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Multi-scale patterns in movement and space use of sharks on inshore reefs

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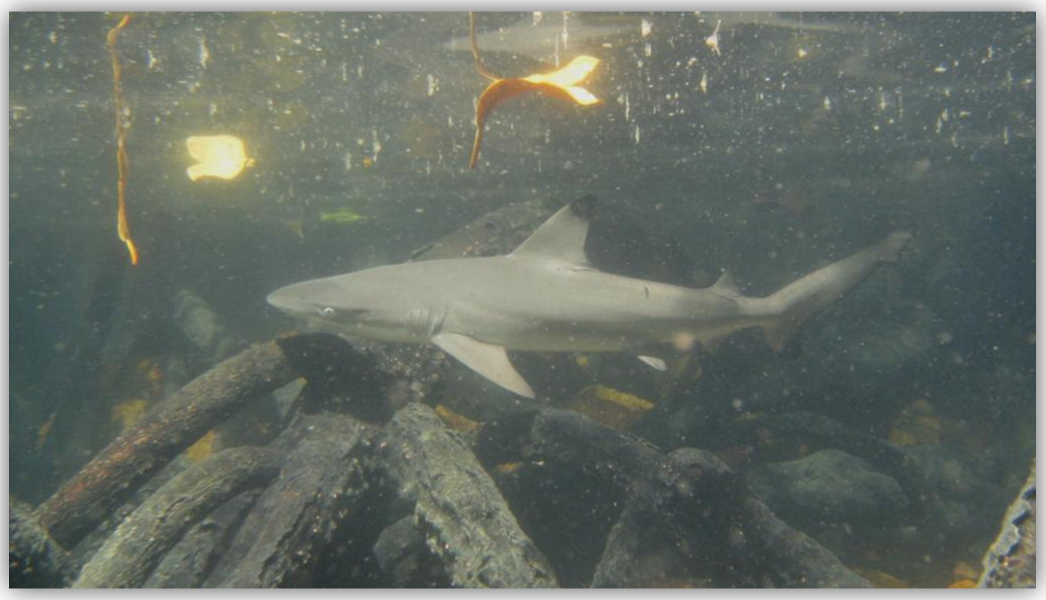

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Copyright and Collaboration

To the best of my knowledge and belief, this thesis contains no material previously published by any other person except where due acknowledgment has been made. Permission from external copyright holders and collaborators has been obtained when necessary.

Ethics and Approvals

All applicable national and institutional guidelines for the care and use of animals were followed. All procedures involving animals were conducted in accordance with the ethical standards of James Cook University"s Animal Ethics Committee (permit A1566) and under research permits from the Great Barrier Reef Marine Park Authority (G10/33754.1 and G10/33240.1).

Publications Arising from Thesis

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Ancillary Works during Candidature

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Abstract

Information on the spatial ecology of reef sharks is critical to understanding life-history patterns, yet gaps remain in our knowledge of how these species move and occupy space. Previous studies have focused primarily on offshore reefs and atolls with little information available on the movement and space use of sharks utilising reef habitats closer to shore. By comparison, tropical inshore regions are dynamic environments, characterised by large and often rapid changes in environmental conditions. Proximity to land and sources of freshwater, for example, expose fishes residing on inshore reefs to fluctuating environmental conditions (e.g. high freshwater run-off/low salinity events), while in many parts of the tropical Indo-Pacific, inshore reef habitats are also subjected to large tidal changes, making them unavailable or difficult to access at lower tides. Research has shown fluctuations in the environment to trigger movement and changes in behaviour and habitat use for many shark and ray species (*Chapter 2*). However, site-attachment in many reef residents, such as reef sharks, could mean that relocation in response to unfavourable environmental conditions may not be feasible. Furthermore, cross-shelf differences in physical and biological properties between reefs inshore and those in offshore or more remote locations can alter regional ecosystem processes significantly, resulting in different movement patterns for resident sharks.

This thesis used a multi-method approach to examine the movement and space use of blacktip reef sharks, *Carcharhinus melanopterus*, on an inshore reef off the coast of Queensland, Australia, and determine their response to changes within their environment. Passive acoustic telemetry was used to examine the residency, space use and depth use of sharks and assess any temporal or biological influences (*Chapter 3*). All sharks showed strong site-attachment to inshore reefs with residency highest among adult females. Sharks exhibited a sex-based, seasonal pattern in space use where males moved more, occupied more space and explored new areas during the reproductive season, while females utilised the same amount of space throughout the year, but shifted the location of the space used. A positive relationship was also observed between space use and size. There was evidence of seasonal site fidelity and long-distance movement with the coordinated, annual migration of two adult

males to the study site during the mating season. Depth use was segregated with some small sharks occupying shallower depths than adults throughout the day and year, most likely as refuge from predation. Results highlight the importance of inshore reef habitats to blacktip reef sharks and provide evidence of connectivity with offshore reefs, at least for adult males.

Passive acoustic telemetry data was then analysed alongside environmental monitoring data to determine the effects of environmental variation on the movement and space use of sharks (*Chapter 4*). Activity space of sharks was modelled against combinations of environmental (wind speed, rain, salinity and water temperature) and biological (size, sex) factors. Size was the most influential predictor of space use, with larger sharks having larger activity spaces. Sex also appeared in top performing models, showing that juvenile males use more space than juvenile females, although effects were marginal. Model results also indicated a relationship between shark activity space and salinity, where space use increased with decreasing salinity. A similar, but weaker relationship was observed with water temperature. These results show blacktip reef sharks respond to even minor changes in salinity, suggesting that they may be able to relocate when conditions are unfavourable, and help define the resilience of this species to disturbance and change.

Lastly, a combination of passive acoustic telemetry and video monitoring techniques were used to examine the movement, behaviour and fine-scale habitat use of sharks within an intertidal bay (*Chapter 5*). Telemetry data was used to investigate diel and tidal effects on coarse-scale habitat use of sharks, while non-baited stationary cameras recorded their fine-scale habitat use and behaviour; data were also examined for size and seasonal differences. We found movement and habitat use of sharks to be strongly associated with the tide, with the smallest juveniles moving into shallow-water mangrove and nearshore habitats as soon as they became available. During high tides, young sharks were observed more frequently within mangrove stands and mangrove-edge habitats than nearby sand flats, and spent longer whilst there, particularly within mangrove stands. There was also evidence of size-based habitat partitioning, with larger sharks remaining mostly in deeper waters off the reef slope. Preferential use of shallow-water by juvenile sharks is well-documented; however, few studies have examined fine-scale habitat use within these areas. Although a growing number of studies have

suggested that intertidal mangrove forests and associated adjacent habitats may play an important role as nursery areas for many elasmobranch species, resolving the use and importance of these habitats is often complicated by their shallow-water nature and intermittent availability. Results from this study indicate that mangrove habitats provide an important ecosystem service for blacktip reef sharks at a critical stage in their life history, with preferential use of these areas most likely a predator avoidance strategy by young sharks.

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Chapter 1: General Introduction

Tropical inshore regions are complex, dynamic environments, characterised by large and often rapid changes in conditions, such as temperature, salinity and tide (Mann 2000, Devlin & Schaffelke 2009). Heat can build quickly within shallow, inshore areas during summer, while offshore areas adjacent to deeper water and locations of upwelling are typically cooler (Mann 2000). Proximity to shore means that inshore areas are also frequently exposed to wet-season flooding effects such as high freshwater run-off, and areas of decreased salinity and greater turbidity within flood plumes (King et al. 2002, Devlin & Schaffelke 2009). Perhaps particularly important to parts of the tropical Indo-Pacific is tide, as water volume change is much greater there than in the Atlantic, resulting in inshore habitats being exposed to a greater degree and for longer periods. For example, intertidal flats and mangrove forests on the Great Barrier Reef (GBR) are often completely exposed during low tides and the ecosystem services they provide to many marine species cannot be accessed during these periods (Sheaves 2005). In contrast, mangrove areas in many parts of the Caribbean remain partially or even fully submerged during low tide periods and therefore continuously available to residents, which may explain the site-specific differences observed in abundance and distribution of some coral-reef associated fish between these two regions, as well as in their degree of dependency on mangrove habitat (Igulu et al. 2014). Despite the environmental variation intrinsic to these areas, tropical inshore regions are also highly productive, and provide important habitat and ecosystem services to many marine species, including elasmobranchs.

Many shark and ray species are observed to utilise discrete habitats within tropical inshore areas for all or part of their life cycle (Knip et al. 2010, Yates et al. 2015). Warm, shallow-water areas, for example, are thought to be important to both reproduction (Wallman & Bennett 2006, Hight & Lowe 2007) and as nursery grounds (Simpfendorfer & Milward 1993, Heupel et al. 2019a). In order to utilise key habitats within inshore areas, however, sharks and rays must develop mechanisms to cope with the frequent and often rapid changes in their environment, or risk decreased fitness or death. For mobile species such as sharks, movement is one such mechanism.

Both acute (e.g. severe weather events) and chronic (e.g. seasonal) environmental changes have been linked to movement in coastal shark populations. Juvenile blacktip sharks, *Carcharhinus limbatus*, for example, were observed to move out of a nursery area in Florida, southeast coast of the United States, in response to a rapid drop in barometric pressure associated with the passage of Tropical Storm Gabrielle (Heupel et al. 2003) – a similar flight response has also been observed in other tropical shark species (Udyawer et al. 2013, Strickland et al. 2019). Whereas multiple studies in temperate areas have shown the distribution and abundance of sharks to fluctuate with chronic, seasonal changes in water temperature, with individuals leaving summer grounds as water temperatures decrease in autumn and returning in spring when temperatures start to increase (Hopkins & Cech 2003, Heupel 2007, Carlisle & Starr 2009). Environmental factors also influence movement over different spatio-temporal scales. As discussed, seasonal temperature changes such as rapid drops in water temperature can trigger emigration from habitats used during summer for some sharks, a cue that allows individuals to avoid lethal winter temperatures (Heupel 2007). In contrast, daily temperature changes have been linked to movement in some species, with individuals moving to occupy warmer areas within a site as temperatures fluctuate throughout the day (Hight & Lowe 2007, Speed et al. 2012b). For example, female leopard sharks, *Triakis semifasciata*, off the coast of California, were found to actively seek out the warmest part of an embayment during the day, with individuals thought to benefit reproductively by using warmer waters (Hight & Lowe 2007).

In addition to the above, several other environmental factors are known to influence movement, behaviour and habitat use of sharks in inshore areas, such as salinity (Heupel & Simpfendorfer 2008, Ubeda et al. 2009), dissolved oxygen (Heithaus et al. 2009, Espinoza et al. 2011), tide (Ackerman et al. 2000, Knip et al. 2011a), photoperiod (Grubbs et al. 2005, Kneebone et al. 2012) and pH (Ortega et al. 2009). Juvenile pigeye sharks, *Carcharhinus amboinensis*, in a nearshore tropical bay in north Queensland, Australia, for example, were observed to move away from sources of freshwater flow and areas of decreased salinity during flooding events (Knip et al. 2011b). Furthermore, several studies have reported tidally-influenced movements, with sharks moving with the tide to conserve energy (Conrath & Musick 2010) or access preferred prey within intertidal areas (Ackerman et al. 2000, Campos et al. 2009). Importantly, environmental changes have the potential to alter the distribution of individuals or even populations over both the short- and long-term which could significantly affect entire ecosystems. Most studies linking environmental changes to movement of sharks within inshore areas, however, have focused primarily on estuarine species or on nearshore species occupying coastal embayments (Hopkins & Cech 2003, Froeschke et al. 2010). Which means that we still lack a full understanding of the role environmental variation plays in the spatial ecology of sharks within inshore areas and there is a need to include species from a broader range of habitat types.

Little information is currently available on the effects of environmental change on reef sharks, particularly for „reef-resident‟ species found at or near coral reefs year-round (Heupel et al. 2019b), such as the grey reef (*Carcharhinus amblyrhynchos*), whitetip reef (*Triaenodon obesus*) and blacktip reef (*Carcharhinus melanopterus*) shark. Although typically associated with clear-water reefs, some reef shark species are also known to occur in turbid coastal bays (Chin et al. 2013c), and habitats adjacent to reefs such as non-estuarine mangrove forests (Guttridge et al. 2012, George et al. 2019). Unlike sharks that use continuous coastal habitats and have the ability to relocate when environmental conditions deteriorate, movement away from patchily distributed coral reef habitats may not be a viable option for reef-resident species due to their documented strong site-attachment to reefs (Barnett et al. 2012, Bond et al. 2012, Heupel & Simpfendorfer 2015) and the risk of not finding new suitable habitats. In a risk assessment of sharks and rays on the GBR, reef sharks were determined to be among the most vulnerable to the effects of climate change, driven mainly by habitat degradation and a loss of overall resiliency based on their strong site-attachment to reefs (Chin et al. 2010). However, to date, studies that have observed movement in response to environmental variation for reef sharks have been conducted mainly on offshore reefs, remote high islands or at atolls, with little information available on the effects of environmental change on sharks resident in inshore reef habitats.

In contrast to inshore areas, offshore reefs and atolls typically have clear-water and comparatively stable environmental conditions. There is often less habitat diversity in offshore locations and also lower movement potential as these areas lack the interconnectivity typical of inshore areas (i.e. less suitable habitat nearby). In addition, the deeper surrounding depths found at offshore reefs, oceanic atolls and remote high islands may also prohibit long-distance movements by resident sharks due to the presumed higher risk of predation when making deep-ocean crossings (Heupel et al. 2010). Importantly, site-specific differences in habitat quality between reefs in inshore areas and those in offshore and more remote locations – including differences in the frequency and magnitude of environmental fluctuations – may result in very different movement and space use patterns for resident sharks. Examining the differences and similarities in the spatial ecology of sharks resident on inshore reefs and those found on reefs in offshore/remote areas can help to resolve the use and importance of certain habitat types or characteristics, as well as inform on possible life-history strategies. Mangrove habitats, for example, are rarely present on offshore reefs and atolls yet some reef shark species, particularly juveniles, are observed in close proximity to them in inshore areas (Chin et al. 2012). For lemon sharks, *Negaprion brevirostris*, at Bimini (Bahamas), use of complex mangrove structure may be a predator avoidance strategy, providing small sharks with protection from larger predators when sheltering among the prop roots (i.e. the habitat is most important; Stump et al. 2017). Alternatively, presence of juveniles within mangrove habitats may simply be a by-product of shallow-water habitat use observed during early life-history stages for many sharks (i.e. the shallow-water characteristic is most important; Morrissey & Gruber 1993). Collectively, the use and importance of inshore habitats to reef sharks may be best indicated by patterns in their movement and space use, and in their response to changes in local environmental conditions.

Despite the importance that inshore habitats are thought to play for some reef sharks, the temporal and spatial use of inshore reef habitats by these species are still not well understood. The degree of dependence on mangrove habitats for any shark species, for example, is virtually unknown despite their known occurrence in these habitats. In addition, the effects of environmental variation on movement and habitat use of sharks resident on inshore reefs also remains relatively unknown, despite the higher frequency and magnitude of environmental fluctuations intrinsic to tropical inshore areas and the identification of these species as some of the most vulnerable to climate change (but see

Rummer et al. 2020); this includes the environmental cues and/or thresholds that may trigger emigration from the area or changes in behaviour. Both environmental cues and thresholds for sharks resident on inshore reefs may differ significantly from those of non-reef dependent coastal shark species as well as reef sharks resident on offshore reefs and atolls. Furthermore, inshore areas are some of the most degraded due to intense coastal development (e.g. dredging, construction and mangrove deforestation) linked to wide-spread habitat alteration and destruction (Edgar et al. 2000, Lotze et al. 2006) and deteriorated water quality (e.g. pesticides and sediments found in river run-off) which can have a negative impact on ecosystem health and productivity (Fabricius 2005, Hutchings et al. 2005, Schaffelke et al. 2005). In order to more fully understand the spatial ecology of reef sharks, we must understand the use and importance of inshore reef habitats to these species, as well as the site-specific factors that influence their movement and space use. Understanding the dynamics of habitat use and movement for sharks on inshore reefs is critical to defining how resilient these populations are to disturbance and change.

This thesis used a multi-method approach to fill gaps in our understanding of the spatial ecology of reef sharks on an inshore island coral reef within the Great Barrier Reef Marine Park. The study site, Orpheus Island, part of the Palm Island Group in north Queensland, Australia, was chosen as it has a good representation of a typical inshore island reef system with several available habitat types (reefs, mangroves, intertidal reef flats), prevalent water conditions (higher turbidity/lower visibility compared to offshore reefs), and proximity to the coast and sources of freshwater flow. The blacktip reef shark, *Carcharhinus melanopterus* (Quoy & Gaimard 1824-25), was chosen as the focal species for this project as it is the most commonly encountered reef shark within inshore waters of the GBR (Chin et al. 2012). In addition, although frequently associated with clear-water reefs, this species is also found on turbid inshore reefs (Chin et al. 2013c) and in close proximity to mangrove habitat (Speed et al. 2016, George et al. 2019). Blacktip reef sharks are one of the three most commonly encountered sharks on offshore reefs of the GBR (Heupel et al. 2009) and, importantly, previous research has been conducted on this species in oceanic locations (Papastamatiou et al. 2010, Mourier et al. 2013), enabling comparisons with the current study. These oceanic reefs are not exposed to environmental fluctuations to the same degree as Orpheus Island and also lack the interconnectivity and habitat diversity that is characteristic of the GBR with its extensive complex of thousands of individual reefs. Results from this study will help to fill knowledge gaps on how site-attached species such as reef sharks move and occupy space in inshore reef habitats, including any site-specific differences in their response to changes in local environmental conditions.

Broadly, this thesis looked at answering two main core questions:

i. *What are the movement and space use patterns of reef sharks in inshore reef ecosystems?*
ii. *How are movement and space use patterns affected by fluctuations in the environment?*

The overarching aims of this thesis were to use multiple field methods to fill gaps in our understanding of the spatial ecology of blacktip reef sharks on inshore reefs by:

1. Examining the long-term patterns in movement, residency and space use of reef sharks on inshore reefs (i.e. broad-scale view)
2. Describing the fine-scale movement, behaviour and habitat selection patterns of reef sharks on inshore reefs
3. Determining how changes in environmental conditions influence movement and activity space of reef sharks on inshore reefs

This thesis is structured as stand-alone scientific manuscripts, some of which have already been published in peer-reviewed journals. Repetition within individual chapters is limited to mostly descriptions of the study site and sampling methods used. Chapter content is summarised briefly below:

Chapter 1 (this chapter): broadly introduces the importance of inshore areas to sharks, the role of environmental variation on their movement and space use, and site-specific differences between inshore and offshore or remote coral reef ecosystems that may affect the spatial ecology of reef sharks resident to these areas. It introduces the core questions and individual aims of this research as well as outlines the thesis structure.

Chapter 2: a literature review on the effects of environmental factors on elasmobranch movement, behaviour and habitat use. This review synthesizes current information on the environmental factors known to influence movement patterns and space use of sharks and rays. This review also highlights the complexities associated with determining environmental drivers of movement as well as the need for inclusion of species from underrepresented habitats in future studies. This review has been published in *Reviews in Fish Biology and Fisheries*.

Chapter 3: uses passive acoustic telemetry to examine the long-term patterns in movement, residency and space use of reef sharks on inshore reefs. This data chapter looks at the broad-scale use of inshore reef habitats by blacktip reef sharks as well as changes associated with sex and ontogeny. This chapter has been published in *PLoS ONE*.

Chapter 4: uses passive acoustic telemetry and environmental monitoring data to determine the effects of environmental changes on the movement and activity space of blacktip reef sharks. This chapter has been published in *Marine Ecology Progress Series*.

Chapter 5: combines passive acoustic telemetry and non-baited, remote stationary video monitoring to examine the fine-scale movement and habitat selection patterns of reef sharks. This manuscript is currently in preparation for publication.

Chapter 6: consists of the general discussion which synthesises the components of each chapter and puts results into a wider context. This chapter also offers suggestions for future research.

Chapter 2: Influence of Environmental Factors on Shark and Ray Movement, Behaviour and Habitat Use

2.1 Introduction

Sharks and rays are predators within the marine environment and many species are thought to play an important role in coastal and oceanic ecosystems worldwide (Bascompte et al. 2005, Ferretti et al. 2008, Heithaus et al. 2008). Several studies have suggested that the removal of large predators from marine systems can lead to drastic and lasting effects in the form of trophic cascades and/or the collapse of marine communities (Dulvy et al. 2000, Shepherd & Myers 2005, Polovina et al. 2009). To date, most studies examining predator removal from marine systems have focused on the effects of overfishing (Stevens et al. 2000, Baum & Worm 2009, Polovina et al. 2009). However, other drivers exist that may affect the distribution and abundance of sharks and rays within marine ecosystems and, by association, the broader marine community. Abiotic factors are easily measured and may form some of the main drivers for behavioural patterns within marine ecosystems. Biotic factors such as prey density and availability (Heithaus 2001, Heithaus et al. 2002, Torres et al. 2006, Goetze & Fullwood 2013), and predator avoidance (Heupel & Hueter 2002, Collins et al. 2007, Heithaus et al. 2009) have also been shown to play a role in the spatial ecology of elasmobranchs. These studies illustrate that a range of drivers influence shark and ray populations and the ecosystems where they occur.

Recent studies have shown that abiotic factors may be significant drivers of movement among sharks and rays. Both acute (e.g. severe weather events; Heupel et al. 2003, Matich & Heithaus 2012) and chronic (e.g. seasonal temperature change; Hopkins & Cech 2003, Heupel 2007, Carlisle & Starr 2009) changes have been linked to movement. For example, Matich and Heithaus (2012) found that juvenile bull sharks, *Carcharhinus leucas*, either permanently left an estuarine system or died during an extreme “cold snap.” In Tomales Bay, California, the bat ray, *Myliobatis californica*, leopard shark, *Triakis semifasciata*, and brown smooth-hound shark, *Mustelis henlei*, were observed to emigrate from the bay in response to a seasonal decrease in water temperature (Hopkins & Cech 2003). In addition to temperature, abiotic factors such as salinity (Collins et al. 2008, Heupel & Simpfendorfer 2008, Ubeda et al. 2009, Simpfendorfer et al. 2011), dissolved oxygen (Parsons & Hoffmayer 2005, Heithaus et al. 2009, Craig et al. 2010, Espinoza et al. 2011), tide (Medved & Marshall 1983, Ackerman et al. 2000, Knip et al. 2011a, Campbell et al. 2012), photoperiod (Grubbs et al. 2005, Heupel 2007, Kneebone et al. 2012, Nosal et al. 2014), barometric pressure (Heupel et al. 2003, Udyawer et al. 2013) and pH (Ortega et al. 2009) have all been reported to play a role in the location and movement of sharks and rays.

Understanding how species respond to changes in their environment is increasingly important given reports of growing human-mediated environmental effects on marine systems. Sharks and rays currently face an array of anthropogenic threats, especially in coastal ecosystems (Knip et al. 2010, Dulvy et al. 2014). For example, chemical pollutants and pesticides found in river run-off have been shown to have a negative impact on both ecosystem health and productivity (Fabricius 2005, Hutchings et al. 2005, Schaffelke et al. 2005). Most notably, Gelsleichter et al. (2005) documented a possible link between exposure to organochloride contaminants found in Florida estuaries and reproductive health in the bonnethead shark, *Sphyrna tiburo*. Intense coastal development such as dredging, construction and deforestation has also been linked to wide-scale habitat alteration and destruction (Edgar et al. 2000, Lotze et al. 2006). Perhaps unsurprisingly, recent studies have reported changes in abundance and distribution of several elasmobranch species associated with human-altered habitats (Jennings et al. 2008, Jirik & Lowe 2012, Werry et al. 2012, Curtis et al. 2013). It is important to note, however, that the effects of utilising modified habitats for sharks and rays are not necessarily negative. Research into use of restored estuarine habitat by round stingrays, *Urobatis halleri*, suggested that female rays may have benefited from the significantly higher mean water temperatures found in restored estuarine basins than in adjacent natural areas (Jirik & Lowe 2012). Collectively, these studies highlight how human-mediated environmental changes have the potential to alter local environmental conditions, affecting the health and spatial ecology of sharks and rays, both positively and negatively.

Compounding anthropogenic changes in coastal systems is the fact that key inshore habitats for many species are often characterised by fluctuating environmental conditions such as high freshwater run-off/low salinity events (Mann 2000, Devlin & Schaffelke 2009), tropical storms (Conner et al. 1989) and large and/or rapid changes in temperature (Mann 2000). With the global population expected to reach an estimated 9 billion by 2050 (Cohen 2003, 2005), and with future climate change scenarios predicting substantial changes in a range of environmental parameters (Emanuel 2005, Webster et al. 2005, Hoegh-Guldberg et al. 2007, Rahmstorf 2007), most of these environmental changes are expected to be exacerbated.

In light of current and projected environmental changes on marine systems, and given the important role predators such as sharks and rays play in the trophic dynamics of coastal and oceanic ecosystems globally, it is vital to understand the drivers behind movement. As movement plays a critical role in defining the use and importance of key habitats for sharks and rays, resolving whether abiotic factors drive movement will provide essential information on spatial ecology and provide data valuable to the successful management of these species and habitats. This review paper outlines and discusses: (1) abiotic factors linked to movement of sharks and rays; (2) complexities associated with determining environmental drivers of movement; and (3) the role of environmental change on spatial ecology.

2.2 Abiotic Factors Linked to Movement of Sharks and Rays

Abiotic factors may influence movement either indirectly (e.g. altering patterns of abundance and distribution of principal prey species) or directly. Given that the energetic demands of key metabolic and physiological processes (e.g. digestion, osmoregulation) for sharks and rays are known to fluctuate in response to changes in abiotic factors such as temperature and salinity (Bernal et al. 2012), the primary way in which abiotic factors are thought to influence elasmobranch movement is directly, via their effect on physiology. Specifically, movement may occur in response to a physiological limit being reached or to a physiological preference, where individuals move to maintain abiotic factors at levels that provide them with some form of advantage.

As mobile marine predators, most sharks and rays have the ability to leave an area should local environmental conditions change sufficiently that the energetic costs of maintaining key metabolic and physiological processes become too demanding. Individuals that leave, however, risk the inability to find new suitable habitat and an increased chance of predation, while those that stay must exist in a stressed state or, at worst, suffer death. Whether or not individuals that leave return to their original habitat or relocate permanently often depends on the length and severity of environmental fluctuations. The following section outlines abiotic factors currently linked to movement of sharks and rays.

2.2.1 *Temperature*

Temperature is well-known to have an effect on the physiology of ectotherms (Fry 1971, Crawshaw 1977, Bernal et al. 2012). The rate of important metabolic and physiological functions such as digestion, somatic growth, and reproduction is determined by the core body temperature of fish which, in turn, is directly controlled by the temperature in their surrounding environment. This is in contrast to endothermic species that are able to regulate their internal body temperature and help maintain metabolic rates using specialized circulatory mechanisms that retain heat (Anderson & Goldman 2001, Dickson & Graham 2004, Donley et al. 2007). Most sharks and rays are ectothermic with the only exceptions found within the family Lamnidae, comprising just five species (Bernal et al. 2012). Given the role that ambient temperature plays in influencing key metabolic and physiological processes for ectotherms, it is perhaps unsurprising that many sharks and rays are sensitive to changes in temperature.

Temperature-related mortality events (i.e. “cold kills”) have been documented for some sharks and rays in response to extreme drops in temperature (Snelson & Bradley 1978, Poulakis et al. 2011, Matich & Heithaus 2012). In contrast, laboratory-held Atlantic stingrays, *Dasyatis sabina*, acclimated to temperatures at or lower than those experienced in their natural habitat (Fangue & Bennett 2003). The authors suggested that by being able to adapt to temperatures lower than those present in their natural habitat rays were able to exploit a wider range of resources than competitors and/or use thermal gradients as a refuge from predators. While sharks and rays that choose to remain within their home range area when temperatures fluctuate must either adapt to the new conditions or suffer death, many species respond through movement.

Temperature-mediated seasonal (Dunbrack & Zielinski 2003, Hopkins & Cech 2003, Heupel 2007, Vaudo & Heithaus 2009) and diel (Carey & Scharold 1990, Economakis & Lobel 1998, Matern et al. 2000, Sims et al. 2006) movements are well-documented in the literature. For example, juvenile blacktip sharks, *Carcharhinus limbatus*, in nearshore waters of the Gulf of Mexico used decreases in water temperature as a cue to leave their summer nursery area – a seasonal exodus to avoid lethal winter temperatures (Heupel 2007). In addition to movement in response to seasonal temperature change, many species are thought to use movement to actively seek out preferred temperatures throughout the day. Common thresher sharks, *Alopias vulpinus*, displayed diel patterns in depth distribution and activity, indicating a nocturnal preference for the warmer mixed layer after daytime activity in deeper, cooler water (Cartamil et al. 2010). Collectively, studies documenting temperature-mediated seasonal and diel movements indicate that temperature often works on shark and ray populations at a variety of temporal scales.

Movement to locate a spatially variable preferred temperature range (i.e. behavioural thermoregulation) may be important to foraging (Carey & Scharold 1990, Matern et al. 2000, Sims et al. 2006, Thums et al. 2013) and reproductive (Economakis & Lobel 1998, Hoisington & Lowe 2005, Hight & Lowe 2007, Jirik & Lowe 2012, Speed et al. 2012b) strategies among sharks and rays. Thermoregulatory behaviour may confer biological advantages to the individual that offset movement costs. Benefits often include energy savings that could be allocated to growth or other biological functions (e.g. reproduction).

The use of behavioural thermoregulation as a foraging strategy may be the reason why deep dives by blue sharks, *Prionace glauca*, were punctuated by frequent short periods at the surface (Carey & Scharold 1990). Since muscle warms more quickly than it cools, blue sharks were thought to re-warm quickly at the surface between dives, allowing them to extend their foraging time below the thermocline. Similarly, a recent study investigating movement of whale sharks, *Rhincodon typus*, off the coast of Western Australia found post-dive surface duration to be negatively correlated with the minimum temperature of dives, thought to be a thermoregulatory strategy where sharks re-warm at the surface after foraging in cooler, deep waters (Thums et al. 2013). Movement into cooler water after feeding has been suggested to decrease the rate of gastric evacuation and increase assimilation efficiency for several species (Matern et al. 2000, Sims et al. 2006, Di Santo & Bennett 2011). A 10°C decrease in water temperature, for example, resulted in a 30% increase in overall food absorption in Atlantic stingrays (Di Santo & Bennett 2011). By adopting a "hunt warm, rest cool" strategy male dogfish, *Scyliorhinus canicula*, were thought to lower their daily energetic costs by just over 4% (Sims et al. 2006). Increases in assimilation efficiency and extended foraging times are examples of how sharks and rays use temperature-mediated movement to conserve energy and improve individual foraging success.

In contrast, movement of female sharks and rays into warm, shallow water is thought to provide reproductive benefits (Economakis & Lobel 1998, Hoisington & Lowe 2005, Hight & Lowe 2007, Jirik & Lowe 2012, Nosal et al. 2013, Nosal et al. 2014). Female leopard sharks off the coast of California actively sought out the warmest part of an embayment as temperatures fluctuated throughout the day (Hight & Lowe 2007). The authors estimated that elevated core body temperatures could increase metabolic rates by up to 17% and augment physiological functions, possibly increasing the rate of embryonic development and decreasing gestation period. By shortening the gestation period, female sharks would have more time to replenish energy reserves following parturition before the onset of winter and the next reproductive cycle (Wallman & Bennett 2006, Jirik & Lowe 2012). Jirik and Lowe (2012) suggested that preferential use of warm, restored estuarine habitat by female round stingrays during gestation may increase the size of offspring at birth, presumably enhancing the survival rates of newborn rays. Alternatively, as females of some shark species are thought to reach sexual maturity at a size greater than their male conspecifics, it has been suggested that aggregations of female sharks in warm waters may increase somatic growth rates, allowing them to reach reproductive maturity more quickly (Economakis & Lobel 1998, Robbins 2007). Whether due to a physiological limitation or as a thermoregulatory strategy in response to physiological preferences, it is clear that temperature is an important driver of movement and space use.

2.2.2 *Salinity*

Salinity is also well-known to have a strong influence on physiology (Pang et al. 1977, Bernal et al. 2012). Although some species are euryhaline and able to exploit a wide range of salinities (Thorson 1972, 1974, Montoya & Thorson 1982, Hazon et al. 2003), the vast majority of sharks and rays are strictly stenohaline and occupy a narrow salinity range (Froeschke et al. 2010, Martin et al. 2012). Regardless of individual salinity tolerances, however, optimal habitat requirements for sharks and rays must be balanced against the energetic costs of osmoregulation, resulting in species-specific responses to changes in salinity.

Salinity has been reported to influence both distribution (Simpfendorfer et al. 2005, Collins et al. 2008, Ubeda et al. 2009, Knip et al. 2011b, Francis 2013) and local abundance (Hopkins & Cech 2003, Carlisle & Starr 2009, Poulakis et al. 2011) of sharks and rays. For example, juvenile pigeye sharks, *Carcharhinus amboinensis*, in a tropical nearshore environment shifted their home range areas during extreme wet season flooding events to avoid freshwater inflow and decreased salinity (Knip et al. 2011b). Similarly, cownose rays, *Rhinoptera bonasus*, monitored in a southwest Florida estuary occurred farther upriver during periods of decreasing flow and increasing salinity (Collins et al. 2008). Given that most sharks and rays are stenohaline, movement in response to salinity change may simply be a means to avoid physiological stress and possible mortality when salinity levels fall outside of individual tolerances. It is important to note that, as a driver of movement, salinity most likely has a greater influence on nearshore species than species that occur further from shore as sharks and rays utilising inshore habitats are more frequently exposed to freshwater run-off and associated salinity fluctuations.

Similar to behavioural thermoregulation, some species have been shown to use movement to actively seek out spatially variable preferred salinity ranges, a type of behavioural osmoregulation thought to confer a biological advantage (Collins et al. 2008, Heupel & Simpfendorfer 2008, Froeschke et al. 2010, Simpfendorfer et al. 2011). Juvenile bull sharks within a Florida estuary selected habitat based on salinity, avoiding areas of low salinity and moving to remain within a preferred salinity range (Simpfendorfer et al. 2005, Heupel & Simpfendorfer 2008). Selection for a preferred salinity range may minimize the energetic costs associated with osmoregulation, energy that presumably could be allocated to growth or other physiological processes (Simpfendorfer et al. 2005, Heupel & Simpfendorfer 2008, Froeschke et al. 2010).

In addition to reducing the energetic costs of osmoregulation, movement to remain within a specific salinity range may also be a means of predator avoidance for some species (Poulakis et al. 2011, Simpfendorfer et al. 2011). Simpfendorfer et al. (2011) found that young smalltooth sawfish, *Pristis pectinata*, demonstrated an affinity for different salinities than those of most marine predators. Within this estuarine system large bull sharks used salinities ranging from 7-20 psu (dimensionless "units" of the Practical Salinity Scale) while juvenile sawfish occupied salinities from 18-24 psu. By moving to remain within a different salinity range than that used by bull sharks, young sawfish presumably lowered their risk of predation and increased survival. Whether as a means to reduce the energetic costs associated with osmoregulation, or to avoid predation, it is apparent that salinity plays a role in moderating distribution and movement patterns of some sharks and rays.

2.2.3 ***Dissolved Oxygen***

Although comparatively fewer studies have focused on the role of dissolved oxygen in spatial ecology, this abiotic factor has been shown to influence both distribution (Grubbs & Musick 2007, Carlisle & Starr 2009, Espinoza et al. 2011, Knip et al. 2011b, Drymon et al. 2013) and abundance (Parsons & Hoffmayer 2005, Heithaus et al. 2009) of several shark and ray species. Heithaus et al. (2009) found dissolved oxygen concentrations to be the best predictor of bull shark abundance within a Florida estuary. The authors suggested that, over small spatial and temporal scales movement was driven largely by the effort of individuals to remain within optimal dissolved oxygen conditions. Similarly, habitat use and movement of the gray smooth-hound shark, *Mustelus californicus*, in a newly restored estuary in southern California, indicated individuals avoided the warmest inner basin during the day due to spatial differences in dissolved oxygen levels (Espinoza et al. 2011). These studies indicate that fluctuations in dissolved oxygen levels may be a significant driver of movement for some species. It is important to note, however, that as a driver of movement, dissolved oxygen most likely has a greater influence on those species utilising comparatively lower oxygen habitats.

In contrast to studies documenting movement in response to changes in dissolved oxygen concentrations, several studies have shown that some species display a degree of tolerance to fluctuations in dissolved oxygen levels. Epaulette sharks, *Hemiscyllium ocellatum*, provide perhaps the best example of hypoxia tolerance in elasmobranchs (Wise et al. 1998, Routley et al. 2002, Nilsson & Renshaw 2004, Speers-Roesch et al. 2012). A study by Wise et al. (1998) found epaulette sharks to be tolerant to both mild hypoxia (20% of normoxia) and to cyclic exposure to extreme hypoxia (5% of normoxia). As a resident on shallow reef platforms characterised by large tidal fluctuations, epaulette sharks are exposed to progressively longer and more severe hypoxic conditions as tides become lower, a natural preconditioning regimen that elicits an enhanced physiological response to hypoxia, allowing it to better exploit its niche environment (Routley et al. 2002, Nilsson & Renshaw 2004).

Laboratory studies on the bonnethead shark (Parsons & Carlson 1998, Carlson & Parsons 2001, 2003) and blacknose shark, *Carcharhinus acronotus* (Carlson & Parsons 2001), determined that these species were able to tolerate at least moderate hypoxic conditions. The authors speculated that behavioural (i.e. increase in swimming activity, mouth gape) and associated physiological (i.e. increase in oxygen uptake) mechanisms employed by these two species may allow them to exploit warm shallow environments (where dissolved oxygen levels can be variable) more effectively than other species (Parsons & Carlson 1998, Carlson & Parsons 2001). Similarly, the observed ability of the scalloped hammerhead shark, *Sphyrna lewini* (Jorgensen et al. 2009), and cownose ray (Craig et al. 2010) to penetrate hypoxic environments may mean these species have access to prey not accessible to other predators. Therefore, dissolved oxygen levels may play an important role in the spatial ecology of some sharks and rays, with individuals driven by a need to remain within optimal dissolved oxygen conditions or as a means to exploit habitats and/or resources inaccessible to others and hence reduce competition.

2.2.4 *Tide*

Tidally-influenced movement has been observed for both sharks (Medved & Marshall 1983, Ackerman et al. 2000, Wetherbee & Rechisky 2000, Carlisle & Starr 2010) and rays (Smith & Merriner 1985, Whitty et al. 2009, Campbell et al. 2012). In separate studies examining movement patterns of juvenile sandbar sharks, *Carcharhinus plumbeus*, off the east coast of the United States, young sharks were observed to move predominantly in the direction of tidal current flow (Medved & Marshall 1983, Wetherbee & Rechisky 2000). Tidally-driven movement patterns are thought to be related to foraging tactics (Smith & Merriner 1985, Ackerman et al. 2000, Campos et al. 2009, Carlisle & Starr 2010), energy conservation strategies (Ackerman et al. 2000, Ortega et al. 2009, Whitty et al. 2009, Campbell et al. 2012), and predator avoidance (Wetherbee et al. 2007, Knip et al. 2011a, Guttridge et al. 2012). For example, species typically found in nearshore waters such as the leopard shark (Ackerman et al. 2000, Carlisle & Starr 2009, 2010), brown smoothhound shark (Campos et al. 2009) and cownose ray (Smith & Merriner 1985) move into shallow water on incoming tides, presumably to forage. Movement with the tide allows individuals to maximise their foraging area by utilising regions only available at high tide (Smith & Merriner 1985, Gilliam & Sullivan 1993, Ackerman et al. 2000, Carlisle & Starr 2010) as well as providing access to comparatively rich prey resources found only in intertidal areas (Carlisle & Starr 2009).

Movement with the tide may also serve to minimize energy expenditure for some sharks (Ackerman et al. 2000, Ortega et al. 2009, Conrath & Musick 2010) and rays (Whitty et al. 2009, Campbell et al. 2012). Conrath and Musick (2010) found that 53.6% of the net movements of juvenile sandbar sharks were with the tide. Due to strong tidal currents within the area the authors speculated that it was energetically costly for young sharks to swim against tidal currents. Energy conservation was also suggested to explain why 98% of young-of-the-year (0+) freshwater sawfish, *Pristis microdon*, moved in the direction of the tide (Whitty et al. 2009). In addition, Ackerman et al. (2000) estimated that tidally-assisted swimming could potentially conserve up to 6% of total energy expenditure for leopard sharks, suggesting that energy savings acquired by young sharks and rays through tidally-directed movement may be considerable.

Movement with the tide may also be a means for juvenile sharks and rays to avoid larger predators (Wetherbee et al. 2007, Guttridge et al. 2012). Movement patterns of juvenile lemon sharks, *Negaprion brevirostris*, on a Brazilian atoll revealed the smallest individuals were most strongly influenced by tides, restricting their movements to the shallowest tide pools at low tide (Wetherbee et al. 2007). Similarly, Knip et al. (2011a) concluded that changes in water depth associated with the tide had the strongest influence on the youngest individuals within a population of pigeye sharks. It is important to note that depth is associated with tide and both authors speculated that, as small individuals are likely to be the most vulnerable to predation, tidally-based movement may be a mechanism to avoid predators by remaining in shallow water. These studies indicate that tide may be an important environmental driver of movement among sharks and rays, as a refuging strategy, a foraging tactic, or as a means to conserve energy.

