George *et al.* 2019). Once mangrove habitats are flooded during higher parts of the tidal cycle, mangrove whiprays return to refuging locations inside mangroves that they have used previously and rest among the root structures (Davy *et al.* 2015; Kanno *et al.* 2019). Juvenile blacktip reef sharks swim inside mangroves during daytime high tides and close to the mangrove edge while adults swim near the mangrove edge but not inside mangroves due to structural complexity (George *et al.* 2019; Kanno *et al.* 2019; Schlaff et al 2020; CHAPTER 5). Blacktip reef sharks avoid mangrove habitats at nighttime, mostly swimming on the reef flat and mangrove edge areas. Cowtail stingrays occasionally rest at the mangrove edge but are mainly found on the reef flat even during high tide (Kanno *et al.* 2019; Martins *et al.* 2020b; CHAPTER 5). Overall, juveniles of blacktip reef sharks, mangrove whiprays and cowtail stingrays use either mangrove refuge or shallow water depending on tidal height so that they can stay safe from potential predators (e.g. adult blacktip reef sharks, sicklefin lemon sharks *N. acutidens* and great hammerhead *Sphyrna mokarran*). As a consequence of selecting safe locations, mangrove whiprays may aggregate with conspecifics due to limited availability of mangrove refuge at a given tidal height particularly during falling tide phase.

6.4 Bimini lemon shark research and comparison with Orpheus Island

Close association between mangroves and lemon sharks *N. brevirostris* has been studied for more than three decades in Bimini, the Bahamas (e.g. Gruber *et al.* 1988; Morrissey and Gruber 1993b, 1993a). As summarised in CHAPTER 2, a broad range of studies have been conducted for a long time (e.g. movement, home range, diet, genetics) and our current understanding of mangrove use by elasmobranchs has been somewhat extrapolated based on the findings from this population. Environmental settings of mangrove habitats are similar between Bimini and Orpheus Island, where spatial ecology research has likewise been a focus, provide for an interesting comparison. Both sites are mainly fringing mangrove habitats in nearshore marine systems with clear water and mesotidal regime (between 2 and 4 m tidal range). Although species composition is different between the two regions, the function of mangroves is homologous. For example, mangrove habitats in the intertidal zone are used as an important nursery by juvenile sharks and rays and predation risk is one of the main drivers for mangrove use, while warm water may benefit shark and ray metabolism. Movement and habitat use patterns of species in the mangrove systems are tidally influenced, and during high tide, individuals stay close to the mangrove edge while during low tide, they move out to the offshore area or adjacent reef flat (e.g. Guttridge *et al.* 2012; Davy *et al.* 2015; George *et al.* 2019; CHAPTER 5).

Trophic linkages between mangroves and elasmobranchs may be different between the two regions. While lemon sharks are known to be reliant on mangrove-derived food resources in Bimini (Hussey *et al.* 2017), mangrove whiprays and cowtail stingrays are not at Orpheus Island (Martins *et al.* 2021). This potential difference needs more examination as feeding modes and diet types are different between lemon sharks and these stingray species, and mangrove food chains are not simple as they depend on mangrove-associated faunal composition, adjacent system types and local context (Sheaves and Molony 2000; Abrantes and Sheaves 2009). While diet and feeding habits of lemon sharks are well studied in Bimini (e.g. Cortés and Gruber 1990; Newman *et al.* 2010; Newman *et al.* 2012), they are poorly understood for the species at Orpheus Island. There is a lot more to investigate about elasmobranch fauna and the functions of mangroves for them at Orpheus Island. Genetic studies and long-term monitoring revealed natal philopatry and duration of nursery use of lemon sharks in Bimini, while similar phenomena are yet to be investigated at Orpheus Island. Furthermore, the negative effect of degradation of mangrove habitats due to coastal development was assessed at Bimini, with a reduction in juvenile lemon shark's survival when mangroves were removed (Jennings *et al.* 2008). Based on the long-term and comprehensive research on lemon sharks in the mangrove system at Bimini, the design of no-take MPAs were assessed to consider how they might protect this mangrove-associated threatened species (van Zinnicq Bergmann *et al.* 2022). A series of multidisciplinary studies in Bimini is good example of long-term scientific effort and accumulation of knowledge can be translated from basic biology to conservation applications.

6.5 Future directions

This research has provided detailed observations on mangrove use of juvenile sharks and rays using acoustic telemetry within mangrove habitats for the first time. As CHAPTER 2 discussed, however, there are knowledge gaps in association between mangroves and elasmobranchs and this dissertation does not provide a complete understanding of mangrove use by elasmobranchs. Below are some future study directions for examining functions of mangrove habitats for elasmobranch species at the present study site as broader implications were previously discussed in CHAPTER 2.