2.2.5 *Photoperiod and Light*

Few studies have identified photoperiod as a potential driver of movement for sharks and rays (Grubbs et al. 2005, Heupel 2007, Kneebone et al. 2012, Nosal et al. 2014). However, long-term movements of juvenile sandbar sharks indicated that winter migration from a summer nursery area was highly correlated with decreasing day length (Grubbs et al. 2005). As an abiotic driver of movement, photoperiod is perhaps more important for species found in temperate regions that are subject to greater differences in seasonal day length. It is also important to note that photoperiod on a seasonal scale is probably an indicator for correlated temperature changes. For example, Grubbs et al. (2005) speculated that the return of juvenile sandbar sharks to nursery areas in the spring was triggered by both photoperiod and temperature with day length a signal to begin northward migrations and temperature the primary driver stimulating movement into the nursery. Similarly, emigration of juvenile sand tiger sharks, *Carcharias taurus*, from a Massachusetts estuary was correlated to both day length and water temperature (Kneebone et al. 2012). Although both factors may be influential, the authors speculated that photoperiod was a stronger, more consistent cue driving movement.

In addition to day length, light intensity has been suggested to drive movement for some species (Nelson et al. 1997, Cartamil et al. 2003, Andrews et al. 2009, Whitty et al. 2009). Andrews et al. (2009) suggested that changes in light intensity during crepuscular periods may initiate nocturnal foraging behaviour in sixgill sharks, *Hexanchus griseus*. Similarly, diel patterns of movement observed in the Hawaiian stingray, *Dasyatis lata*, were thought to be more influenced by light intensity than temperature or tidal stage (Cartamil et al. 2003). Finally, Nelson et al. (1997) revealed crepuscular vertical migrations of the megamouth shark, *Megachasma pelagios*, closely tracked specific isolumes. The authors concluded that depth selection was related to light level. As potential drivers of movement, both photoperiod and light intensity have been shown to play a key role in the spatial ecology of several elasmobranch species, but remain relatively understudied to date.

2.2.6 *Other Factors*

Two other abiotic factors have been identified as drivers of movement among sharks and rays, but neither has been examined in detail. The first of these is barometric pressure. Changes in barometric pressure associated with tropical storms can trigger movement in sharks (Heupel et al. 2003, Udyawer et al. 2013). Heupel et al. (2003) found that juvenile blacktip sharks left a nursery area in response to a decrease in barometric pressure associated with a tropical storm. Findings by Udyawer et al. (2013), however, indicate movement in response to extreme storm events may be species-specific. Five species of coastal shark (*Carcharhinus limbatus*, *C. tilstoni*, *C. melanopterus*, *C. sorrah*, and *C. amboinensis*) responded differently to changes in barometric pressure before, during and after a severe tropical storm. A short-term flight response was observed in all monitored species except the blacktip reef shark (*C. melanopterus*) which did not depart or change location. The authors speculated that blacktip reef sharks are perhaps more tolerant to the adverse conditions associated with tropical storms or that the benefits gained by individuals who remain in their preferred habitat outweigh the benefits of departing.

The second rarely examined environmental driver of movement for elasmobranch species is pH (Ortega et al. 2009). Juvenile bull sharks within a Florida river were tracked before and after an influx of freshwater revealing two distinct movement patterns. Movement and location of individuals were either primarily nocturnal and correlated with salinity, temperature and dissolved oxygen, or diurnal in nature and correlated with temperature, dissolved oxygen, turbidity and pH (Ortega et al. 2009). Although under-represented in the literature, changes in barometric pressure and pH may play a role in influencing movement and their role should be explored further.

2.3 Complexities Associated with Determining Environmental Drivers of Movement

Although there are multiple studies linking shark and ray movement with abiotic factors, these studies often present unique problems. For example, links between movement and environment are inherently correlative and do not provide conclusive evidence that abiotic factors and not some other driver (e.g. predator avoidance, prey distribution/availability) are behind such movement. In addition, if abiotic factors are shown to be responsible for movement, it often remains unclear whether species are actively seeking specific conditions or merely reacting to them. Finally, abiotic factors rarely occur in isolation, making it difficult to determine which factor is of highest importance or whether synergistic interactions between different factors are occurring. The influence of other factors confounds interpretation of abiotic cues for movement including biological and physiological processes and geographic variability. Here we discuss some of the complexities associated with determining environmental drivers of movement for elasmobranchs.

2.3.1 *Biotic Factors*

Several biotic factors have been shown to trigger movement and changes in behaviour among sharks and rays. In particular, prey density and availability (Heithaus et al. 2002, Shepard et al. 2006, Torres et al. 2006, Jaine et al. 2012) and predator avoidance (Heupel & Hueter 2002, Collins et al. 2007, Heithaus et al. 2009) are thought to influence movement patterns and habitat choice for many species. Movements of several planktivorous sharks and rays, for example, have been linked to tidally-concentrated plankton aggregations (Sims & Quayle 1998, Shepard et al. 2006, Priede & Miller 2009, Jaine et al. 2012). Similarly, spatial patterns in abundance for the gray smooth-hound shark (Espinoza et al. 2011), tiger shark (Heithaus 2001) and sixgill shark (Andrews et al. 2010) were shown to be influenced by both water temperature and prey availability, most likely due to these species following a seasonal shift in prey resources. As biotic factors may work alongside and/or mask the effects of abiotic factors, it is often a challenge to decipher the exact effects of abiotic factors on movement.

2.3.2 *Variation between Seasons*

Seasonal variability in abiotic factors may complicate resolution of important drivers of movement for sharks and rays. For example, Campbell et al. (2012) observed that while movement of the freshwater whipray, *Himantura dalyensis*, was dominated by the diel cycle during the wet season, whipray movement patterns during the dry season were related to the tidal/lunar cycle. The authors concluded that the observed shift from tidal/lunar to diel periodicity in movement was related to the seasonal suppression of tidal flow during the wet season. Similarly, seasonal differences in diving patterns were observed for the blue shark where individuals made frequent diurnal excursions to depth resting at the surface between dives during winter, but did not show this pattern in summer (Carey & Scharold 1990). The authors speculated that seasonal changes in the type or availability of prey, or sexual activity associated with the onset of mating season, may be responsible for the observed change in swimming behaviour. Since conditions often vary between seasons, it is important that studies include long-term monitoring of individuals when possible to encompass seasonal differences.

2.3.3 *Variation between Sexes*

Sexual segregation is a common characteristic of shark and ray populations (Klimley 1987, Sims 2005, Robbins 2007, Wearmouth & Sims 2008, Mucientes et al. 2009) so it is perhaps unsurprising that research has also shown variability in response to abiotic factors between sexes. Male Atlantic stingrays, for example, exhibited little change in preferred temperature while females showed thermal preferences based on feeding and reproductive state (Wallman & Bennett 2006). The authors concluded that female selection for a preferred temperature range may be due to higher energetic demands to maintain a larger body size, the reproductive cost of yolking eggs, or to meet nutritional demands of pups during gestation. Sexual segregation was also observed in round stingrays monitored in a restored Californian estuary (Jirik & Lowe 2012). Preferential use of warmer, shallow waters of the restored basin by female stingrays was thought to provide some reproductive benefit. Given that energetic demands vary due to sex-specific costs in reproduction, it may not be uncommon for environmental drivers of movement to differ between sexes, making consideration of sex-based differences important to data interpretation.

2.3.4 *Variation between Size Classes*

Ontogenetic shifts in movement, behaviour and habitat use have been widely documented (Gruber et al. 1988, Papastamatiou et al. 2009b, Andrews et al. 2010, Heupel et al. 2010) and several studies have shown environmental drivers of movement to vary between size classes (Wetherbee et al. 2007, Heupel & Simpfendorfer 2008, Whitty et al. 2009, Knip et al. 2011a). For example, bull sharks in the Caloosahatchee River, Florida, partitioned habitat among size classes, with the youngest, smallest individuals typically found upriver while older, larger juveniles occurred farther downstream in adjacent embayments (Simpfendorfer et al. 2005, Heupel & Simpfendorfer 2008). As the youngest individuals displayed an affinity for salinities between 7-20 psu, and given that the Caloosahatchee River was the only place within the system where salinities less than 20 psu regularly occurred, the authors speculated that salinity was an important factor in the observed size-based partitioning, possibly as a means to reduce intraspecific predation.

Similarly, studies on movement patterns of juvenile pigeye sharks (Knip et al. 2011a), freshwater sawfish (Whitty et al. 2009) and lemon sharks (Wetherbee et al. 2007) all reported movement by the youngest, smallest individuals into the shallowest habitat with the tides. This behaviour is thought to be a refuging strategy from larger predators. Ontogenetic differences in habitat requirements among sharks and rays may translate into different abiotic drivers of movement between size classes and highlights the need to include a range of age groups within a given sampling pool before population level conclusions are drawn.

2.3.5 *Variation between and Within Geographic Locations*

To further complicate identification of triggers for movement, environmental drivers may differ between and within regions for a given species. For example, the primary abiotic factor influencing the distribution of bull sharks in the Caloosahatchee River was salinity (Simpfendorfer et al. 2005, Heupel & Simpfendorfer 2008), whereas in the Florida Everglades dissolved oxygen was reported to be the greatest predictor of bull shark abundance (Heithaus et al. 2009). Heithaus et al. (2009) speculated that differences in primary environmental drivers of movement between regions may be due to site-specific differences in the physical structure and hydrological dynamics of the two estuaries. Specifically, the Caloosahatchee River estuary is affected by acute low salinity/high freshwater run-off events while the Everglades estuary is not, resulting in salinity having a lower influence in this region. Similarly, residency and movement patterns of cownose rays in a southwest Florida estuary indicated no relationship between ray activity and tidal stage (Collins et al. 2007), contrasting with previous results from Chesapeake Bay (Smith & Merriner 1985, 1987). Collins et al. (2007) speculated that site-specific differences in foraging profitability may explain the differing drivers of movement observed between these two regions.

Abiotic factors triggering movement and changes in behaviour may also differ over smaller spatial scales. Carlisle and Starr (2010) reported that distribution and movement of leopard sharks within an estuarine system on the coast of California were strongly influenced by the tides, but that the pattern of movement depended on what section of the site sharks were using. In the main channel sharks were observed to move with the tide, maximising their foraging area over a more dispersed prey field, while in the adjacent Elkhorn Slough National Estuarine Research Reserve sharks swam against tidal currents, most likely in an effort to remain close to intertidal mudflats where prey resources were abundant. Similarly, Rechisky and Wetherbee (2003) examined the short-term movements of young sandbar sharks within a nursery ground in Delaware Bay and found movement patterns of sharks to differ between sections of the same bay. On the shallow shelf of western Delaware Bay shark movements were tidally-based while movements on the deeper eastern side of the bay were independent from tidal currents. Studies on spatial ecology of elasmobranchs must consider differences in species response to environmental drivers over both broad and small spatial scales and ensure that all habitat types are represented within a sample to provide sufficient resolution of species behaviour.

2.4 The Role of Environmental Change on Spatial Ecology

A wide range of abiotic factors are expected to fluctuate within the next century as a result of climate change. Current estimates by the Intergovernmental Panel on Climate Change (IPCC) predict a 1 to 6°C rise in average sea surface temperature (SST) by 2100 (IPCC 2007). In addition, projected increases in both the frequency and intensity of tropical storms and associated high rainfall events (Emanuel 2005, Webster et al. 2005) will most likely result in acute fluctuations in barometric pressure and salinity levels. Atmospheric carbon dioxide levels are expected to exceed 500 parts per million by the end of this century, dramatically altering the pH of oceans due to ocean acidification (Hoegh-Guldberg et al. 2007). Given that many of the abiotic factors predicted to fluctuate under future climate change scenarios have been shown to trigger movement and changes in behaviour and habitat use of sharks and rays, it is important to consider their responses to future changes in their environment.

A recent integrated risk assessment looking at the vulnerability of sharks and rays on Australia‟s Great Barrier Reef (GBR) to climate change found that vulnerability was driven by case-specific interactions of multiple factors (e.g. water temperature, ocean acidification) and species attributes (e.g. habitat specificity, mobility) (Chin et al. 2010). Based on this, the authors concluded that freshwater/estuarine and reef-associated sharks and rays are particularly vulnerable to climate change impacts since key habitats for these species are affected by an array of anthropogenic and environmental impacts, thus reducing the overall resilience of these species. Although there is an argument to be made that changing conditions may benefit species by making some habitats available that previously were not, movement to alternative locations may not be possible or desirable for many species. For freshwater/estuarine and reef-associated sharks and rays, the risks of moving to find new, suitable habitat (e.g. increased chance of predation, inability to find new suitable habitat) must be weighed against the energetic costs of remaining in an altered environment. Individuals that choose to remain in these habitats may exist in a stressed state, forced to allocate energy to physiological processes such as osmoregulation that could be put towards growth and/or reproduction, resulting in a loss to overall fitness or, at worst, mortality. Furthermore, although laboratory studies have demonstrated that some elasmobranch species are able to acclimate to higher than average temperatures, adaptation to extreme environmental fluctuations remains poorly studied.

Temperature and salinity are the two abiotic factors predicted to have the greatest effects on sharks and rays under current climate change projections (Chin et al. 2010). Given that many species have been shown to behaviourally regulate these two factors, fluctuations in either may cause alteration of movement, changing the way species interact with and utilise habitat, or departure from affected areas should conditions become intolerable. If adverse conditions persist they could induce permanent range contractions or shifts as individuals attempt to locate and/or remain in suitable habitat (Last et al. 2011, Hazen et al. 2013). Range contractions could negatively affect populations by making them more susceptible to localised depletion (i.e. fishing impacts) or mortality due to site-specific degradation and loss of habitat. Range shifts have already been observed for many temperate marine fishes (Holbrook et al. 1997, Perry et al. 2005, Munday et al. 2007) and some sharks (Last et al. 2011, Hazen et al. 2013) in response to higher than average ocean temperatures. Hazen et al. (2013) predicted substantial northward displacement of a range of predators under current climate change scenarios, with an up to 35% change in core habitat for some species. The authors concluded that the shark guild showed the greatest risk of pelagic habitat loss. Ultimately, selection of preferred environmental conditions via movement may dictate the distribution of not just individuals, but populations and could significantly alter entire ecosystems and their associated marine communities.

2.5 Conclusion and Future Work

This review has shown that many shark and ray species actively select for or exploit specific environmental conditions, often forgoing their home range areas to access a spatially variable resource. Movement to seek out and/or remain within preferred environmental conditions highlights the important role abiotic factors play in the spatial ecology of many marine predators. However, abiotic factors rarely act in isolation and behavioural responses may differ between species, sex, ontogenetic stage, season and geographic location. Movement of sharks and rays is most likely driven by a suite of factors – both abiotic and biotic – with habitat selection by individuals representing a compromise between the need to optimize metabolic/physiological function and maintain access to valuable resources (e.g. food, shelter from predators). Recent studies looking at aggregation behaviour in female leopard sharks, for example, have shown drivers of movement to be complex and influenced by preferred environmental conditions (i.e. low wave intensity, warm water temperatures) as well as proximity to key foraging grounds (Nosal et al. 2013, Nosal et al. 2014). Future research should consider both abiotic and biotic factors and their potential roles in shaping movement behaviour.

Resolution of the specific role abiotic factors play in shark and ray movement, behaviour and habitat use may be improved through long-term monitoring studies examining movement at multiple scales and through laboratory research. A long-term acoustic monitoring study on the ray community in Shark Bay, Western Australia, found that previously observed differences in seasonal abundance of rays was most likely due to seasonal changes in habitat use rather than large-scale migrations as was previously thought (Vaudo & Heithaus 2009, 2012). The authors were able to compare movement patterns of tracked individuals to abundance data and speculated that observed decreases in ray density during winter may be due to more time spent in deep water habitats rather than emigration from the bay. Laboratory studies can help clarify response to abiotic factors by separating out and testing individual factors while controlling for others. For example, results from controlled experiments that display species actively seeking out a preferred temperature range (Casterlin & Reynolds 1979, Wallman & Bennett 2006) or improving digestive efficiency through post-feeding thermotaxis (Di Santo & Bennett 2011) serve to provide support for behavioural thermoregulation.

Past studies on elasmobranch response to environmental change have focused primarily on coastal species and are heavily biased to sharks. Reasons for this are multifold, but typically include economic constraints, the highly variable nature of coastal systems and ease-of-access to nearshore shark species. As such, the current body of literature concerning the effects of abiotic factors on movement, behaviour and habitat use of elasmobranchs is not necessarily reflective of all species traits or habitat types. Information on response to abiotic factors for sharks resident on coral reefs, for example, remains relatively unknown despite their identification as some of the species most at risk from climate change effects (Heupel & Simpfendorfer 2014). Future studies examining the role of environmental drivers on elasmobranch spatial ecology should include species from a broad range of habitats to gain a better understanding of the importance of these variables across this diverse family.

Chapter 3: Long-term Patterns in Movement, Residency and Space Use of Reef Sharks on Inshore Reefs

3.1 Introduction

The link between movement and population dynamics is complex and manifests at least on a small-scale through behavioural decisions that affect reproduction and survival (Börger et al. 2008, Morales et al. 2010). Movement patterns can reveal sex- (Wearmouth & Sims 2008) and/or ontogenetic-based (Dahlgren & Eggleston 2000, Gibson et al. 2002, Pittman & McAlpine 2003) differences within a sample population that inform on individual life-history strategies (e.g. mating tactics, predator avoidance). In addition, analysis of site fidelity and home range estimation can identify important habitats through the continued or repetitive use of specific areas by individuals restricting their movements to a region much smaller than that which they are capable of using (Powell 2000, Kernohan et al. 2001). Underpinning movement theory is the idea that the costs of establishing and maintaining a home range in terms of overall fitness should not exceed the lifetime benefits (Switzer 1993, Powell 2000) related to reproductive success (e.g. mate encounter rates, offspring care) and/or survival (e.g. food availability, predation risk). However, movement patterns (e.g. home range size, location and shape) are the result of dynamic and often synergistic processes between individual characteristics and the external environment, and as such are subject to change (Switzer 1993). Examining how individuals of different sexes and life-history stages move and occupy space within a range of unique habitats is critical to understanding the biology and ecology of the species as a whole.

Highly mobile marine species such as sharks exhibit complex movement patterns across a wide range of spatial and temporal scales. These patterns can range from small daily movements with the tide to access preferred prey (Campos et al. 2009, Carlisle & Starr 2010) to yearly seasonal migrations (Heithaus et al. 2007, Barnett et al. 2011) spanning hundreds of kilometres. Many species have been shown to exhibit some degree of residency, site fidelity or philopatry over their lifetime (Chapman et al. 2015), as well as changes in behaviour and habitat use associated with ontogeny (Whitty et al.

2009, Grubbs 2010, Knip et al. 2011a) and sex (Sims 2005, Wearmouth & Sims 2008, Wearmouth & Sims 2010). Preferential use of shallow-water habitats by juveniles, for example, has been attributed to predator avoidance strategies (Wetherbee et al. 2007, Whitty et al. 2009, Knip et al. 2011a, Simpfendorfer et al. 2011, Stump et al. 2017), growth optimization (Whitty et al. 2009, Poulakis et al. 2011), foraging tactics (Ebert & Ebert 2005, Whitty et al. 2009, Knip et al. 2011a) and to avoid intraspecific competition (Knip et al. 2011a). Sex-based differences in movement and space use among adults may result from competitive exclusion or reflect a reproductive strategy to improve mate-encounter rates (Heupel & Simpfendorfer 2014), conserve energy during the mating season (Sims et al. 2001), increase somatic growth rates/decrease time to reproductive maturity (Klimley 1987) or utilize preferred habitats during parturition (Feldheim et al. 2002, Ebert & Ebert 2005, DiBattista et al. 2008). Movement and habitat use of sharks are also known to vary between sites with different environmental, geographic and hydrodynamic properties (Schlaff et al. 2014).

Inshore habitats are complex heterogeneous environments ranging from soft-sediment, estuarine and seagrass habitats to highly structured fringing reef systems, which greatly influences observed movement patterns in shark species that inhabit them. To date, most studies examining the spatial ecology of reef sharks have focused primarily on offshore reefs (Heupel & Simpfendorfer 2014, Espinoza et al. 2015) and atolls (Pikitch et al. 2005, Papastamatiou et al. 2010, Field et al. 2011, Bond et al. 2012, Tickler et al. 2017), with little information available on the movement and space use of sharks occupying reef habitats closer to shore (but see Chin et al. 2016). Cross-shelf differences in physical (e.g. currents/upwelling) and biological (e.g. benthos/fish assemblages; Williams & Hatcher 1983, Wismer et al. 2009, Malcolm et al. 2010) properties of reefs may result in regional variations in richness/diversity of prey species, trophic structures and ecosystem processes for resident sharks. In addition, the isolated and often patchy nature of atolls and offshore reefs, respectively, along with documented high site-attachment of reef sharks to coral reef habitat (Barnett et al. 2012, Bond et al. 2012, Heupel & Simpfendorfer 2015), may mean that these species have different movement potential compared to those utilising inshore reef systems where habitat is less fragmented and adjacent to a continuous coastline (Heupel & Simpfendorfer 2014). Residency and movement patterns of grey reef sharks, *Carcharhinus amblyrhynchos*, for example, have been observed to differ between reefs with different degrees of isolation; in near continuous reef habitat on the northern Great Barrier Reef (GBR), Australia, sharks exhibited low residency and large-scale movement between reefs (Heupel et al. 2010), while on comparatively more isolated offshore reefs further south (Heupel & Simpfendorfer 2014, Espinoza et al. 2015) and elsewhere (Field et al. 2011, Barnett et al. 2012) sharks were observed to be highly resident and displayed limited inter-reef movement.

Differences in movement and degree of site fidelity may reflect site-specific differences in habitat quality and resource availability (Papastamatiou et al. 2011, Espinoza et al. 2015), indicate level of exposure to predation risk or tolerance to environmental changes (Heupel & Simpfendorfer 2014). Studies have shown that, for reef sharks, both the presence (Chin et al. 2012) and quality of coral reef habitat is important, with shark abundance positively correlated to the amount of coral cover (Espinoza et al. 2014). However, regional declines in coral cover (De‟ath et al. 2012) along with deteriorating water quality associated with increasing coastal development (McCulloch et al. 2003, Lotze et al. 2006, Wooldridge et al. 2006) could result in some inshore shark species avoiding degraded habitats. Proximity to shore also means that sharks utilising inshore reef habitats are more accessible to recreational and commercial fishers where they are caught as targeted species or, more commonly, as bycatch (Gribble et al. 2005, Chin et al. 2012). Overfishing, including localised depletion of shark species, and habitat degradation within fished areas have been linked to ecosystem-wide changes (Blaber et al. 2000, Kaiser et al. 2000, Stevens et al. 2000, Sandin et al. 2008). Collectively, environmental and anthropogenic effects on inshore reef systems may result in very different movement and space use patterns for resident sharks compared to their counterparts offshore.

The purpose of this research was to investigate the movement patterns and space use of reef sharks within an inshore reef environment. We examined residency, space use and depth use patterns of the blacktip reef shark, *Carcharhinus melanopterus*, on an inshore reef in order to determine how a species common to offshore reefs and atolls, moves and occupies space when utilising inshore reef systems. Movement metrics were analysed across time and included sex and size effects to determine if biological factors significantly influence movement and space use of sharks. Results from this study were compared to those conducted on the same or similar species within offshore reef environments to put movement of *C. melanopterus* on inshore reefs into a wider context. Examining how resident sharks utilise space within inshore reef systems will improve our knowledge of reef shark spatial ecology and help to clarify the importance of inshore reef habitats for these species (Osgood & Baum 2015).

3.2 Materials and Methods

3.2.1 *Study Site*

Orpheus Island (18.37°S, 146.30°E) is a tropical island located approximately 16 km off the northeast coast of Queensland, Australia, within inshore waters of the Great Barrier Reef Marine Park (**Figure 3.1**). Part of the larger Palm Island Group, Orpheus Island is 12 km long and 1-2.5 km wide and separated from the nearest island to the south (Fantome) by a shallow (~8 m) sand flat and to the north (Pelorus) by a deeper (~18 m) sandy channel (**Figure 3.1**a, b). Several bays located around the island are characterised by shallow sand and/or coral rubble reef flats with most containing sections of non-estuarine mangrove habitat (mostly *Rhizophora* spp.). Average depth in the bays is less than 5 m and maximum tidal range reaches 4 m with some bays becoming completely dry at lowest tide levels. The island is surrounded by a fringing reef system with depths ranging from 8-20 m.

3.2.2 *Study Species*

The blacktip reef shark, *C. melanopterus* (Quoy & Gaimard 1824-25), is a medium-sized shark common to shallow sand flats and coral reefs throughout the Indo-West and Central Pacific, including tropical waters around Australia from Shark Bay (Western Australia) northeast to Moreton Bay (Queensland) (Last & Stevens 2009). It is the third most commonly encountered shark in the GBR reef line fishery (Heupel et al. 2009) and the most common reef shark caught in the commercial net fishery operating within inshore waters of the GBR (Chin et al. 2012). High site-attachment is reported for *C. melanopterus* on atolls (Stevens 1984, Papastamatiou et al. 2009a, Papastamatiou et al. 2009b), remote high islands (Mourier & Planes 2012) and in several coastal bays (Speed et al. 2011, Chin et al. 2013c)

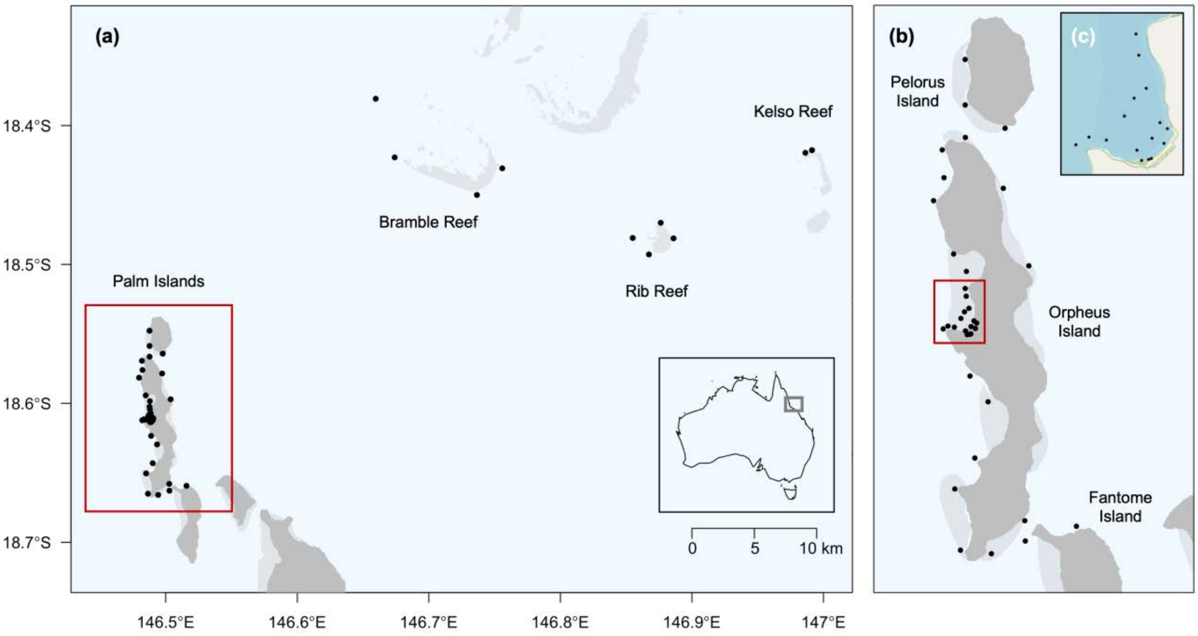

Figure 3.1: Study site: Palm Islands, Queensland, Australia. (a-b) Location of acoustic receivers (*circles*) around offshore reefs and Pelorus, Orpheus and Fantome islands (country map *inset*). (c) Close-up of Pioneer Bay.

with localised movement and comparatively small home ranges observed across various habitat types and life history stages (Stevens 1984, Papastamatiou et al. 2011, Speed et al. 2011, Chin et al. 2013c). Males reach sexual maturity at ~ 1000 mm, females between 1100 – 1335 mm (reviewed in Mourier et al. 2013), with mating and parturition reported to occur locally between November and March (Lyle 1987, Chin et al. 2013b, Chin et al. 2013c).

3.2.3 *Field Methods*

Passive acoustic telemetry was used to examine the movement and space use of *C. melanopterus* within reef habitats at Orpheus Island. Thirty-six VR2W acoustic receivers (Vemco Ltd, Canada) deployed around the study site in August 2010 as part of the Integrated Marine Observing System were used to monitor the movement of tagged individuals (**Figure 3.1**). Most receivers were distributed around Orpheus Island, however some were deployed at Pelorus (n = 3) and Fantome (n = 2) islands to track movements of individuals between islands. Receivers were fastened to a nylon rope with a float and anchored 2-3 m above the seabed using stainless steel chain shackled to a coral head. In areas without reef substrate, receivers were attached to star pickets embedded into the sea floor (n = 12). To track movement of sharks to and from shallow-water sand/mangrove habitats and the adjacent fringing reef, several receivers were placed within Pioneer Bay, a 400 m-wide intertidal reef flat located on the western side of Orpheus Island (**Figure 3.1**c). Intertidal receivers were partially buried in the substrate with the hydrophone approximately 10 cm above the surface in order to maximise possible detection time. We assumed that once the receiver hydrophone was out of the water, the habitat was too shallow for sharks to access and thus did not bias the estimation of time spent in intertidal areas. Within Pioneer Bay, receivers located closest to shore (n = 5) and mid-bay (n = 3) became completely exposed during low tides (tidal heights ≤ 160 cm and 140 cm, respectively, relative to the lowest astronomical tide). Detection range of receivers within the bay was ~125 m (Welsh et al. 2012), with detection range likely greater in deeper habitats along the adjacent reef. Acoustic receivers were downloaded twice per year. A separate study run concurrently to this one, deployed receivers at Bramble (18.24°S, 146.42°E), Rib (18.29°S, 146.52°E) and Kelso (18.26°S, 147.00°E) reefs, located approximately 29 km, 43 km and 57 km north-east of Orpheus Island (**Figure 3.1**a), respectively, with data made available for analysis.

Individuals were captured on multi-hook long-lines or rod and reel. Long-lines consisted of a 500 m mainline (8 mm nylon rope) with gangions (1 m of 5 mm nylon cord with 1 m wire trace and size 14 Mustad tuna circle hooks) attached at 8-10 m intervals. Lines were baited with either butterfly bream (*Nemipterus* spp.) or squid (*Loligo* spp.), anchored at both ends and left to soak for 1 hour. Individuals collected using rod and reel were caught using 8/0 Mustad hooks baited with squid or pilchard (*Sardinops* spp.). Sharks were measured to the nearest millimetre, sexed and tagged with a rototag in the first dorsal fin for external identification. V13-1L (13 mm x 36 mm), V13P-1H (13 mm x 48 mm) or V16-4H (16 mm x 68 mm) acoustic transmitters (Vemco Ltd., Canada) were surgically implanted into the body cavity of sharks via a 3-4 cm incision and the wound closed using dissolvable surgical sutures in the muscle and skin layers. Prior to internal fitting, transmitters were coated with a 70:30 mixture of paraffin and beeswax to prevent transmitter rejection (Heupel & Hueter 2001).

Sharks were retained for approximately 10 minutes during measuring and tagging procedures. All surgical procedures were conducted according to protocols approved by James Cook University‟s Animal Ethics committee (permit A1566) and under research permits from the Great Barrier Reef Marine Park Authority (G10/33754.1 and G10/33240.1).

Acoustic transmitters pulsed at 69 kHz on a pseudo-random repeat rate of 50-130 (V13-1L), 120-200 (V13P-1H) and 45-75 (V16-4H) seconds and had an estimated battery life of 881, 364 and 858 days, respectively. Each transmitter emitted a unique ID code specific to the individual tagged. V13P-1H acoustic transmitters also recorded depth information up to a maximum depth of 50 m and accurate to ± 2.5 m, although the accuracy of tags has been shown to be greater *in situ* (± 0.64; Matley et al. 2015).

3.2.4 *Data Analysis*

Data from acoustic receivers were used to investigate movement patterns and space use of *C. melanopterus*. Sharks had to be detected within the array for ≥ 30 days to be included in analysis. Single detections per day were classified as possible false detections and were removed before further analysis. All analyses were conducted in the R environment (R).

3.2.4.1 Residency

Residency of sharks was examined via calculation of a Residency Index which was defined by first assembling a presence history (i.e. days for which an individual was detected at least twice within the array). Presence histories were then used to calculate the ratio of days detected within the acoustic array to days at liberty, assigning each individual a value between 0-1 for low to high residency, respectively. „Days at liberty‟ (i.e. total detection days possible) was defined as either the maximum transmitter life or, for tags that were still active after the study period, the number of days from tag deployment to the final download date (20 January 2014). A „Roaming Index‟ was calculated as a proxy for movement within the array and represented the ratio of receivers where an individual was detected to the total number of receivers within the array (Udyawer et al. 2015). Roaming Index values ranged from 0 (no detections) to 1 (detected on all receivers). Residency and roaming indices were tested for normality and transformed if required then analysed using generalised additive mixed models (GAMMs) to determine if there were any effects of sex and size across all tagged individuals. GAMMs were conducted using the *mgcv* package in R (Wood 2004) with individuals (animal „ID" code) included as random effects within models.

3.2.4.2 Space Use Estimates

Space use metrics for tagged individuals were estimated using fixed kernel utilisation distributions (KUDs) calculated from short-term centres of activity positions (COA). COA estimates were calculated for each individual using a customised R script (Simpfendorfer et al. 2002) and represented the mean position of each shark over a 30-minute time step weighted by the number of detections at each receiver. COA positions were calculated prior to estimating KUDs to account for the inherent spatio-temporal autocorrelation within the data structure, and account for varying transmission settings among different models of acoustic transmitters used in the study (Udyawer et al. 2018). The *adehabitatHR* package in R (Calenge 2006) was used to calculate monthly space use using 50 and 95% KUDs. Areas of core use (50% KUD) and extent of space use (95% KUD) were examined over monthly intervals to investigate changes in movement patterns and space use over time. Months with ≤ 30 unique locations for an individual were excluded from subsequent analyses for that individual to prevent inaccurate estimates of space use. It is important to note that COA estimates assume a homogenous detection probability and could not be determined when individuals utilised habitats outside of the listening range of the receiver array, making it possible that calculated metrics underestimated true space used by individuals.

The proportion of overlap in 50 and 95% KUDs between consecutive months was used to quantify if individuals consistently reused space over the full tagging period or exploited new areas (Heupel & Simpfendorfer 2015). Using the *adehabitatHR* package in R, overlap was calculated as a proportion of the previous month"s value to quantify the area of core and extent of space used from month-to-month. To determine whether individuals were utilising new areas, monthly cumulative 50 and 95% KUDs were calculated by adding each new month"s position data to that of the previous month and recalculating the KUD. The difference in KUD size between consecutive months was calculated as a function of the previous month"s value, enabling comparisons of monthly cumulative KUDs between individuals and indicating periods of expanded movement to include previously unused areas.

Linear mixed effects models (LMM) were used to analyse all space use metrics (50 and 95% KUDs, KUD overlap and cumulative KUD) for sex, size and temporal (month) effects using the *lme4* package in R (Bates et al. 2015). Individual (animal „ID" code) was incorporated as a random factor within models to account for the repeated-measures nature of the data (Bolker et al. 2009). Prior to running analyses, 50 and 95% KUD data were checked for normality and log-transformed if required; as KUD overlap and cumulative KUD were proportional data, an arcsine-transformation was used (Heupel & Simpfendorfer 2015). Variance inflation factors were calculated using the R package *car* (Fox & Weisberg 2011) to test models for multicollinearity. Graphs were produced using the „Animal Tracking Toolbox" within the *VTrack* package (Udyawer et al. 2018). The „dredge" function in the *MuMIn* package in R (Barton 2013) was used to generate a series of candidate additive models for 50 and 95% KUDs that represented every possible combination of fixed (size, sex and month) and random (individual) factors (global model: ~ month × sex + length + [1|ID]). Candidate models were compared to each other and ranked using Akaike"s information criterion corrected for small sample bias (AICc) with models with the lowest AICc value considered to best explain observed effects on space use. Maximum likelihood ratio tests were used to test for significant differences ($\alpha = 0.05$) between candidate models and the null model.

3.2.4.3 Depth Analysis

A subset of twenty *C. melanopterus* fitted with transmitters containing depth sensors were used to examine depth use by individuals at Orpheus Island. Patterns in depth use of sharks were investigated at monthly and hourly intervals, between sexes and with size in order to determine if there were any temporal or biological effects on depth use. Seasonal patterns in mean monthly depth data, and diel patterns in the hourly depth data, from the twenty individuals were assessed using a GAMM with individual (animal ID) included as random effects. An AR1 correlation structure was utilised with the corCAR1 function in the „nlme" package (Pinheiro et al. 2019) to account for autocorrelation in the seasonal and diel depth data (Pedersen et al. 2019).

3.3 Results

Fifty-nine *C. melanopterus* were tagged with acoustic transmitters at Orpheus Island between December 2010 and February 2013. Transmitters were fitted to 20 sharks tagged in December 2010 (14 female, 6 male), 23 sharks in December 2011 (10 female, 13 male), 2 in March 2012 (female), 8 in December 2012 (3 female, 5 male) and 6 in February 2013 (3 female, 3 male). Two individuals were never detected and another 17 were excluded from analyses due to limited data. Of the 40 individuals included in the final analyses (**Table 3.1**), detection periods ranged from 40-889 days with sharks tracked for an average of 424 days (± 47 SE). Individuals detected for less than the period of maximum transmitter life either departed the monitored area permanently, died outside of the array or experienced tag failure; the timing of detection loss was random and did not appear to be coordinated among individuals (**Figure 3.2**a). The sample population had a nearly even number of females (n = 21) and males (n = 19), 60% of which were sexually immature. Size of tagged individuals ranged from 510 mm STL (stretch total length) to 1452 mm STL which is close to the minimum and maximum size reported locally for this species (Chin et al. 2013b). Only small sharks (510-812 mm STL) were caught within Pioneer Bay and larger sharks (998-1452 mm STL) on the adjacent reef, with individuals measuring between these two size groups not encountered. Given that two distinct size classes utilising very different habitats were monitored during the study, individuals were further categorised as "small" (< 1000 mm STL) or "large" (> 1000 mm STL) in subsequent analyses; size classes corresponded to conservative estimates for size at maturity.

Table 3.1: Details of acoustically tagged blacktip reef sharks at Orpheus Island. ID code, individual; STL, stretch total length; Residency Index, ratio of days detected within the array to days at liberty; Roaming Index, proportion of receivers at which each individual was detected.

ID code	STL (mm)	Sex	Release date	Days at liberty	Days detected	Residency Index	Roaming Index
6523	685	F	10/12/2011	374	268	0.72	0.58
6525	570	M	10/12/2011	374	203	0.54	0.45
6526	510	M	10/12/2011	374	144	0.39	0.54
6527	1050	F	11/12/2011	374	367	0.98	0.12
6530	700	M	12/12/2011	374	347	0.93	0.42
6531	770	M	13/12/2011	374	369	0.99	0.64
6532	1070	F	13/12/2011	374	373	1.00	0.76
6533	1030	F	13/12/2011	374	369	0.99	0.34
6534	1070	F	13/12/2011	374	374	1.00	0.76
6535	750	M	13/12/2011	374	367	0.98	0.24
6539	1350	F*	13/12/2011	374	374	1.00	0.43
6540	1260	F*	14/12/2011	374	374	1.00	0.84
6541	1350	F*	24/03/2012	364	232	0.64	0.27
7950	584	F	20/12/2012	368	104	0.28	0.27
7955	812	M	22/12/2012	368	332	0.90	0.34
7956	588	F	22/12/2012	368	345	0.94	0.28
7957	559	M	26/12/2012	368	52	0.14	0.25
7958	593	M	13/02/2013	341	51	0.15	0.22
7959	610	M	13/02/2013	341	199	0.58	0.30
7962	559	M	16/02/2013	338	134	0.40	0.22
46999	1070	M*	13/12/2011	769	769	1.00	0.87
47000	1274	M*	12/12/2011	770	73	0.09	1.00
47001	1040	M*	11/12/2011	771	622	0.81	0.28
47003	1120	M*	13/12/2011	769	767	1.00	0.79
62310	615	F	7/12/2010	889	876	0.99	0.76
62311	675	F	7/12/2010	889	85	0.10	0.28
62315	620	M	7/12/2010	889	413	0.46	0.76
62316	580	F	23/3/2012	668	73	0.11	0.10
62318	765	M	7/12/2010	889	878	0.99	0.72
62319	1320	F*	8/12/2010	889	844	0.95	0.66
62320	1320	F*	8/12/2010	889	877	0.99	0.15
62321	1271	M*	8/12/2010	889	40	0.04	0.91
62322	1452	F*	8/12/2010	889	873	0.98	0.36
62323	1442	F*	8/12/2010	889	257	0.29	0.09
62324	1416	F*	8/12/2010	889	889	1.00	0.85
62326	758	F	9/12/2010	889	175	0.20	0.42
62327	1371	F*	9/12/2010	889	860	0.97	0.91
62329	1080	M*	9/12/2010	889	520	0.58	0.28
62332	998	F	9/12/2010	889	889	1.00	0.84
62333	1252	M*	9/12/2010	889	792	0.89	0.81

* Indicates mature individuals.

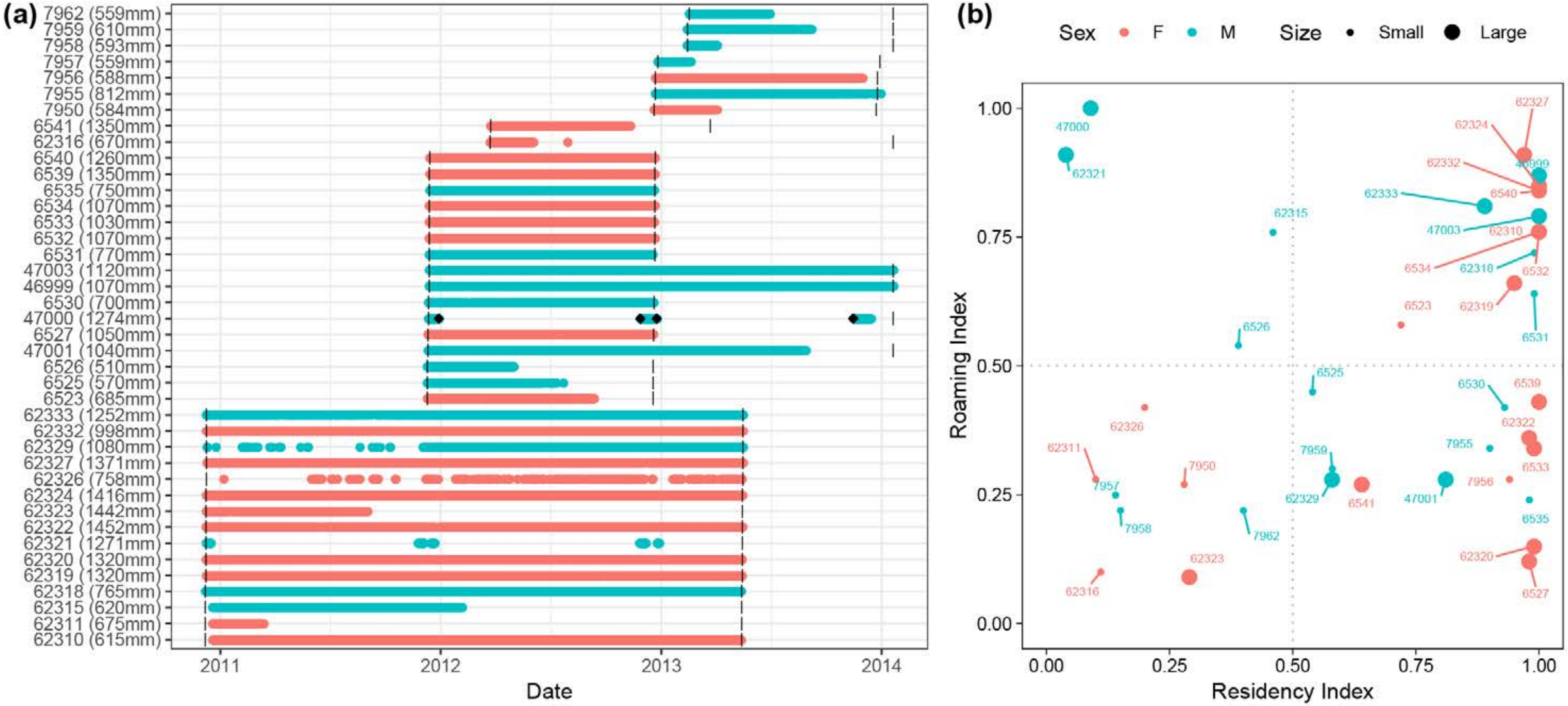

Figure 3.2: Presence plot and residency-roaming analysis of acoustically tagged blacktip reef sharks at Orpheus Island. (a) Presence plot of 40 blacktip reef sharks captured and released at Orpheus Island (females: *red*; males: *blue*) showing presence at the study site (*circles*) and offshore reefs (*black diamonds*) and *grey bars* indicating maximum transmitter life. (b) Residency-roaming analysis of small (<1000 mm STL) and large (>1000 mm STL) individuals, indicated by *small* and *large circles*, respectively, with values ranging from 0-1 for low to high residency/roaming.

3.3.1 *Residency*

Residency index results indicated strong site-attachment to reef habitats with over two thirds (n = 28) of individuals remaining at the study site (residency index > 0.5) for the majority of the monitoring period (**Table 3.1**; **Figure 3.2**). Over half of the sharks (n = 25) were detected ≥ 70% of the monitoring period and nineteen individuals never left the study site. Just under half (43%) of the sample population had a roaming index above 0.5 indicating that the majority of sharks used less than half of the monitored area (**Table 3.1**; **Figure 3.2**). There was an effect of size (STL) on roaming (p = 0.025), but not on residency (p = 0.059) and sex was not significant for either metric (residency: p = 0.540; roaming: p = 0.188). The general trend was for residency and roaming indices to increase with size. However, large females appeared to be more resident and roam less throughout the array than large males, while residency patterns among small sharks were generally similar with roaming indices of juvenile males only marginally higher than that of females.

Two adult males were absent from the array for most of the study, but returned around the same time each year (November/December) where they remained for approximately 1 month. During this time, one individual (ID: 47000, 1274 mm STL) was also detected at Kelso (30 December 2011), Bramble (24 December 2012) and Rib (27 November 2012, 16 November 2013) Reefs (**Figure 3.1**a) – a linear distance of 57, 29 and 43 km, respectively. Single-day detections on offshore reefs either immediately preceded or followed extended periods of stay at Orpheus Island, suggesting this individual was in transit to/from the study site. The second adult male (ID 62321, 1271 mm STL) was never detected outside of the array and its whereabouts for much of the monitoring period remain unknown. Between consecutive years, times of arrival and departure fell within 1-2 weeks of each other, indicating that movements were highly coordinated. Average duration of stay for the two males while at Orpheus was 29 days ± 1.5 SE each year.

3.3.2 *Space Use*

Size of animals (STL) was the biggest predictor of space use for sharks with both 50 and 95% KUDs observed to increase with size (50%: $p = 0.014$; 95%: $p < 0.001$; **Table 3.2**; **Figure 3.3**a, c), although the strength of this relationship differed between sexes with males likely driving the observed pattern. The extent of space use and core space used by large sharks were 48% (large: 1.12 km² ± 0.21 SE; small: 0.54 km² ± 0.05 SE) and 65% larger (large: 0.16 km² ± 0.03 SE; small: 0.11 km² ± 0.01 SE), respectively, than their smaller conspecifics. There was also an effect of month ($p = 0.030$) and the interaction of sex and month ($p = 0.024$) on 95% KUD indicating that males and females used space differently throughout the year (**Table 3.2**). This is supported by model selection results which showed best-fit models for 50% KUD incorporated size and sex, and for 95% KUD size, sex and month (**Table 3.3**). Maximum likelihood ratio tests showed best-fit models to be significantly better than the null model. The trend was for average monthly space used by males and females to be similar for much of the year before diverging in November and December when males used nearly twice as much space as females (**Figure 3.3**b, d).

Table 3.2: Factors affecting size of space used by blacktip reef sharks, proportional overlap and change in cumulative space use.

	Space Use		**Overlap**		**Cumulative**	
	50% KUD	**95% KUD**	**50% KUD**	**95% KUD**	**50% KUD**	**95% KUD**
Month	0.0685	**0.0304**	0.0585	0.0652	0.3690	0.0744
Sex	0.0786	0.1694	**0.0010**	**0.0107**	0.9765	0.2387
STL	**0.0136**	**<0.0001**	0.1008	0.4119	0.3020	0.6127
Month:sex	0.0843	**0.0237**	**0.0463**	0.3443	0.2252	0.1985

Global model: ~ month × sex + STL + [1|ID]); STL, stretch total length.

Significant values indicated by bold text.

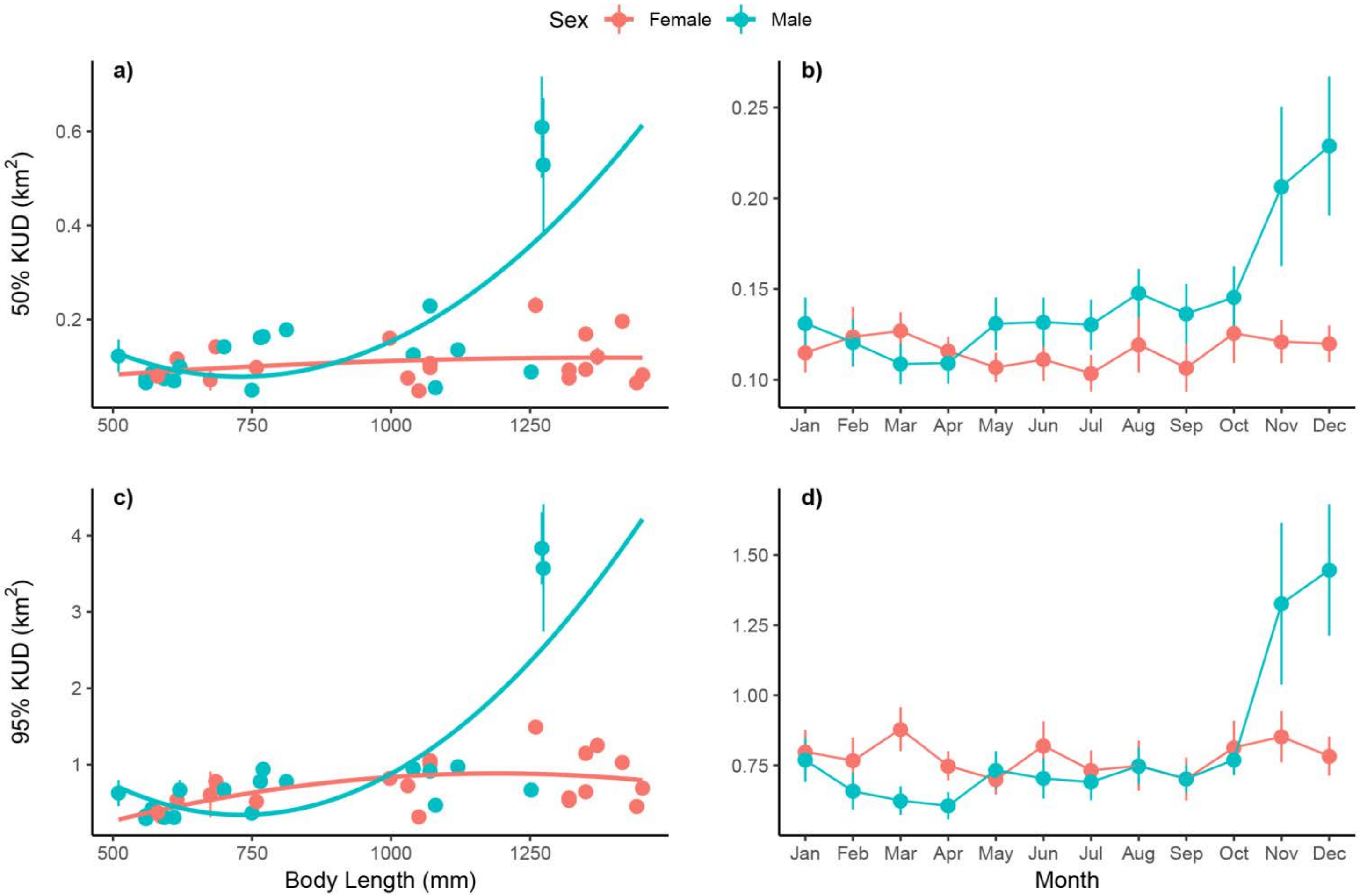

Figure 3.3: Biological and temporal effects on space use of acoustically tagged blacktip reef sharks at Orpheus Island. (a-b) Effects of size (STL [mm]) and month on core space use (50% KUD) of 40 blacktip reef sharks at Orpheus Island (females: *red*; males: *blue*). (c-d) Effects of size and month on extent of space use (95% KUD). Panels include mean and standard error.

Table 3.3: Top-ranked models showing factors affecting core (50% KUD) and extent (95% KUD) of space used by blacktip reef sharks.

Model rank	**Model**	***df***	**50% KUD AICc**	**50% KUD ΔAICc**	***w***
1	**log(as) ~STL+sex**	**5**	**371.03**	**0.00**	**0.30**
2	log(as) ~STL+sex+mon	16	371.05	0.02	0.29
3	log(as) ~STL+mon	15	372.81	1.78	0.12
4	log(as) ~STL	4	373.13	2.09	0.10
5	log(as) ~mon	14	374.51	3.48	0.05
6	log(as) ~	3	374.76	3.73	0.05
7	log(as) ~sex+mon	15	375.44	4.41	0.03
8	log(as) ~sex	4	375.44	4.41	0.03
9	log(as) ~STL+sex+mon+mon×sex	27	376.32	5.29	0.02
10	log(as) ~sex+mon+mon×sex	26	380.67	9.64	0.00

Model rank	**Model**	***df***	**95% KUD AICc**	**95% KUD ΔAICc**	***w***
1	**log(as) ~STL+sex+mon**	**16**	**373.72**	**0.00**	**0.44**
2	log(as) ~STL+sex+mon+mon×sex	27	374.60	0.89	0.28
3	log(as) ~STL+mon	15	374.66	0.94	0.27
4	log(as) ~STL+sex	5	385.13	11.42	0.00
5	log(as) ~STL	4	386.46	12.74	0.00
6	log(as) ~mon	14	388.27	14.55	0.00
7	log(as) ~sex+mon	15	390.37	16.65	0.00
8	log(as) ~sex+mon+mon×sex	26	391.34	17.63	<0.00
9	log(as) ~	3	399.42	25.70	<0.00
10	log(as) ~sex	4	401.40	27.69	<0.00

ΔAICc, Akaike difference; *w*, Akaike weight; STL, stretch total length; log(as), log-transformed space use metric; mon, month.

Best-fit model shown in bold.

Differences between sexes were observed in the amount of overlap in space use between consecutive months (50%: p = 0.001; 95%: p = 0.011; **Table 3.2**), indicating a difference between males and females in their level of fidelity to home ranges (**Figure 3.4**a, b). Female *C. melanopterus* consistently reused an average of 55-75% of core areas between consecutive months. However, a significant decline in the amount of overlap was observed in December when the mean level dropped to 45%. Similar to core space use patterns, mean overlap in female monthly 95% KUDs ranged from

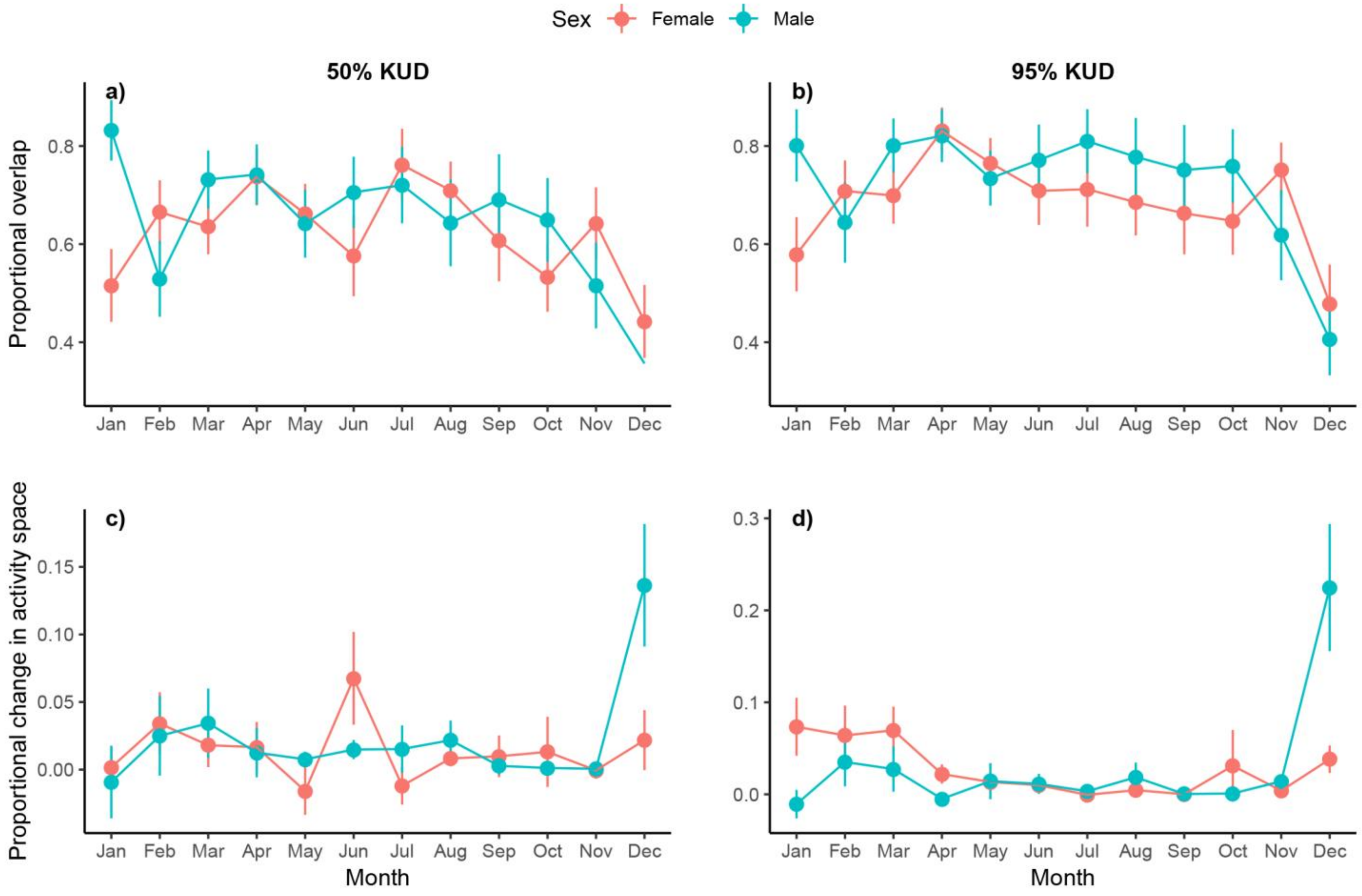

Figure 3.4: Monthly space use estimates for acoustically tagged blacktip reef sharks at Orpheus Island. (a-b) Proportional overlap of monthly 50 and 95% KUDs of 40 blacktip reef sharks at Orpheus Island (females: *red*; males: *blue*); high values of overlap indicate little change in the location of KUDs between consecutive months. (c-d) Proportional change in monthly cumulative 50 and 95% KUDs; high positive values indicate sharks are expanding their space use to include previously unused areas. Panels include mean and standard error.

60% to over 80% before declining to below 50% in December. Patterns of overlap for males also indicated a high reuse of areas throughout most of the year. Mean overlap of monthly 50% KUDs for males predominantly ranged from 55-85% and averaged over 75% for 95% KUDs, higher than that of females. After stabilizing at the beginning of the year, a sharp decline was observed from October to December for both metrics where mean overlap dropped to below 40%. Decreases in mean overlap observed for males and females at the end of the year suggest an increase in movement or change in behaviour during this period. The interaction term for 50% KUDs was also significant ($p = 0.046$), perhaps reflecting the divergence in January when overlap in core space use of males was over 30% higher than that of females.

No significant differences were observed in the change in monthly cumulative 50 and 95% KUDs between sexes or with size (**Table 3.2**). The general trend was for size of space used by males and females to remain relatively constant throughout most of the year with less than 5% change observed between consecutive months (**Figure 3.4**c, d). Core and extent of space use by females was marginally higher than males in June and from January to March, respectively; males showed little change throughout the year followed by a sharp increase from November to December. Increases in monthly cumulative space used by males indicate periods of expansion into previously unused areas and corroborate observed decreases in the amount of overlap and increases in the size of space used by individuals during this period.

3.3.3 *Depth Use*

A total of 20 individuals were fitted with acoustic depth tags: 7 adults (all females) and 13 juveniles (3 females, 10 males). Examination of depth use across the year revealed differences between sexes and with size (**Figure 3.5**a, c). Monthly depth use averaged across all large females ranged from 3.1-5.2 m (individual means: 1-8.5 m), in contrast to smaller females which mostly remained within 1 m of the surface (mean: 0.1-0.8 m). Deepest mean depths used by large females occurred between August and November followed by a move into shallower water in December. An examination of differences in depth use between large and small males was not possible since no

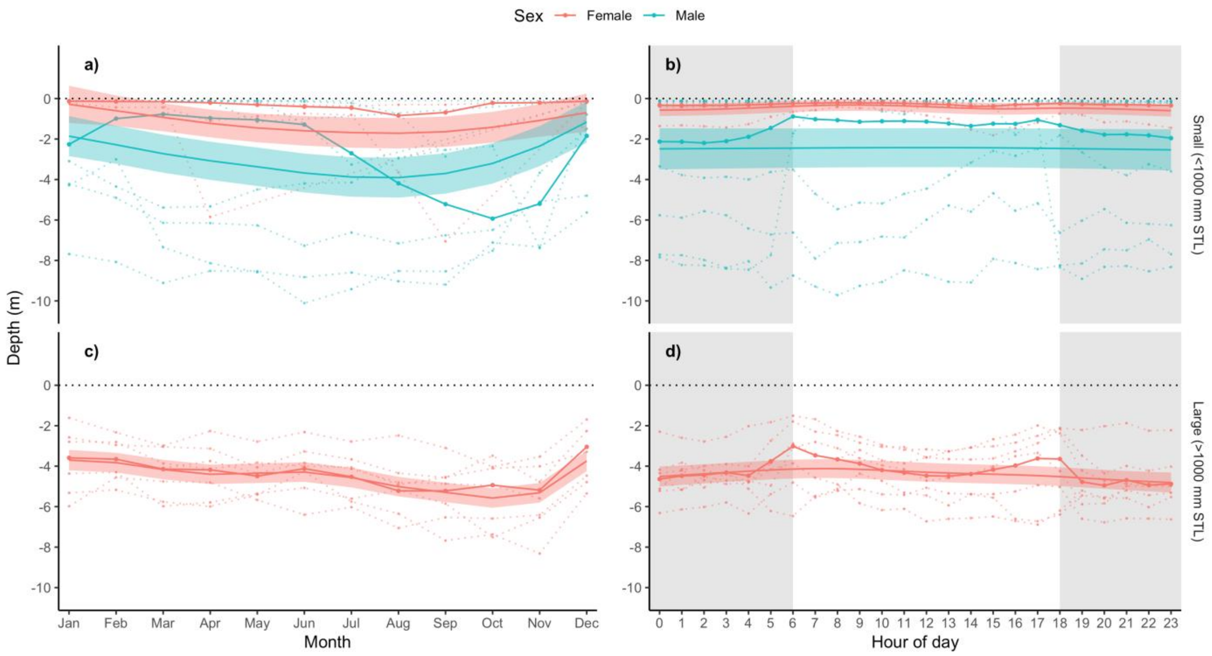

Figure 3.5: Monthly and diel depth use of acoustically tagged blacktip reef sharks at Orpheus Island. (a-b) Monthly and diel depth use of small (<1000 mm STL) blacktip reef sharks at Orpheus Island (females: *red*; males: *blue*). (c-d) Monthly and diel depth use of large (>1000 mm STL) individuals. Broken lines represent depth use patterns of each individual, with solid lines and points representing mean monthly and hourly depths across all individuals. Trendlines and polygons represent GAMM model predictions with 95% Confidence Interval bounds.

males > 1000 mm STL were fitted with depth sensor tags during the study. Variability in seasonal depth use was larger in small males than females (**Figure 3.5**a), with some small males consistently using deeper waters throughout the year. Small males that did use shallower waters in the first half of the year, displayed a shift to deeper waters in September and October, increasing the mean depth use during this period of the year.

Diel depth use of most large females followed a crepuscular pattern with the shallowest mean depths across all individuals (3-3.5 m) observed at dawn and dusk and deepest mean depths (5 m) at night (**Figure 3.5**d). In contrast, averaged depth use across all small females showed that they remained within a half metre of the surface throughout the day (**Figure 3.5**b). Patterns of mean hourly depth use by small males mimicked that of large females, although there was greater variability between individuals; crepuscular depths averaged across all males were approximately 1 m while the deepest mean depths were just over 2 m.

3.4 Discussion

Results from this study revealed distinct sex- and size-based patterns in how *C. melanopterus* move and occupy space on inshore reefs. Sharks exhibited a seasonal pattern in movement and space use that differed between males and females; during the reproductive season males moved more, occupying more space and exploring new areas within the array while females utilised the same amount of space throughout the year, but shifted the location of their core and home ranges during this period. In addition, the highly coordinated, annual migration of two adult males to the study site corresponding with the onset of mating season indicated long-term, seasonal site fidelity likely related to reproduction and provided evidence of connectivity with offshore reefs. Movement patterns by males may represent mate-searching behaviour while females may be driven more by habitat selection, re-locating during the reproductive season to areas favourable for gestation or parturition. Size effects were also observed with some smaller sharks, particularly females, using less space and shallower depths than adults, most likely a product of refuge behaviour by juveniles utilising protective shallow-water mangrove and sand flat habitats within the study site. Results from this study support previous research conducted on atolls, remote islands and within separate coastal bays showing *C. melanopterus* to be strongly site-attached to coral reefs, indicating that this is most likely a universal species trait and thus highlighting the importance of inshore reef habitats.

3.4.1 *Residency and Long-Distance Movement*

To date, most studies examining movement and space use of reef sharks have been conducted on offshore reefs, remote islands or atolls with high site fidelity and restricted space use a common trait observed for many species including the lemon shark, *Negaprion brevirostris* (Gruber et al. 1988, DeAngelis et al. 2008, Chapman et al. 2009), Caribbean reef shark, *Carcharhinus perezi* (Garla et al. 2006, Bond et al. 2012), whitetip reef shark, *Triaenodon obesus* (Barnett et al. 2012) and *C.*

amblyrhynchos (Field et al. 2011, Barnett et al. 2012, Espinoza et al. 2015, Heupel & Simpfendorfer 2015). Similarly, results from the current study showed *C. melanopterus* to be strongly site-attached to reef habitats inshore, supporting previous research conducted on this species in remote reef (Papastamatiou et al. 2009b, Papastamatiou et al. 2010, Papastamatiou et al. 2011, Mourier & Planes 2012) and coastal environments (Speed et al. 2011, Chin et al. 2013c). High residency and low roaming values at Orpheus Island remained relatively constant throughout most of the study period indicating limited movement and high reuse of inshore reef areas across the sample population. Results reflect the importance of reef habitats to these species with likely benefits to survival and reproductive success in the form of increases in food availability and mate encounter rates, as well as lowered risk of predation (Switzer 1993, Powell 2000).

While overall residencies were high, larger sharks appeared to be more site-attached. Similarly, juvenile *C. melanopterus* in separate coastal bays were observed to be less resident than adult females (Chin et al. 2013c, Chin et al. 2016, Speed et al. 2016). Outwardly this seems counter-intuitive given that studies on similar species such as *N. brevirostris* (Gruber et al. 1988, Wetherbee et al. 2007, Wiley & Simpfendorfer 2007, Chapman et al. 2009), *C. perezi* (Garla et al. 2006) and *C. amblyrhynchos* (Heupel et al. 2010) have documented higher site-attachment among juveniles, presumably due to the benefits acquired by remaining within area-restricted nursery habitats (e.g. lower predation risk, higher prey availability). As days at liberty were calculated using maximum transmitter life and not the date of last detection, individuals that died early on in the study would appear less resident. It is therefore possible that the lower residency values observed for smaller sharks were, in fact, an artefact of the high mortality rate documented for juveniles of many shark species (Gruber et al. 2001, Heupel & Simpfendorfer 2002). Alternatively, low residency rates may simply reflect the real departure of juvenile sharks from the monitored area.

Several studies have documented an absence of *C. melanopterus* of intermediate size (population modes at 500, 1100 mm: Papastamatiou et al. 2009a, 950-1050 mm: Chin et al. 2013b, 850-1050 mm: Chin et al. 2013c, 750-850 mm: Mourier et al. 2013), suggesting this may indicate periods of fast growth (Mourier et al. 2013), reflect gear selectivity (Papastamatiou et al. 2009a) or represent an ontogenetic change in habitat use to areas outside of these study sites (Chin et al. 2013c, Mourier et al. 2013). As methods used to capture juveniles within Pioneer Bay were also employed on the adjacent reef, it is unlikely that gear selectivity influenced observed size distributions at Orpheus. Chin et al. (2013c) speculated that juvenile *C. melanopterus* may depart nursery habitats as subadults just prior to the onset of sexual maturity (Chin et al. 2013a), possibly as a means to meet changing energetic requirements, reduce intraspecific competition and/or promote genetic mixing (Chin et al. 2016). Similarly, subadult *C. melanopterus* in Moorea were observed to become more mobile upon leaving nursery habitats (Mourier & Planes 2012). As the size range of individuals absent in the current study (~800-1000 mm) approached the minimum size at maturity reported for this species, it is possible that low residency rates among tagged juveniles represent an ontogenetic shift in habitat use to areas outside of the array. However, given that juveniles resident for less than half of the monitoring period were smaller (mean: 600 mm ± 22 SE; range: 510-758 mm STL) than that of the missing size class at Orpheus and size at reproductive maturity for this species, it is more likely that natural mortality was responsible for observed low residency patterns.

Residency was highest among adult females while large males roamed more widely within the array. Similarly, adult female *C. melanopterus* in a tropical coastal bay 100 km south of Orpheus exhibited high levels of long-term site-attachment while adult males were rarely encountered and, when present, moved more within the study site (Chin et al. 2013c, Chin et al. 2016). Sex-based differences in movement and space use documented among reef sharks are usually associated with reproduction (Ebert & Ebert 2005, Whitney et al. 2012, Mourier et al. 2013, Heupel & Simpfendorfer 2015). Adult male *C. amblyrhynchos* on the GBR, for example, were observed to roam more and make long-distance movements indicative of possible mate-searching behaviour while females were largely residential (Espinoza et al. 2015, Heupel & Simpfendorfer 2015). Alternatively, higher roaming among adult males at Orpheus Island may be a means to reduce intraspecific competition with resident females. Here, the annual return of two adult males largely absent from the study site corresponded with known times of mating and parturition for this species locally (Lyle 1987, Chin et al. 2013b), a repeated pattern suggesting long-term, seasonal site fidelity most likely related to reproduction.

The detection of an adult male on 3 separate reefs up to 57 km offshore and over multiple years indicates cross-shelf linkage and has important implications for connectivity. Although known to be highly resident, long-distance movements (i.e. ≥ 10 km) have been observed for several reef shark species including *C. amblyrhynchos* (16 km: McKibben & Nelson 1986, 134 km: Heupel et al. 2010, 250 km: Barnett et al. 2012, 81 km: Speed et al. 2016), *C. perezi* (50 km: Chapman et al. 2005) and *C. melanopterus* (80 km: Chin et al. 2013a, 138 km: Speed et al. 2016), among others (Lowe et al. 2006, Whitney et al. 2012, Dudgeon et al. 2013). While large-scale movements are primarily observed for adults (Chapman et al. 2005, Heupel et al. 2010), they have also been documented among juveniles (Lowe & Bray 2006, Chin et al. 2013a) and are thought to assist with gene dispersal, reducing inter- and intra-specific competition and identifying new suitable habitats/resources (Grubbs 2010). Several studies on *C. melanopterus* have documented occasional long-range excursions within reef systems for reasons likely related to reproduction (Papastamatiou et al. 2009b, Mourier & Planes 2012, Speed et al. 2016). For example, inter-island migrations were observed for adult female *C. melanopterus* in French Polynesia, with sharks observed to travel 50 km over open ocean to give birth in natal habitats (Mourier & Planes 2012). Individuals utilising near continuous habitats within the GBR are believed to have greater movement potential than those on more fragmented and remote reefs through a presumed lowered risk of predation (i.e. no open ocean crossings) and better chance of finding suitable habitat nearby. For example, while large movements may be less common for *C. amblyrhynchos* resident on isolated reef platforms (Barnett et al. 2012), in a comparatively well-connected network of habitats such as the GBR, this species has been observed to move routinely within and between reef systems (Heupel et al. 2010, Espinoza et al. 2015). Results from the current study provide further support for direct linkage of *C. melanopterus* populations between inshore and offshore regions (Chin et al. 2013a) and highlight the importance of inshore habitats to this species.

3.4.2 ***Space Use and Seasonal Patterns***

Similar to previous studies, *C. melanopterus* used small, well-defined spaces typical of many sedentary, site-attached reef shark species (Papastamatiou et al. 2010, Papastamatiou et al. 2011, Osgood & Baum 2015, Speed et al. 2016). Mean space use (95% KUDs) of adults at Orpheus Island (1.12 km² ± 0.21 SE) were largely consistent with those observed in remote (0.55 km² ± 0.24 SE: Papastamatiou et al. 2009b, 10.05 km² ± 0.95 SE: Papastamatiou et al. 2010) and coastal (12.8 km² ± 3.12 SE: Speed et al. 2016) regions. However, space use estimates were much smaller than those observed for sharks utilising a nearby coastal bay (25.42 km² ± 4.54 SE: Chin et al. 2016). Differences between this study and Chin et al. (2016) are likely due to site-specific differences in geography and receiver coverage. Here, 36 receivers covered a linear distance of approximately 18 km along a fringing reef compared to an array of 69 receivers spanning 140 km² of an intertidal bay; greater coverage and a lack of complex topography may have resulted in the larger space use calculated by Chin et al. (2016).

Space used by adults was roughly twice the size of that used by juveniles. Results were similar to those of Speed et al. (2016) who observed space use of juveniles (7.2 km² ± 1.33 SE) to be approximately half that of adults (12.8 km² ± 3.12 SE). Increases in space use with body size are well-documented among reef sharks (Gruber et al. 1988, Chapman et al. 2005, Garla et al. 2006, Wetherbee et al. 2007, Chapman et al. 2009, Heupel et al. 2010) and may be due to: 1) growing metabolic requirements and the need to find adequate resources (Jetz et al. 2004, Lowe & Bray 2006); 2) changes in morphology (e.g. mouth gape) and/or biomechanics (e.g. increased swimming speed), as well as skills acquisition leading to improved hunting ability and a shift in diet/habitat use (Wetherbee et al. 2004, McElroy et al. 2006, Tamburello et al. 2015); 3) a decrease in predation pressure/refuge function or; 4) the onset of maturity. Ontogenetic shifts in diet have been observed for several reef and reef-associated shark species (Lowe et al. 1996, Ebert & Ebert 2005, Papastamatiou et al. 2006, Newman et al. 2012), including *C. melanopterus* (Speed et al. 2012a). Neonate *N. brevirostris*, for example, have a broad diet comprised of small prey items while adults exhibit selective piscivory, consuming fewer, larger prey (Newman et al. 2012). Similarly, Speed et al. (2012a) found adult *C. melanopterus* to feed higher in the food web than juvenile conspecifics. It is possible then that space use patterns of sharks at Orpheus may be due to juveniles preferentially foraging on smaller prey items found within restricted areas of the study site while adults foraged more widely in order to meet their larger resource requirements. For neonate *N. brevirostris*, foraging opportunistically on slow-moving benthic invertebrates and small teleosts may also reduce the risk of predation by avoiding costly pursuits of prey (Newman et al. 2012). As such, smaller space use among juveniles may also reflect a predator avoidance strategy, with individuals remaining close to shallow-water sand and mangrove habitats where they were captured as protection from larger predators utilising the wider array (Morrissey & Gruber 1993, Wetherbee et al. 2007, Papastamatiou et al. 2009b, Poulakis et al. 2011, DiGirolamo et al. 2012, Guttridge et al. 2012, Stump et al. 2017, George et al. 2019). Juvenile *C. melanopterus*, for example, were observed to remain largely within a coastal bay in Western Australia while adults moved more, most likely due to the availability of protective shallow sand flat and mangrove habitats (Speed et al. 2016).

Sharp increases in the overall and cumulative space used by male *C. melanopterus* between October and December along with concurrent declines in monthly overlap indicate a change in behaviour during this period, with sharks moving more and exploring new areas. In contrast, the amount of space used by females remained comparatively constant throughout much of the year while patterns in overlap mirrored that of males, indicating a shift in the location of core and home ranges. Similarly, the amount of space used by male *C. amblyrhynchos* in the southern GBR was shown to increase during the mating season along with movement into new regions (Heupel & Simpfendorfer 2014, 2015); the authors speculated that this may be a mating tactic to improve the ability of males to locate responsive females or due to an increased need for resources to sustain reproductive activity during this period. In contrast, for mature female *C. amblyrhynchos* in the central GBR, changes in space use observed during times of reported parturition may be due to sharks moving to undetected areas of the reef, possibly into shallow-water habitats to give birth (Espinoza et al. 2015). Likewise, for adult female *C. melanopterus* in Moorea, parturition was observed to occur outside of their usual home range (Mourier & Planes 2012). Changes in space use at Orpheus corresponded with known times of mating and parturition for this species locally and were thus likely related to reproduction as movement would not be expected to differ significantly between sexes if either a response to a seasonal shift in prey resources (Heithaus 2001, Barnett et al. 2011) or change in environmental conditions (Schlaff et al. 2014) were responsible for patterns in space use. Increases in space use and movement into new regions by males during the reproductive season may be an attempt to improve mate encounter rates or re-provision spent resources (Heupel & Simpfendorfer 2014, 2015), while shifts in the location of space used by females may be due to sharks spending more time in areas important for parturition (e.g. optimize gestation, embryonic development: Economakis & Lobel 1998, Hight & Lowe 2007) or that provide refuge from male harassment and energy demanding mating activities (Economakis & Lobel 1998, Sims 2003, Wearmouth & Sims 2008, Mucientes et al. 2009, Jacoby et al. 2010, Wearmouth & Sims 2010). Apart from seasonal changes, space use metrics of all sharks remained relatively consistent throughout the year indicating that both sexes had similar dietary and environmental requirements.

3.4.3 *Depth Use and Diel Behaviour*

Overall, small sharks were observed to spend most of their time in the shallowest part of the study area with adults occupying deeper areas, although there was considerable variability among small males in how they utilised depth seasonally and over a diel period, with some individuals restricting their movements to shallow waters and others consistently using deeper depths. Studies have shown some reef shark species to partition habitat according to size, with juveniles typically occupying shallow-water habitats and adults comparatively deeper water (Gruber et al. 1988, Pikitch et al. 2005). Ontogenetic shifts in habitat use have been reported for *C. melanopterus*, with juveniles selecting shallow reef flats (Hobson 1963, Papastamatiou et al. 2009b), lagoons (Speed et al. 2016) and turbid, coastal foreshores (Chin et al. 2013c, Chin et al. 2016). For example, at Palmyra Atoll juvenile *C. melanopterus* were only ever observed in shallow sand flat habitats close to shore while adults showed strong site fidelity to deeper ledge habitats (Papastamatiou et al. 2009b). As size segregation likely reduces predation on young sharks (Wearmouth & Sims 2008), depth use patterns at Orpheus may reflect the preferential use of shallow sand and mangrove habitats by juveniles as a strategy to avoid larger predators, including conspecifics, which were observed to consistently use deeper depths within the array and are often unable to easily access these habitats due to their larger size (Morrissey & Gruber 1993, DiGirolamo et al. 2012). Similar results were reported from a manual tracking study where juvenile *C. melanopterus* were observed to remain within shallow waters (<1 m) of the reef flat and crest during low tides and refuge in mangrove habitats at higher tides, most likely to avoid predators (George et al. 2019). Alternatively, size segregation may help individuals avoid intraspecific competition over shared resources (Ebert & Ebert 2005, Knip et al. 2011a) or reflect an ontogenetic shift in diet (Papastamatiou et al. 2006, Newman et al. 2012) or physiological development (Wetherbee et al. 2004, McElroy et al. 2006, Tamburello et al. 2015). It is likely, though, that the benefits of using shallow-water habitats for juvenile sharks are multi-fold and not mutually exclusive.

The shallowest depths used by large females were during known times of mating and parturition locally. Warmer temperatures found on reef flats may speed up gestation in elasmobranch species and/or improve survival rates of neonates through a larger size at birth (Economakis & Lobel 1998, Hoisington & Lowe 2005, Hight & Lowe 2007, Jirik & Lowe 2012). Off the coast of Western Australia, for example, adult female *C. melanopterus* (some pregnant) were observed to aggregate within a shallow inshore bay with detection rate of sharks highest during spring/summer when water temperatures were warmer (Speed et al. 2011). In addition, there is evidence that adult females may behaviourally thermoregulate, with biotelemetry revealing body temperatures of sharks to be up to 1.3 degrees above the average ambient water temperature, a strategy thought to aid in reproduction (Speed et al. 2012b). As such, adult female *C. melanopterus* at Orpheus Island may be spending more time in warm, shallow waters during the reproductive season to decrease gestation periods, giving them time to replenish before the onset of winter, or to provide offspring with a biological advantage. Use of shallow-water habitats during this period may also provide pregnant females refuge from male harassment post-mating (Sims 2003). However, as no mature males were fitted with depth tags in the current study, it was impossible to determine if adult sharks partitioned depth use between sexes during this time.