Mangrove habitats can be a difficult place to conduct research due to both physical and ecological complexity. Methods and activities may be limited due to physical restraints, such as complex structures, occurrence of dangerous animals, low water visibility and tides. To successfully conduct research in mangrove habitats, we need to understand sampling limitations as well as local context of mangrove habitats (e.g. tidal regime, geomorphology, rainfall etc.). New techniques or methods may be required to overcome and compensate for those sampling difficulties. In this study, the use of passive acoustic telemetry was tested for the first time in dense mangrove habitats. Detailed observations of the associations between mangrove habitats and animals are important to investigate whether the presence of mangroves benefits species that occur in proximity to mangroves. Such fine-scale data will help better understand how species use not only broad mangrove systems but also within mangrove habitats.

Prior to monitoring study, CHAPTER 4 conducted range testing to examine the detection range and receiver performance in mangrove habitats. In CHAPTER 4, the inside mangrove test was conducted for 2 days with 2 transmitters. While the outside test was conducted for a month. Future research could have a longer testing duration in the inside mangrove habitats to reveal a general pattern of acoustic receiver performance and detection range with changes in tides, weather and other environmental factors. Furthermore, the results suggest the importance of mangrove density over the distance between the receiver and transmitter. This study did not quantify the density of mangroves, but future research could identify the complexity or density of mangroves and incorporate it as a factor. Then, the effects of mangrove density will be tested to understand how the density affects the detection range and what the threshold mangrove density is to block the signal from the transmitter.

In CHAPTER 5, habitat use and movement patterns of three focal species were studied for one year. The results demonstrated their high site fidelity to the bay, although some individuals presumably left the bay, and a possible seasonal change in their abundance. Additionally, the duration of nursery use by blacktip reef sharks and mangrove whiprays in Orpheus Island remains unknown. Hence, long-term study is still required to monitor their presence and behaviour, ideally more than two years so that seasonal patterns, if any, could be clearly illustrated. To successfully conduct acoustic telemetry for a longer term, there are a few issues to overcome, such as transmitters battery life and receiver maintenance (cleaning, battery, data download). There are trade-offs to consider among battery life, sensor availability (e.g. temperature, depth, acceleration, oxygen), transmitter size and cost (Simpfendorfer and Heupel 2012), and future research would need to consider what would be the best option for long-term monitoring of small juveniles that are abundant at Orpheus Island and are the focus for research. An alternative approach to study the duration and site fidelity of species is a genetic study. Genetic approaches would reveal reproductive traits, population structure and possible natal philopatry of populations in Orpheus Island (e.g. Feldheim *et al.* 2002; Feldheim *et al.* 2014).

There are a number of sensors available for acoustic transmitters and the sensor data could be used to examine species movement data in relation to additional biotic and abiotic factors. For example, temperature sensor equipped transmitters can be used to test if daily and seasonal changes in mangrove habitat use is driven by changes in temperature, and behavioural thermoregulation. Accelerometer sensor data will be useful to investigate behavioural changes, especially for blacktip reef sharks. Future research with accelerometer data could reveal if blacktip reef sharks change their activity inside and outside of mangrove habitats, and if they hunt at night outside of mangroves.

Physiological traits of individuals play an important role in decisions relating to behaviour and habitat use. For example, water temperature is one of the main drivers for migration and habitat selection in ectothermic elasmobranchs (Heithaus *et al.* 2009; Elston *et al.* 2022b). Although some physiological tests were conducted for stingrays at Orpheus Island (Tenzing 2014; Higgins 2018), more studies are required to examine the extent their physiology affects their habitat use and behaviour. In this study, blacktip reef sharks and mangrove whiprays demonstrated seasonal difference in mangrove use, displaying greater mangrove use in spring (CHAPTER 5). The importance of shade from mangrove trees to some teleost species is known (Cocheret de la Morinière *et al.* 2004; Verweij *et al.* 2006a) and this seasonal pattern may be related to the use of mangrove for shade. Currently, no study has been conducted to address whether mangroves offer thermal refuge to elasmobranch species. Tropical nearshore habitats cyclically experience high temperature and animals may cope with excessive heat by changing their behaviour or habitat use (e.g. Higgins 2018; Elston *et al.* 2022b). Moreover, physiological study, particularly on ambient temperature and metabolic performance, is one of the urgent tasks in this era of climate change crisis (Bouyoucos *et al.* 2020).

Fluctuations in the amount of dissolved oxygen (DO) in mangrove habitats were not tested in this study, but it can be a possible driver that affects movement and habitat use patterns of species. DO level data over tidal and daily time scales could reveal a different aspect of harsh environmental conditions to some species within mangrove habitats. As discussed in CHAPTER 3, mangrove habitats regularly experience low DO levels due to respiration and low water movement (Altieri *et al.* 2021). Especially at night, DO level may be too low for some individuals to use mangrove habitats (Dubuc *et al.* 2019) and this lack of oxygen may cause diel patterns in mangrove use. Monitoring DO levels in the mangrove habitats could reveal if DO factor drives diel shift in habitat use of blacktips reef sharks.

Life history of elasmobranch species needs to be conducted for a wider range of species in general, but it is needed particularly for those species that occur in coastal habitats including mangroves given their threatened status (e.g. Dulvy *et al.* 2021). In CHAPTER 3, relatively small body size and slow growth for graceful sharks were revealed by age and growth analysis, and possible trade-offs of living in mangrove habitats was hypothesised. To test this hypothesis, further studies on this species and ecologically similar species are required, including age validation and data from the different population(s). Life history data is a critical component to assess species' population status and extinction risk and plan and implement their conservation planning gif necessary. Given the status of global mangrove loss, research effort for species that rely on mangrove habitats is urgently required.

Trophic linkages between mangrove ecosystems and elasmobranchs remains unclear. While some studies have found species consumed mangrove-derived food resources (Hussey *et al.* 2017; Lear *et al.* 2019), a recent study from Orpheus Island found the opposite (Martins *et al.* 2022). The flow of mangrove-derived carbon through the food chain is complex (Alongi 2014) and certainly more research is needed to determine the effective approach to detect mangrove-derived sources. The importance of top predators in mangrove food webs is suggested by recent studies (Marley *et al.* 2019; Muro-Torres *et al.* 2020) and elasmobranchs are most likely an important member of mangrove food webs and ecosystem functions. For further understanding of trophic linkages between mangrove habitats and elasmobranch species at Orpheus Island, understandings of trophic interactions between connected systems such as coral reefs, sand flat and offshore systems would be the first critical step. Extensive sampling over a wide area and of potential prey species, and a greater understanding of tissue specific isotopic discrimination factors are required as suggested by Martins *et al.* (2022).

Environmental factors and context are diverse depending on local mangrove sites and therefore, the habitat function of mangroves are likely to be different place to place (Igulu *et al.* 2014; Bradley *et al.* 2020). As discussed in CHAPTER 2, the functions of mangrove habitats vary depending on local context and as shown in CHAPTER 5, species use mangrove habitats differently. Therefore, the functions of mangroves should not be generalised. And the type of mangroves and local context, such as tides, shapes of mangrove forests, biogeography, should be taken into account when examining the association between mangrove habitats and elasmobranchs species.

Given the fundamental role that tides play in species' habitat use and movement patterns, tidal regime may significantly affect habitat use of species in nearshore systems. Tidal regime is generally classified into four categories: microtidal (tidal range <2m), mesotidal (2-4m). macrotidal (4-8m) and megatidal (>8m) (Davies 1972; Levoy *et al.* 2000). Tidal regime varies in regions and influences availability of nearshore habitats to organisms. Igulu *et al.* (2014) reviewed previous research in mangrove and seagrass habitat use by teleost species and found that the difference in tidal regime between the Caribbean and the Indo-West Pacific nearshore habitats is a primary factor to distinguish the functions of mangrove and seagrass habitats between the two regions. That is, small tidal range in the Caribbean offers a safe habitat for juvenile fish for a longer time while large tidal range in the Indo-Pacific forces them to migrate between habitats during low tide, resulting in mangroves being less effective nursery grounds (Igulu *et al.* 2014). As elasmobranchs have a larger body size and larger home range, patterns in mangrove use are most likely different between mangrove habitats in different tidal regimes. Microtidal mangrove habitats may offer longer access to species while the availability of megatidal mangrove habitats may quickly change with tidal cycle. Difference in tidal regime also affects water condition (e.g. DO level, temperature), which is most likely a driving factor for species' mangrove use. Research that investigates the same or similar species between mangrove systems in different tidal regimes would help understand this factor.

Studies from Orpheus Island and Bimini have both been conducted in clear-water mangrove habitats. Water turbidity may affect the function of mangrove habitats as many elasmobranchs are visual predators. CHAPTER 5 revealed that blacktip reef sharks avoided structurally complex mangrove habitats at night possibly and partly because the mangrove habitats are too dark to navigate through. Although elasmobranchs are equipped with other sensory organs, such as electric, motion and olfactory sensors, low visibility may render it difficult to detect predators and locate prey (e.g. Cerutti-Pereyra *et al.* 2014). For teleost species, reduction in hunting success was reported in the turbid water (Johansen and Jones 2013). Thus, the importance and function of mangrove habitats to elasmobranchs may be different between clear-water and non-clear water mangrove habitats. Comparisons of habitat use of the same species between clear and non-clear water mangroves may reveal the differences in functions of mangrove habitats.