Diel depth use patterns of adult females and some juveniles – particularly small males – showed crepuscular peaks in shallow-water depth use and movement by adults into deeper waters at night and throughout the day. Some reef sharks, including *C. melanopterus*, have been shown to increase their activity at night (McKibben & Nelson 1986, Wetherbee et al. 1990, Garla et al. 2006, Whitney et al. 2007, Papastamatiou et al. 2009b) or at dawn and dusk (Vianna et al. 2013, Papastamatiou et al. 2015), usually attributed to foraging. As with many other predators, sharks have vision well-suited to low-light conditions, giving them an advantage over their prey (Gardiner et al. 2012). *C. melanopterus* at Palmyra Atoll, for example, may be most active in the early evenings due, in part, to their sensory advantage during this period and a presumed increase in foraging success (Papastamatiou et al. 2015). Similarly, crepuscular behaviour of *C. amblyrhynchos* in Palau may be the result of sharks attempting to maintain a preferred isolume (Vianna et al. 2013). As ectothermic predators, vertical movements of sharks are also likely influenced by temperature (Schlaff et al. 2014). In contrast to adult females, most juvenile sharks apart from three males remained in shallow water throughout the day, indicating that ontogenetic differences may exist in their depth use requirements. For small sharks, the metabolic costs associated with remaining in warm, shallow waters may be outweighed by the decreased risk of predation gained when using these habitats.

Similar to coastal populations of *C. melanopterus*, (Speed et al. 2011, Chin et al. 2013c, Chin et al. 2016) inshore populations at Orpheus appeared to consist mostly of highly resident females (juveniles and adults) and juvenile males, with adult males largely transient, either roaming more throughout the array or present only during the reproductive season. Adult females may show high residency to inshore reefs as these habitats provide the resources necessary to meet requirements for reproduction, growth and survival (Mourier & Planes 2012, Espinoza et al. 2015) while adult males may roam more to reduce intraspecific competition and/or maintain genetic diversity across broad spatial scales (Grubbs 2010). In addition, evidence of cross-shelf connectivity observed in this and previous studies suggests that inshore reef habitats may play an important role in supporting marine ecosystems offshore. Understanding how *C. melanopterus* moves and occupies space within inshore reef systems helps to clarify the importance of inshore reef habitats to this species and may aid in future management and conservation efforts.

Chapter 4: Environmental Effects on Movement and Activity Space of Reef Sharks on Inshore Reefs

4.1 Introduction

Environmental factors play an important role in the spatial ecology of many elasmobranch species. Studies have documented changes in movement patterns and habitat use of elasmobranchs in response to a variety of factors such as temperature, salinity and tides (Schlaff et al. 2014). As drivers of movement, environmental factors have the potential to alter the distribution of individuals or populations over both short and long temporal scales, which could significantly influence entire ecosystems. To date, most studies linking environmental factors to movement of elasmobranchs have focused primarily on estuarine species or nearshore species occupying coastal embayments (e.g. Hopkins & Cech 2003, Heithaus et al. 2009, Froeschke et al. 2010) and on pelagic species (Vaudo et al. 2016). In order to more fully understand the role environmental factors play in the spatial ecology of elasmobranchs, it is important to examine environmental effects on movement and space use of species from a broader range of habitats.

Little information is currently available on the effects of environmental change on reef sharks. An integrated risk assessment of elasmobranchs in Australia‟s Great Barrier Reef World Heritage Area determined that reef-associated sharks were among the most vulnerable to climate change, with changes in temperature, freshwater input and ocean circulation predicted to have widespread effects on these species (Chin et al. 2010). For reef sharks, vulnerability was driven by habitat degradation and an associated loss of overall resiliency based on their site-attachment to coral reefs and adjacent (e.g. reef flat) habitats (e.g. Gruber et al. 1988, Barnett et al. 2012, Bond et al. 2012, Heupel & Simpfendorfer 2015). Unlike for species that use continuous coastal habitats and have the ability to relocate should environmental conditions deteriorate, movement away from patchily distributed coral reef habitat may not be a viable option for reef sharks because of the risk of not finding new suitable habitat.

In those studies that have documented environmental effects on the spatial ecology of reef sharks, the factors most commonly reported to influence movement and space use are temperature (Economakis & Lobel 1998, DiGirolamo et al. 2012, Guttridge et al. 2012, Speed et al. 2012b) and tide (Wetherbee et al. 2007, Papastamatiou et al. 2010, Guttridge et al. 2012, Filmalter et al. 2013). In contrast, recent, long-term monitoring revealed that space use of grey reef sharks on the Great Barrier Reef (GBR) was not related to environmental factors (Heupel & Simpfendorfer 2014, Espinoza et al. 2015), but rather was likely biologically driven (e.g. prey density, reproduction). Common to all of these studies, however, is that they were conducted on offshore reefs where conditions are expected to be more stable than on inshore reefs. By comparison, inshore regions are highly dynamic and are characterised by environmental fluctuations such as high freshwater run-off/low salinity events (King et al. 2002, Devlin & Brodie 2005, Devlin & Schaffelke 2009) and large and/or rapid changes in temperature (Mann 2000). For sharks resident on inshore reefs, frequent exposure to variable environmental conditions may result in different movement patterns compared to individuals found farther offshore.

The blacktip reef shark, *Carcharhinus melanopterus* (Quoy & Gaimard 1824-25), is a medium-bodied predator, common to reefs throughout the Indo-West and Central Pacific. In Australia, its distribution ranges from Moreton Bay (Queensland) north and west to Shark Bay (Western Australia) (Last & Stevens 2009). It is the third most commonly encountered shark on the GBR after the grey reef shark, *Carcharhinus amblyrhynchos*, and the whitetip reef shark, *Triaenodon obesus* (Heupel et al. 2009, Last & Stevens 2009). Blacktip reef sharks are site-attached, with several studies documenting comparatively small home ranges and localised movement across a wide range of habitats and life history stages (Stevens 1984, Papastamatiou et al. 2011, Speed et al. 2011, Chin et al. 2013c, Chin et al. 2016). Investigations into catch and occurrence of reef sharks within the GBR lagoon showed that blacktip reef sharks dominate the catch (60.2%), making it the most common reef shark found in inshore habitats (Chin et al. 2012). Inshore populations are more regularly exposed to environmental variability, making this species an excellent case study on the effects of environmental factors on the spatial ecology of a reef shark.

The purpose of this research was to examine the response of blacktip reef sharks to environmental changes within an inshore reef environment. Examining how resident sharks respond to fluctuations in their environment will help determine how resilient populations are to disturbance and change. We tested the hypothesis that movement patterns of blacktip reef sharks on an inshore reef will reflect changes in the local environmental conditions (e.g. temperature, salinity). In addition, previous research has documented sex (Papastamatiou et al. 2009a, Speed et al. 2011, Chin et al. 2016) and ontogenetic (Papastamatiou et al. 2009b, Speed et al. 2011, Chin et al. 2016, Speed et al. 2016) differences in movement and space use of blacktip reef sharks believed to be due to sex- and size-specific differences in energetic costs (e.g. reproduction, growth) and habitat requirements (e.g. prey availability, predator avoidance). As biological mechanisms may alter responses to environmental drivers, we also tested the hypotheses that environmental factors influencing movement and space use will differ between sexes and size classes.

4.2 Materials and Methods

4.2.1 *Study Area*

Field work was conducted around Orpheus Island (18.37°S, 146.30°E), part of the Palm Island Group of the GBR approximately 16 km off the coast of Queensland, Australia (**Figure 4.1**a). Orpheus Island is 12 km long, 1 to 2.5 km wide and surrounded by fringing reef, with depths ranging from 8 to 20 m. Several bays are located around the island, which are characterised by sand and/or coral rubble intertidal flats with most containing sections of non-estuarine mangrove habitat (dominated by *Rhizophora* spp.). Average depth in the bays is less than 5 m, and maximum tidal range reaches 4 m. Because of its close proximity to the mainland, Orpheus Island is directly affected by run-off from several rivers along the north Queensland coast, including the Herbert and Burdekin rivers (King et al. 2002), resulting in a variable inshore environment.

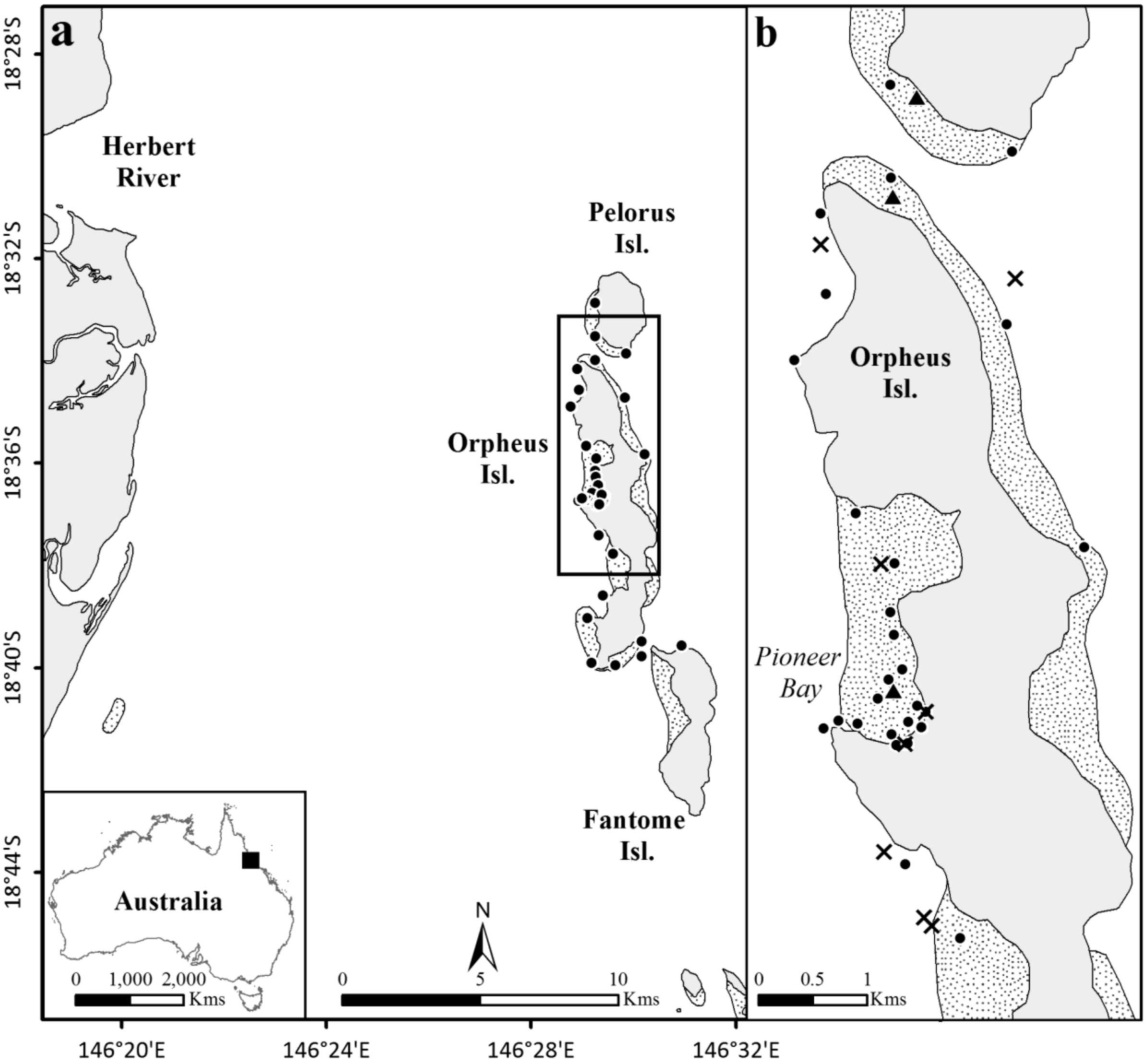

Figure 4.1: Study site: Orpheus Island, Palm Islands, Queensland, Australia (insert shows the location of the study site within Australia). (b) Close-up of Orpheus Island, showing weather stations (*triangles*) and fishing locations (*crosses*). In both panels, the positions of acoustic receivers at Orpheus, Pelorus and Fantome islands are marked with *circles*. Light grey stippling indicates reef habitat.

4.2.2 *Field Methods*

Movement patterns and space use of blacktip reef sharks were examined using passive acoustic telemetry. Thirty-six VR2W acoustic receivers (Vemco) were deployed around the study site to monitor the movement of tagged individuals (**Figure 4.1**). While the majority of receivers were distributed around Orpheus Island, some were deployed on the adjacent Pelorus (n = 3) and Fantome (n = 2) islands to track movements of individuals between islands. Receivers were positioned 2 to 3 m above the seabed, fastened to a nylon rope with a float and anchored to the reef using stainless steel chain shackled to a coral head. Receivers placed in areas without reef substrate (n = 12) were attached to star pickets embedded into the sea floor. Receivers closest to shore (n = 8) within Pioneer Bay, an intertidal reef flat located on the western side of Orpheus Island, became completely exposed at tidal heights of 160 cm or less, relative to the lowest astronomical tide (LAT) and at 140 cm or less, relative to LAT for mid-bay receivers. Detection range of receivers was ~125 m within shallow inshore bays around the island (Welsh et al. 2012), with the detection range likely larger in deeper habitats around the island. Data from receivers were downloaded twice a year.

Tagging took place between December 2011 and February 2013 at several locations around Orpheus Island (**Figure 4.1**b). Sharks were captured using multi-hook long-lines or rod and reel. Long-lines consisted of a 500 m mainline (8 mm nylon rope) anchored at both ends and left to soak for 1 hour. Gangions (1 m of 5 mm nylon cord with 1 m wire trace and size 14 Mustad tuna circle hooks) were attached at 8 to 10 m intervals along the mainline and baited with either frozen butterfly bream (*Nemipterus* sp.) or squid (*Loligo* sp.). Individuals collected by rod and reel were captured on 8/0 Mustad hooks baited with pilchard (*Sardinops* sp.) or squid. All captured individuals were measured to the nearest millimetre, sexed and tagged with a rototag in the first dorsal fin for identification prior to release. V13P acoustic transmitters (69 kHz; 13 mm diameter x 45 mm length; Vemco) were surgically implanted into the body cavity via a small incision (3-4 cm) following the methods of Heupel and Hueter (2001). Transmitters emitted a unique pulse series (i.e. ID code) specific to the individual tagged, as well as depth (maximum depth: 50 m), on a pseudorandom repeat every 120 to 200 seconds and had an estimated battery life of 374 days. Sharks were retained for a maximum of 10 minutes during measuring and tagging procedures, with all surgical procedures conducted according to protocols approved by James Cook University‟s Animal Ethics committee (permit A1566).

The Integrated Marine Observing System‟s (IMOS) Facility for Automated Intelligent Monitoring of Marine Systems manages a network of sensor equipment around Orpheus and Pelorus islands (**Figure 4.1**b) that record data on 12 environmental parameters (e.g. barometric pressure, rainfall). These data are publicly available from IMOS (www.imos.org.au) or Australian Institute of Marine Science (www.aims.gov.au) websites. Environmental data for the period between December 2011 and the end of January 2014 were downloaded and used in analyses (**Figure 4.2**). Salinity measurements were taken at the Pelorus Island weather station (at a depth of 14.6 m), and temperature measurements from the northernmost Orpheus Island station (at a depth of 7.6 m). The weather station within Pioneer Bay measured both temperature and salinity, but was not operational for the full period of the study. Variation in salinity and temperature data between these 2 weather stations and the third station within Pioneer Bay was limited (average of ± 0.23 ppt; ± 0.25°C) when all 3 stations were active; as such, data from the 2 northern stations were selected for use in further statistical analyses as these data sets were the most complete. Given the complex topography at Orpheus Island along with the large tides, it is unlikely that an environmental gradient would develop within the study area. However, it is possible that variability in abiotic conditions exists around the islands that could not be measured. Environmental parameters were recorded at 1 hour intervals and were filtered and later processed to provide summary data at the same time scale as that used for activity space estimates. Data were then centred to have a mean of 0 (Becker et al. 1988) before being tested for correlation. Where environmental parameters of interest were found to be highly correlated ($R > 0.70$), 1 of each pair of correlated co-variates was removed, leaving water temperature, salinity, rainfall and average wind speed to be included in final analyses.

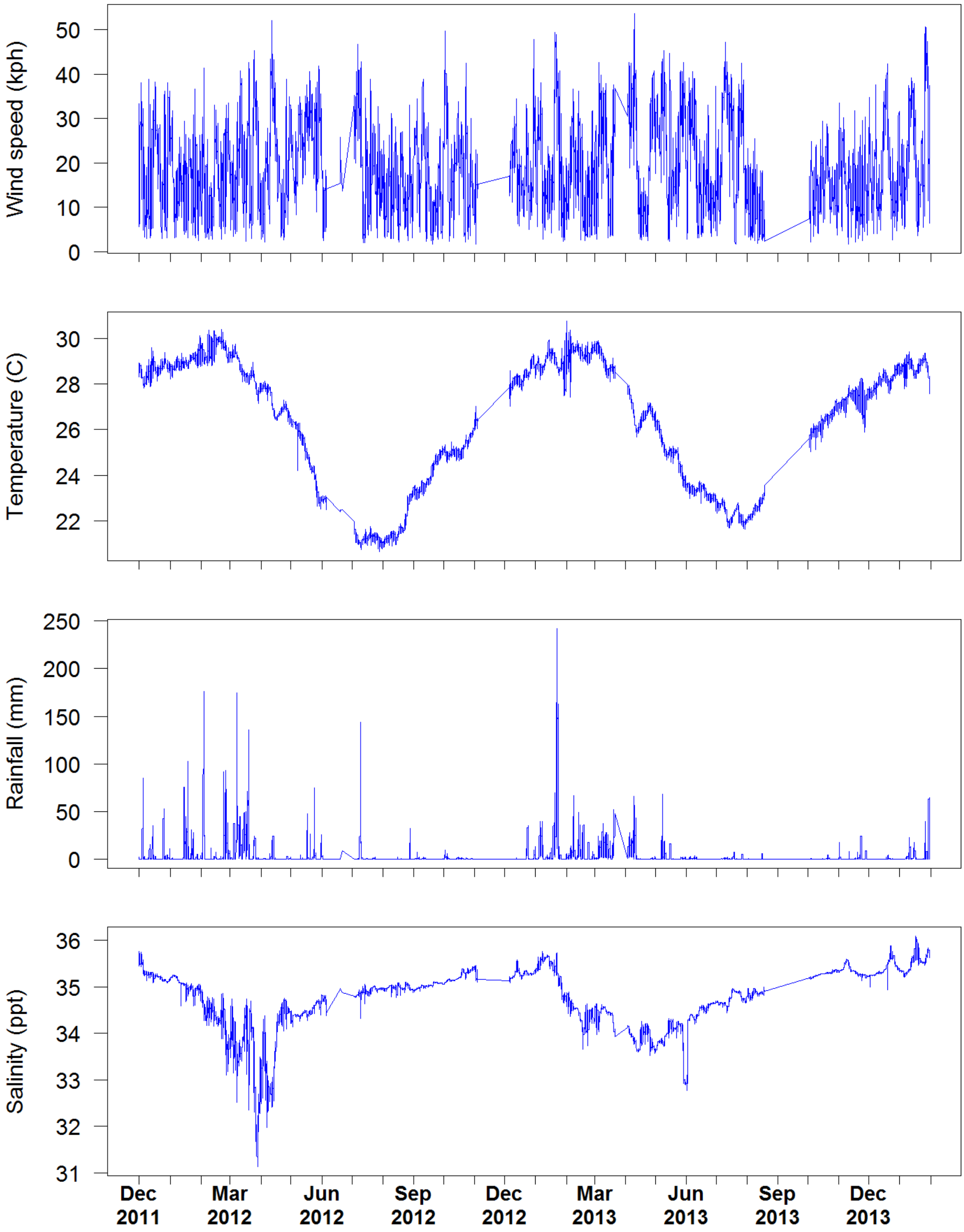

Figure 4.2: Environmental measurements for Orpheus and Pelorus islands from December 2011 to the end of January 2014.

4.2.3 *Data Analysis*

Data from acoustic receivers were examined to investigate changes in activity space and movement patterns of blacktip reef sharks in response to environmental conditions. To be included in the analyses, sharks had to be detected within the array for ≥ 30 days and at least twice on a single receiver on any given day to reduce the chance of including false detections. Residency of individuals was calculated as the ratio of days detected within the acoustic array to days at liberty, with values ranging from 0 to 1 for low to high residency, respectively. „Days at liberty‟ represented the total detection days possible and was defined as the number of days from initial tagging and transmitter activation to the date when the battery was expected to expire (i.e. predicted tag life) for individuals tagged in December 2011/2012 or until the end of the study for sharks tagged in February 2013.

4.2.3.1 Position Estimates

Customised R scripts were used to provide a „centre of activity‟ (COA) estimate for each individual over a 30 minute time period (Simpfendorfer et al. 2002). COA locations represented the mean position of each shark for the given time step weighted by the number of detections at each receiver within the array. Following the methods of Simpfendorfer et al. (2008) and Heupel and Simpfendorfer (2014), the acoustic array was treated as a linear system. Using this approach, the receiver located on the northwest side of Pelorus Island was designated as the starting point, and position of individuals was calculated as the distance from that point. Reef distance values were then combined with mean tag depth values from the same time period to generate a 2-dimensional representation of location averaged over a 30 minute time period.

4.2.3.2 Activity Space

Weekly activity spaces of individuals were calculated using 50 and 95% vertical kernel utilization distributions (vKUDs) based on COA estimates using the *ks* package in R (Duong 2007). Vertical activity space estimates (vKUDs) provided information on depth use with distance along the reef for each individual. Areas of core use (50% vKUD) and extent (95% vKUD) were examined over weekly intervals to investigate changes in movement and space use over time. Weeks with < 10 position estimates for an individual resulted in that week being excluded from subsequent analyses for that individual to avoid inaccurate estimates of activity space. Unless otherwise indicated, analyses were conducted in the R environment (Development Core Team 2013).

4.2.3.3 Factors Influencing Activity Space Size

Linear mixed effects models were used to examine activity space data for size, sex and environmental effects using the *nlme* package in R (Pinheiro et al. 2019). Individual (animal „ID‟ code) was incorporated as a random factor within these models to account for the repeated-measures nature of the data (Bolker et al. 2009). Before running models, activity space estimates were first checked for normality and square root transformed if required (Heupel & Simpfendorfer 2014). Models were also tested for collinearity by calculating the variance inflation factors among the covariates using the R package *car* (Fox & Weisberg 2011). An information theoretic model selection process was used to investigate the effects of fixed (environmental variables, stretch total length [STL], sex) and random (individual) factors on weekly 50 and 95% vKUDs of individuals (Burnham & Anderson 2003). The „dredge‟ function in the *MuMIn* package in R (Barton 2013) was used to generate a series of candidate models that were compared to each other using Akaike‟s information criterion corrected for small-sample bias (AICc). Candidate models were constructed against all possible combinations of environmental and biological factors and the null model (global model: ~ water temperature + salinity + rainfall + wind speed + STL + sex × week + [1|ID]). Maximum likelihood ratio tests were used to compare candidate models against the null model and test for significant differences ($\alpha = 0.05$). Model averaging was conducted on the top candidate models (ΔAICc < 2) for 50 and 95% vKUD, which weighted environmental and biological parameters with respect to AICc weight. Parameter estimates were then averaged over the subset of candidate models, a process that allowed for incorporation of model uncertainty. Cumulative AICc weights ($0 \leq w_i \leq 1$) were calculated to evaluate strength of evidence for each activity space-modelled covariate within averaged models (Burnham & Anderson 2003). Following Barbieri and Berger (2004), covariates with $w_i > 0.5$ were considered significant drivers of activity space.

4.3 Results

Between December 2011 and February 2013, we tagged 34 blacktip reef sharks with acoustic transmitters at Orpheus Island. No attempt was made to control the number of males and females, and transmitters were fitted to animals regardless of sex. Nineteen sharks were tagged in December 2011 (10 female, 9 male), 1 in March 2012 (female), 8 in December 2012 (3 female, 5 male) and 6 in February 2013 (3 female, 3 male). Sixteen individuals were subsequently either never detected within the array (n = 2) or had limited data (n = 14) and were excluded from analyses. Of the 18 individuals included in the study, the smallest shark (510 mm STL) had a partially open umbilical scar identifying it as a neonate, while the largest shark tagged measured 1350 mm STL (**Table 4.1**). As age and growth studies for this species have reported average size at maturity to be 1050 mm STL for males and 1335 mm STL for females (Chin et al. 2013b), only a single mature adult was included in the final analyses (female, 1350 mm STL).

Minimum detection time of sharks was ~2 months, with half (n = 9) present for the full period of predicted tag life (**Figure 4.3**). Remaining sharks (n = 9) either departed from the monitored area permanently, died outside of the array or experienced tag failure. The timing of detection loss was random and did not appear to be coordinated among individuals or with environmental changes. One individual was detected exclusively on a single receiver for a period of ~ 5.5 months prior to tag expiry and was presumed to have died (these months were excluded from analyses). Blacktip reef sharks showed site-attachment to reef habitats with high residency indices (≥ 0.70) calculated for 11 individuals (**Table 4.1**). Four individuals were detected within the array every day for the duration of the study. It is important to note that, due to the way in which „days at liberty" were determined (i.e. using predicted tag life, not when individual tags were last detected), residency values may be underestimated as individuals go undetected, although present, when using habitats outside of the listening range of the acoustic array.

Table 4.1: Details of acoustically tagged blacktip reef sharks, *Carcharhinus melanopterus* (ID code), with stretch total length (STL), sex, release date (dd/mm/yyyy) and overall 50 and 95% vertical activity space (vKUD) estimates. Residency index was calculated as the ratio of days detected within the array to days at liberty, with values ranging from 0 to 1 for low to high residency.

ID code	STL (mm)	Sex	Release date	Days at liberty	Days detected	Residency index	Overall 50% vKUD (m²)	Overall 95% vKUD (m²)
6523	685	F	10/12/2011	374	268	0.72	796	8000
6525	570	M	10/12/2011	374	203	0.54	370	695
6526	510	M	10/12/2011	374	144	0.39	237	1095
6527	1050	F	11/12/2011	374	367	0.98	1055	10730
6531	770	M	13/12/2011	374	369	0.99	2841	29163
6532	1070	F	13/12/2011	374	373	1.00	982	22245
6533	1030	F	13/12/2011	374	369	0.99	1160	22852
6534	1070	F	13/12/2011	374	374	1.00	2813	31471
6535	750	M	13/12/2011	374	367	0.98	808	10328
6539	1350	F	13/12/2011	374	374	1.00	2538	17390
6540	1260	F	14/12/2011	374	374	1.00	4120	34322
7950	584	F	20/12/2012	374	104	0.28	314	871
7955	812	M	22/12/2012	374	332	0.89	4186	17679
7956	588	F	22/12/2012	374	345	0.92	366	937
7957	559	M	26/12/2012	374	52	0.14	328	2416
7958	593	M	13/02/2013	341	51	0.15	174	1218
7959	610	M	13/02/2013	341	199	0.58	137	2250
7962	559	M	16/02/2013	338	134	0.40	89	1883

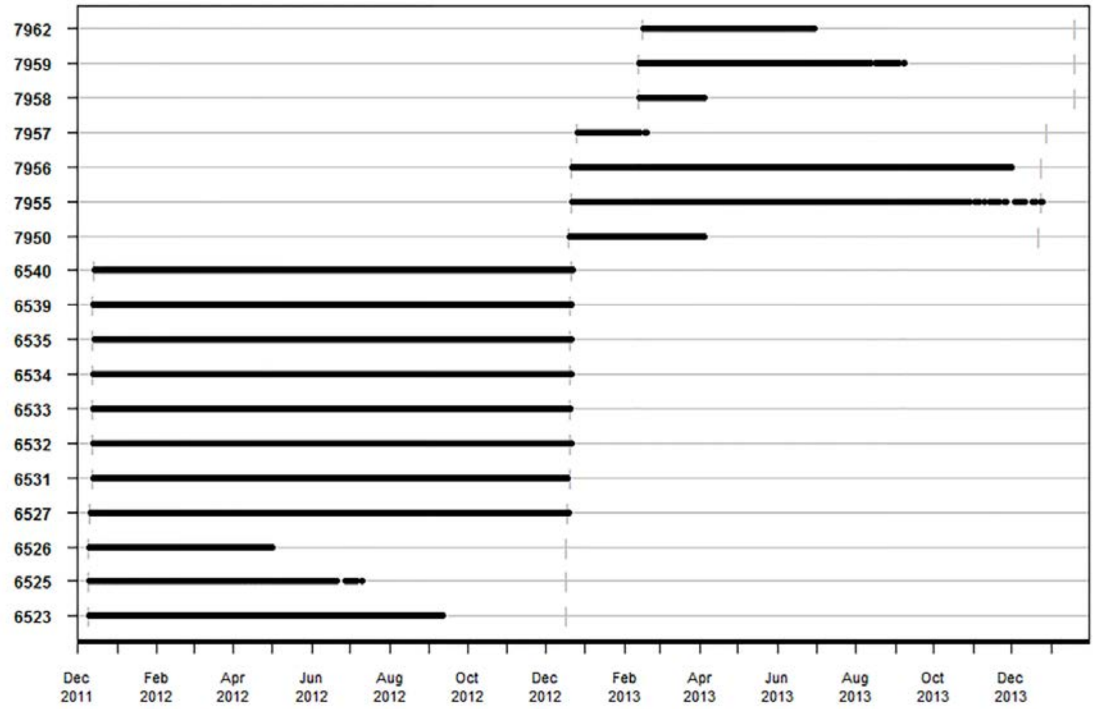

Figure 4.3: Presence plot for 18 blacktip reef sharks, *Carcharhinus melanopterus*, captured and released at Orpheus Island from December 2011 to the end of January 2014; *black circles* indicate presence at the site and light *grey vertical bars* indicate predicted tag life.

Results from modelling indicated that both biological (size, sex) and environmental (salinity, temperature) effects influenced the activity space of monitored sharks. The best-fit model (i.e. lowest AICc value) for 95% vKUD included STL, sex, salinity and temperature (**Table 4.2**) while the best-fit model for 50% vKUD included STL, sex, salinity and week (**Table 4.3**). Neither best-fit model for 50 or 95% vKUD had overwhelming support (i.e. similar low AICc weights among the top 15 models), and all candidate models were significantly better than the null models (maximum likelihood ratio test, $p < 0.01$). Cumulative AICc weights for averaged models (both 50 and 95% vKUD) supported dredge outputs, with all environmental and biological parameters included in best-fit models shown to influence activity spaces of tagged sharks ($w_i > 0.5$; **Table 4.4**). STL had the highest cumulative AICc weight across both metrics of vKUD, indicating that it had the most influence on activity space. After size, salinity had the most significant influence on 95% vKUD of sharks followed by water temperature and sex. Week was the second-most influential factor affecting 50% vKUD, followed by sex and salinity.

Table 4.2: Top-ranked candidate models examining the effects of environmental and biological factors on extent of blacktip reef shark, *Carcharhinus melanopterus*, vertical activity space (95% vKUD; square-root transformed). The best-fit model with the smallest Akaike‟s information criterion corrected for small-sample bias (AICc) is shown in **bold**. Maximum likelihood ratio tests showed all models to be significantly better than the null model. ΔAICc is the Akaike difference and *w* is the Akaike weight. STL: stretch total length; as: activity space; wk: week; sal: salinity; temp: water temperature; rain: rainfall; wind: average wind speed.

Model rank	**Model**	***df***	**95% vKUD AICc**	**95% vKUD ΔAICc**	***w***
1	**sqrt(as) ~STL+sex+sal+temp**	**9**	**4783.54**	**0.00**	**0.11**
2	sqrt(as) ~STL+sal+temp	8	4783.65	0.11	0.10
3	sqrt(as) ~STL+sex+sal	8	4785.40	1.86	0.04
4	sqrt(as) ~STL+sal	7	4785.52	1.98	0.04
5	sqrt(as) ~STL+sex+sal+temp+wind	10	4785.59	2.05	0.04
6	sqrt(as) ~STL+sex+sal+temp+rain	10	4785.61	2.07	0.04
7	sqrt(as) ~wk+STL+sex+sal+temp	10	4785.61	2.07	0.04
8	sqrt(as) ~STL+sal+temp+wind	9	4785.69	2.16	0.04
9	sqrt(as) ~STL+sal+temp+rain	9	4785.71	2.18	0.04
10	sqrt(as) ~wk+STL+sal+temp	9	4785.71	2.18	0.04
11	sqrt(as) ~STL+sex+sal+rain	9	4786.73	3.19	0.02
12	sqrt(as) ~STL+sal+rain	8	4786.82	3.29	0.02
13	sqrt(as) ~STL+sex+temp	8	4786.87	3.34	0.02
14	sqrt(as) ~STL+temp	7	4787.01	3.48	0.02
15	sqrt(as) ~STL+sex+sal+wind	9	4787.47	3.93	0.02

Table 4.3: Top-ranked candidate models examining the effects of environmental and biological factors on core vertical activity space (50% vKUD; square-root transformed) of blacktip reef sharks, *Carcharhinus melanopterus*. The best-fit model with the smallest AICc is shown in **bold**. Maximum likelihood ratio tests showed all models to be significantly better than the null model. Abbreviations as in **Table 4.2**.

Model rank	**Model**	***df***	**50% vKUD AICc**	**50% vKUD ΔAICc**	***w***
1	**sqrt(as) ~wk+STL+sex+sal**	**9**	**4138.29**	**0.00**	**0.07**
2	sqrt(as) ~wk+STL+sex+sal+wk×sex	10	4138.60	0.32	0.06
3	sqrt(as) ~wk+STL+sal	8	4138.63	0.34	0.06
4	sqrt(as) ~wk+STL+sex	8	4138.70	0.41	0.06
5	sqrt(as) ~wk+STL+sex+wk×sex	9	4139.00	0.71	0.05
6	sqrt(as) ~wk+STL	7	4139.08	0.79	0.05
7	sqrt(as) ~wk+STL+sex+sal+temp	10	4139.97	1.68	0.03
8	sqrt(as) ~wk+STL+sex+sal+wind	10	4140.00	1.71	0.03
9	sqrt(as) ~wk+STL+sex+sal+rain	10	4140.04	1.75	0.03
10	sqrt(as) ~wk+STL+sex+sal+temp+wk×sex	11	4140.14	1.86	0.03
11	sqrt(as) ~wk+STL+sal+temp	9	4140.29	2.01	0.03
12	sqrt(as) ~wk+STL+sal+wind	9	4140.33	2.04	0.02
13	sqrt(as) ~wk+STL+sex+sal+wind+wk×sex	11	4140.33	2.04	0.02
14	sqrt(as) ~wk+STL+sex+sal+rain+wk×sex	11	4140.35	2.06	0.02
15	sqrt(as) ~wk+STL+sal+rain	9	4140.35	2.06	0.02

Table 4.4: Cumulative Akaike‟s information criterion (AIC) weights (w_i), parameter estimates and p-values calculated from an averaged subset (ΔAICc < 2) of candidate models showing the relative influence of biological and environmental parameters on vertical activity space (50 and 95% vKUD; square-root transformed) of blacktip reef sharks, *Carcharhinus melanopterus*. Cumulative weights and parameters considered influential drivers of activity space are shown in **bold**. Abbreviations as in **Table 4.2**.

	Parameter	Estimate ± SE	p	w_i
50% vKUD	**STL**	0.056 ± 0.013	<0.001	**1.00**
	sex	8.621 ± 7.829	0.271	**0.77**
	wk	0.103 ± 0.039	0.009	**1.00**
	wk:sex	-0.027 ± 0.056	0.626	0.30
	sal	-0.550 ± 0.576	0.340	**0.67**
	temp	-0.034 ± 0.165	0.838	0.13
	wind	-0.026 ± 0.200	0.895	0.06
	rain	-0.034 ± 0.270	0.900	0.06
95% vKUD	**STL**	0.130 ± 0.035	<0.001	**1.00**
	sex	12.673 ± 17.683	0.474	**0.51**
	sal	-1.906 ± 0.831	0.022	**1.00**
	temp	-0.969 ± 0.838	0.247	**0.72**

Model averaging showed that larger sharks had larger activity spaces, with 50 and 95% vKUDs increasing with size (**Figure 4.4**a, c; **Table 4.4**; ANOVA, $p < 0.01$). Average weekly 50% vKUD of the smallest individual (male, 510 mm STL) was less than 10% that of the largest (female, 1350 mm STL), ranging from 117 ± 91 (SE) m^2 to 1496 ± 97 m^2, respectively; weekly 95% vKUD ranged from an average of 2270 ± 488 m^2 to $12\ 101 \pm 492$ m^2, with the largest individual using over 5 times more space than the smallest. Although not significant, male sharks used marginally larger activity spaces than females (**Figure 4.4**a, c). However, as only a single adult female was detected upon release, sex-specific differences in space use must be interpreted with caution. Interaction plots for sex and STL from averaged models showed juvenile males to be driving observed sex-based patterns in activity space, and therefore data may not reflect true biological trends at the higher end of the size spectrum. In addition, the lower cumulative AICc weight of sex for both 50% ($w_i = 0.77$) and 95% ($w_i = 0.51$) vKUDs indicated that this factor was of less importance to observed patterns in activity space than STL. The sex x week interaction term was not included in either of the best-fit models during model selection nor shown to be important ($w_i < 0.5$; **Table 4.4**), suggesting that patterns in activity space over time did not differ between males and females.

Models incorporating salinity consistently ranked high during the model selection process (**Tables 4.2 & 4.3**). However, cumulative AICc weights from averaged models suggested that salinity was more important to 95% vKUD ($w_i = 1.00$) than to core space use ($w_i = 0.67$), where it had a marginal effect (**Table 4.4**). During the study, salinity levels ranged from 31.1 ppt (March 2012) to 36.1 ppt (January 2014). The general trend was for 95% vKUD to increase with decreasing salinity (**Figure 4.4**d; **Table 4.4**; ANOVA, $p = 0.02$), with increased depth use, increased use of horizontal space or a combination of both accounting for these changes; the marginal effect of salinity on 50% vKUD indicated that core activity spaces were more stable (**Figure 4.4**b; **Table 4.4**). Temperature was also included in the best-fit model for 95% vKUD. Results from model averaging showed the estimated size of activity space to decrease with increasing temperature (**Table 4.4**). Cumulative AICc weights for 95% vKUD suggested that temperature was less important ($w_i = 0.72$) as a predictor of activity space size than salinity – an observation supported by its low relative importance ($w_i = 0.13$)

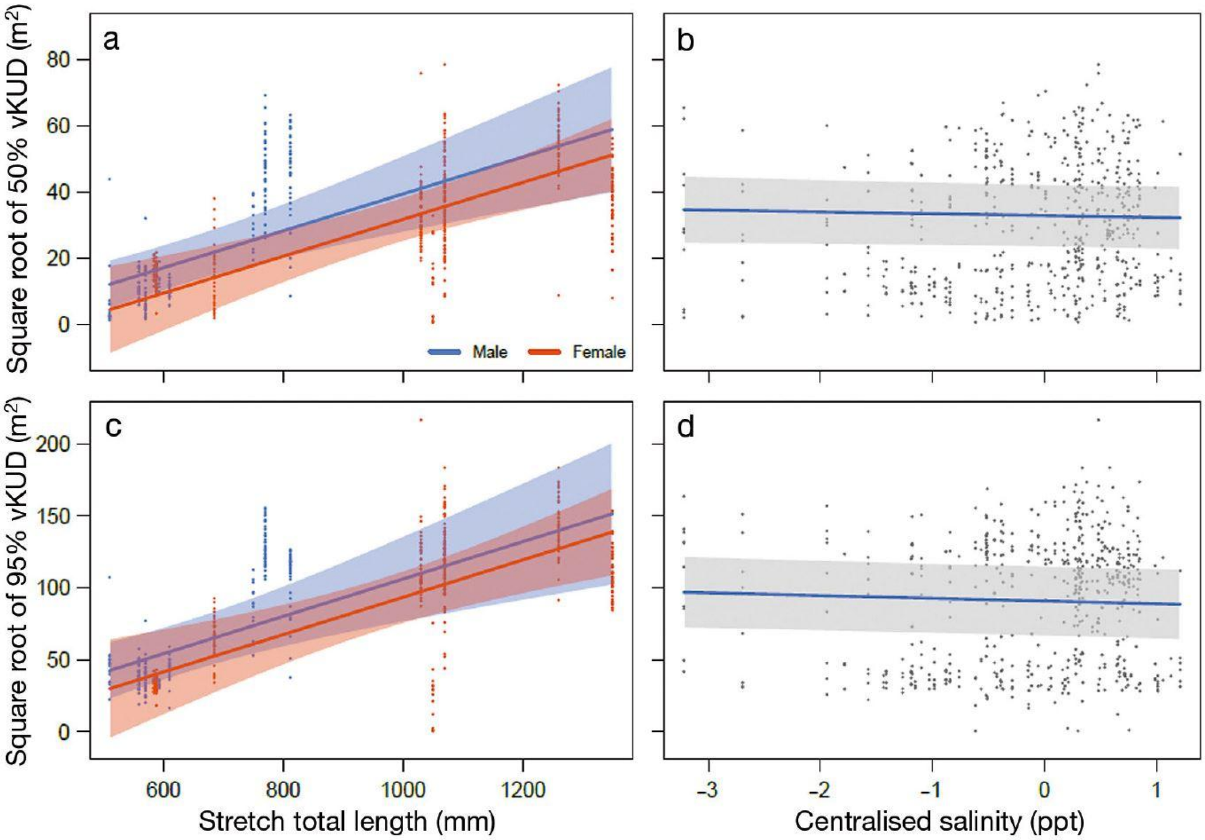

Figure 4.4: Interaction plots from averaged models showing effects of biological and environmental factors on blacktip reef shark, *Carcharhinus melanopterus*, vertical activity space (vKUD; square-root transformed). The left column shows changes in (**a**) 50% and (**c**) 95% vKUD with increasing size (stretch total length, STL) for females (*red*) and males (*blue*). The right column indicates changes in (**b**) 50% and (**d**) 95% vKUD with changes in salinity. *Shaded areas* indicate 95% confidence intervals and points are raw data for STL and centralised raw data for salinity.

and lack of inclusion in the best-fit model for 50% vKUD. It is worth noting that, given the design of the acoustic array, observed patterns in space use were over relatively coarse spatial scales and may not reflect fine-scale movement and behavioural responses to temperature change.