Although the focal species in Orpheus Island research were blacktip reef sharks, mangrove whiprays and cowtail stingrays, there are other elasmobranchs around Orpheus Island, including sicklefin lemon sharks, pink whiprays *Pateobatis fai*, bluespotted lagoon ray *Taeniura lymma*, porcupine rays *Urogymnus asperrimus*, Australian whiprays *Himantura australis* and giant shovelnose rays *Glaucostegus typus* that would provide additional research opportunities. More comprehensive fishing approaches could sample more of those species and future research would expand a range of species to investigate their habitat use and movement patterns in the region. In particular, their global populations are listed as either Endangered or Vulnerable by the IUCN Red List (except Australian whiprays), but Australian populations are relatively stable. Therefore, research on those species in this region would be great implication for better understandings of their biology and ecology and their conservation practice.

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Appendices

Appendix 1 Bibliography of the 65 research articles used to count the number of studies for each species and region in the literature review.

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Appendix 2 Dredge results for mangrove use analysis.

Blacktip reef sharks												
Full model: Presence ~ hour + year-month + magnitude + stage + scale(tideht) + scale(body size) + (1 | tag)												
Model no.	Intercept	Hour	Year-month	Magnitude	Stage	Tidal height	Body size	df	log likelihood	AIC	delta	weight
60	**-7.901**	**+**	**+**	**+**	**+**	**1.347**		**47**	**-6351.5**	**12797.1**	**0**	**0.669**
64	**-7.934**	**+**	**+**	**+**	**+**	**1.347**	**-0.5936**	**48**	**-6351.2**	**12798.5**	**1.41**	**0.331**
44	-7.269	+	+	+		1.446		45	-6380.9	12851.8	54.74	0
48	-7.311	+	+	+		1.446	-0.5999	46	-6380.6	12853.2	56.13	0
58	-6.695	+	+		+	1.421		42	-6384.84	12853.7	56.61	0
62	-6.735	+	+		+	1.421	-0.5948	43	-6384.55	12855.1	58.03	0
42	-6.289	+	+			1.451		40	-6413.08	12906.2	109.09	0
46	-6.329	+	+			1.451	-0.6011	41	-6412.78	12907.6	110.49	0
28	-7.624	+		+	+	1.308		33	-6536.19	13138.4	341.32	0
32	-7.787	+		+	+	1.307	-0.6696	34	-6535.74	13139.5	342.41	0
12	-7.051	+		+		1.409		31	-6560.63	13183.3	386.19	0
16	-7.214	+		+		1.409	-0.6712	32	-6560.17	13184.3	387.27	0
26	-6.221	+			+	1.39		28	-6592.41	13240.8	443.75	0
30	-6.385	+			+	1.39	-0.6737	29	-6591.96	13241.9	444.86	0
10	-5.845	+				1.419		26	-6616.1	13284.2	487.14	0
14	-6.009	+				1.419	-0.6759	27	-6615.65	13285.3	488.23	0
52	-10.65	+	+	+	+			46	-6792.96	13677.9	880.86	0
56	-10.69	+	+	+	+		-0.5741	47	-6792.64	13679.3	882.22	0
20	-10.19	+		+	+			32	-6969.96	14003.9	1206.86	0
24	-10.35	+		+	+		-0.6612	33	-6969.45	14004.9	1207.83	0
59	-6.478		+	+	+	1.335		24	-7525.2	15098.4	2301.34	0
63	-6.506		+	+	+	1.335	-0.5701	25	-7524.88	15099.7	2302.69	0
57	-5.005		+		+	1.54		19	-7567.11	15172.2	2375.16	0
61	-5.028		+		+	1.54	-0.5748	20	-7566.78	15173.6	2376.5	0
43	-6.195		+	+		1.298		22	-7576.66	15197.3	2400.26	0
47	-6.216		+	+		1.298	-0.5698	23	-7576.34	15198.7	2401.61	0
36	-8.475	+	+	+				44	-7601.58	15291.2	2494.09	0
40	-8.479	+	+	+			-0.5651	45	-7601.18	15292.4	2495.29	0
41	-4.774		+			1.454		17	-7638.57	15311.1	2514.08	0
45	-4.796		+			1.454	-0.5742	18	-7638.24	15312.5	2515.42	0
50	-7.014	+	+		+			41	-7623.07	15328.1	2531.08	0
54	-7.018	+	+		+		-0.5883	42	-7622.63	15329.3	2532.19	0
4	-8.143	+		+				30	-7763.95	15587.9	2790.84	0

8	-8.291	+		+			-0.6406	31	-7763.33	15588.7	2791.59	0
18	-6.365	+			+			27	-7898.89	15851.8	3054.72	0
22	-6.529	+			+		-0.7231	28	-7898.09	15852.2	3055.11	0
27	-5.412			+	+	1.229		10	-7993.94	16007.9	3210.82	0
31	-5.593			+	+	1.229	-0.7878	11	-7993.15	16008.3	3211.23	0
25	-3.858				+	1.432		5	-8034.96	16079.9	3282.85	0
29	-4.039				+	1.432	-0.7876	6	-8034.17	16080.3	3283.28	0
11	-5.086			+		1.214		8	-8043.75	16103.5	3306.43	0
15	-5.266			+		1.214	-0.7878	9	-8042.95	16103.9	3306.83	0
51	-9.288		+	+	+			23	-8056.69	16159.4	3362.31	0
55	-9.299		+	+	+		-0.5448	24	-8056.35	16160.7	3363.63	0
9	-3.617					1.36		3	-8100.61	16207.2	3410.15	0
13	-3.797					1.36	-0.7881	4	-8099.82	16207.6	3410.57	0
34	-5.491	+	+					39	-8219.85	16517.7	3720.63	0
38	-5.472	+	+				-0.5833	40	-8219.34	16518.7	3721.61	0
2	-5.072	+						25	-8450.6	16951.2	4154.14	0
6	-5.227	+					-0.6947	26	-8449.75	16951.5	4154.44	0
19	-7.962			+	+			9	-8479.47	16976.9	4179.87	0
23	-8.136			+	+		-0.7731	10	-8478.61	16977.2	4180.15	0
35	-7.19		+	+				21	-8860.57	17763.1	4966.08	0
39	-7.185		+	+			-0.5488	22	-8860.16	17764.3	4967.25	0
7	-6.341			+			-0.7653	8	-9251.16	18518.3	5721.26	0
3	-6.177			+				7	-9252.16	18518.3	5721.26	0
49	-4.47		+		+			18	-9614.29	19264.6	6467.51	0
53	-4.439		+		+		-0.5838	19	-9613.72	19265.4	6468.38	0
21	-3.923				+		-0.7964	5	-9983.87	19977.7	7180.67	0
17	-3.755				+			4	-9985.08	19978.2	7181.1	0
33	-3.421		+					16	-10123.2	20278.5	7481.4	0
37	-3.368		+				-0.5935	17	-10122.6	20279.2	7482.14	0
5	-2.962						-0.7981	3	-10477.1	20960.2	8163.17	0
1	-2.799							2	-10478.4	20960.9	8163.81	0

Mangrove whiprays

Full model: Presence ~ hour + year-month + magnitude + stage + scale(tideht) + (1 | tag)

Model no.	Intercept	Hour	Year-month	Magnitude	Stage	Tidal height	df	log likelihood	AIC	delta	weight
32	**-0.9797**	**+**	**+**	**+**	**+**	**1.699**	**46**	**-7332.9**	**14757.7**	**0**	**1**
31	-1.345		+	+	+	1.648	23	-7455.25	14956.5	198.77	0
24	-1.623	+	+	+		1.713	44	-7438.34	14964.7	206.94	0
23	-1.6		+	+		1.723	21	-7574.52	15191	433.29	0
30	1.607	+	+		+	2.219	42	-7564.07	15212.1	454.4	0
29	1.482		+		+	2.179	19	-7695.81	15429.6	671.87	0
22	0.6648	+	+			2.042	40	-7744.17	15568.3	810.6	0
21	0.7621		+			2.026	17	-7845.95	15725.9	968.16	0
16	-5.465	+		+	+	1.481	32	-8182.14	16428.3	1670.55	0
28	-4.977	+	+	+	+		45	-8229.52	16549	1791.3	0
8	-5.926	+		+		1.538	30	-8299.73	16659.5	1901.72	0
27	-5.23		+	+	+		22	-8342.31	16728.6	1970.88	0
15	-5.105			+	+	1.422	9	-8382.37	16782.7	2025	0
14	-2.729	+			+	1.988	28	-8453.05	16962.1	2204.35	0
7	-5.212			+		1.54	7	-8516.45	17046.9	2289.15	0
6	-3.522	+				1.848	26	-8622.36	17296.7	2538.98	0
13	-2.278				+	1.953	5	-8657.13	17324.3	2566.52	0
5	-2.916					1.831	3	-8803.41	17612.8	2855.08	0
12	-8.472	+		+	+		31	-8963.22	17988.4	3230.7	0
11	-8.103			+	+		8	-9144.34	18304.7	3546.94	0
20	-4.123	+	+	+			43	-9521.73	19129.5	4371.73	0
19	-3.894		+	+			20	-9891.01	19822	5064.28	0
4	-7.325	+		+			29	-10237.2	20532.3	5774.6	0
3	-6.592			+			6	-10661.3	21334.5	6576.78	0
26	0.275	+	+		+		41	-11276	22633.9	7876.2	0
25	0.3743		+		+		18	-11626.6	23289.2	8531.44	0
18	0.2236	+	+				39	-11926.5	23931	9173.25	0
10	-2.737	+			+		27	-11997.7	24049.3	9291.59	0
17	0.6239		+				16	-12364.5	24761.1	10003.32	0
9	-2.382				+		4	-12416.5	24841.1	10083.35	0
2	-2.709	+					25	-12630.7	25311.5	10553.72	0
1	-2.1						2	-13134.5	26273.1	11515.31	0