4.4 Discussion

The results of this research demonstrated that both biological and environmental factors influence how blacktip reef sharks occupy space within inshore reef habitats. Size was the most influential predictor of space use, with activity space positively correlated with this factor. Similar patterns were observed for this species in coastal habitats in Western Australia, where larger activity spaces were observed for adults (Speed et al. 2016). Ontogenetic shifts in movement, behaviour and habitat use have been recorded for several reef-associated sharks (Garla et al. 2006, Wetherbee et al. 2007, Grubbs 2010, Heupel et al. 2010), including blacktip reef sharks (Papastamatiou et al. 2009b, Chin et al. 2013a, Chin et al. 2016, Speed et al. 2016). Many of these studies showed that juvenile sharks primarily use shallow-water habitats (e.g. mangrove stands, sand flats), which differ from movements of adults that use both shallow intertidal and the adjacent deep reef habitats (Wetherbee et al. 2007, Papastamatiou et al. 2009b, Knip et al. 2011a, DiGirolamo et al. 2012). Studies suggest that juvenile sharks expand their space use as they grow, with broader movements of adults likely related to energetic requirements and the need to find adequate resources (Lowe & Bray 2006, Tamburello et al. 2015). Thus, activity spaces of blacktip reef sharks at Orpheus Island are likely increasing with animal size as a response to growing energetic demands as well as a more developed ability to capture larger and faster-moving prey in varied habitats. Observations from stable isotope studies on this species show evidence of size-based differences in diet, with larger individuals feeding higher in the food web (Speed et al. 2012a).

A marginal influence of sex was observed on space use in the present study, where juvenile males displayed larger activity spaces than juvenile females. Previously, studies on adult grey reef sharks in Australia have documented sex-dependent activity spaces and movements by mature males during the mating seasons, most likely to find suitable mates (Heupel & Simpfendorfer 2014, 2015). Similarly, adult female blacktip reef sharks utilising a shallow, turbid coastal habitat were highly resident while males had larger activity spaces and were transient (Chin et al. 2016). While these studies suggest that differences in space use between males and females may be related to reproductive requirements, in the present study only a single adult female was obtained, making it impossible to examine changes in activity space in response to seasonal biological processes (e.g. mate-searching, breeding, parturition). Nevertheless, activity spaces of juvenile male sharks at Orpheus Island were larger than those of juvenile females, indicating that movement drivers in juveniles may be more complex. Responses to environmental factors among juvenile blacktip reef sharks was not expected to differ given the similar energy requirements and associated space use of both sexes. However, as sex-specific costs in reproduction have different energetic demands, it is possible that further research will reveal differences in response to environmental drivers between sexes.

Our results indicated that salinity plays an important role in the spatial ecology of blacktip reef sharks on inshore reefs. Of the four environmental factors modelled (wind speed, rain, salinity and water temperature), salinity had the greatest influence on activity space, with 95% vKUDs increasing with decreasing salinity. Most sharks, including blacktip reef sharks, are stenohaline and occupy a narrow salinity range (Pang et al. 1977). When salinity levels fall outside of individual tolerances, sharks may use movement to avoid physiological stress and possible mortality (Heupel & Simpfendorfer 2008, Simpfendorfer et al. 2011). As such, one explanation for changes in activity space with salinity was that sharks moved to avoid unfavourable environmental conditions and that their corresponding space use increased as they sought more suitable conditions. In nearshore regions, seasonal fluctuations in rates of freshwater inflow and associated changes in salinity levels have been linked to movement of elasmobranchs as individuals avoid areas of high freshwater inflow and decreased salinity (Collins et al. 2008, Knip et al. 2011b, Francis 2013). A similar movement response based on freshwater inflow has been reported for bonnethead sharks, *Sphyrna tiburo*, where sharks left the area at lower salinity levels (Heupel et al. 2006). It is also possible that activity spaces of sharks increased as individuals actively sought out a preferred salinity range within the study area in an effort to reduce the energetic costs associated with osmoregulation, a behavioural strategy observed in other elasmobranch species (Simpfendorfer et al. 2005, Froeschke et al. 2010). In addition, response by sharks to salinity changes may be due to the effects of this factor on resource distribution as opposed to physiological limitations, although this was not possible to measure in the current study.

While blacktip reef sharks reacted to salinity decreases by increasing their activity space, they did not permanently leave the study site during these periods. This suggests that this species may be somewhat resilient to environmental fluctuations, an observation supported by research showing that blacktip reef sharks may be more tolerant of the effects of a tropical cyclone than other inshore shark species (Udyawer et al. 2013). The failure to move under cyclonic and low-salinity conditions may also serve to highlight the importance of coral reef habitat to this species. Resilience to environmental changes may allow individuals to remain in reef habitats and be able to access the key ecosystem services reefs provide until conditions recover. Similarly, neonate sawfish, *Pristis pectinata*, were observed to remain in shallow-water estuarine habitats longer than older juveniles when salinity levels increased, possibly due to the improved chance of survival gained from remaining in these protected habitats outweighing the energetic costs of osmoregulation (Simpfendorfer et al. 2011) or because they are better adapted to survive in these conditions. It is also possible that salinity conditions at Orpheus Island simply did not reach a level that would cause emigration. Salinity levels declined to below 16 ppt before bonnethead sharks emigrated from a Florida (USA) estuary (Heupel et al. 2006). Similarly, catch data from an inshore reef at Magnetic Island, approximately 100 km south of Orpheus Island, reported a substantial decline in catch rate of blacktip reef sharks when salinity decreased to 16 ppt following a heavy rainfall event (A. Chin, pers. comm.). In comparison, salinity fluctuations at Orpheus Island were quite small (range: 31-36 ppt), and thus may not have been low enough to cause sharks to depart the reef despite altering their movement patterns.

Our study indicates that temperature may have an effect on activity space of sharks, although less pronounced than salinity. Previous studies have shown temperature to be an important driver of movement and space use for this species (Speed et al. 2011, Speed et al. 2012b, Papastamatiou et al. 2015). The lack of variation in salinity experienced in offshore (Papastamatiou et al. 2015) or freshwater–limited (Speed et al. 2011, Speed et al. 2012b) areas may mean that temperature plays a greater role for those populations than salinity, although this has not been tested. In comparison, Orpheus Island is only 16 km from the mainland and the catchments which affect salinities can experience rainfall of up to 600 ml over only a few days causing large and rapid changes (Bureau of Meteorology 2015). Freshwater plumes associated with wet season flooding have been shown to regularly extend offshore past Orpheus and the Palm Islands, with salinity levels decreasing to at least 30 ppt (Wolanski & Jones 1981, King et al. 2002, Devlin & Brodie 2005, Devlin & Schaffelke 2009).

Blacktip reef sharks resident to these inshore reef systems have likely developed mechanisms to cope with fluctuations in salinity in order to remain in coral reef habitat. Given that previous studies documenting temperature effects on space use of blacktip reef sharks looked at fine-scale (i.e. diel) changes in movement and behaviour, it is also possible that the coarser resolution of the data in the present study (i.e. over larger temporal scales) may have masked temperature effects.

4.5 Conclusion

This study demonstrated the importance of biological and environmental factors on movement and activity space of a common reef shark on inshore reefs. Size had the greatest effects on space use, with larger sharks using larger activity spaces, presumably due to growing energetic demands and the need to find adequate resources. Sex effects were also observed, with juvenile males using marginally more space than juvenile females; reasons for this are not immediately clear and results should be treated cautiously due to limitations in the data (i.e. only 1 adult tagged). After size, salinity was the best predictor of activity space of juvenile blacktip reef sharks at Orpheus Island. Sharks increased their activity spaces as salinity levels decreased; however, further study is required to determine if response was due to a physiological limitation, individuals actively seeking out more favourable conditions (i.e. behavioural osmoregulation) or some other factor (e.g. movement of prey species; Heupel & Simpfendorfer 2014). Water temperature had a similar but weaker effect on activity space size. Results add to previous studies on this species that have documented environmental effects on space use and serve to highlight how site-specific differences in physical structure and conditions can drive movement. While sharks reacted to salinity decreases by increasing their activity space, they did not permanently leave the study site, which suggests that this species may be somewhat resilient to environmental change or that conditions did not reach a level that would cause departure. Furthermore, blacktip reef sharks appear to use more than just reef environments (Chin et al. 2012, Chin et al. 2016), displaying an ecological flexibility that may have allowed them to seek out higher-salinity areas within the study region during low-salinity events.

Both the frequency and intensity of tropical storms are projected to increase in the future (Emanuel 2005, Webster et al. 2005), leading to associated increases in the number of high rainfall/freshwater run-off events. Practically, this means that sharks resident on inshore reefs will encounter greater and more frequent fluctuations in local salinity levels than they do currently and will need to develop mechanisms to cope if they are to survive on inshore reefs. As reef sharks are site-attached to reef habitats, they may be limited in their ability to avoid unfavourable conditions. While the current study shows that these sharks are able to handle salinity fluctuations to some degree, should conditions deteriorate past a physiological threshold or persist for an extended period of time, they may be forced to leave, risking decreased fitness or, at worst, mortality. As salinity is predicted to have some of the greatest effects on reef sharks under future climate change scenarios (Chin et al. 2010) and given current and projected declines in coral reef habitat (Hoegh-Guldberg et al. 2007, Diaz-Pulido et al. 2009), an examination of the effects of salinity on movement and activity space of reef sharks is timely and will help to better predict how they may respond in the future.

Chapter 5: Fine-Scale Movement, Behaviour and Habitat Selection Patterns of Reef Sharks on Inshore Reefs

5.1 Introduction

Tropical inshore regions are complex, heterogeneous environments (Pitcher et al. 2009) that provide important ecosystem services for many marine species, including sharks and rays (Knip et al. 2010, Yates et al. 2015). Coastal mangrove forests and intertidal mud-flats, for example, are highly productive habitats known to act as foraging grounds and nursery areas for many teleost (Beck et al. 2001, Blaber 2007, Kimirei et al. 2013) and elasmobranch (Simpfendorfer & Milward 1993, Cerutti-Pereyra et al. 2014, Heupel et al. 2019a, Martins et al. 2020) species. The use of shallow-water inshore habitats, particularly during early life-history stages, is thought to benefit individuals through enhanced feeding opportunities and protection from predators afforded within these areas (Castro 1993, Mumby et al. 2004, Blaber 2007, Heupel et al. 2007, Vaudo & Heithaus 2009). However, while many studies have documented preferential use of shallow water by juvenile sharks and rays (Wetherbee et al. 2007, Whitty et al. 2009, Knip et al. 2011a), few have examined fine-scale habitat use within these areas (Kanno et al. 2019, Martins et al. 2020). Complicating the resolution of inshore habitat use by juveniles is that these areas are often unavailable or difficult to access at lower tides (Sheaves 2005). Nonetheless, intertidal habitats may play an important role as juvenile habitat for some shark and ray species (Tobin et al. 2014, Oh et al. 2017).

Intertidal and subtidal mangrove forests occupy approximately 170,000 km² of coastline in the tropics and subtropics (Valiela et al. 2001), with many fish species dependent on them for all or part of their life cycle (Nagelkerken et al. 2002, Nagelkerken et al. 2008, Kimirei et al. 2013); however, less is known about the use and importance of mangrove habitats to elasmobranchs. For juvenile reef fish, use of mangrove habitats may reflect ease of access to an increased or specialised food supply (Robertson & Duke 1987, Ellison & Farnsworth 2000, Laegdsgaard & Johnson 2001) and/or a reduced risk of predation when sheltering within mangrove prop roots (Laegdsgaard & Johnson 2001, Mumby et al. 2004, Chittaro et al. 2005, Nagelkerken et al. 2008), although the degree to which these ecosystem services are provided is still debated (Smith & Hindell 2005, Sheaves et al. 2016, Dubuc et al. 2019). Similarly, mangrove habitats may be attractive nursery habitat to young sharks and rays due to the abundant food resources and protection that they provide (Simpfendorfer et al. 2010, Guttridge et al. 2012, Kanno et al. 2019). In fact, Chin et al. (2012), found that the presence of mangrove and seagrass habitats within 2 km of a sample increased the probability of capturing juvenile blacktip reef sharks, *Carcharhinus melanopterus*, within a tropical nearshore embayment.

Although studies have shown several elasmobranch species to occur in association with mangrove stands, (White & Potter 2004, Chin et al. 2012, Cerutti-Pereyra et al. 2014, Morgan et al. 2015), few have looked at the utilisation of these habitats as potential nursery areas and those that did focused mainly on just two species: lemon sharks, *Negaprion brevirostris* (Gruber et al. 1988, Guttridge et al. 2012) and smalltooth sawfish, *Pristis pectinata* (Simpfendorfer et al. 2010, Poulakis et al. 2011); in addition, these studies took place mostly within the Western Atlantic and Gulf of Mexico where tidal volume change is much lower compared to that of the Indo-Pacific region, resulting in mangrove habitats remaining submerged and available to individuals for longer periods of time. More recently, two species of tropical ray, the mangrove whipray, *Urogymnus granulatus,* and cowtail stingray, *Pastinachus ater*, have been observed to use mangrove stands within an intertidal bay in northern Australia as a possible refuge area and foraging ground (Davy et al. 2015, Kanno et al. 2019, Martins et al. 2020), indicating that these habitats may still be important to juveniles even when only intermittently accessible. However, apart from the aforementioned studies, little information is available on the use and importance of mangrove habitats for other shark and ray species.

Habitat edges – or the interface between two distinct habitats – may also play an important ecological role for some species. Edge effects in fragmented habitats are thought to influence the population dynamics of many terrestrial species either *directly*, through changes to their distribution and abundance, and/or *indirectly*, through changes to species interactions, such as competition or predation (Murcia 1995, Fagan et al. 1999, Ries et al. 2004, Fletcher et al. 2007). Less is known, however, about the importance of habitat edges within marine systems, particularly for sharks and rays. Heithaus et al. (2006) observed tiger sharks to show a strong preference for shallow edge habitats within seagrass ecosystems, a strategy thought to maximize encounter rates with primary prey species which are greater along edges. In fact, several studies have shown predation risk for fish to be highest along habitat edges, which often serve as a transition zone between refuges (e.g. mangrove prop roots, seagrass beds) and nearby foraging grounds (Gorman et al. 2009, Hammerschlag et al. 2010). In mobile animals, predation effects can occur through either direct consumption or as a behavioural response to predation risk; these „non-consumptive‟ risk effects can alter the movement, habitat use and/or distribution patterns of individuals as they attempt to balance maximising growth rates through foraging in high resource areas with minimising risk of mortality by avoiding predators (Dahlgren & Eggleston 2000, Grol et al. 2008, Guttridge et al. 2012, Stump et al. 2017). For example, perceived predation threats are most likely the reason why juvenile lemon sharks in Bimini, Bahamas were observed to refuge in artificial mangrove structures when predators were present (Stump et al. 2017).

To date, studies examining the role of edge effects in the spatial ecology of marine species have been conducted mostly within seagrass ecosystems (Bologna & Heck 2002, Dorenbosch et al. 2005, Tanner 2005, Smith et al. 2008, Macreadie et al. 2010, Carroll et al. 2019), and with a focus on changes in abundance and/or distribution of teleosts. A recent study on Australia‟s Great Barrier Reef (GBR) suggests that edge habitats may also play a critical role in structuring communities for coral reef fish, with 43% of 51 coral reef fish species found to have significantly higher or lower abundances along a coral reef-sand edge than in either of the adjacent habitats (Sambrook et al. 2016). Little information is currently available, however, regarding edge effects within mangrove ecosystems (Reis-Filho et al. 2016, Dubuc et al. 2019, Kanno et al. 2019, Martins et al. 2020). It is suggested that, at least for juvenile fish, utilising mangrove edges may provide an optimal medium, conferring site-specific benefits usually only acquired within adjacent habitats (e.g. opportunistic feeding, refuge; Dubuc et al. 2019). Although juveniles of several elasmobranch species are observed to regularly patrol near mangrove borders (White & Potter 2004, DiGirolamo et al. 2012, Cerutti-Pereyra et al. 2014), few studies have examined the fine-scale spatial and temporal habitat use patterns of individuals within these areas, so the mechanisms that drive movement, especially for young sharks, are still not fully understood (but see Davy et al. 2015, George et al. 2019, Kanno et al. 2019, Martins et al. 2020).

The blacktip reef shark, *Carcharhinus melanopterus* (Quoy & Gaimard 1824-25), is a medium-bodied shark commonly found on coral reefs throughout the Indo-West and Central Pacific, including Australia (Last & Stevens 2009). Localised movement and restricted space use is reported throughout their range and across various life-history stages (Stevens 1984, Papastamatiou et al. 2009a, Speed et al. 2011, Chin et al. 2016, Schlaff et al. 2020), along with ontogenetic shifts in diet (Speed et al. 2012a) and habitat use (Papastamatiou et al. 2009b, Chin et al. 2013a). Juveniles, in particular, are observed to be strongly site-attached to shallow reef-associated habitats such as sand flats (Papastamatiou et al. 2009b, Speed et al. 2016, Oh et al. 2017), with young sharks also frequently seen in close proximity to, or within, mangrove stands (Chin et al. 2012, Speed et al. 2016, George et al. 2019). However, despite the suspected importance of shallow sand flat and mangrove habitats during early life history stages, little is known about how blacktip reef sharks utilise these inshore environments or what ecosystem services they may provide.

The overall aim of this study was to investigate the fine-scale movement and habitat selection patterns of reef sharks on an inshore reef. We used passive acoustic telemetry and non-baited, remote stationary cameras to investigate patterns in movement, behaviour and habitat use of blacktip reef sharks on an intertidal reef flat in order to determine how these individuals utilise a time-restricted environment. Presence, relative abundance, residency time and behaviour of sharks were examined within three unique shallow-water habitats – sand flat, edge and mangrove stand. Movement and habitat use patterns were examined for diel, tidal, seasonal and size effects, as these factors have previously been shown to influence mangrove and intertidal fish assemblages (Robertson & Duke 1987, Rooker & Dennis 1991, Guttridge et al. 2012, Kimball & Able 2012, Igulu et al. 2014, Reis-Filho et al. 2016) as well as movement and space use of blacktip reef sharks (Papastamatiou et al. 2009b, Speed et al. 2011, Schlaff et al. 2020). Examining the fine-scale movement and habitat use of reef sharks within a shallow, tidally-restricted inshore reef system will help fill crucial knowledge gaps on the importance of inshore reef habitats for these species and the advantages they may provide.

5.2 Materials and Methods

5.2.1 *Study Site*

This study took place within Pioneer Bay, a 0.35 km² intertidal bay situated on the western side of Orpheus Island, part of the Palm Island group located approximately 16 km off the coast of far north Queensland, Australia (18.6161°S, 146.4972°E; **Figure 5.1**a). Non-estuarine mangrove stands (mostly red mangrove, *Rhizophora stylosa*) lined the bay, with a sand and coral reef flat extending approximately 400 m from the shoreline to the reef edge where it sloped ~8-10 m to the seabed. Substrate within the bay consisted mostly of sand and dead micro atolls transitioning to coral on the reef flat and soft mud within mangrove areas (see Martins et al. 2020). Average depth in the bay was 5 m and maximum tidal range ~4 m, resulting in mangrove stands and parts of the reef flat becoming completely exposed at the lowest tides.

5.2.2 *Field Methods*

To examine the movement patterns and fine-scale habitat use of blacktip reef sharks within an intertidal bay we combined passive acoustic telemetry and video monitoring using non-baited stationary cameras. Data from acoustic receivers were used to look at movement of tagged individuals within Pioneer Bay in relation to the tide and time of day. However, while acoustic data were able to provide information on when individuals were present within the bay and their estimated positions, it could not identify which habitats they were using whilst there. Video monitoring was thus used to supplement passive acoustic tracking data in order to provide information on fine-scale habitat use of sharks.

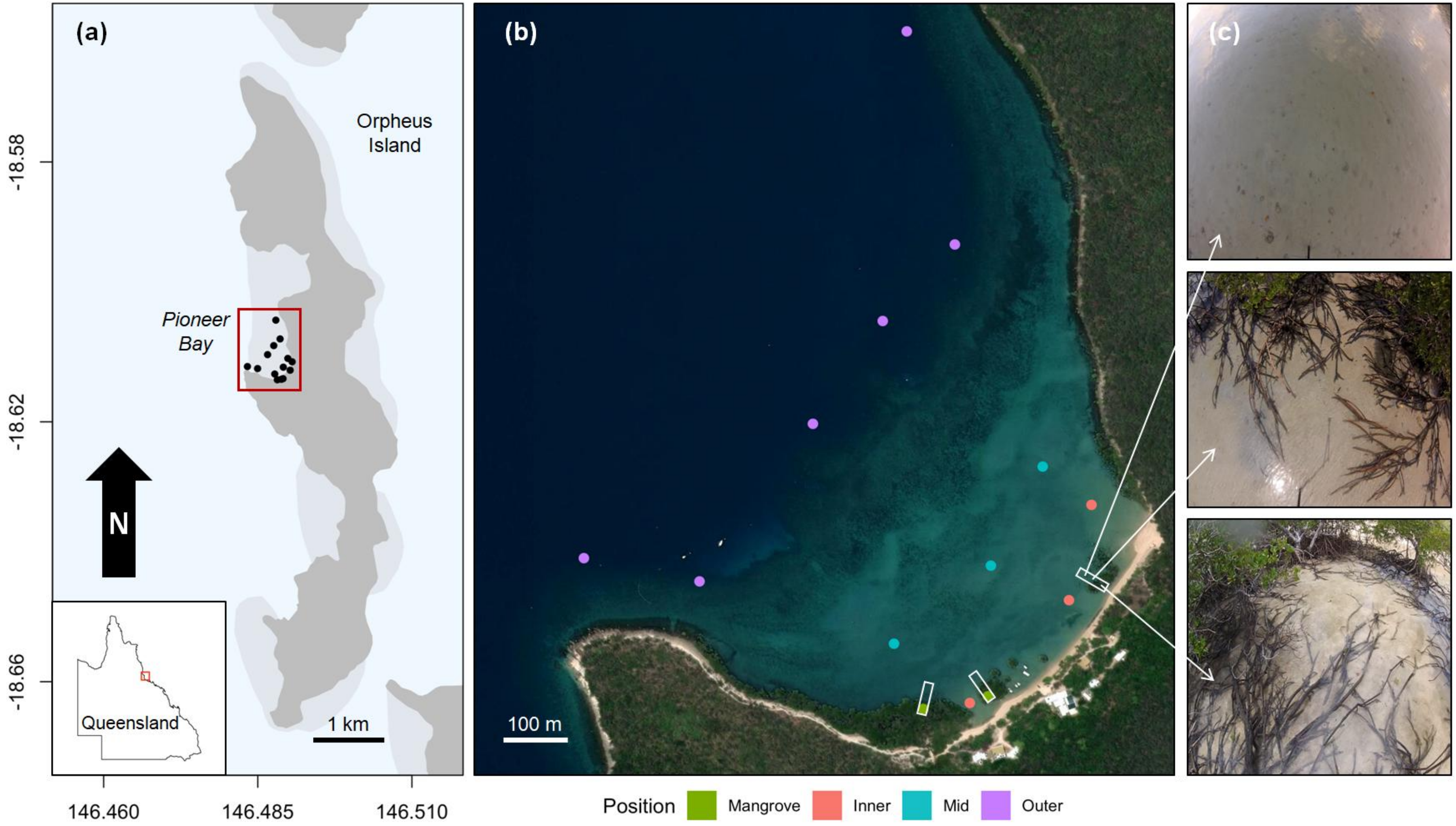

Figure 5.1: Study site: Pioneer Bay, Orpheus Island, Queensland, Australia. (a-b) Location of acoustic receivers (*circles*) within Pioneer Bay, Orpheus Island (country map *inset*); coloured *circles* indicate receiver positions and white *rectangles* denote locations of video transects. (c) Close-up of habitat types sampled within video transects: sand flat (*top*), edge (*middle*) and mangrove stand (*bottom*).

5.2.2.1 Passive Acoustic Telemetry

As part of a larger study (Schlaff et al. 2020), eight VR2W acoustic receivers (Vemco Ltd, Canada) were placed on the Pioneer Bay reef flat to look at shallow-water habitat use of tagged blacktip reef sharks (**Figure 5.1**b). Receivers were placed within dense mangrove stands (n = 2) and in rows parallel to the coastline, one close to shore (n = 3) and the other mid-bay (n = 3). Receivers were attached to star pickets and partially buried in the substrate, with the hydrophone sitting ~20 cm above the seabed. Receivers located within mangrove stands became exposed at tidal heights ≤ 180-200 cm, relative to the lowest astronomical tide, ≤ 160 cm for those closest to shore and at 140 cm for mid-bay receivers. In addition, another six receivers were placed within deeper waters (~8-10 m) of the bay, just off the reef edge. Deep-water receivers were attached to a nylon rope with float and anchored ~2-3 m above the seabed. Maximum detection range of receivers within the bay was ~125 m (Welsh et al. 2012), with detection likely greater in deeper waters adjacent to the reef flat. Acoustic receivers were downloaded twice per year.

Acoustic transmitters were surgically implanted into the abdominal cavities of sharks in order to track their movements within the study site. Sharks were captured using multi-hook long-lines and rod-and-reel, and then measured, sexed and tagged with an internal acoustic tag (V13-1L, V13P-1H or V16-4H; Vemco Ltd., Canada) and external Rototag® prior to release (see Schlaff et al. 2020 for detailed methods). Acoustic transmitters pulsed at 69 kHz on a pseudo-random repeat rate of 50-130 (V13-1L), 120-200 (V13P-1H), and 45-75 (V16-4H) seconds and had an estimated battery life of 881, 364 and 858 days, respectively. Transmitters emitted a unique ID code specific to the individual tagged. Sharks were retained for approximately 10 minutes during measuring and tagging, with all surgical procedures conducted according to protocols approved by James Cook University"s Animal Ethics committee (permit A1566).

5.2.2.2 Video Monitoring

Video transects were placed in three separate locations within Pioneer Bay for 1 week in austral summer (6−13 February 2013) and winter (17−24 August 2013) to record habitat use and behaviour of blacktip reef sharks (**Figure 5.1**b). High-definition stationary cameras (GoPro Hero 3®; 8 cm x 5 cm x 5 cm) were installed along transects, one in each of three unique shallow-water habitats: mangrove stand, sand flat and edge (i.e. the interface between mangrove and sand flat habitats) (**Figure 5.1**c). Cameras placed on sand flat and edge habitats were suspended from a 3 m wooden dowel (diameter: 25 mm) with a 1 m horizontal extension, attached to a star picket and anchored to the seabed. Cameras placed within mangrove stands were mounted to tree branches in the canopy (approximate height: 3 m) using a clamp (Gorilla Clip®). Cameras faced directly downward and had a field of view of ~35-45 m^2. Transects were deployed twice a day when daylight permitted, once on the rising tide (i.e. flood) and again on the falling tide (i.e. ebb). On the flood tide, recording was initiated prior to the waterline reaching the camera field of view. On the ebb tide, recording was initiated approximately 3.5 – 5 hours before estimated water depth dropped to ~20 cm in order to maximise recording time, as sharks were never observed to swim in depths shallower than this (AM Schlaff, pers. obs.). Cameras filmed for approximately 3.5 – 5 hours (i.e. battery life with and without extended GoPro BacPac®), before being retrieved and the footage downloaded for analysis.

5.2.3 *Data Analysis*

Detection data from acoustic receivers were used to investigate tidal and diel patterns in movement and use of Pioneer Bay by blacktip reef sharks at Orpheus Island. Data from video transects were used to investigate fine-scale, shallow-water habitat use of sharks within the bay through examination of their relative abundance, residence time and behaviour both within and between each unique habitat type. Unless otherwise stated, all statistical analyses were conducted in the R environment (R Development Core Team 2018).

5.2.3.1 Passive Acoustic Telemetry

To be considered „present‟ and included in analysis, sharks had to be detected at least twice on any given receiver on the same day, with single detections per day classified as possible false detections and removed. In addition, telemetry data collected outside of the video collection periods were excluded from analyses, which enabled a more direct comparison with video monitoring results.

Receivers were grouped into one of four position categories: „mangrove‟ units, „inner‟ intertidal units, „mid-bay‟ intertidal units and „outer‟ reef units (**Figure 5.1**b). Raw detection data were put into 30 minute time bins and analysed alongside tide data to determine the location of individuals throughout the tidal cycle and check for any patterns in movement and habitat use associated with the tide and time of day. Tide heights were determined using the local hourly tide chart at Lucinda Port (National Tide Centre, Bureau of Meteorology, Commonwealth of Australia), modelled to provide an estimate of tide height per minute. A random intercept Generalised Linear Model (GLM) with a binomial logit link error structure was then used to examine the proportion of detections at each receiver position to test for biological (size) effects across seasons [formula: prop ~ Size + Position + Season]. Only five of the nineteen individuals were represented across the two seasons, therefore a GLM model structure was selected over a mixed model framework.

Cyclic patterns in detection rates for individuals at the shallowest receivers were examined using a spectral analysis. Numbers of detections at „mangrove‟ and „inner‟ intertidal units were summed by every hour for each individual monitored. A Lomb-Scargle periodogram was generated for each tagged individual in R using the „lomb‟ package (Ruf 1999). A Fast Fourier Transform with Hamming window was applied to the data, and peaks in cyclic detections at receivers examined across a range of time-steps (0 – 100 hour steps) to identify any tidal (~12.4h) or diel (~24h) peaks in the calculated normalised power spectral density. An average periodogram was calculated across juvenile and adult life-stages, and significance limits at $\alpha = 0.05$ were estimated to identify significant cyclic peaks.

5.2.3.2 Video Monitoring

Video footage was analysed in Event Measure Version 4.43 downloaded from SeaGIS (www.seagis.com.au), with information collected on: species ID; estimated stage of maturity (juvenile, adult or unknown); time of entry and departure and; behaviour when present. Species recorded included all sharks as well as large teleosts assumed to be capable of hunting and consuming small sharks (e.g. giant trevally, *Caranx ignobilis*). Stage of maturity was determined by estimating the body size of sharks using stationary objects of known size within the video, with "juveniles" categorised as individuals < 1000 mm stretch total length (STL) and "adults" > 1000 mm STL, which corresponded to conservative estimates for size at maturity (see review in Mourier et al. 2013). The amount of time individuals spent within each habitat was used as a proxy for residency and calculated using observed times of entry and departure. Each individual was assigned a behaviour classification: „transiting‟ (straight-line swimming without changing direction), „searching‟ (swimming while changing direction regularly) or „feeding‟ (actively chasing fish or feeding).

Relative abundance and residence time of sharks within each habitat type were analysed for biological (maturity stage) and environmental (tidal) effects. The density of shark sightings during the full period on video monitoring was used as a proxy for relative abundance. Patterns in the relative abundance of adults and juveniles were examined across the full tidal range and between sampled habitats and analysed using a two-way ANOVA which compared the mean tidal height between each size class and habitat type. Residence time was defined as the total amount of time an individual was continuously present when in the video and calculated as the difference between an individual‟s last sighting time and that of their initial appearance. Mean residence time of sharks while in each habitat was calculated for the full tidal period, with tide height placed into 25cm bins for analysis. A random intercept GLM was used to compare residency time of observed sharks across the full tidal range and across habitats for each life-stage. Residency time was log-transformed to improve normality of residuals. The influence of the tidal cycle was explored using another GLM which modelled the residency time of sharks within each habitat between periods of rising and falling tides.

Behaviour of each individual was recorded while "resident" and analysed using a chi-squared goodness of fit test to determine whether the proportion of behaviour varied: (1) between each habitat type within the same season (i.e. proportional difference between mangrove stand, sand flat and edge habitats during summer or winter), (2) seasonally within the same habitat (i.e. between summer and winter for each habitat type) and (3) across habitats between rising and falling tidal stages.

5.3 Results

5.3.1 *Passive Acoustic Telemetry*

Eighteen blacktip reef sharks were monitored within the study site in summer (11 adults, 7 juveniles) and six in winter (3 adults, 3 juveniles) (**Figure 5.2**). Body size of juvenile sharks ranged from 559 mm STL to 998 mm STL and adults from 1040 mm STL to 1498 mm STL (**Table 5.1**), which is close to the minimum and maximum sizes reported for this species locally (Chin et al. 2013b). While the ratio of males to females was nearly even during the summer monitoring period for both juveniles (4 females, 3 males) and adults (6 females, 5 males), only adult males were monitored within the array in winter (juveniles: 2 females, 1 male). Lower sample size and the absence of adult females in winter were largely due to transmitters reaching the end of their predicted battery life prior to this video recording period. Sharks were highly resident during both monitoring periods, with adults detected every day during the summer and most days during winter; juveniles never left the study site.

Tide height had a significant influence on location of juvenile sharks within Pioneer Bay. In general, young sharks moved progressively toward shore on the incoming tide, making use of shallow, intertidal habitats as soon as they became available (**Figure 5.2**). The opposite pattern was observed during falling tides, when juveniles gradually moved away from shore as water levels receded within the bay. During high tides, when all habitats were considered available (tide heights ≥ 180 cm), the smallest sharks were primarily detected on mangrove and intertidal units while larger juveniles and adults were mostly detected on outer reef receivers. During low tides, the number of detections of the smallest juveniles decreased considerably, with most either only occasionally detected on the outer receiver line or not at all, indicating these individuals were most likely occupying shallow waters near

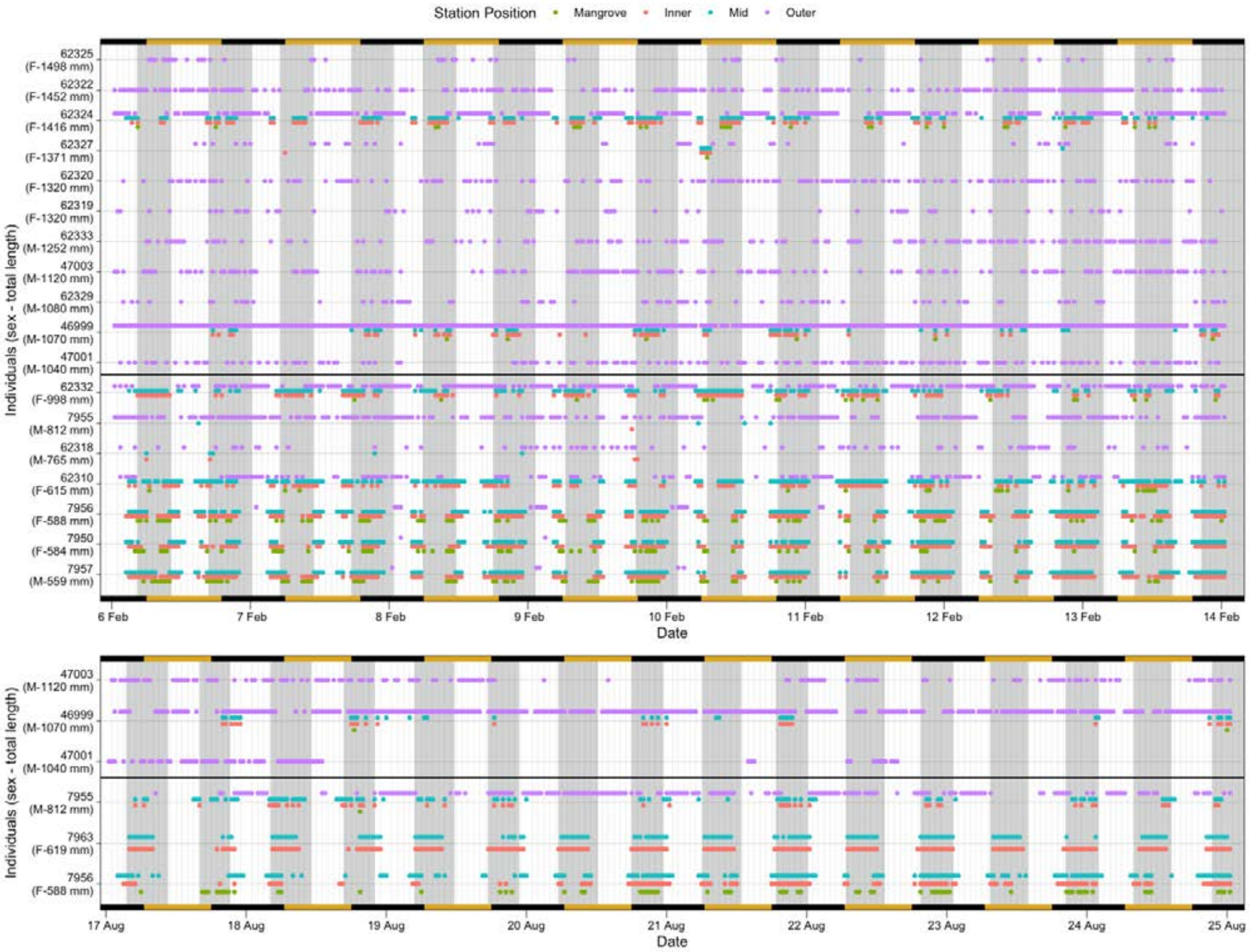

Figure 5.2: Presence plot of acoustically tagged blacktip reef sharks in Pioneer Bay, Orpheus Island, over 1 week in austral summer (*top*) and winter (*bottom*). Coloured *circles* indicate detections at mangrove (*green*), inner intertidal (*red*), mid-bay intertidal (*blue*) and outer reef (*purple*) receivers. *Horizontal black lines* separate adult (*above*) and juvenile (*below*) sharks, *shaded vertical bars* indicate times when all habitats were available, and *black* and *gold checkered banner*s denote nighttime and daytime periods, respectively.

Table 5.1: Details of acoustically tagged blacktip reef sharks, *Carcharhinus melanopterus* (ID code), with stretch total length (STL), sex and proportion of detections at „mangrove‟, „inner‟ intertidal, „mid-bay‟ and „outer‟ reef receivers over 1 week in austral summer (Feb) and winter (Aug).

ID code	**STL (mm)**	**Sex**	**% Mangrove**		**% Inner**		**% Mid**		**% Outer**	
			Feb	**Aug**	**Feb**	**Aug**	**Feb**	**Aug**	**Feb**	**Aug**
7957	559	M	11.21		47.02		41.37		0.41	
7950	584	F	11.27		48.48		40.13		0.12	
7956	588	F	9.71	10.89	46.49	46.60	42.45	42.51	1.35	
62310	615	F	2.80		26.87		51.31		19.03	
7963	619	F				68.32		31.68		
62318	765	M			2.88		4.32		92.81	
7955	812	M		0.21	0.29	14.48	0.72	32.34	98.99	52.98
62332	998	F	1.25		21.67		36.14		40.95	
47001	1040	M*							100	100
46999	1070	M*	0.07	0.05	3.31	2.36	3.90	3.25	92.72	94.34
62329	1080	M*							100	
47003	1120	M*							100	100
62333	1252	M*							100	
62319	1320	F*							100	
62320	1320	F*							100	
62327	1371	F*	0.81		24.39		24.39		50.41	
62324	1416	F*	2.24		25.62		37.45		34.70	
62322	1452	F*							100	
62325	1498	F*							100	

* Indicates mature individuals.

the reef crest and largely out of range of reef receivers. In contrast, larger juveniles and adults were frequently detected at outer receivers during low tide periods, indicating they remained in deeper water near the reef slope. Four individuals displayed detection patterns which appeared to combine characteristics of both adults and juveniles. Animal 7955, (male, 812 mm), 62332 (female, 998 mm), 46999 (male, 1070 mm) and 62324 (female, 1416 mm) were frequently detected on intertidal and mangrove receivers during high tide periods and on outer receivers during lower tides.