Cowtail stingrays

Full model: Presence ~ daynight + year-month + magnitude + stage + scale(tideht) + (1 | tag)

Model no.	Intercept	Day-night	Year-month	Magnitude	Tidal height	df	log likelihood	AIC	delta	weight
16	**-4.462**	**+**	**+**	**+**	**1.278**	**17**	**-1197.1**	**2428.1**	**0**	**1**
15	-4.114		+	+	1.319	16	-1213.87	2459.7	31.63	0
14	-3.555	+	+		1.386	15	-1228.64	2487.3	59.18	0
13	-2.975		+		1.495	14	-1252.64	2533.3	105.18	0
8	-4.923	+		+	1.314	6	-1286.19	2584.4	156.27	0
7	-4.764			+	1.331	5	-1290.81	2591.6	163.52	0
6	-3.915	+			1.446	4	-1326.56	2661.1	233.02	0
5	-3.729				1.49	3	-1331.97	2669.9	241.83	0
12	-4.592	+	+	+		16	-1369.64	2771.3	343.17	0
11	-4.136		+	+		15	-1404.17	2838.3	410.22	0
4	-5.181	+		+		5	-1483.87	2977.7	549.63	0
3	-4.919			+		4	-1497.44	3002.9	574.77	0
10	-2.447	+	+			14	-1518.94	3065.9	637.78	0
9	-1.604		+			13	-1595.36	3216.7	788.61	0
2	-3.304	+				3	-1664	3334	905.89	0
1	-2.772					2	-1702.82	3409.6	981.54	0

Appendix 3 Dredge results for reuse of high tide location analysis.

Blacktip reef shark

Full model: dist ~ hour + year-month + magnitude + scale(size) + (1 | tag)

Model no.	Intercept	Hour	Year-month	Magnitude	Size	df	log Likelihood	AICc	delta	weight
16	**215.3**	**+**	**+**	**+**	**26.7**	**46**	**-16235.25**	**32564.2**	**0**	**0.984**
12	206.9	+	+	+		45	-16240.41	32572.4	8.24	0.016
14	221.2	+	+		26.57	41	-16255.33	32594	29.82	0
10	212.7	+	+			40	-16260.49	32602.2	38.06	0
8	201.9	+		+	28.63	32	-16305.94	32676.7	112.52	0
4	192	+		+		31	-16311.18	32685.1	120.95	0
6	192.3	+			28.28	27	-16324.9	32704.4	140.2	0
2	182.5	+				26	-16330.11	32712.8	148.59	0
15	178.2		+	+	26.85	23	-16348.01	32742.4	178.27	0
11	169.1		+	+		22	-16353.16	32750.7	186.53	0
13	211.5		+		26.12	18	-16379.83	32795.9	231.75	0
9	202.6		+			17	-16384.93	32804.1	239.92	0
7	162.1			+	28.58	9	-16419.75	32857.6	293.4	0
3	151.6			+		8	-16424.97	32866	301.83	0
5	180.6				27.43	4	-16449.03	32906.1	341.89	0
1	170.5					3	-16454.16	32914.3	350.15	0

Mangrove whipray

Full model: dist ~ hour + year-month + magnitude + (1 | tag)

Model no.	Intercept	Hour	Year-month	Magnitude	df	log Likelihood	AICc	delta	weight
8	**74.61**	**+**	**+**	**+**	**45**	**-19371.44**	**38834.2**	**0**	**1**
6	74.26	+	+		40	-19390.42	38861.9	27.7	0
4	85.07	+		+	31	-19442.88	38948.4	114.22	0
2	93.34	+			26	-19463.67	38979.8	145.62	0
7	61.07		+	+	22	-19471.71	38987.7	153.58	0
5	58.79		+		17	-19494.74	39023.7	189.51	0
3	73.88			+	8	-19544.46	39105	270.8	0
1	79.04				3	-19571.08	39148.2	314	0