Diel patterns in movement were also observed amongst the smallest juveniles across both seasons, with detections on intertidal and mangrove receivers more numerous and consistent during high tide periods at night than those during the day (**Figure 5.2**). It is unlikely that drops in the number of detections during the day were due to juveniles having exited the bay, as they were detected within intertidal habitats both immediately preceding and following their availability. Furthermore, variations in tidal volume (i.e. depth and duration), and thus availability of intertidal habitats, were not responsible for the diel effects observed, as this pattern was clear during both sampling periods even though the highest high tides occurred at night during summer and in the daytime during winter (**Figure 5.3**). Welsh et al. (2012) observed no diel differences in receiver performance or detection

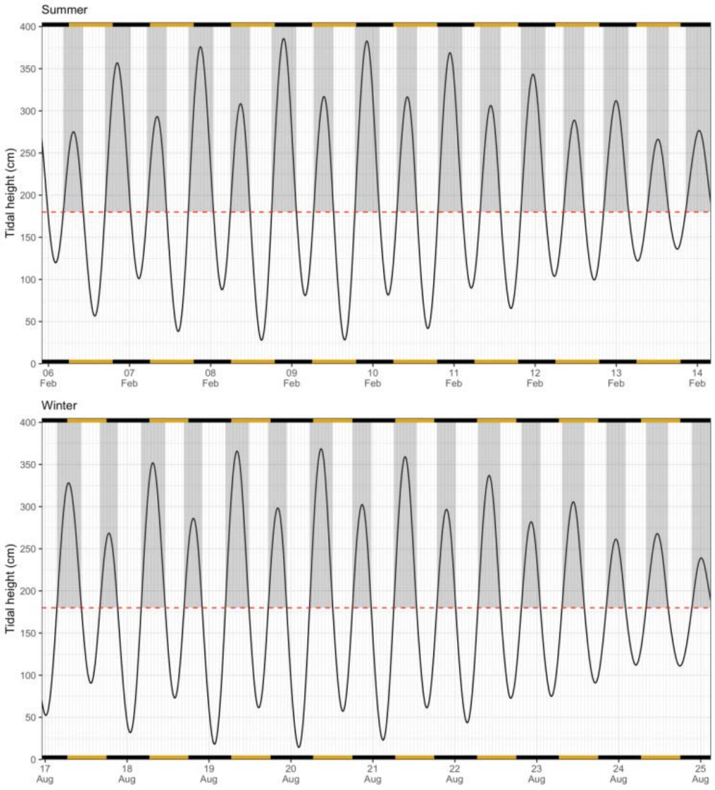

Figure 5.3: Tide predictions for Pioneer Bay, Orpheus Island, over the study period, 1 week in austral summer (*top*) and winter (*bottom*). *Black* and *gold checkered banner*s denote nighttime and daytime periods, respectively.

capabilities within Pioneer Bay, so it is also unlikely that nocturnal increases in biological noise within intertidal areas compromised detections. There was no apparent diel pattern in detection on outer reef receivers amongst adults. Of the two adults frequently detected on intertidal and mangrove receivers, animal 62324 was present within these habitats during any high tide period, day or night, as was animal 46999 during summer.

A tidal and diel signature was reflected in results from spectral analysis for juveniles only, with two main peaks in normalised spectral densities at 12.4 and 24 hours (**Figure 5.4**). There was considerable variability in cyclic detection patterns on inshore receivers between individuals; however the average periodogram for juveniles indicated a significant peak at both diel and tidal cycles.

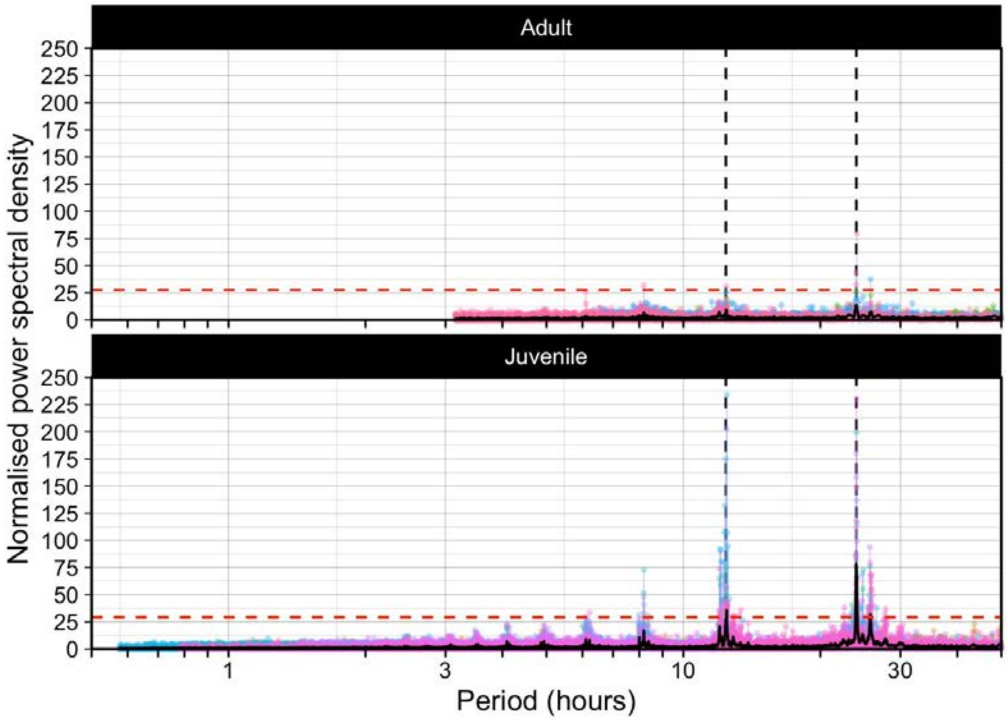

Figure 5.4: Spectral density of hourly detections of tagged blacktip reef sharks on „mangrove" and „inner" intertidal receivers in Pioneer Bay, Orpheus Island. *Black line* is the rolling average for adults (*top*) and juveniles (*bottom*), and *dashed red lines* indicate significance limits at α = 0.05, with peaks above these lines indicating significant cyclic peaks.

There were no significant seasonal differences in the proportion of detections at different receiver positions within the bay ($p = 0.746$); however there was a clear pattern between the proportion of detections and size of sharks, with larger individuals detected on outer reef receivers significantly more than on inner, mid-bay and mangrove receivers ($z_{1,63} = 2.66$, $p < 0.01$; **Figure 5.5**). For adults, the majority of detections in both summer (89 ± 7%) and winter (98 ± 2%) were recorded on outer reef receivers (**Table 5.1**), while the opposite pattern was observed for juveniles, with most detections coming from intertidal and mangrove units (summer: 64 ± 16%; winter: 82 ± 18%). Of the five individuals detected during both summer and winter, two displayed noticeably different patterns in movement between seasons. Animal 7955 was almost exclusively detected on outer reef receivers in summer, but during the winter was regularly detected on intertidal and mangrove receivers when these habitats became available (**Figure 5.2**). In contrast, while animal 46999 was detected within intertidal and mangrove habitats across both seasons, detections in summer occurred during both daytime and nighttime high tides, but primarily only at night during winter.

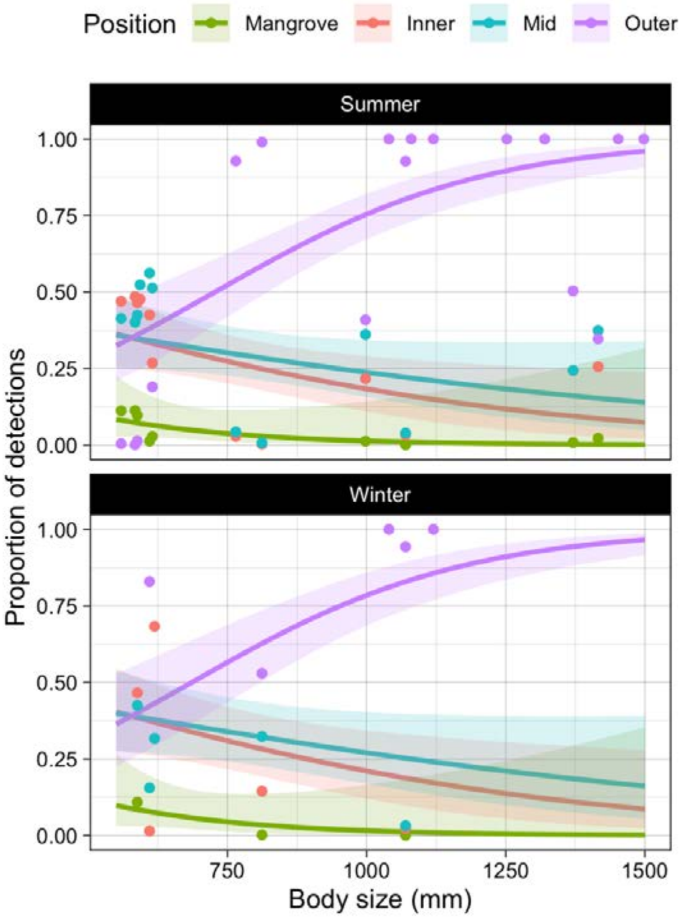

Figure 5.5: Proportion of detections of tagged blacktip reef sharks at „mangrove‟, „inner‟ intertidal, „mid-bay‟ and „outer‟ reef receivers over 1 week in austral summer (*top*) and winter (*bottom*). *Shaded areas* indicate 95% confidence intervals and points are raw data for body size (stretch total length).

5.3.2 *Video Monitoring*

A total of 63 videos were analysed in summer (21 in each habitat) and 89 in winter (30 in sand flat and edge habitats, 29 in mangrove stands). Video recording times ranged from 0.9 – 3.7 hours (mean: 2.7 ± 0.02 SE) in summer and 0.8 – 4.0 hours (mean: 2.6 ± 0.01 SE) in winter. Total observations of juvenile and adult blacktip reef sharks, respectively, were 268 and 25 in summer and 52 and 15 in winter. In addition, 10 juvenile lemon sharks, *Negaprion acutidens*, were observed in summer and nine in winter; however, as sub-adults these individuals were most likely incapable of hunting and consuming small blacktip reef sharks and were thus excluded from subsequent analyses.

Results from video monitoring revealed size and tidal influences on habitat use of sharks. Analysis of the relative abundance of sharks showed no significant difference in the tidal height at which adults were observed across all habitats ($F_{1,2} = 1.28$, $p = 0.28$), however there was a significant difference in variance of observations between juveniles and adults across all habitats ($F_{1,1} = 24.50$, $p = < 0.01$); juveniles were observed in mangrove stands and edge habitats at significantly higher tides than in adjacent sand flat habitats ($F_{1,2} = 92.56$, $p = < 0.01$). In general, the relative abundance of juveniles was greatest within sand flat habitats on lower tides, peaking just below the point at which mangrove and edge habitats became available (tide height: ~180 cm; **Figure 5.6**). At tide heights above 180 cm, relative abundance of young sharks was greatest within edge and mangrove habitats, with individuals observed most frequently within mangrove stands at the highest tides. In contrast, adults were almost exclusively observed in sand and edge habitats regardless of tide height. Similarly, residency time of adult sharks when present in sand flat and edge habitats remained much the same irrespective of tide height, while juveniles were observed to spend more time when in mangrove habitats on higher tides than in either edge or sand flat habitats (**Figure 5.7**).

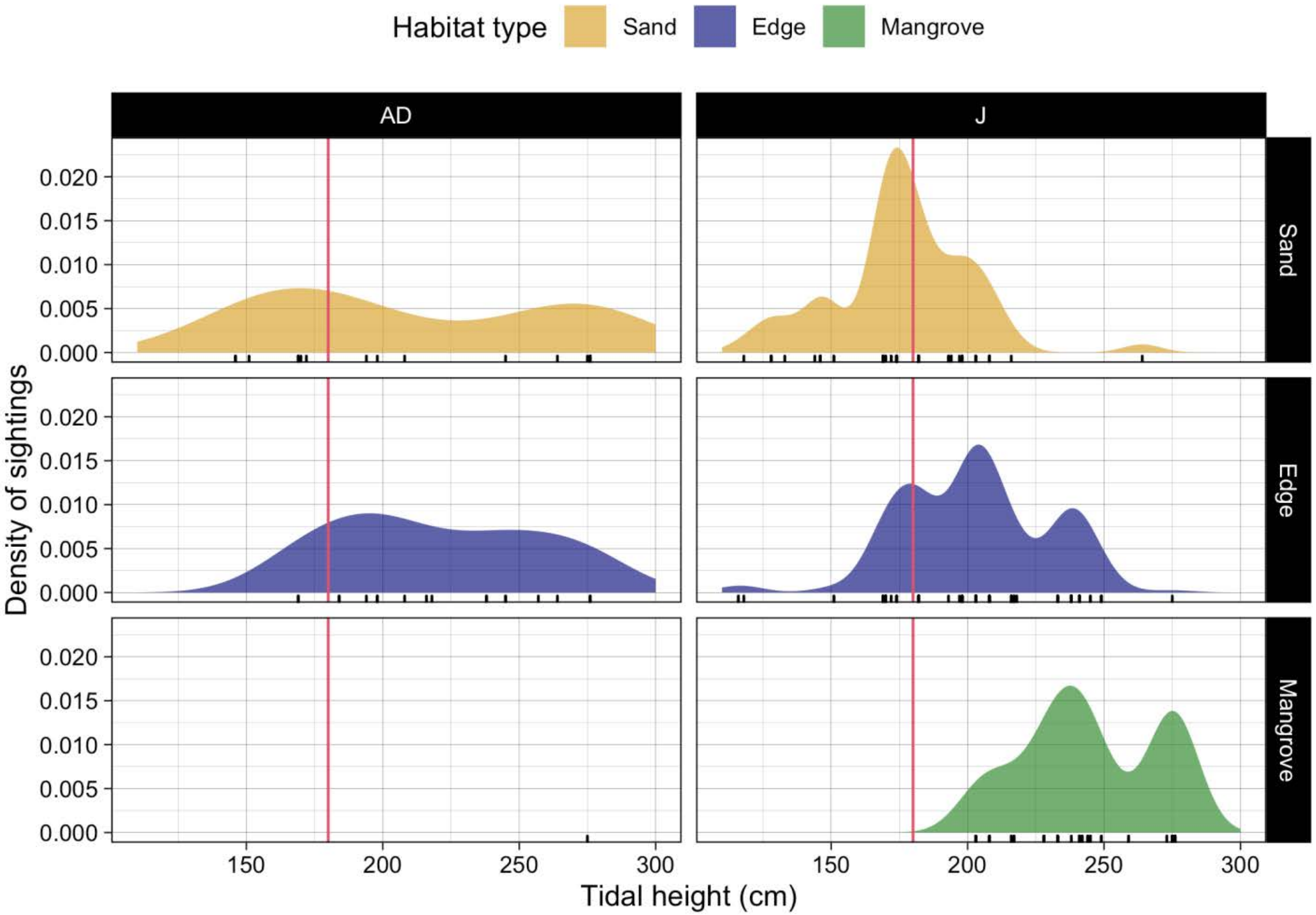

Figure 5.6: Relative abundance of adult (*left*) and juvenile (*right*) blacktip reef sharks within 3 unique shallow-water habitats in Pioneer Bay, Orpheus Island. Panels denote sand flat (*top*), edge (*middle*) and mangrove (*bottom*) habitats, and *red line* indicates tide height at which all habitats became available.

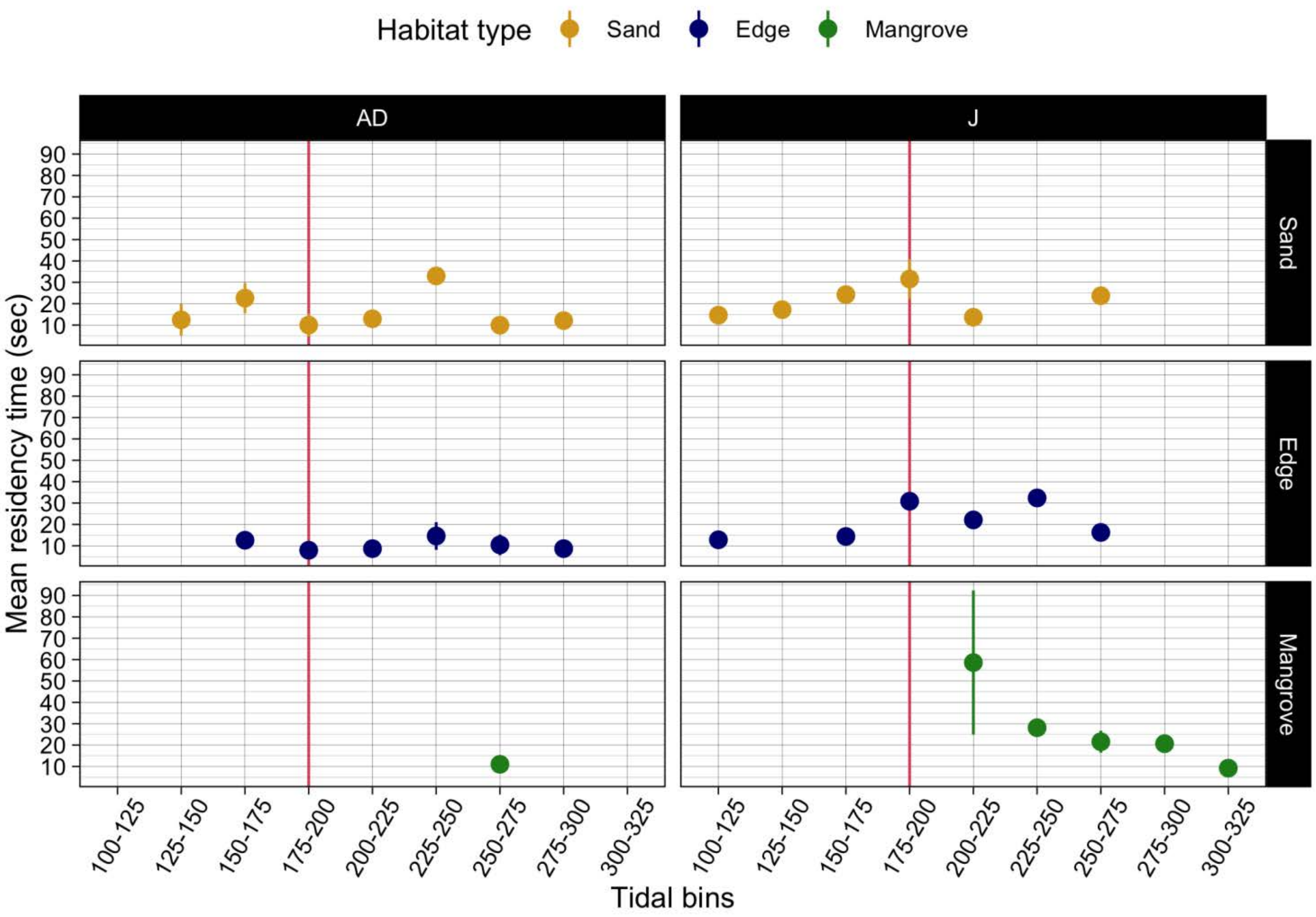

Figure 5.7: Mean and standard error residency time of adult (*left*) and juvenile (*right*) blacktip reef sharks within 3 unique shallow-water habitats in Pioneer Bay, Orpheus Island. Panels denote sand flat (*top*), edge (*middle*) and mangrove (*bottom*) habitats, and *red line* indicates tide height at which all habitats

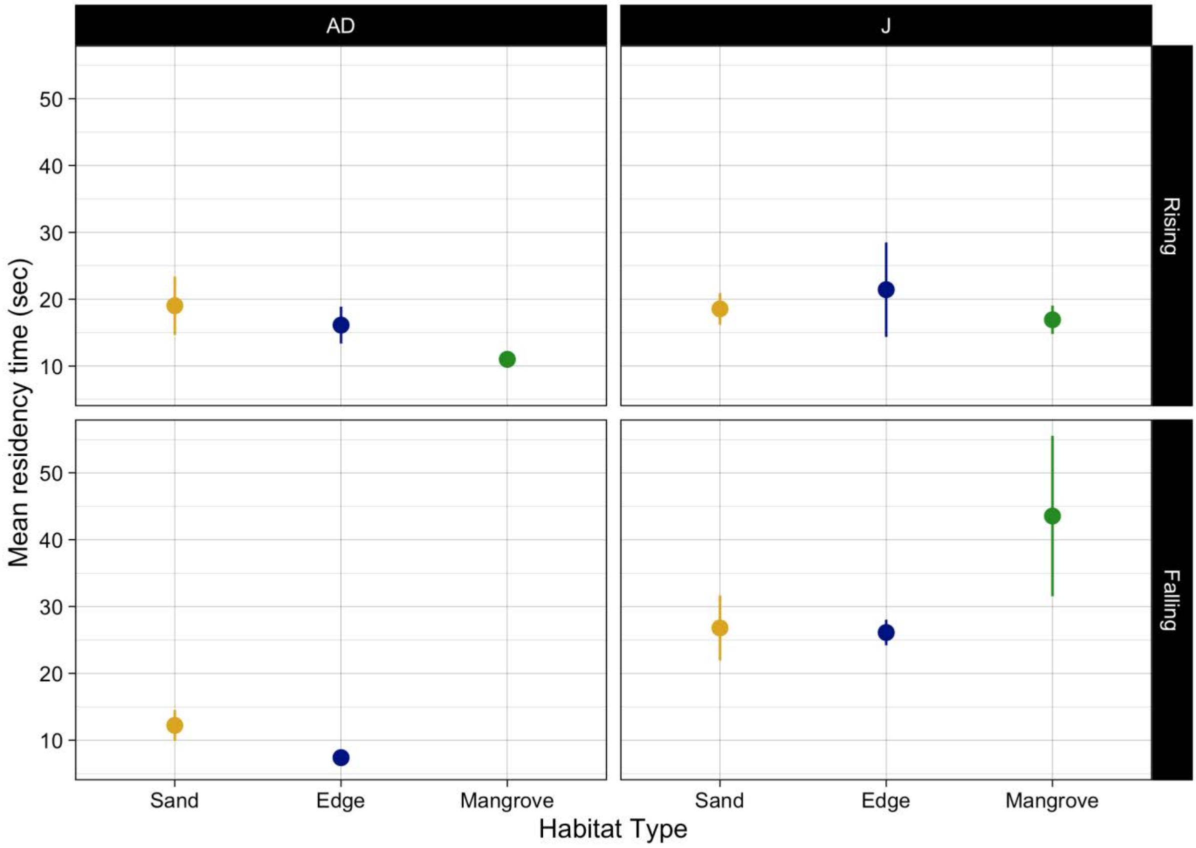

Figure 5.8: Mean and standard error residency time of adult (*left*) and juvenile (*right*) blacktip reef sharks within 3 unique shallow-water habitats in Pioneer Bay, Orpheus Island over periods of rising (*top*) and falling (*bottom*) tides.

There was no significant difference in mean residency times of adults observed across tidal heights ($t_{1,349} = 0.47$, $p = 0.64$) and across habitats ($t_{1,349} = 0.42$, $p = 0.56$). However, juveniles were observed to be significantly more resident at higher tidal heights in the mangrove stands as compared to the other two habitats ($t_{1,349} = 3.18$, $p = < 0.01$). Mean residency times within habitat types also differed with tidal stage for both juveniles and adults; in general, juveniles spent more time within mangrove stands on falling tides ($t_{1,349} = 2.88$, $p < 0.01$), while adults spent more time within edge and sand flat habitats on the rising tides ($t_{1,349} = 2.04$, $p < 0.01$) and were only ever recorded in mangrove habitats during this period as well (**Figure 5.8**).

Proportion of observed behaviour differed significantly between adults and juveniles over both summer and winter (summer: $\chi^2 = 8.02$, $p < 0.01$, winter: $\chi^2 = 36.2$, $p < 0.01$), with juveniles spending more time searching while adults were largely observed to be transiting through the area (**Figure 5.9**). Among juveniles, proportion of observed behaviours were not significantly different across habitat types in winter ($\chi^2 = 0.22$, $p = 0.89$), however significantly differed across habitats in summer ($\chi^2 = 10.8$, $p = 0.02$). Young sharks spent an average of ~20-25% more time searching while in mangrove habitats in summer than in either edge or sand flat habitats, respectively (**Figure 5.9**). Juvenile sharks were never observed actively feeding when in mangrove stands (**Figure 5.9**). Behaviour of adult sharks differed between habitat types ($\chi^2 = 27.2$, $p < 0.01$), however was not significantly different across seasons due to low numbers of observations ($\chi^2 = 3.52$, $p = 0.06$). Large sharks were never observed searching when in mangrove habitats and only ever observed searching in edge habitats during winter. The proportion of observed behaviours differed significantly with tidal stage for both juveniles ($\chi^2 = 11.01$, $p < 0.01$) and adults ($\chi^2 = 17.07$, $p < 0.01$). The general trend was for juveniles to spend more time searching on the falling tide than the rising, while the opposite pattern was observed for adults (**Figure 5.10**).

5.4 Discussion

Analysis of the fine-scale movement patterns and habitat use of juvenile blacktip reef sharks within a tropical inshore bay showed them to be strongly associated with tide, with young sharks moving to occupy shallow nearshore habitats on the intertidal reef flat as soon as they became available. There was also clear size-based habitat partitioning within the bay, with the smallest individuals utilising shallow intertidal and mangrove habitats disproportionately while adults and larger juveniles mostly occupied deeper areas off of the reef slope. Preferential use of mangrove habitats by smaller juveniles was most likely a predator avoidance strategy, with young sharks refuging among prop-roots in areas inaccessible to predators due to their larger size. Although previous studies have observed juvenile blacktip reef sharks in close proximity to mangrove stands (Chin et al. 2012, Speed et al. 2016), limitations in the ability to effectively monitor intertidal and

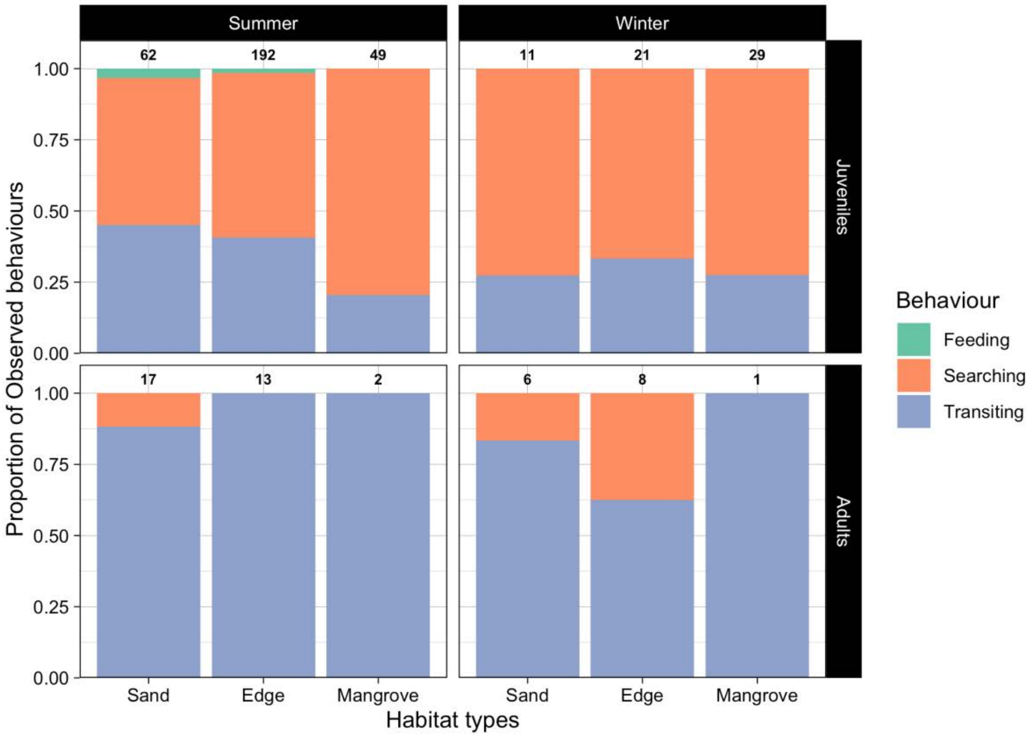

Figure 5.9: Proportion of observed behaviours among juvenile (*top*) and adult (*bottom*) blacktip reef sharks within sand, edge and mangrove habitats in Pioneer Bay, Orpheus Island, over 1 week in austral summer (*left*) and winter (*right*). Number of behavioural observations indicated above column.

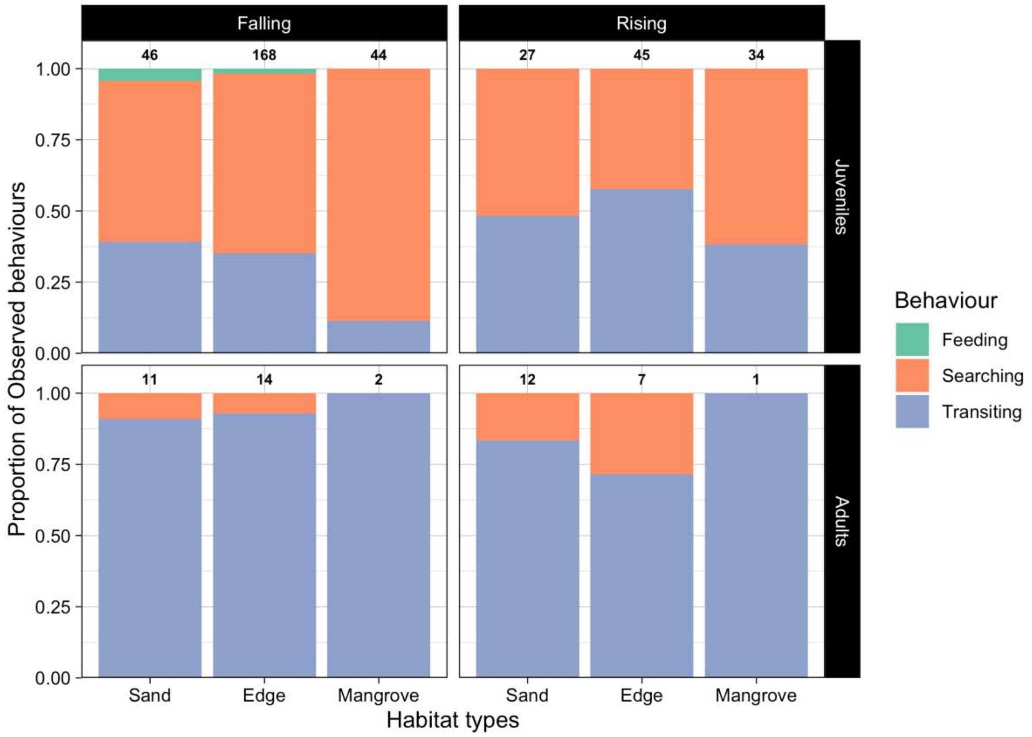

Figure 5.10: Proportion of observed behaviours among juvenile (*top*) and adult (*bottom*) blacktip reef sharks within sand, edge and mangrove habitats in Pioneer Bay, Orpheus Island, over periods of falling (*left*) and rising (*right*) tides. Number of behavioural observations indicated above column.

mangrove areas using acoustic telemetry means that fine-scale temporal and spatial use of mangrove habitats has remained largely unstudied (but see George et al. 2019). Results from video monitoring support observations from telemetry studies and indicate that mangrove habitats likely provide important ecosystem services for blacktip reef sharks at a critical stage in their life-history.

Juvenile blacktip reef sharks were observed to undertake regular, tidally-driven migrations onto the reef flat in Pioneer Bay, with young sharks moving progressively into shallow-water areas on the incoming tide and retreating as the tide fell. In contrast, adults largely occupied deeper water habitats off of the reef slope throughout the day. Ontogenetic differences in habitat use are well-documented among elasmobranchs, including reef sharks, with studies typically reporting preferential use of shallow-water habitats for juveniles and adults to occupy deeper water (Gruber et al. 1988, Wetherbee et al. 2007, Grubbs 2010, Knip et al. 2011a). Similarly, blacktip reef sharks are reported to partition habitat with size, with juveniles selecting shallower habitats than adults throughout their range (Papastamatiou et al. 2009b, Speed et al. 2016, Oh et al. 2017, Schlaff et al. 2020). As vulnerability to predation and resource requirements change with increasing animal size (Jetz et al. 2004, Lowe & Bray 2006), it is perhaps unsurprising for patterns in movement and habitat use to change in response to the shifting needs of individuals. Two individuals observed to display movement patterns that combined those of adults and the smallest sharks were larger juveniles, and thus may have simply represented an ontogenetic transition period where vulnerability to predation and a need to refuge was being balanced with increasing resource requirements and a need to forage more widely. The other two individuals that displayed combined patterns were both adults. Shipley et al. (2018) found adult Caribbean reef sharks, *Carcharhinus perezi*, to largely occupy deeper water habitats, with occasional forays onto the reef shelf likely related to foraging. Similarly, larger blacktip reef sharks at Orpheus Island may primarily occupy deeper habitats off of the reef slope, with some individuals moving into intertidal areas to forage opportunistically when these habitats become available. Given this pattern was consistently observed for the same two individuals over time, however, also suggests individual specialisation in an intertidal hunting strategy, which is consistent with observations of stable isotopes in bull sharks, *Carcharhinus leucas*, which show individual specialisation in diet (Matich et al. 2011).

Tidally-mediated movements have been observed for blacktip reef sharks elsewhere, with pups and young-of-the-year at Palmyra Atoll moving with the tide to occupy shallow sand flat habitats that were inaccessible at lower tides (Papastamatiou et al. 2009b). In a separate study that actively tracked juvenile blacktip reef sharks in Pioneer Bay, individuals also appeared to move in synchrony with the tide (George et al. 2019). Similar movement patterns have been observed for juveniles of other tropical reef-associated elasmobranchs, namely lemon sharks (Wetherbee et al. 2007, Guttridge et al. 2012) and mangrove whiprays (Davy et al. 2015), and are thought to be a predator avoidance strategy. As relative predation risk has been shown to increase with water depth (Rypel et al. 2007), young sharks may move with the tide in order to remain within shallow-water areas, which larger predators cannot easily access due to their size. Turbid conditions within shallow-water habitats may also offer a degree of protection to young sharks from visual predators, thus reducing predation pressure and allowing them to forage without disruption (Chin et al. 2013c, Cerutti-Pereyra et al. 2014).

George et al. (2019) observed juvenile blacktip reef sharks in Pioneer Bay to never move beyond the reef crest or enter into deeper water beyond the fringing reef even at the lowest tides. For species that regularly utilise intertidal areas, movement to and from these habitats may carry a significant risk of predation and young sharks must possess strategies to minimise this risk. Juvenile mangrove whiprays, for example, exhibited high rates of movement and travelled along a more linear path when transiting between low- and high tide refuges on the incoming tide, with rays remaining in very shallow water at all times (Davy et al. 2015). Similar behaviour was also observed for juvenile cowtail stingrays (Martins et al. 2020) and blacktip reefs sharks (George et al. 2019) on the same reef. By remaining near the reef crest at low tides, and then moving quickly with the tide to shelter in shallow-water habitats during high tide periods, juvenile sharks may decrease encounter rates with possible predators and thus minimise their risk of mortality.

Intertidal habitats are also known to be important foraging grounds for several reef-associated fish species (Lugendo et al. 2007, Castellanos-Galindo et al. 2010) and some sharks and rays (Ackerman et al. 2000, Campos et al. 2009, Vaudo & Heithaus 2012, Kanno et al. 2019), so it is possible that juvenile sharks here may be moving with the tide in order to forage within the bay. A stable isotope study by Speed et al. (2012a), suggests that young blacktip reef sharks feed from lower in the food web compared with their larger conspecifics. As such, juvenile sharks at Orpheus Island may be selectively foraging on smaller prey items within intertidal habitats while larger juveniles and adults remain in deeper water and feed from higher in the food chain.

Alternatively, consistent use of shallow-water, intertidal areas by the smallest sharks may be a thermoregulatory strategy, whereby individuals obtain some physiological benefit (e.g. increase in somatic growth, digestion) when moving with the tide to occupy warmer water areas within the bay. Preferential use of extremely shallow water (< 0.6m) by 0+ freshwater sawfish, *Pristis microdon*, may be due, in part, to individuals optimizing growth rates by occupying warmer water (Whitty et al. 2009) – a strategy possibly employed by smalltooth sawfish (Poulakis et al. 2011), lemon sharks (Morrissey & Gruber 1993) and mangrove whiprays (Higgins 2018). Juvenile lemon sharks have also been observed to select progressively warmer waters throughout the day within a thermally heterogeneous nursery, thought to prolong feeding activities and/or digestion (DiGirolamo et al. 2012). More recently, juvenile mangrove whiprays utilising shallow-water habitats within Pioneer Bay have been shown to select temperatures close to their maximum thermal threshold as a possible predator avoidance strategy, as these conditions are physiologically challenging and may be prohibitive to predators (Higgins 2018). Evidence of possible behavioural thermoregulation has also been observed for blacktip reef sharks. Adult females aggregating in coastal waters in Western Australia are observed to seek out the warmest waters within a bay, a behavioural strategy thought to aid in reproduction (Speed et al. 2012b). In contrast, adult females at a tropical Pacific atoll may swim in warmer waters at the surface during the day in order to increase digestion rates and maximise subsequent foraging (Papastamatiou et al. 2015). Both studies focused on adult females, however, and as it was beyond the scope of the current study, it remains unknown whether juvenile blacktip reef sharks at Orpheus Island behaviourally thermoregulate.

During high tide periods when predators were able to access most habitats within the bay, the smallest individuals were frequently detected within mangrove habitats, lending support to a behavioural strategy aimed at minimising encounter rates with predators and possible mortality

(Sheaves 2005). Young sharks were also sighted more frequently on cameras within mangrove habitats at higher tides and stayed for longer periods of time whilst there; this coincided with the presence of larger sharks in edge and adjacent sand flat habitats. Similarly, greater numbers of juvenile lemon sharks were observed to use mangrove-inlets at higher tides and for longer periods of time when predators were in the area (Guttridge et al. 2012). Neonate smalltooth sawfish have also been observed to refuge among mangrove prop roots in extremely shallow water when a shark was seen feeding nearby (Poulakis et al. 2011). Use of mangrove habitats at Orpheus Island likely provides the smallest sharks with refuge from predation, similar to juveniles of other tropical reef-associated shark and ray species (DiGirolamo et al. 2012, Davy et al. 2015, Stump et al. 2017, Kanno et al. 2019). Predator avoidance strategies may also be responsible for the observed diel patterns in habitat use. During the day, when vulnerability to predation is likely higher due to greater visibility, young sharks may take advantage of high tidal volumes to refuge deep within complex mangrove habitats where they are out of reach of predators, but also out of range of receivers. At night, when visibility is reduced, juveniles may move more freely throughout the bay.

In fact, predation risk has been shown to be up to two times higher outside of mangrove habitats for some reef fish (Chittaro et al. 2005). Lowered risk of mortality within mangrove habitats has been attributed to various characteristics intrinsic to these environments including: depth (Rypel et al. 2007); turbidity (Nagelkerken 2009); structural complexity (Laegdsgaard & Johnson 2001, de la Moriniere et al. 2004, Verweij et al. 2006, Nagelkerken & Faunce 2008, Nagelkerken 2009) and/or; shade (Helfman 1981, de la Moriniere et al. 2004, Ellis & Bell 2004, Verweij et al. 2006). Helfman (1981), for example, determined that a shaded observer could see a sunlit object at more than 2.5 times the distance at which an unshaded observer could see a shaded target. As such, young sharks sheltering among mangrove prop roots are both better able to see approaching predators and, at the same time, themselves more difficult to see. Juvenile blacktip reef sharks actively tracked within Pioneer Bay were observed to predominately restrict their movements to mangrove stands during high tide periods, spending approximately 70% of their time within these areas (George et al. 2019). As such, use of mangrove habitats by young sharks here does not appear to be simply a result of shallow-water depth use as has been suggested elsewhere (Morrissey & Gruber 1993), but rather selection for a preferred habitat type during a critical stage in their life-history.

It has been suggested that where refuge from predation is the primary motivation to use mangrove habitats, remaining in these habitats as long as possible would maximise the advantage (Sheaves 2005). During falling tides, however, a trade-off exists between maximising protection from predation and the risk of becoming stranded in shallow water. Juveniles of some estuarine species, for example, have been observed to leave sheltered mangrove habitats at roughly the same depth at which they arrived, a strategy thought to ensure safe passage back to lower tide refuges (Reis-Filho et al. 2016). For juvenile blacktip reef sharks, lower mean residency and more time spent transiting within intertidal habitats during rising tides indicates that sharks were not lingering in these areas. In turn, higher residency times within mangrove stands on falling tides may be due to sharks delaying departure from these protective habitats as long as possible to mitigate their risk of predation when transiting to low-tide refuges on the reef crest. Similar movement patterns were observed for actively tracked juvenile blacktip reef sharks in Pioneer Bay (George et al. 2019); individuals moved quickly and in a directed manner through exposed areas during incoming tides, thought to minimise predation risk, whereas during high and ebbing tides sharks remained in mangrove habitats as long as possible before moving quickly towards low tide refuges, most likely to avoid stranding. For adults, higher residency times on rising tides may simply be a foraging strategy, with larger sharks focusing hunting efforts on the incoming tide when juveniles may not yet have access to protective mangrove habitats and there is no risk of stranding.

Mangrove habitats may also provide access to favourable environmental conditions or specialised food resources compared to open areas (e.g. sand flats). During the day, water temperatures in Pioneer Bay were observed to be cooler under the mangrove canopy than on the adjacent sand flat during summer, but warmer in winter (Davy 2012); this may explain the preferential use of these habitats by juvenile mangrove whiprays, with individuals thought to obtain physiological benefits in the form of decreased maintenance costs or increases in digestive efficiency (Davy et al. 2015, Higgins 2018). Similarly, juvenile blacktip reef sharks may be exploiting thermal heterogeneity at this site by moving to access advantageous conditions within mangrove stands during high tide periods, although this was not tested. It is also possible that habitat selection of young sharks may reflect movement to access preferred prey species found within mangrove areas. Blacktip reef sharks are opportunistic feeders, observed to feed predominantly on teleost fish (Stevens 1984) and, to a lesser degree, crustaceans and cephalopods (Lyle 1987, Cortes 1999). It is possible that the high abundance of invertebrate species found among mangrove prop roots (Ellison & Farnsworth 2000) along with the high number of coral reef fish species that have been documented within mangrove habitats in Pioneer Bay specifically (Barnes et al. 2012) may be responsible for attracting juvenile sharks to these habitats. Kanno et al. (2019) frequently observed juvenile mangrove whiprays feeding within mangrove habitats in Pioneer Bay. Unlike the previous study, however, we observed few feeding events by juvenile blacktip reef sharks and those were exclusively within sand flat habitats, making it unlikely that mangrove habitat use was primarily driven by prey availability.

Although young sharks were more frequently sighted within mangrove habitats at higher tides, they were also observed to utilise edge habitats during this period as well. Similarly, juvenile cowtail stingrays showed a strong affinity for mangrove edge habitats, with these areas presumed to provide both ample food resources for young rays and possibly reduce encounters with potential predators (Martins et al. 2020). Dahlgren and Eggleston (2000) suggested that juveniles will shift their habitat use to minimise the ratio of mortality risk to growth rate, affecting distribution patterns within populations as predation risk changes with body size. Stump et al. (2017), for example, showed size to be an important factor influencing antipredator behavior in juvenile lemon sharks, with increased use of artificial mangrove habitats by small sharks when larger conspecifics were present. While young blacktip reef sharks may benefit from access to resources from adjacent habitats when using mangrove edges, the clear preference for mangrove habitats at higher tides indicates that a trade-off exists between growth rate/food abundance and risk of predation (Grol et al. 2008). Thus, young sharks may spend more time along mangrove edges when these habitats first become available as they have access to both potential foraging areas (i.e. sand flats) and protective prop root habitats at a time when predators may be present, but likely still in low numbers due to the shallow water depths. Later, as tide heights increase and larger predators are able to access nearshore areas within the bay, young sharks may move deeper into the mangrove forest complex as the risk of predation outweighs any benefits gained through increased foraging opportunities in open areas.

As relative abundance of juvenile sharks in Pioneer Bay was greater along mangrove edges than on the adjacent sand flat during high tide periods, it could be assumed that larger sharks would spend more time within edge habitats to increase their chances of encountering potential prey, however this was not observed. Some predators are thought to increase their hunting success by searching along edges (Gorman et al. 2009), where abundance of fish (Smith et al. 2008) and fauna (e.g. crustaceans, polychaetes; Bologna & Heck 2002, Tanner 2005) are often greater. Preferential use of shallow edge habitats has been documented among tiger sharks, for example, with adults thought to increase encounter rates with primary prey species which are more abundant along edges (Heithaus et al. 2006). Similarly, lower rates of movement and selection for coral reef ledges by adult blacktip reef sharks at Palmyra Atoll was indicative of possible searching behaviour, with sharks thought to either obtain a higher forage base and/or greater encounter rates with prey within these areas (Papastamatiou et al. 2009b). Within Pioneer Bay, occasional predation attempts on juvenile cowtail stingrays by adult blacktip reef sharks have been observed (Martins et al. 2020); as these rays are most commonly found on sand flats and along mangrove edges, sharks may be foraging equally within these areas to increase their likelihood of encountering them, along with other potential prey. The absence of a strong edge effect for adult sharks may also be due to the variable patch size of mangrove stands included in this study, as this factor has been shown to influence whether or not edge effects are observed (Smith et al. 2010). It is also possible that edge effects were not observed due to the short time frame with which tides were both high enough for adults to access mangrove edges, but still too low for juveniles to penetrate deeply into the forest. During the highest tides when young sharks were found mostly within mangrove stands, larger sharks may concentrate their foraging activities elsewhere.

The advent of cheap and compact video recording technology (e.g. GoPro®) has given rise to new, non-invasive methods of studying the spatial ecology of marine species *in situ* (Mallet & Pelletier 2014, Reis-Filho et al. 2016), particularly with regards to their habitat use and behaviour. In addition, video monitoring is often more cost effective and less labour intensive than other monitoring techniques and able to overcome sampling issues which may confound results, such as behaviour modification due to the presence of observers or bait. Underwater video has been successfully used in studies examining fine-scale, spatio-temporal habitat use of teleost fish (Ellis & Bell 2008, Kimball & Able 2012, Reis-Filho et al. 2016, Sheaves et al. 2016, Dubuc et al. 2019). Drone technology offers promising new avenues with which to explore small-scale movement and habitat use patterns of sharks (Raoult et al. 2018), however their applicability is limited in mangrove areas due to the dense canopy. Use of suspended, stationary video cameras in the current study presented some limitations worth consideration for future studies, namely the inability to record during adverse weather conditions, at night or during extreme high tides. Nonetheless, in a sheltered area such as Pioneer Bay, we were able to successfully employ video monitoring to study the fine-scale habitat use and behaviour of juvenile blacktip reef sharks – particularly effective as it was used alongside existing acoustic telemetry (Mallet & Pelletier 2014).

This study explored movement and fine-scale habitat use of juvenile blacktip reef sharks within a shallow, time-restricted inshore reef nursery. Understanding how young sharks partition time between and within different habitats helps us to better understand the ecological importance of these habitats to reef sharks during early life-history stages. Globally, mangrove forests have declined by roughly a third since the 1980s (Valiela et al. 2001, Alongi 2002), with an estimated loss rate of 2.1% per year. Given the continuing decline of mangrove habitats world-wide, and the heightened threat to mangrove species in high intertidal and estuarine areas, in particular (Polidoro et al. 2010), an examination of the importance of mangrove habitats to reef sharks is both necessary and timely. As limited information is currently available on the fine-scale spatio-temporal habitat use and movement patterns of young sharks within shallow-water nursery areas, the knowledge generated by this research will help to inform management and conservation efforts within the GBR Marine Park and elsewhere.

Chapter 6: General Discussion and Future Directions

6.1 General Discussion

Information on the spatial ecology of reef sharks is critical to understanding life-history strategies and identifying key habitat requirements, which aid in both predicting the effects of natural and anthropogenic threats on populations (Brooks et al. 2006), and in developing strategies for their conservation and management (Roberts et al. 2003). However, a heavy focus on reefs in offshore and remote areas in previous studies (i.e. oceanic atolls, high islands), means that gaps remain in our knowledge of how these species move and occupy space, particularly in inshore reef environments along continental margins. Conditions in tropical inshore areas may differ significantly from those offshore with respect to the type, frequency and magnitude of environmental fluctuations, level of productivity, and degree of connectivity between reefs, which may result in different movement patterns for resident sharks. As such, examining the movement and space use patterns of sharks resident on inshore reefs – including their response to environmental variation – is critical to determining the use and importance of inshore reef habitats to these species, and in defining how resilient these populations are to disturbance and change. Broadly, this thesis looked at answering two main research questions. In this chapter, I synthesise the data presented in this thesis to answer the questions posed and to put results into a wider context. This chapter also offers suggestions for future directions in this area of research.

1. *What are the movement and space use patterns of reef sharks in inshore reef ecosystems?*

Multi-scale patterns in the movement and space use of blacktip reef sharks, *Carcharhinus melanopterus*, were examined, revealing distinct sex- and size-based differences in how this species moved and occupied space on an inshore reef. Broad-scale patterns in movement and space use based on long-term acoustic telemetry data (*Chapter 3*) indicated that, similar to previous studies on this species, blacktip reef sharks were strongly site-attached to inshore reefs, although males generally used more of the available habitat. While space use was largely consistent throughout the year for both sexes, during the reproductive season, adult males increased their activity, moving more broadly throughout the study site and undertaking long-distance migrations to/from offshore reefs while adult females utilised the same amount of space, but shifted the location of the space used. Analysis of fine-scale patterns in movement and habitat use based on combined acoustic telemetry and video monitoring (*Chapter 5*) revealed size-based habitat partitioning within the sampled population. Smaller individuals were observed to utilise shallow-water intertidal habitats, particularly mangrove stands, disproportionately, while larger juveniles and adults primarily occupied deeper water areas off the reef slope.

Similar to coastal populations that have been studied elsewhere in Australia (Speed et al. 2011, Chin et al. 2013c, Chin et al. 2016), the blacktip reef shark population at Orpheus Island consisted mainly of highly resident adult females and juveniles, with mature males less resident, either roaming more throughout the site or transient. Lower overall residency among adult males may be a means to reduce competition with resident females or to meet sex-specific resource requirements (Klimley 1987, Wearmouth & Sims 2008). The timing of return among transient adult males corresponded with mating season (Chin et al. 2013b), and was thus likely related to reproduction (e.g. mate-searching); this is supported by the observed patterns in movement and space use of resident adult males which increased significantly during this same time period. Male-mediated dispersal to offshore reefs may also be an agent for gene flow across broad spatial scales (e.g. cross-shelf) while regional genetic differences are maintained by females remaining within reproductively important habitats (Mourier & Planes 2012, Espinoza et al. 2015). Strong genetic structure (Vignaud et al. 2013, Vignaud et al. 2014) and high levels of inbreeding (Mourier & Planes 2012) were observed for blacktip reef sharks on fragmented reefs in French Polynesia, likely due to the high residency and limited movement (i.e. low dispersal and gene exchange) reported for this and similar species in more remote reef habitats (Stevens 1984, McKibben & Nelson 1986, Chapman et al. 2005, Papastamatiou et al. 2009b, Field et al. 2011). In contrast, genetic diversity of sharks was found to be greater on reefs in the GBR and Red Sea where connectivity is higher and available habitat in closer proximity (Vignaud et al. 2014).

Higher residency and localised movement observed for adult females and juveniles reflects the quality of inshore reef habitats as reproductive areas and as nursery grounds, enhancing juvenile growth and survival (Chin et al. 2013c). During the reproductive season, shifts in the location of space used by females may be due to individuals re-locating to areas favourable for gestation or pupping (Porcher 2005, Mourier & Planes 2012). Similar to inshore blacktip reef shark populations in Western Australia (Speed et al. 2012b), mature females may be exploiting thermal heterogeneity within warm, shallow-water embayments such as Pioneer Bay (Higgins 2018) to gain a reproductive advantage; this is supported by an observed decrease in depth use at this time, however without fine-scale information on temperature or biotelemetry data (Speed et al. 2012b) it was impossible to determine if sharks were behaviourally thermoregulating. Adult females may be relocating at this time for other reasons related to reproduction, such as to seek refuge from male harassment and energy-demanding mating activities (Jacoby et al. 2010) and/or to re-provision spent resources. Similar to findings by Chin et al. (2016), juveniles at Orpheus Island were less resident than adult females and also exhibited higher variability in residency between individuals, especially among males. Adult females appear to be long-term residents on reefs in inshore areas, displaying limited movement over multiple years, while juveniles may disperse at the onset of maturity, as evidenced by the missing size classes in this study and in research by Chin et al. (2013c), along with juvenile migration onto offshore reefs (Chin et al. 2013a).

High site fidelity and restricted movement has been reported for both juvenile and adult blacktip reef sharks on atolls (Papastamatiou et al. 2009b, Papastamatiou et al. 2010, Lea et al. 2016) and oceanic high islands (Mourier et al. 2012, Bouyoucos et al. 2020b). In contrast to this study and others conducted within inshore areas (Speed et al. 2011, Chin et al. 2013c), there were no clear differences in spatial and/or temporal habitat use patterns between sexes at atolls (Stevens 1984, Papastamatiou et al. 2009a, Papastamatiou et al. 2010), and no evidence of large-scale movements by sharks or migrations over deep ocean, at least for Palmyra Atoll (Papastamatiou et al. 2010). Furthermore, the amount of space used by individuals at atolls was generally similar regardless of sex or size (Stevens 1984, Papastamatiou et al. 2009b), although ontogenetic differences were observed in the location of the space used at Palmyra Atoll (Papastamatiou et al. 2009b). There was some evidence of sex structuring at Aldabra (Stevens 1984) and Palmyra atolls (Papastamatiou et al. 2009a), although not strongly supported in either location. Strong sexual segregation was documented among adult blacktip reef sharks off Moorea, French Polynesia, however, with females observed to use lagoons while males primarily occupied the fore-reef (Mourier et al. 2013); genetic analyses at this location also indicated that adult females regularly make inter-island migrations between their home range and natal grounds up to 50km away and across deep ocean to give birth. It is worth noting when making these comparisons that research at Palmyra and Aldabra atolls was conducted exclusively within the lagoons, and therefore did not quantify movement and space use patterns of individuals on the outer reef slope, where conditions are very different from the inner lagoons. Collectively, however, it is clear that differences exist in how blacktip reef sharks move and occupy space on inshore reefs compared to reefs in more remote locations.

Regional variations in movement and space use patterns of blacktip reef sharks paralleled those of another reef-resident species, the grey reef shark, *Carcharhinus amblyrhynchos*. Similar to blacktip reef sharks, grey reef sharks were observed to display limited dispersal and more restricted movements, in general, on isolated oceanic reefs (Field et al. 2011, Barnett et al. 2012) than on mid- to outer-shelf reefs in the Great Barrier Reef Marine Park (GBRMP), which were more closely-spaced and could be considered near-continuous habitat (Heupel et al. 2010, Espinoza et al. 2015). Differences in movement and space use patterns between reef sharks resident on isolated reef platforms (i.e. atolls, seamounts) and remote high islands, and those utilising inshore or near-continuous reef habitats within the GBRMP are likely due to site-specific differences in the degree of connectivity and habitat quality. Oceanic islands and atolls are surrounded by deep oceans that may not be easily traversable for highly site-attached reef shark species such as blacktip reef and grey reef sharks, due to the risk of predation and a lack of suitable habitat nearby. In turn, greater connectivity within inshore and well-connected reef areas may allow resident sharks to more easily access and capitalize on sites of regional productivity, favourable environmental conditions or that offer important ecosystem services (e.g. nursery habitats), compared to remote islands and coral reef platforms where these habitats may be absent entirely or isolated by deep water and largely inaccessible. Lower movement potential on isolated reefs compared to well-connected coastal habitats, for example, along with differences in productivity and resource availability may be the reason for regional variations in blacktip reef shark size and growth; smaller sizes at birth, lower growth rates and smaller maximum sizes were observed for this species at atolls and remote high islands (Stevens 1984, Papastamatiou et al. 2009a, Mourier et al. 2013) compared with coastal regions (Chin et al. 2013b). This may result from resource limitations on oceanic reefs, such as lower prey availability and/or quality, and higher intra-specific competition for shared resources (Weideli et al. 2019).

Limited spatial overlap was observed between adult and juvenile blacktip reef sharks at Orpheus Island. Size-based habitat partitioning is a common trait for this species regardless of geographic location, with juvenile blacktip reef sharks selecting shallow-water habitats (i.e. reef flats, lagoons, coastal foreshores) and adults occupying comparatively deeper water (Papastamatiou et al. 2009b, Speed et al. 2016, Oh et al. 2017). Ontogenetic shifts in habitat use have been attributed to perceived level of predation risk, a need to reduce competition for shared resources, access to preferred prey in order to meet size-specific energetic requirements, and the onset of maturity (Grubbs 2010). Use of shallow-water habitats within Pioneer Bay likely provides young blacktip reef sharks with a degree of protection from predation by reducing encounter rates with larger sharks, including conspecifics, which occupy deeper waters off of the reef slope. While shallow-water depth use alone may help to mitigate predation risk (Rypel et al. 2007), in inshore areas where mangrove habitats are also available, small sharks may further decrease their risk of mortality by maximising the time spent in these habitats – particularly during high tide periods when larger sharks can access most inshore areas and predation risk is higher. Habitat partitioning between juveniles and adults may also aid in reducing competitive interactions or to meet changing physiological requirements (e.g. energetic budgeting). Warmer temperatures within shallow-water areas in Pioneer Bay may give young sharks a biological advantage, such as increasing somatic growth rates or optimising metabolic performance, as has been suggested for juveniles of other tropical reef-associated shark and ray species (Morrissey & Gruber 1993, DiGirolamo et al. 2012, Higgins 2018). For young sharks, the benefits of using shallow-water habitats are likely multi-fold and not mutually exclusive.

2. *How are movement and space use patterns affected by fluctuations in the environment?*

This thesis examined how sharks resident on inshore reefs within the GBR Marine Park responded to changes within the local environment, using multiple survey techniques and over various spatial and temporal scales. Passive acoustic telemetry was analysed alongside environmental monitoring data over a two-year period to look at changes in broad-scale movement and space use of blacktip reef sharks in response to changes within the local environment (*Chapter 4*). As consideration of vertical space use for mobile species is important when looking at response to environmental changes within marine systems, this thesis incorporated depth data into the analysis of activity spaces. Results showed that blacktip reef sharks responded the most to changes in salinity over other environmental factors tested, with sharks either shifting their space use horizontally or moving deeper within the water column in response to salinity decreases following a period of heavy rainfall. Fine-scale movement and habitat selection patterns within Pioneer Bay were examined over diel (day and night) and daily scales using passive acoustic telemetry combined with non-baited, stationary video monitoring (*Chapter 5*). Movements of the smallest sharks were tidally-influenced, with individuals moving progressively onto the intertidal reef flat with the incoming tide. In addition, despite access to several habitat types within Pioneer Bay, young sharks displayed a clear preference for mangrove habitats during the highest tides. The affinity young blacktip reef sharks displayed to mangrove stands during high tide periods indicates that these habitats provide important ecosystem services to this species during a critical stage in their life-history.

Results from this thesis indicate that even minor fluctuations in salinity levels can lead to measurable changes in the space use of blacktip reef sharks on inshore reefs. Coastal regions are more variable than offshore areas and atolls, and resident species must be able to cope with large daily and seasonal fluctuations in their environment (Knip et al. 2010, Higgins 2018). In contrast, the comparatively stable conditions typical of mid- to offshore reefs and remote coral reef platforms may allow resident species to adapt to these areas without the need to undertake seasonal movements or alter their space use in response to environmental disturbances (Heupel & Simpfendorfer 2014, Espinoza et al. 2015). Grey reef sharks, for example, appear well-adapted to a wide range of environmental conditions at offshore reefs in the southern GBRMP, attributed to their high site-attachment and potential isolation from other suitable coral reef habitat (Heupel & Simpfendorfer 2014). Since previous studies have not examined the effects of salinity on movement and activity space of blacktip reef sharks, it is unknown whether this species would respond similarly to this factor in offshore and more remote areas. Given the greater connectivity within inshore areas, however, along with proximity to shore and regular exposure to freshwater influxes through wet-season flood plumes (King et al. 2002, Devlin & Brodie 2005, Devlin & Schaffelke 2009), it is likely salinity has a greater influence on blacktip reef shark populations on inshore reefs than it does for sharks resident on reefs in offshore or more remote locations. While blacktip reef sharks at Orpheus Island altered their space use patterns in response to decreases in salinity levels, they did not emigrate from the area. Similarly, blacktip reef shark populations within inshore areas have been shown to remain resident during drops in barometric pressure preceding tropical cyclones, neither departing or changing location from reef habitats (Udyawer et al. 2013). As such, blacktip reef sharks are perhaps more tolerant to adverse environmental conditions such as those associated with tropical storms and wet-season flooding effects, with the benefits gained by individuals who remain in these inshore reef habitats outweighing those of departing.

There was also a clear tidal signature in the fine-scale movement and habitat selection patterns of young sharks, with the smallest individuals moving with the tide into shallow-water habitats on the reef flat as soon as they became available, and using mangrove habitats disproportionately during high-tide periods. Ecological theory suggests that animals use habitat optimally, selecting habitat (e.g. habitat profitability) and/or modifying their behaviour (e.g. predator avoidance) in order to maximize their level of fitness (Rosenzweig 1974, Mittelbach 1981, Werner et al. 1983a, Werner et al. 1983b). Shallow-water habitats such as intertidal flats and mangrove stands are thought to play an important role as nursery areas (Castro 1993, Simpfendorfer & Milward 1993, White & Potter 2004, Heupel et al. 2007, Vaudo & Heithaus 2009), conferring biological advantages to reef sharks during early life-history stages in the form of enhanced growth and/or survival through the provision of abundant prey, reduced intraspecific competition and/or refuge from predation. Tidally-influenced movement patterns within shallow-water areas have been observed for juveniles of several reef-associated shark and ray species (Wetherbee et al. 2007, Guttridge et al. 2012, Davy et al. 2015, Martins et al. 2020), including blacktip reef sharks (Papastamatiou et al. 2009b, George et al. 2019, Lea et al. 2020), and were largely attributed to predator avoidance strategies. As depth is associated with tide, tidally-based movement in Pioneer Bay may simply be a means for the young sharks to minimise predation risk by remaining in shallow water (Rypel et al. 2007), selectively occupying habitats on the intertidal reef flat that are inaccessible to predators at lower tide heights due to their larger body size. Given the clear preference for mangrove habitats displayed by the smallest individuals during the highest tide periods when large sharks were able to access nearshore areas, it is likely that use of these habitats also mitigates predation risk for young sharks.

While restricting movements to shallow-water intertidal and mangrove habitats may decrease predation risk for young reef sharks, these are comparatively inhospitable environments and can be physiologically challenging to individuals that use them (Lear et al. 2019). Intertidal habitats such as Pioneer Bay regularly experience large and sometimes rapid diel changes in temperature, dissolved oxygen (DO), salinity and water level (Rummer et al. 2009, Mattone & Sheaves 2017, Higgins 2018), and residents must be able to adapt to these conditions accordingly. Large tidal fluctuations, for example, expose residents to progressively longer and more severe hypoxic conditions as tide levels decrease. Cryptic niche species such as the epaulette shark, *Hemiscyllium ocellatum*, are well-adapted to living on intertidal reef flats, and able to successfully exploit resources within these areas due to their tolerance to cyclic exposure to extreme hypoxia (Wise et al. 1998, Routley et al. 2002, Nilsson & Renshaw 2004). Temperatures within intertidal areas can also fluctuate dramatically throughout the tidal cycle, resulting in spatio-temporal differences as water levels rise and fall (Dabruzzi et al. 2012, Higgins 2018). Juveniles of some reef-associated shark and ray species, such as the mangrove whipray, *Urogymnus granulatus* (Higgins 2018), ribbontail stingray, *Taeniura lymma* (Dabruzzi et al. 2012), and lemon shark, *Negaprion brevirostris* (DiGirolamo et al. 2012), may be physiologically adapted to withstand higher temperatures within shallow-water areas (Lear et al. 2019); this would allow them to exploit the thermal heterogeneity within these environments, obtaining biological advantages such as predator avoidance, an increase in somatic growth or digestion efficiency.

Recent research suggests that neonate blacktip reef sharks may also be particularly well-adapted to living in environmentally hostile areas such as intertidal reef flats, displaying a tolerance to elevated sea temperatures and low dissolved oxygen concentrations (Bouyoucos et al. 2020a). Juvenile sharks confined to habitats within discrete, shallow-water areas, such as Pioneer Bay, spend substantially more time above their optimum temperature than adults, which often occupy deeper water areas and range more widely (Lear et al. 2019). While occupying temperatures outside of usual ranges may compromise individuals metabolically, the energetic costs of occupying these areas must be outweighed by the benefits acquired. For young blacktip reef sharks, thermal tolerance would allow individuals to remain within shallow-water areas for as long as possible, presumably lowering their risk of predation and increasing survival (Bouyoucos et al. 2020a). Neonate blacktip reef sharks in Moorea, French Polynesia, appeared to actively avoid higher temperatures within the study site, which suggests that juveniles of this species may use behaviour to avoid unfavourable environmental temperatures (Bouyoucos et al. 2020a). In Pioneer Bay, the widest range of temperatures are found within mangrove habitats, and juvenile mangrove whiprays at this location are thought to mitigate extreme temperatures during the hottest periods of the day by seeking out cooler temperatures beneath the mangrove canopy (Higgins 2018). Extreme variations in dissolved oxygen levels within mangrove forests, however, means that the use of these habitats is likely constrained by the ability of individuals to withstand low DO levels (Mattone & Sheaves 2017). For young blacktip reef sharks, the ability to tolerate low dissolved oxygen concentrations may allow individuals to seek thermal respite within mangrove habitats when necessary, ultimately allowing them to remain in and utilise habitats within these shallow-water systems. Tolerance to substantial fluctuations in DO may also allow young sharks to penetrate deeply within the mangrove complex during high tide periods, and out of reach of larger predators. For individuals able to adapt to the extreme environmental conditions within these inshore environments, it is clear that the advantages provided may be great.

The use and importance of inshore reef habitats by sharks may be dictated by patterns in their movement and behaviour and in their response to environmental changes. Inshore reefs are some of the most exposed regions for natural and human-mediated environmental effects. Fluctuations in environmental conditions, particularly within inshore areas, are expected to be exacerbated under future climate change scenarios (Emanuel 2005, Webster et al. 2005, Rahmstorf 2007), with coral reef habitats predicted to be among some of the worst affected (Hoegh-Guldberg et al. 2007, Diaz-Pulido et al. 2009). In conjunction with the effects of fishing pressure (Heupel et al. 2009), inshore reef shark populations on the GBR are at the frontline of natural and human impacts on marine systems (Chin et al. 2010, Heupel et al. 2019b). This thesis has shown that inshore reef habitats provide important ecosystem services to blacktip reef sharks throughout various stages in their life-history. While conditions within inshore regions can fluctuate dramatically, blacktip reef sharks appear well-adapted to life in these dynamic environments, with juvenile sharks, in particular, able to exploit time-restricted intertidal habitats to their advantage despite the physiological challenges that accompany them. Although young blacktip reef sharks occupying shallow-water nearshore habitats appear robust to temperature changes within their current seasonal range (Bouyoucos et al. 2020a), this may change as global warming pushes populations closer to their upper thermal limits. While larger individuals may be able to mitigate long-term temperature changes by shifting their geographic distribution to more thermally favourable areas (Hazen et al. 2013), this may not be possible for smaller individuals that are bound to specific habitats, such as mangrove forests. These individuals may have to mitigate the physiological effects of increasing temperatures by altering their behavioural patterns, which could impact success and long-term fitness of individuals (Lear et al. 2019); as conditions become more thermally taxing, young sharks may avoid or limit time in key habitats which may affect foraging opportunities and/or interactions with predator species. Furthermore, the continued degradation and loss of mangrove habitats (Valiela et al. 2001, Alongi 2002) in particular, may have significant consequences for young blacktip reef sharks in inshore areas, limiting their ability to seek thermal refuge and negatively impacting populations that are resident on reefs within these regions.

6.2 Future Directions

Understanding the importance of inshore reef habitats to resident shark species and the effects of environmental change on these populations is key to understanding their movement and distribution patterns, especially within the context of a changing climate. While this thesis has filled some knowledge gaps regarding the movement and space use of sharks within inshore reef systems and their environmental drivers, it has also raised additional questions that require further information to resolve. Although results from this research have shown mangrove habitats near inshore reefs to be important to blacktip reef sharks, particularly during early life history stages, this species is strongly site-attached to reefs and therefore movement and habitat selection patterns observed here may not reflect those of less resident or transient reef shark species within inshore reef areas (Heupel et al. 2019b). The sicklefin lemon shark, *Negaprion acutidens*, for example, is common to inshore areas throughout the Indo-Pacific, with juveniles often observed on shallow reef flats and around mangroves (White & Potter 2004). Although juvenile sicklefin lemon sharks co-occur with blacktip reef sharks at Orpheus Island (AM Schlaff, pers. obs.), this species is considered a non-resident reef shark (Heupel et al. 2019b), and it remains unknown how and to what extent they use mangrove habitats.

Furthermore, although the youngest sharks were observed to habitually use mangrove habitats during high tide periods, it was unknown how far within the mangrove complex they penetrated. Although studies show these individuals are able to tolerate hypoxic conditions to a degree (Bouyoucos et al. 2020a), it has yet to be seen whether they regularly utilise areas with low dissolved oxygen concentrations *in situ*, particularly mangrove habitats where fluctuations in DO can vary from normoxic to hypoxic within the same tidal cycle (Mattone & Sheaves 2017). Establishing an environmental profile within mangrove areas over the full tidal cycle and with increasing distance from the mangrove edge, analysed alongside fine-scale monitoring data (acoustic telemetry, video monitoring) of individuals within these areas could help to resolve habitat use patterns for young sharks (Heupel et al. 2019b).

The location of the current study was subjected to large tidal changes, and therefore movement and habitat selection patterns observed here, particularly for young sharks, may differ considerably from areas where tidal amplitudes are smaller and nearshore habitats remain submerged to a greater degree or for a longer period of time. Studies conducted in the Caribbean have shown a greater dependency on mangrove habitats for some juvenile coral reef fish than that observed for similar species in parts of the Indo-Pacific where tidal ranges are greater (Igulu et al. 2014). Compared to Orpheus Island where mangrove and intertidal habitats became completely exposed at the lowest tides, inshore reef areas with smaller tides and continuous or near-continuous access to nearshore habitats may result in different movement and space use patterns for young sharks; juvenile sharks may have a higher dependency on habitats in these areas, making them more susceptible to habitat loss (e.g. mangrove deforestation). Furthermore, environmental conditions (e.g. salinity, dissolved oxygen, temperature) in areas with low tidal changes may differ significantly from areas such as Orpheus Island where large tides promote more mixing and less stratification of the water column, which could affect movement and habitat use patterns of resident sharks.

Lastly, although this thesis documented habitat partitioning between juveniles and adults, future studies that incorporate stable isotope analysis could help to determine if these individuals are feeding on different prey items (Hussey et al. 2011, Heupel et al. 2019b), providing support for the size-based habitat partitioning observed here. Similarly, stable isotope values could help resolve whether males and females had similar dietary contributions, which could help explain the observed differences in residency and roaming between sexes. Depth use information for mature males would also be useful; determining whether adult males and females partition habitat vertically within the water column, during reproductive periods only or throughout the year, would provide insight into sex-specific behaviour and/or resource requirements (Heupel & Simpfendorfer 2015).

References

Ackerman JT, Kondratieff MC, Matern SA, Cech JJJ (2000) Tidal influence on spatial dynamics of leopard sharks, *Triakis semifasciata*, in Tomales Bay, California. Environmental Biology of Fishes 58:33-43

Alongi DM (2002) Present state and future of the world's mangrove forests. Environmental Conservation 29:331-349

Anderson SD, Goldman KJ (2001) Temperature measurements from salmon sharks, *Lamna ditropis*, in Alaskan waters. Copeia 3:794-796

Andrews KS, Williams GD, Farrer D, Tolimieri N, Harvey CJ, Bargmann G, Levin PS (2009) Diel activity patterns of sixgill sharks, *Hexanchus griseus*: the ups and downs of an apex predator. Animal Behaviour 78:525-536

Andrews KS, Williams GD, Levin PS (2010) Seasonal and ontogenetic changes in movement patterns of sixgill sharks. PLoS ONE 5:e12549

Barbieri MM, Berger JO (2004) Optimal predictive model selection. The Annals of Statistics 32:870-897

Barnes L, Bellwood DR, Sheaves M, Tanner JK (2012) The use of clear-water non-estuarine mangroves by reef fishes on the Great Barrier Reef. Marine Biology 159:211-220

Barnett A, Abrantes KG, Seymour J, Fitzpatrick R (2012) Residency and spatial use by reef sharks of an isolated seamount and its implications for conservation. PLoS ONE 7:e36574

Barnett A, Abrantes KG, Stevens JD, Semmens JM (2011) Site fidelity and sex-specific migration in a mobile apex predator: implications for conservation and ecosystem dynamics. Animal Behaviour 81:1039-1048

Barton K (2013) MuMIn: multi-model inference. R package version 1:5

Bascompte J, Melian CJ, Sala E (2005) Interaction strength combinations and the overfishing of a marine food web. Proceedings of the National Academy of Sciences of the United States of America 102:5443-5447

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1-48

Baum JK, Worm B (2009) Cascading top-down effects of changing oceanic predator abundances. Journal of Animal Ecology 78:699-714

Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51:633-641

Becker RA, Chambers JM, Wilks AR (1988) The new S language: a programming environment for data analysis and graphics. Wadsworth and Brooks/Cole Advanced Books & Software, Monterey, CA

Bernal D, Carlson JK, Goldman KJ, Lowe CG (2012) Energetics, metabolism, and endothermy in sharks and rays. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of Sharks and Their Relatives. CRC Press, Boca Raton

Blaber SJ (2007) Mangroves and fishes: issues of diversity, dependence, and dogma. Bulletin of Marine Science 80:457-472

Blaber SJM, Cyrus DP, Albaret JJ, Ching CV, Day JW, Elliott M, Fonseca MS, Hoss DE, Orensanz J, Potter IC, Silvert W (2000) Effects of fishing on the structure and functioning of estuarine and nearshore ecosystems. ICES Journal of Marine Science 57:590-602

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127-135

Bologna PA, Heck KL (2002) Impact of habitat edges on density and secondary production of seagrass-associated fauna. Estuaries 25:1033-1044

Bond ME, Babcock EA, Pikitch EK, Abercrombie DL, Lamb NF, Chapman DD (2012) Reef sharks exhibit site-fidelity and higher relative abundance in marine reserves on the Mesoamerican Barrier Reef. PLoS ONE 7:e32983

Börger L, Dalziel BD, Fryxell JM (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. Ecology Letters 11:637-650

Bouyoucos IA, Morrison PR, Weideli OC, Jacquesson E, Planes S, Simpendorfer CA, Brauner CJ, Rummer JL (2020a) Thermal tolerance and hypoxia tolerance are associated in blacktip reef shark (*Carcharhinus melanopterus*) neonates. Journal of Experimental Biology 223:jeb221937

Bouyoucos IA, Romain M, Azoulai L, Eustache K, Mourier J, Rummer JL, Planes S (2020b) Home range of newborn blacktip reef sharks (*Carcharhinus melanopterus*), as estimated using mark-recapture and acoustic telemetry. Coral Reefs 39:1209–1214

Brooks TM, Mittermeier RA, da Fonseca GA, Gerlach J, Hoffmann M, Lamoreux JF, Mittermeier CG, Pilgrim JD, Rodrigues AS (2006) Global biodiversity conservation priorities. Science 313:58-61

Bureau (2015) Flood Warning System for the Herbert River. Accessed 1 August. http://www.bom.gov.au/qld/flood/brochures/herbert/herbert.shtml

Burnham KP, Anderson D (2003) Model selection and multi-model inference: a practical information-theoretic approach. Springer-Verlag, New York, NY

Calenge C (2006) The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516-519

Campbell HA, Hewitt M, Watts ME, Peverell S, Franklin CE (2012) Short- and long-term movement patterns in the freshwater whipray (*Himantura dalyensis*) determined by the signal processing of passive acoustic telemetry data. Marine and Freshwater Research 63:341-350

Campos BR, Fish MA, Jones G, Riley RW, Allen PJ, Klimley PA, Cech Jr JJ, Kelly JT (2009) Movements of brown smoothhounds, *Mustelus henlei*, in Tomales Bay, California. Environmental Biology of Fishes 85:3-13

Carey FG, Scharold JV (1990) Movements of blue sharks (*Prionace glauca*) in depth and course. Marine Biology 106:329-342

Carlisle AB, Starr RM (2009) Habitat use, residency, and seasonal distribution of female leopard sharks *Triakis semifasciata* in Elkhorn Slough, California. Marine Ecology Progress Series 380:213-228

Carlisle AB, Starr RM (2010) Tidal movements of female leopard sharks (*Triakis semifasciata*) in Elkhorn Slough, California. Environmental Biology of Fishes 89:31-45

Carlson JK, Parsons GR (2001) The effects of hypoxia on three sympatric shark species: physiological and behavioral responses. Environmental Biology of Fishes 61:427-433

Carlson JK, Parsons GR (2003) Respiratory and hematological responses of the bonnethead shark, *Sphyrna tiburo*, to acute changes in dissolved oxygen. Journal of Experimental Marine Biology and Ecology 294:15-26

Carroll JM, Keller DA, Furman BT, Stubler AD (2019) Rough Around the Edges: Lessons Learned and Future Directions in Marine Edge Effects Studies. Current Landscape Ecology Reports:1-12

Cartamil D, Wegner NC, Aalbers S, Sepulveda CA, Baquero A, Graham JB (2010) Diel movement patterns and habitat preferences of the common thresher shark (*Alopias vulpinus*) in the Southern California Bight. Marine and Freshwater Research 61:596-604

Cartamil DP, Vaudo JJ, Lowe CG, Wetherbee BM, Holland KN (2003) Diel movement patterns of the Hawaiian stingray, *Dasyatis lata*: implications for ecological interactions between sympatric elasmobranch species. Marine Biology 142:841-847

Castellanos-Galindo GA, Krumme U, Willis TJ (2010) Tidal influences on fish distributions on tropical eastern Pacific rocky shores (Colombia). Marine Ecology Progress Series 416:241-254

Casterlin ME, Reynolds WW (1979) Shark thermoregulation. Comparative Biochemistry and Physiology Part A, Physiology 64:451-453

Castro JI (1993) The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. Environmental Biology of Fishes 38:37-48

Cerutti-Pereyra F, Thums M, Austin C, Bradshaw C, Stevens J, Babcock R, Pillans R, Meekan M (2014) Restricted movements of juvenile rays in the lagoon of Ningaloo Reef, Western

Australia–evidence for the existence of a nursery. Environmental Biology of Fishes 97:371-383

Chapman DD, Babcock EA, Gruber SH, Dibattista JD, Franks BR, Kessel SA, Guttridge T, Pikitch EK, Feldheim KA (2009) Long-term natal site-fidelity by immature lemon sharks (*Negaprion brevirostris*) at a subtropical island. Molecular Ecology 18:3500-3507

Chapman DD, Feldheim KA, Papastamatiou YP, Hueter RE (2015) There and back again: a review of residency and return migrations in sharks, with implications for population structure and management. Annual Review of Marine Science 7:547-570

Chapman DD, Pikitch EK, Babcock E, Shivji MS (2005) Marine reserve design and evaluation using automated acoustic telemetry: a case-study involving coral reef-associated sharks in the Mesoamerican Caribbean. Marine Technology Society Journal 39:42-55

Chin A, Heupel MR, Simpendorfer CA, Tobin AJ (2016) Population organisation in reef sharks: new variations in coastal habitat use by mobile marine predators. Marine Ecology Progress Series 544:197-211

Chin A, Heupel MR, Simpfendorfer CA, Tobin AJ (2013a) Ontogenetic movements of juvenile blacktip reef sharks: evidence of dispersal and connectivity between coastal habitats and coral reefs. Aquatic Conservation: Marine and Freshwater Ecosystems 23:468-474

Chin A, Kyne PM, Walker TI, McAuley RB (2010) An integrated risk assessment for climate change: analysing the vulnerability of sharks and rays on Australia's Great Barrier Reef. Global Change Biology 16:1936-1953

Chin A, Simpfendorfer C, Tobin A, Heupel M (2013b) Validated age, growth and reproductive biology of *Carcharhinus melanopterus*, a widely distributed and exploited reef shark. Marine and Freshwater Research 64:965-975

Chin A, Tobin A, Simpendorfer C, Heupel M (2012) Reef sharks and inshore habitats: patterns of occurrence and implications for vulnerability. Marine Ecology Progress Series 460:115-125

Chin A, Tobin AJ, Heupel MR, Simpfendorfer CA (2013c) Population structure and residency patterns of the blacktip reef shark *Carcharhinus melanopterus* in turbid coastal environments. Journal of Fish Biology 82:1192-1210

Chittaro PM, Usseglio P, Sale P (2005) Variation in fish density, assemblage composition and relative rates of predation among mangrove, seagrass and coral reef habitats. Environmental Biology of Fishes 72:175-187

Cohen JE (2003) Human population: the next half century. Science 302:1172-1175

Cohen JE (2005) Human population grows up. Scientific American 293:48-55

Collins AB, Heupel MR, Motta PJ (2007) Residence and movement patterns of cownose rays *Rhinoptera bonasus* within a south-west Florida estuary. Journal of Fish Biology 71:1159-1178

Collins AB, Heupel MR, Simpfendorfer CA (2008) Spatial distribution and long-term movement patterns of cownose rays *Rhinoptera bonasus* within an estuarine river. Estuaries and Coasts 31:1174-1183

Conner WH, Day JW, Baumann RH, Randall JM (1989) Influence of hurricanes on coastal ecosystems along the northern Gulf of Mexico. Wetlands Ecology and Management 1:45-56

Conrath CL, Musick JA (2010) Residency, space use and movement patterns of juvenile sandbar sharks (*Carcharhinus plumbeus*) within a Virginia summer nursery area. Marine and Freshwater Research 61:223-235

Cortes E (1999) Standardized diet compositions and trophic levels of sharks. ICES Journal of Marine Science 56:707-717

Craig JK, Gillikin PC, Magelnicki MA, May LN (2010) Habitat use of cownose rays (*Rhinoptera bonasus*) in a highly productive, hypoxic continental shelf ecosystem. Fisheries Oceanography 19:301-317

Crawshaw LI (1977) Physiological and behavioral reactions of fishes to temperature change. Journal of the Fisheries Research Board of Canada 34:730-734

Curtis TH, Parkyn DC, Burgess GH (2013) Use of human-altered habitats by bull sharks in a Florida nursery area. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 5:28-38

Dabruzzi TF, Bennett WA, Rummer JL, Fangue NA (2012) Juvenile Ribbontail Stingray, *Taeniura lymma* (Forsskal, 1775) (Chondrichthyes, Dasyatidae), demonstrate a unique suite of physiological adaptations to survive hyperthermic nursery conditions. Hydrobiologia 701:37-49

Dahlgren CP, Eggleston DB (2000) Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology 81:2227-2240