Cowtail stingray

Full model: dist ~ hour + year-month + magnitude + (1 | tag)

Model no.	Intercept	Hour	Year-month	Magnitude	df	log Likelihood	AICc	delta	weight
8	**195.5**	**+**	**+**	**+**	**45**	**-7683.195**	**15459.7**	**0**	**1**
6	125.8	+	+		40	-7707.473	15497.6	37.86	0
4	240.3	+		+	31	-7797.883	15659.3	199.63	0
7	173.6		+	+	22	-7816.529	15677.9	218.14	0
2	176.6	+			26	-7821.511	15696.1	236.42	0
5	128.1		+		17	-7840.254	15715	255.27	0
3	219.4			+	8	-7927.03	15870.2	410.46	0
1	174.6				3	-7949.426	15904.9	445.15	0

Appendix 4 Dredge results for aggregation analysis.

Full model: aggregation ~ hour + yrmon + stage + scale(tideht) + neapcat

Model no.	Intercept	Hour	Magnitude	Tidal height	Stage	Year-month	df	log likelihood	AICc	delta	weight
31	**-0.9858**		**+**	**-0.1221**	**+**	**+**	**17**	**-2827.529**	**5689.2**	**0**	**0.764**
27	**-0.747**		**+**		**+**	**+**	**16**	**-2829.709**	**5691.5**	**2.35**	**0.236**
32	-0.7744	+	+	-0.1399	+	+	40	-2812.216	5705	15.82	0
28	-0.491	+	+		+	+	39	-2814.915	5708.4	19.19	0
29	0.3404			0.1471	+	+	12	-2861.197	5746.4	57.29	0
30	0.5611	+		0.1035	+	+	35	-2842.736	5755.9	66.73	0
25	0.2695				+	+	11	-2868.738	5759.5	70.36	0
26	0.5028	+			+	+	34	-2846.14	5760.7	71.52	0
24	-1.392	+	+	-0.2359		+	38	-2873.647	5823.8	134.63	0
23	-1.731		+	-0.2166		+	15	-2908.407	5846.9	157.73	0
20	-1.132	+	+			+	37	-2890.447	5855.4	166.21	0
19	-1.499		+			+	14	-2923.766	5875.6	186.44	0
18	-0.0647	+				+	32	-2926.733	5917.8	228.66	0
22	-0.06738	+		-0.04349		+	33	-2925.895	5918.2	229	0
17	-0.4306					+	9	-2967.73	5953.5	264.33	0
21	-0.4306			0.001735		+	10	-2967.729	5955.5	266.33	0
12	-2.023	+	+		+		31	-3028.625	6119.6	430.42	0
16	-2.179	+	+	-0.07739	+		32	-3027.731	6119.8	430.65	0
15	-1.933		+	-0.08299	+		9	-3071.642	6161.3	472.15	0
11	-1.771		+		+		8	-3072.745	6161.5	472.35	0
14	-0.6358	+		0.1753	+		27	-3067.848	6189.9	500.79	0
10	-0.7155	+			+		26	-3079.085	6210.4	521.24	0
8	-2.801	+	+	-0.2007			30	-3081.117	6222.5	533.38	0
13	-0.5147			0.189	+		4	-3115.056	6238.1	548.96	0
4	-2.571	+	+				29	-3094.25	6246.8	557.63	0
9	-0.6012				+		3	-3128.933	6263.9	574.71	0
7	-2.661		+	-0.1961			7	-3146.567	6307.2	617.99	0
3	-2.446		+				6	-3160.254	6332.5	643.36	0

2	-1.193	+		24	-3153.823	6355.8	666.69	0
6	-1.192	+	0.01786	25	-3153.666	6357.5	668.39	0
1	-1.225			1	-3222.776	6447.6	758.39	0
5	-1.225		0.0368	2	-3222.055	6448.1	758.95	0

Appendix 5 Dredge results for straightness analysis.

Full model: straight ~ hour + year-month + magnitude + stage + scale(size) + sex + (1|tag)

Model No.	Intercept	Hour	Magnitude	Size	Sex	Stage	Year-month	df	log likelihood	AICc	delta	weight
51	**0.4481**		**+**			**+**	**+**	**26**	**-182.91**	**418**	**0**	**0.745**
55	**0.4472**		**+**	**-0.0201**		**+**	**+**	**27**	**-183.1**	**420.4**	**2.39**	**0.225**
59	0.4425		+		+	+	+	27	-185.46	425.1	7.13	0.021
49	0.5004					+	+	20	-194.062	428.2	10.23	0.004
63	0.4494		+	-0.02131	+	+	+	28	-186.15	428.5	10.52	0.004
53	0.5013			-0.01846		+	+	21	-194.781	431.7	13.68	0.001
57	0.4962				+	+	+	21	-196.771	435.7	17.66	0
19	0.418		+			+		12	-205.834	435.7	17.7	0
23	0.4118		+	-0.02568		+		13	-205.491	437	19.02	0
61	0.504			-0.02017	+	+	+	22	-197.769	439.7	21.67	0
17	0.4464					+		6	-214.805	441.6	23.61	0
27	0.4093		+		+	+		13	-208.289	442.6	24.62	0
21	0.4405			-0.02553		+		7	-214.691	443.4	25.38	0
31	0.4191		+	-0.02886	+	+		14	-208.157	444.4	26.36	0
25	0.4385				+	+		7	-217.295	448.6	30.59	0
35	0.4197		+				+	23	-201.938	450	32.02	0
29	0.4487			-0.02906	+	+		8	-217.284	450.6	32.57	0
39	0.4186		+	-0.02099			+	24	-201.743	451.7	33.64	0
33	0.4716						+	17	-210.596	455.3	37.27	0
43	0.4135		+		+		+	24	-204.406	457	38.97	0
37	0.4727			-0.01928			+	18	-210.945	458	39.97	0
47	0.4204		+	-0.02198	+		+	25	-204.846	459.9	41.87	0
41	0.467				+		+	18	-213.233	462.6	44.55	0
3	0.3905		+					9	-223.368	464.8	46.75	0
7	0.3846		+	-0.02623				10	-222.696	465.4	47.41	0
1	0.4194							3	-229.995	466	47.98	0
45	0.4749			-0.02072	+		+	19	-213.993	466.1	48.08	0
5	0.414			-0.02595				4	-229.601	467.2	49.19	0
11	0.3811		+		+			10	-225.788	471.6	53.59	0
15	0.3912		+	-0.02913	+			11	-225.427	472.9	54.88	0
9	0.4109				+			4	-232.461	472.9	54.91	0
13	0.4215			-0.0292	+			5	-232.257	474.5	56.51	0
18	0.3729	+				+		29	-213.232	484.7	66.7	0
50	0.4163	+				+	+	43	-200.018	486.6	68.57	0
22	0.3682	+		-0.02124		+		30	-213.918	488.1	70.09	0
54	0.4175	+		-0.01846		+	+	44	-200.944	490.5	72.45	0
26	0.3685	+			+	+		30	-215.944	492.2	74.14	0
52	0.3789	+	+			+	+	49	-197.213	493.1	75.12	0
58	0.4122	+			+	+	+	44	-202.736	494	76.03	0
30	0.3773	+		-0.02517	+	+		31	-216.438	495.2	77.15	0
56	0.3787	+	+	-0.01959		+	+	50	-197.763	496.3	78.25	0
62	0.4202	+		-0.02023	+	+	+	45	-203.884	498.4	80.35	0
20	0.3617	+	+			+		35	-214.867	500.1	82.09	0
60	0.3737	+	+		+	+	+	50	-199.825	500.4	82.38	0
24	0.3564	+	+	-0.02209		+		36	-215.294	503	84.96	0
64	0.3809	+	+	-0.02094	+	+	+	51	-200.767	504.3	86.29	0
28	0.3559	+	+		+	+		36	-217.525	507.4	89.42	0
32	0.3645	+	+	-0.02562	+	+		37	-217.898	510.2	92.19	0
2	0.3452	+						26	-230.723	513.6	95.63	0
6	0.3408	+		-0.02183				27	-231.097	516.4	98.4	0
34	0.3877	+					+	40	-218.757	518	99.97	0
10	0.3401	+			+			27	-233.414	521	103.03	0
38	0.389	+		-0.01938			+	41	-219.319	521.1	103.12	0
14	0.3492	+		-0.02546	+			28	-233.688	523.6	105.6	0
42	0.3831	+			+		+	41	-221.404	525.3	107.29	0
36	0.351	+	+				+	46	-218.166	529	110.94	0
46	0.3914	+		-0.02086	+		+	42	-222.317	529.2	111.14	0
40	0.3506	+	+	-0.02058			+	47	-218.344	531.3	113.33	0
4	0.3339	+	+					32	-234.335	533	114.96	0
8	0.3288	+	+	-0.02275				33	-234.422	535.2	117.15	0
44	0.3451	+	+		+		+	47	-220.695	536	118.03	0
48	0.3524	+	+	-0.02166	+		+	48	-221.395	539.5	121.46	0
12	0.3274	+	+		+			33	-236.962	540.2	122.23	0
16	0.3363	+	+	-0.02599	+			34	-237.095	542.5	124.52	0