Davy L (2012) Spatial ecology of two stingray species (*Pastinachus atrus* and *Himantura granulata*) in a nearshore environment. Honours, James Cook University,

Davy LE, Simpfendorfer CA, Heupel MR (2015) Movement patterns and habitat use of juvenile mangrove whiprays (*Himantura granulata*). Marine and Freshwater Research 66:481-492

de la Moriniere EC, Nagelkerken I, van der Meij H, van der Velde G (2004) What attracts juvenile coral reef fish to mangroves: habitat complexity or shade? Marine Biology 144:139-145

De‟ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27–year decline of coral cover on the Great Barrier Reef and its causes. Proceedings of the National Academy of Sciences 109:17995-17999

DeAngelis BM, McCandless CT, Kohler NE, Recksiek CW, Skomal GB (2008) First characterization of shark nursery habitat in the United States Virgin Islands: evidence of habitat partitioning by two shark species. Marine Ecology Progress Series 358:257-271

Devlin M, Schaffelke B (2009) Spatial extent of riverine flood plumes and exposure of marine ecosystems in the Tully coastal region, Great Barrier Reef. Marine and Freshwater Research 60:1109-1122

Devlin MJ, Brodie J (2005) Terrestrial discharge into the Great Barrier Reef Lagoon: nutrient behavior in coastal waters. Marine Pollution Bulletin 51:9-22

Di Santo V, Bennett WA (2011) Is post-feeding thermotaxis advantageous in elasmobranch fishes? Journal of Fish Biology 78:195-207

Diaz-Pulido G, McCook LJ, Dove S, Berkelmans R, Roff G, Kline DI, Weeks S, Evans RD, Williamson DH, Hoegh-Guldberg O (2009) Doom and boom on a resilient reef: climate change, algal overgrowth and coral recovery. PLoS ONE 4:1-9

DiBattista JD, Feldheim KA, Thibert-Plante X, Gruber SH, Hendry AP (2008) A genetic assessment of polyandry and breeding-site fidelity in lemon sharks. Molecular Ecology 17:3337-3351

Dickson KA, Graham JB (2004) Evolution and consequences of endothermy in fishes. Physiological and Biochemical Zoology 77:998-1018

DiGirolamo AL, Gruber SH, Pomory C, Bennett WA (2012) Diel temperature patterns of juvenile lemon sharks *Negaprion brevirostris*, in a shallow-water nursery. Journal of Fish Biology 80:1436-1448

Donley JM, Shadwick RE, Sepulveda CA, Syme DA (2007) Thermal dependence of contractile properties of the aerobic locomotor muscle in the leopard shark and shortfin mako shark. Journal of Experimental Biology 210:1194-1203

Dorenbosch M, Grol MG, Nagelkerken I, Van der Velde G (2005) Distribution of coral reef fishes along a coral reef–seagrass gradient: edge effects and habitat segregation. Marine Ecology Progress Series 299:277-288

Drymon JM, Carassou L, Powers SP, Grace M, Dindo J, Dzwonkowski B (2013) Multiscale analysis of factors that affect the distribution of sharks throughout the northern Gulf of Mexico. Fishery Bulletin 111:370-380

Dubuc A, Waltham NJ, Baker R, Marchand C, Sheaves M (2019) Patterns of fish utilisation in a tropical Indo-Pacific mangrove-coral seascape, New Caledonia. PLoS ONE 14:e0207168

Dudgeon CL, Lanyon JM, Semmens JM (2013) Seasonality and site fidelity of the zebra shark, *Stegostoma fasciatum*, in southeast Queensland, Australia. Animal Behaviour 85:471-481

Dulvy NK, Fowler SL, Musick JA, Cavanagh RD, Kyne PM, Harrison LR, Carlson JK, Davidson LN, Fordham SV, Francis MP (2014) Extinction risk and conservation of the world's sharks and rays. Elife 3:e00590

Dulvy NK, Metcalfe JD, Glanville J, Pawson MG, Reynolds JD (2000) Fishery stability, local extinctions, and shifts in community structure in skates. Conservation Biology 14:283-293

Dunbrack R, Zielinski R (2003) Seasonal and diurnal activity of sixgill sharks (*Hexanchus griseus*) on a shallow water reef in the Strait of Georgia, British Columbia. Canadian Journal of Zoology 81:1107-1111

Duong T (2007) ks: Kernel density estimation and kernel discriminant analysis for multivariate data in R. Journal of Statistical Software 21:1-16

Ebert DA, Ebert TB (2005) Reproduction, diet and habitat use of leopard sharks, *Triakis semifasciata* (Girard), in Humboldt Bay, California, USA. Marine and Freshwater Research 56:1089-1098

Economakis A, Lobel P (1998) Aggregation behavior of the grey reef shark, *Carcharhinus amblyrhynchos*, at Johnston Atoll, Central Pacific Ocean. Environmental Biology of Fishes 51:129-139

Edgar GJ, Barrett NS, Graddon DJ, Last PR (2000) The conservation significance of estuaries: a classification of Tasmanian estuaries using ecological, physical and demographic attributes as a case study. Biological Conservation 92:383-397

Ellis WL, Bell SS (2004) Conditional use of mangrove habitats by fishes: depth as a cue to avoid predators. Estuaries 27:966-976

Ellis WL, Bell SS (2008) Tidal influence on a fringing mangrove intertidal fish community as observed by in situ video recording: implications for studies of tidally migrating nekton. Marine Ecology Progress Series 370:207-219

Ellison AM, Farnsworth EJ (2000) Mangrove communities. In: Bertness MD, Gaines SD, Hay ME (eds) Marine Community Ecology. Sinauer Associates, New York, USA

Emanuel K (2005) Increasing destructiveness of tropical cyclones over the past 30 years. Nature 436:686-688

Espinoza M, Cappo M, Heupel MR, Tobin AJ, Simpfendorfer CA (2014) Quantifying shark distribution patterns and species-habitat associations: implications of marine park zoning. PLoS ONE 9:e106885

Espinoza M, Farrugia TJ, Lowe CG (2011) Habitat use, movements and site fidelity of the gray smooth-hound shark (*Mustelus californicus* Gill 1863) in a newly restored southern California estuary. Journal of Experimental Marine Biology and Ecology 401:63-74

Espinoza M, Heupel MR, Tobin AJ, Simpfendorfer CA (2015) Residency patterns and movements of grey reef sharks (*Carcharhinus amblyrhynchos*) in semi-isolated coral reef habitats. Marine Biology 162:343-358

Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Marine Pollution Bulletin 50:125-146

Fagan WF, Cantrell RS, Cosner C (1999) How habitat edges change species interactions. The American Naturalist 153:165-182

Fangue NA, Bennett WA (2003) Thermal tolerance responses of laboratory-acclimated and seasonally acclimatized Atlantic stingray, *Dasyatis sabina*. Copeia:315-325

Feldheim KA, Gruber SH, Ashley MV (2002) The breeding biology of lemon sharks at a tropical nursery lagoon. Proceedings of the Royal Society of London B: Biological Sciences 269:1655-1661

Ferretti F, Myers RA, Serena F, Lotze HK (2008) Loss of large predatory sharks from the Mediterranean Sea. Conservation Biology 22:952-964

Field IC, Meekan MG, Speed CW, White W, Bradshaw CJA (2011) Quantifying movement patterns for shark conservation at remote coral atolls in the Indian Ocean. Coral Reefs 30:61-71

Filmalter JD, Dagorn L, Cowley PD (2013) Spatial behaviour and site fidelity of the sicklefin lemon shark *Negaprion acutidens* in a remote Indian Ocean atoll. Marine Biology 160:2425-2436

Fletcher J, Robert J, Ries L, Battin J, Chalfoun AD (2007) The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined? Canadian Journal of Zoology 85:1017-1030

Fox J, Weisberg S (2011) An R companion to applied regression. Sage Publications, Thousand Oaks, CA

Francis MP (2013) Temporal and spatial patterns of habitat use by juveniles of a small coastal shark (*Mustelus lenticulatus*) in an estuarine nursery. PLoS ONE 8:e57021

Froeschke J, Stunz GW, Wildhaber ML (2010) Environmental influences on the occurrence of coastal sharks in estuarine waters. Marine Ecology Progress Series 407:279-292

Fry FEJ (1971) The effect of environmental factors on the physiology of fish. In: Hoar WS, Randall DJ (eds) Fish physiology: environmental relations and behavior. Academic Press, New York

Gardiner JM, Hueter RE, Maruska KP, Sisneros JA, Casper BM, Mann DA, Demski LS (2012) Sensory physiology and behavior of elasmobranchs. In: Carrier J, Musick J, Heithaus M (eds) Biology of Sharks and Their Relatives. CRC Press, Boca Raton

Garla RC, Chapman DD, Wetherbee BM, Shivji M (2006) Movement patterns of young Carribean reef sharks, *Carcharhinus perezi*, at Fernando de Noronha Archipelago, Brazil: the potential of marine protected areas for conservation of a nursery ground. Marine Biology 149:189-199

Gelsleichter J, Manire CA, Szabo NJ, Cortes E, Carlson J, Lombardi-Carlson L (2005) Organochlorine concentrations in bonnethead sharks (*Sphyrna tiburo*) from four Florida estuaries. Archives of Environmental Contamination and Toxicology 48:474-483

George L, Martins APB, Heupel M, Simpendorfer C (2019) Fine-scale movements of juvenile blacktip reef sharks *Carcharhinus melanopterus* in a shallow nearshore nursery. Marine Ecology Progress Series 623:85-97

Gibson R, Robb L, Wennhage H, Burrows M (2002) Ontogenetic changes in depth distribution of juvenile flatfishes in relation to predation risk and temperature on a shallow-water nursery ground. Marine Ecology Progress Series 229:233-244

Gilliam D, Sullivan KM (1993) Diet and feeding habits of the southern stingray *Dasyatis Americana* in the central Bahamas. Bulletin of Marine Science 52:1007-1013

Goetze JS, Fullwood LAF (2013) Fiji's largest marine reserve benefits reef sharks. Coral Reefs 32:121-125

Gorman AM, Gregory RS, Schneider DC (2009) Eelgrass patch size and proximity to the patch edge affect predation risk of recently settled age 0 cod (Gadus). Journal of Experimental Marine Biology and Ecology 371:1-9

Gribble N, Whybird O, Williams L, Garrett R (2005) Fishery assessment update 1988-2003: Queensland east coast shark. In: Fisheries QGDoPIa (ed). DPI Animal Science, Northern Fisheries Centre, Cairns

Grol MG, Dorenbosch M, Kokkelmans EM, Nagelkerken I (2008) Mangroves and seagrass beds do not enhance growth of early juveniles of a coral reef fish. Marine Ecology Progress Series 366:137-146

Grubbs RD (2010) Ontogenetic shifts in movements and habitat use. In: Carrier J, Musick JA, Heithaus M (eds) Sharks and their relatives II: Biodiversity, adaptive physiology, and conservation. CRC Press, Boca Raton, FL

Grubbs RD, Musick JA (2007) Spatial delineation of summer nursery areas for juvenile sandbar sharks in Chesapeake Bay, Virginia. In: McCandless CT, Kohler NE, Jr. HLP (eds) Shark nursery grounds of the Gulf of Mexico and east coast waters of the United States, Book 50. American Fisheries Society Symposium, Bethesda, MD

Grubbs RD, Musick JA, Conrath CL, Romine JG (2005) Long-term movements, migration, and temporal delineation of a summer nursery for juvenile sandbar sharks in the Chesapeake Bay region. In: McCandless CT, Kohler NE, Jr. HLP (eds) Shark nursery grounds of the Gulf of Mexico and east coast waters of the United States, Book 50. American Fisheries Society Symposium, Bethesda, MD

Gruber SH, De Marignac JR, Hoenig JM (2001) Survival of juvenile lemon sharks at Bimini, Bahamas, estimated by mark–depletion experiments. Transactions of the American Fisheries Society 130:376-384

Gruber SH, Nelson DR, Morrissey JF (1988) Patterns of activity and space utilization of lemon sharks, *Negaprion brevirostris*, in a shallow Bahamian lagoon. Bulletin of Marine Science 43:61-76

Guttridge TL, Gruber SH, Franks BR, Kessel ST, Gledhill KS, Uphill J, Krause J, Sims DW (2012) Deep danger: intra-specific predation risk influences habitat use and aggregation formation of juvenile lemon sharks *Negaprion brevirostris*. Marine Ecology Progress Series 445:279-291

Hammerschlag N, Morgan AB, Serafy JE (2010) Relative predation risk for fishes along a subtropical mangrove–seagrass ecotone. Marine Ecology Progress Series 401:259-267

Hazen EL, Jorgensen S, Rykaczewski RR, Bograd SJ, Foley DG, Jonsen ID, Shaffer SA, Dunne JP, Costa DP, Crowder LB (2013) Predicted habitat shifts of Pacific top predators in a changing climate. Nature Climate Change 3:234-238

Hazon N, Wells A, Pillans RD, Good JP, Gary Anderson W, Franklin CE (2003) Urea based osmoregulation and endocrine control in elasmobranch fish with special reference to euryhalinity. Comparative Biochemistry and Physiology Part B, Biochemistry & Molecular Biology 136:685-700

Heithaus MR (2001) The biology of tiger sharks, *Galeocerdo cuvier*, in Shark Bay, Western Australia: sex ratio, size distribution, diet, and seasonal changes in catch rates. Environmental Biology of Fishes 61:25-36

Heithaus MR, Delius BK, Wirsing AJ, Dunphy-Daly MM (2009) Physical factors influencing the distribution of a top predator in a subtropical oligotrophic estuary. Limnology and Oceanography 54:472-482

Heithaus MR, Dill LM, Marshall GJ, Buhleier B (2002) Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. Marine Biology 140:237-248

Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. TRENDS in Ecology and Evolution 23:202-210

Heithaus MR, Hamilton IM, Wirsing AJ, Dill LM (2006) Validation of a randomization procedure to assess animal habitat preferences: microhabitat use of tiger sharks in a seagrass ecosystem. Journal of Animal Ecology 75:666-676

Heithaus MR, Wirsing AJ, Dill LM, Heithaus LI (2007) Long-term movements of tiger sharks satellite-tagged in Shark Bay, Western Australia. Marine Biology 151:1455-1461

Helfman GS (1981) The advantage to fishes of hovering in shade. Copeia 2:392-400

Heupel M, Simpfendorfer C (2002) Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. Canadian Journal of Fisheries and Aquatic Sciences 59:624-632

Heupel MR (2007) Exiting Terra Ceia Bay: examination of cues stimulating migration from a summer nursery area. In: McCandless CT, Kohler NE, Jr. HLP (eds) Shark nursery grounds of the Gulf of Mexico and east coast waters of the United States, Book 50. American Fisheries Society Symposium, Bethesda, MD

Heupel MR, Carlson JK, Simpfendorfer CA (2007) Shark nursery areas: concepts, definition, characterization and assumptions. Marine Ecology Progress Series 337:287-297

Heupel MR, Hueter RE (2001) Use of an automated acoustic telemetry system to passively track juvenile blacktip shark movements. In: Sibert J, Nielsen J (eds) Electronic tagging and tracking in marine fisheries. Kluwer Academic Publishers, Dordrecht

Heupel MR, Hueter RE (2002) Importance of prey density in relation to the movement patterns of juvenile blacktip sharks (*Carcharhinus limbatus*) within a coastal nursery area. Marine and Freshwater Research 53:543-550

Heupel MR, Kanno S, Martins AP, Simpfendorfer CA (2019a) Advances in understanding the roles and benefits of nursery areas for elasmobranch populations. Marine and Freshwater Research 70:897-907

Heupel MR, Papastamatiou YP, Espinoza M, Green ME, Simpfendorfer CA (2019b) Reef shark science – key questions and future directions. Frontiers in Marine Science 6:12

Heupel MR, Simpfendorfer CA (2008) Movement and distribution of young bull sharks *Carcharhinus leucas* in a variable estuarine environment. Aquatic Biology 1:277-289

Heupel MR, Simpfendorfer CA (2014) Importance of environmental and biological drivers in the presence and space use of a reef-associated shark. Marine Ecology Progress Series 496:47-57

Heupel MR, Simpfendorfer CA (2015) Long-term movement patterns of a coral reef predator. Coral Reefs 34:679-691

Heupel MR, Simpfendorfer CA, Collins AB, Tyminski JP (2006) Residency and movement patterns of bonnethead sharks, *Sphyrna tiburo*, in a large Florida estuary. Environmental Biology of Fishes 76:47-67

Heupel MR, Simpfendorfer CA, Fitzpatrick R (2010) Large-scale movement and reef fidelity of grey reef sharks. PLoS ONE 5:5

Heupel MR, Simpfendorfer CA, Hueter RE (2003) Running before the storm: blacktip sharks respond to falling barometric pressure associated with Tropical Storm Gabrielle. Journal of Fish Biology 63:1357-1363

Heupel MR, Williams AJ, Welch DJ, Ballagh A, Mapstone BD, Carlos G, Davies C, Simpfendorfer CA (2009) Effects of fishing on tropical reef associated shark populations on the Great Barrier Reef. Fisheries Research 95:350-361

Higgins E (2018) How hot is too hot? The effects of elevated temperatures upon two species of juvenile stingrays. Honours, James Cook University, Townsville

Hight BV, Lowe CG (2007) Elevated body temperatures of adult female leopard sharks, *Triakis semifasciata*, while aggregating in shallow nearshore embayments: evidence for behavioral thermoregulation? Journal of Experimental Marine Biology and Ecology 352:114-128

Hobson ES (1963) Feeding behavior in three species of sharks. Pacific Science 17:171-194

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007) Coral reefs under rapid climate change and ocean acidification. Science 318:1737-1742

Hoisington G, Lowe CG (2005) Abundance and distribution of the round stingray, *Urobatis halleri*, near a heated effluent outfall. Marine Environmental Research 60:437-453

Holbrook SJ, Schmitt RJ, Stephens JS (1997) Changes in an assemblage of temperate reef fishes associated with a climate shift. Ecological Applications 7:1299-1310

Hopkins TE, Cech JJ (2003) The influence of environmental variables on the distribution and abundance of three elasmobranchs in Tomales Bay, California. Environmental Biology of Fishes 66:279-291

Hussey NE, Dudley SF, McCarthy ID, Cliff G, Fisk AT (2011) Stable isotope profiles of large marine predators: viable indicators of trophic position, diet, and movement in sharks? Canadian Journal of Fisheries and Aquatic Sciences 68:2029-2045

Hutchings P, Haynes D, Goudkamp K, McCook L (2005) Catchment to Reef: Water quality issues in the Great Barrier Reef Region - An overview of papers. Marine Pollution Bulletin 51:3-8

Igulu MM, Nagelkerken I, Dorenbosch M, Grol MG, Harborne AR, Kimirei IA, Mumby PJ, Olds AD, Mgaya YD (2014) Mangrove habitat use by juvenile reef fish: meta-analysis reveals that tidal regime matters more than biogeographic region. PLoS ONE 9:e114715

IPCC (2007) Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds). Cambridge University Press, Cambridge, UK

Jacoby DM, Busawon DS, Sims DW (2010) Sex and social networking: the influence of male presence on social structure of female shark groups. Behavioral Ecology 21:808-818

Jaine FRA, Couturier LIE, Weeks S, Townsend KA, Bennett MB, Fiora K, Richardson AJ (2012) When giants turn up: sighting trends, environmental influences and habitat use of the manta ray *Manta alfredi* at a coral reef. PLoS ONE 7:e46170

Jennings DE, Gruber SH, Franks BR, Kessel ST, Robertson AL (2008) Effects of large-scale anthropogenic development on juvenile lemon shark (*Negaprion brevirostris*) populations of Bimini, Bahamas. Environmental Biology of Fishes 83:369-377

Jetz W, Carbone C, Fulford J, Brown JH (2004) The scaling of animal space use. Science 306:266-268

Jirik KE, Lowe CG (2012) An elasmobranch maternity ward: female round stingrays *Urobatis halleri* use warm, restored estuarine habitat during gestation. Journal of Fish Biology 80:1227-1245

Jorgensen SJ, Klimley AP, Muhlia-Melo AF (2009) Scalloped hammerhead shark *Sphyrna lewini*, utilizes deep-water, hypoxic zone in the Gulf of California. Journal of Fish Biology 74:1682-1687

Kaiser M, Ramsay K, Richardson C, Spence F, Brand A (2000) Chronic fishing disturbance has changed shelf sea benthic community structure. Journal of Animal Ecology 69:494-503

Kanno S, Schlaff A, Heupel M, Simpendorfer C (2019) Stationary video monitoring reveals habitat use of stingrays in mangroves. Marine Ecology Progress Series 621:155-168

Kernohan BJ, Gitzen RA, Millspaugh JJ (2001) Analysis of animal space use and movements. In: Millspaugh JJ, Marzluff JM (eds) Radio tracking and animal populations. Academic Press, San Diego

Kimball ME, Able KW (2012) Tidal migrations of intertidal salt marsh creek nekton examined with underwater video. Northeastern Naturalist 19:475-486

Kimirei IA, Nagelkerken I, Mgaya YD, Huijbers CM (2013) The mangrove nursery paradigm revisited: otolith stable isotopes support nursery-to-reef movements by Indo-Pacific fishes. PLoS ONE 8:e66320

King B, McAllister F, Done TJ (2002) Modelling the impact of the Burdekin, Herbert, Tully and Johnstone River plumes on the central Great Barrier Reef. CRC Reef Research Centre Technical Report No 44. CRC Reef Research Centre, Townsville

Klimley AP (1987) The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. Environmental Biology of Fishes 18:27-40

Kneebone J, Chisholm J, Skomal GB (2012) Seasonal residency, habitat use, and site fidelity of juvenile sand tiger sharks *Carcharias taurus* in a Massachusetts estuary. Marine Ecology Progress Series 471:165-181

Knip DM, Heupel MR, Simpfendorfer CA (2010) Sharks in nearshore environments: models, importance, and consequences. Marine Ecology Progress Series 402:1-11

Knip DM, Heupel MR, Simpfendorfer CA, Tobin AJ, Moloney J (2011a) Ontogenetic shifts in movement and habitat use of juvenile pigeye sharks *Carcharhinus amboinensis* in a tropical nearshore region. Marine Ecology Progress Series 425:233-246

Knip DM, Heupel MR, Simpfendorfer CA, Tobin AJ, Moloney J (2011b) Wet-season effects on the distribution of juvenile pigeye sharks, *Carcharhinus amboinensis*, in tropical nearshore waters. Marine and Freshwater Research 62:658-667

Laegdsgaard P, Johnson C (2001) Why do juvenile fish utilise mangrove habitats? Journal of Experimental Marine Biology and Ecology 257:229-253

Last PR, Stevens J (2009) Sharks and rays of Australia. CSIRO Publishing, Collingwood

Last PR, White WT, Gledhill DC, Hobday AJ, Brown R, Edgar GJ, Pecl G (2011) Long-term shifts in abundance and distribution of a temperate fish fauna: a response to climate change and fishing practices. Global Ecology and Biogeography 20:58-72

Lea JS, Humphries NE, Bortoluzzi J, Daly R, Von Brandis RG, Patel E, Patel E, Clarke CR, Sims DW (2020) At the turn of the tide: space use and habitat partitioning in two sympatric shark species is driven by tidal phase. Frontiers in Marine Science 7:624

Lea JS, Humphries NE, von Brandis RG, Clarke CR, Sims DW (2016) Acoustic telemetry and network analysis reveal the space use of multiple reef predators and enhance marine protected area design. Proceedings of the Royal Society B: Biological Sciences 283:20160717

Lear KO, Whitney NM, Morgan DL, Brewster LR, Whitty JM, Poulakis GR, Scharer RM, Guttridge TL, Gleiss AC (2019) Thermal performance responses in free-ranging elasmobranchs depend on habitat use and body size. Oecologia 191:829-842

Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson CH, Jackson JBC (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806-1809

Lowe CG, Bray RN (2006) Fish movement and activity patterns. In: Allen LG, Horn MH, Pondella DJ (eds) The Ecology of California Marine Fishes. University of California Press, Berkeley, CA

Lowe CG, Wetherbee BM, Crow GL, Tester AL (1996) Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. Environmental Biology of Fishes 47:203-211

Lowe CG, Wetherbee BM, Meyer CG (2006) Using acoustic telemetry monitoring techniques to quantify movement patterns and site fidelity of sharks and giant trevally around French Frigate Shoals and Midway Atoll. Atoll Research Bulletin 543:281-303

Lugendo BR, Nagelkerken I, Kruitwagen G, Van Der Velde G, Mgaya YD (2007) Relative importance of mangroves as feeding habitats for fishes: a comparison between mangrove habitats with different settings. Bulletin of Marine Science 80:497-512

Lyle JM (1987) Observations on the biology of *Carcharhinus cautus* (Whitley), *Carcharhinus melanopterus* (Quoy and Gaimard) and *Carcharhinus fitzroyensis* (Whitley) from northern Australia. Australian Journal of Marine and Freshwater Research 38:701-710

Macreadie PI, Hindell JS, Keough MJ, Jenkins GP, Connolly RM (2010) Resource distribution influences positive edge effects in a seagrass fish. Ecology 91:2013-2021

Malcolm HA, Jordan A, Smith SD (2010) Biogeographical and cross-shelf patterns of reef fish assemblages in a transition zone. Marine Biodiversity 40:181-193

Mallet D, Pelletier D (2014) Underwater video techniques for observing coastal marine biodiversity: a review of sixty years of publications (1952–2012). Fisheries Research 154:44-62

Mann KH (2000) Ecology of coastal waters: with implications for management. Blackwell Science, Malden, MA

Martin CS, Vaz S, Ellis JR, Lauria V, Coppin F, Carpentier A (2012) Modelled distributions of ten demersal elasmobranchs of the eastern English Channel in relation to the environment. Journal of Experimental Marine Biology and Ecology 418:91-103

Martins A, Heupel M, Bierwagen S, Chin A, Simpfendorfer C (2020) Diurnal activity patterns and habitat use of juvenile *Pastinachus ater* in a coral reef flat environment. PLoS ONE 15:e0228280

Matern SA, Cech Jr JJ, Hopkins TE (2000) Diel movements of bat rays, *Myliobatis californica*, in Tomales Bay, California: evidence for behavioural thermoregulation? Environmental Biology of Fishes 58:173-182

Matich P, Heithaus MR (2012) Effects of an extreme temperature event on the behavior and age structure of an estuarine top predator, *Carcharhinus leucas*. Marine Ecology Progress Series 447:165-178

Matich P, Heithaus MR, Layman CA (2011) Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. Journal of Animal Ecology 80:294-305

Matley J, Heupel M, Simpfendorfer C (2015) Depth and space use of leopard coralgrouper *Plectropomus leopardus* using passive acoustic tracking. Marine Ecology Progress Series 521:201-216

Mattone C, Sheaves M (2017) Patterns, drivers and implications of dissolved oxygen dynamics in tropical mangrove forests. Estuarine, Coastal and Shelf Science 197:205-213

McCulloch M, Fallon S, Wyndham T, Hendy E, Lough J, Barnes D (2003) Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. Nature 421:727

McElroy WD, Wetherbee BM, Mostello CS, Lowe CG, Crow GL, Wass RC (2006) Food habits and ontogenetic changes in the diet of the sandbar shark, *Carcharhinus plumbeus*, in Hawaii. Environmental Biology of Fishes 76:81-92

McKibben JN, Nelson DR (1986) Patterns of movement and grouping of gray reef sharks, *Carcharhinus amblyrhynchos*, at Enewetak, Marshall Islands. Bulletin of Marine Science 38:89-110

Medved RJ, Marshall JA (1983) Short-term movements of young sandbar sharks, *Carcharhinus plumbeus* (Pisces, Carcharhinidae). Bulletin of Marine Science 33:87-93

Mittelbach GG (1981) Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology 62:1370-1386

Montoya RV, Thorson TB (1982) The bull shark (*Carcharhinus leucas*) and largetooth sawfish (*Pristis perotteti*) in Lake Bayano, a tropical man-made impoundment in Panama. Environmental Biology of Fishes 7:341-347

Morales JM, Moorcroft PR, Matthiopoulos J, Frair JL, Kie JG, Powell RA, Merrill EH, Haydon DT (2010) Building the bridge between animal movement and population dynamics. Philosophical Transactions of the Royal Society of London B: Biological Sciences 365:2289-2301

Morgan D, Allen M, Ebner B, Whitty J, Beatty S (2015) Discovery of a pupping site and nursery for critically endangered green sawfish *Pristis zijsron*. Journal of Fish Biology 86:1658-1663

Morrissey JF, Gruber SH (1993) Habitat selection by juvenile lemon sharks, *Negaprion brevirostris*. Environmental Biology of Fishes 38:311-319

Mourier J, Mills SC, Planes S (2013) Population structure, spatial distribution and life-history traits of blacktip reef sharks *Carcharhinus melanopterus*. Journal of Fish Biology 82:979-993

Mourier J, Planes S (2012) Direct genetic evidence for reproductive philopatry and associated fine-scale migrations in female blacktip reef sharks (*Carcharhinus melanopterus*) in French Polynesia. Molecular Ecology 22:201-214

Mourier J, Vercelloni J, Planes S (2012) Evidence of social communities in a spatially structured network of a free-ranging shark species. Animal Behaviour 83:389-401

Mucientes GR, Queiroz N, Sousa LL, Tarroso P, Sims DW (2009) Sexual segregation of pelagic sharks and the potential threat from fisheries. Biology Letters 5:156-159

Mumby PJ, Edwards AJ, Arias-Gonzalez JE, Lindeman KC, Blackwell PG, Gall A, Gorczynska MI, Harborne AR, Pescod CL, Renken H, Wabnitz CCC, Llewellyn G (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. Nature 427:533-536

Munday PL, Jones GP, Sheaves M, Williams AJ, Goby G (2007) Vulnerability of fishes on the Great Barrier Reef to climate change. In: Johnson JE, Marshall PA (eds) Climate change and the Great Barrier Reef. Great Barrier Reef Marine Park Authority and Australian Greenhouse Office, Australia

Murcia C (1995) Edge effects in fragmented forests: implications for conservation. Trends in Ecology & Evolution 10:58-62

Nagelkerken I (2009) Evaluation of nursery function of mangroves and seagrass beds for tropical decapods and reef fishes: patterns and underlying mechanisms. In: Nagelkerken I (ed) Ecological connectivity among tropical coastal ecosystems. Springer, Dordrecht

Nagelkerken I, Blaber SJM, Bouillon S, Green P, Haywood M, Kirton LG, Meynecke JO, Pawlik J, Penrose HM, Sasekumar A, Somerfield PJ (2008) The habitat function of mangroves for terrestrial and marine fauna: a review. Aquatic Botany 89:155-185

Nagelkerken I, Faunce C (2008) What makes mangroves attractive to fish? Use of artificial units to test the influence of water depth, cross-shelf location, and presence of root structure. Estuarine, Coastal and Shelf Science 79:559-565

Nagelkerken I, Roberts Cv, Van Der Velde G, Dorenbosch M, Van Riel M, De La Moriniere EC, Nienhuis P (2002) How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale. Marine Ecology Progress Series 244:299-305

Nelson DR, McKibben JN, Strong WR, Lowe CG, Sisneros JA, Schroeder DM, Lavenberg RJ (1997) An acoustic tracking of a megamouth shark, *Megachasma pelagios*: a crepuscular vertical migrator. Environmental Biology of Fishes 49:389-399

Newman SP, Handy RD, Gruber SH (2012) Ontogenetic diet shifts and prey selection in nursery bound lemon sharks, *Negaprion brevirostris*, indicate a flexible foraging tactic. Environmental Biology of Fishes 95:115-126

Nilsson GE, Renshaw GMC (2004) Hypoxic survival strategies in two fishes: extreme anoxia tolerance in the North European crucian carp and natural hypoxic preconditioning in a coral-reef shark. Journal of Experimental Biology 207:3131-3139

Nosal AP, Caillat A, Kisfaludy EK, Royer MA, Wegner NC (2014) Aggregation behavior and seasonal philopatry in male and female leopard sharks *Triakis semifasciata* along the open coast of southern California, USA. Marine Ecology Progress Series 499:157-175

Nosal AP, Cartamil DC, Long JW, Luhrmann M, Wegner NC, Graham JB (2013) Demography and movement patterns of leopard sharks (*Triakis semifasciata*) aggregating near the head of a submarine canyon along the open coast of southern California, USA. Environmental Biology of Fishes 96:865-878

Oh BZ, Thums M, Babcock RC, Meeuwig JJ, Pillans RD, Speed C, Meekan MG (2017) Contrasting patterns of residency and space use of coastal sharks within a communal shark nursery. Marine and Freshwater Research 68:1501-1517

Ortega LA, Heupel MR, Van Beynen P, Motta PJ (2009) Movement patterns and water quality preferences of juvenile bull sharks (*Carcharhinus leucas*) in a Florida estuary. Environmental Biology of Fishes 84:361-373

Osgood G, Baum J (2015) Reef sharks: recent advances in ecological understanding to inform conservation. Journal of Fish Biology 87:1489-1523

Pang PKT, Griffith RW, Atz JW (1977) Osmoregulation in elasmobranchs. American Zoologist 17:365-377

Papastamatiou YP, Cartamil DP, Lowe CG, Meyer CG, Wetherbee BM, Holland KN (2011) Scales of orientation, directed walks and movement path structure in sharks. Journal of Animal Ecology 80:864-874

Papastamatiou YP, Caselle JE, Friedlander AM, Lowe CG (2009a) Distribution, size frequency, and sex ratios of blacktip reef sharks *Carcharhinus melanopterus* at Palmyra Atoll: a predator-dominated ecosystem. Journal of Fish Biology 75:647-654

Papastamatiou YP, Friedlander AM, Caselle JE, Lowe CG (2010) Long-term movement patterns and trophic ecology of blacktip reef sharks (*Carcharhinus melanopterus*) at Palmyra Atoll. Journal of Experimental Marine Biology and Ecology 386:94-102

Papastamatiou YP, Lowe CG, Caselle JE, Friedlander AM (2009b) Scale-dependent effects of habitat on movements and path structure of reef sharks at a predator-dominated atoll. Ecology 90:996-1008

Papastamatiou YP, Watanabe YY, Bradley D, Dee LE, Weng K, Lowe CG, Caselle JE (2015) Drivers of daily routines in an ectothermic marine predator: hunt warm, rest warmer? PLoS ONE 10:e0127807

Papastamatiou YP, Wetherbee BM, Lowe CG, Crow GL (2006) Distribution and diet of four species of carcharhinid shark in the Hawaiian Islands: evidence for resource partitioning and competitive exclusion. Marine Ecology Progress Series 320:239-251

Parsons GR, Carlson JK (1998) Physiological and behavioral responses to hypoxia in the bonnethead shark, *Sphyrna tiburo*: routine swimming and respiratory regulation. Fish Physiology and Biochemistry 19:189-196

Parsons GR, Hoffmayer ER (2005) Seasonal changes in the distribution and relative abundance of the Atlantic sharpnose shark *Rhizoprionodon terraenovae* in the North Central Gulf of Mexico. Copeia 4:914-920

Pedersen EJ, Miller DL, Simpson GL, Ross N (2019) Hierarchical generalized additive models in ecology: an introduction with mgcv. PeerJ 7:e6876

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. Science 308:1912-1915

Pikitch EK, Chapman DD, Babcock EA, Shivji MS (2005) Habitat use and demographic population structure of elasmobranchs at a Caribbean atoll (Glover‟s Reef, Belize). Marine Ecology Progress Series 302:187-197

Pinheiro J, Bates D, DebRoy S, Sarkar D (2019) nlme: Linear and nonlinear mixed effects models. R package, Book 3.1-142

Pitcher C, Doherty P, Anderson T (2009) Seabed environments, habitats and biological assemblages. In: Hutchings P, Kingsford M, Hoegh-Guldberg O (eds) The Great Barrier Reef: biology, environment and management. CSIRO Publishing Collingwood

Pittman S, McAlpine C (2003) Movements of marine fish and decapod crustaceans: process, theory and application. Advances in Marine Biology 44:205-294

Polidoro BA, Carpenter KE, Collins L, Duke NC, Ellison AM, Ellison JC, Farnsworth EJ, Fernando ES, Kathiresan K, Koedam NE (2010) The loss of species: mangrove extinction risk and geographic areas of global concern. PLoS ONE 5:e10095

Polovina JJ, Abecassis M, Howell EA, Woodworth P (2009) Increases in the relative abundance of mid-trophic level fishes concurrent with declines in apex predators in the subtropical North Pacific, 1996-2006. Fishery Bulletin 107:523-531

Porcher IF (2005) On the gestation period of the blackfin reef shark, *Carcharhinus melanopterus*, in waters off Moorea, French Polynesia. Marine Biology 146:1207-1211

Poulakis GR, Stevens PW, Timmers AA, Wiley TR, Simpfendorfer CA (2011) Abiotic affinities and spatiotemporal distribution of the endangered smalltooth sawfish, *Pristis pectinata*, in a south-western Florida nursery. Marine and Freshwater Research 62:1165-1177

Powell RA (2000) Animal home ranges and territories and home range estimators. In: Boitani L, Fuller TK (eds) Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York

Priede IG, Miller PI (2009) A basking shark (*Cetorhinus maximus*) tracked by satellite together with simultaneous remote sensing II: New analysis reveals orientation to a thermal front. Fisheries Research 95:370-372

Quoy JRC, Gaimard P (1824-25) Description de poissons. In: Freycinet Ld (ed) Voyage autour de monde execute sur les corvettes de LM "L'Uranie" et "La Physicienne", pendant les annees 1817, 1818, 1819, et 1820. Pillet Aine, Paris

R Development Core Team (2018) A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rahmstorf S (2007) A semi-empirical approach to projecting future sea-level rise. Science 315:368-370

Raoult V, Tosetto L, Williamson JE (2018) Drone-based high-resolution tracking of aquatic vertebrates. Drones 2:37

Rechisky EL, Wetherbee BM (2003) Short-term movements of juvenile and neonate sandbar sharks, *Carcharhinus plumbeus*, on their nursery grounds in Delaware Bay. Environmental Biology of Fishes 68:113-128

Reis-Filho JA, Giarrizzo T, Barros F (2016) Tidal migration and cross-habitat movements of fish assemblage within a mangrove ecotone. Marine Biology 163:111

Ries L, Fletcher Jr RJ, Battin J, Sisk TD (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. Annual Review of Ecology Evolution and Systematics 35:491-522

Robbins RL (2007) Environmental variables affecting the sexual segregation of great white sharks *Carcharodon carcharias* at the Neptune Islands South Australia. Journal of Fish Biology 70:1350-1364

Roberts CM, Branch G, Bustamante RH, Castilla JC, Dugan J, Halpern BS, Lafferty KD, Leslie H, Lubchenco J, McArdle D (2003) Application of ecological criteria in selecting marine reserves and developing reserve networks. Ecological Applications 13:215-228

Robertson A, Duke N (1987) Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. Marine Biology 96:193-205

Rooker J, Dennis G (1991) Diel, lunar and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. Bulletin of Marine Science 49:684-698

Rosenzweig ML (1974) On the optimal aboveground activity of bannertail kangaroo rats. Journal of Mammalogy 55:193-199

Routley MH, Nilsson GE, Renshaw GMC (2002) Exposure to hypoxia primes the respiratory and metabolic responses of the epaulette shark to progressive hypoxia. Comparative Biochemistry and Physiology Part A, Molecular & Integrative Physiology 131:313-321

Ruf T (1999) The Lomb-Scargle periodogram in biological rhythm research: analysis of incomplete and unequally spaced time-series. Biological Rhythm Research 30:178-201

Rummer J, Fangue N, Jordan H, Tiffany B, Blansit K, Galleher S, Kirkpatrick A, Kizlauskas A, Pomory C, Bennett W (2009) Physiological tolerance to hyperthermia and hypoxia and effects on species richness and distribution of rockpool fishes of Loggerhead Key, Dry Tortugas National Park. Journal of Experimental Marine Biology and Ecology 371:155-162

Rummer JL, Bouyoucos IA, Mourier J, Nakamura N, Planes S (2020) Responses of a coral reef shark acutely exposed to ocean acidification conditions. Coral Reefs https://doi.org/10.1007/s00338-020-01972-0

Rypel AL, Layman CA, Arrington DA (2007) Water depth modifies relative predation risk for a motile fish taxon in Bahamian tidal creeks. Estuaries and Coasts 30:518-525

Sambrook K, Jones GP, Bonin MC (2016) Life on the edge: Coral reef fishes exhibit strong responses to a habitat boundary. Marine Ecology Progress Series 561:203-215

Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos JE, Obura D, Pantos O, Paulay G, Richie M, Rohwer F, Schroeder RE, Walsh S, Jackson JBC, Knowlton N, Sala E (2008) Baselines and degradation of coral reefs in the Northern Line Islands. PLoS ONE 3:1-11

Schaffelke B, Mellors J, Duke NC (2005) Water quality in the Great Barrier Reef region: responses of mangrove, seagrass and macroalgal communities. Marine Pollution Bulletin 51:279-296

Schlaff AM, Heupel MR, Simpfendorfer CA (2014) Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review. Reviews in Fish Biology and Fisheries 24:1089-1103

Schlaff AM, Heupel MR, Udyawer V, Simpfendorfer CA (2020) Sex-based differences in movement and space use of the blacktip reef shark, *Carcharhinus melanopterus*. PLoS ONE 15:e0231142

Sheaves M (2005) Nature and consequences of biological connectivity in mangrove systems. Marine Ecology Progress Series 302:293-305

Sheaves M, Johnston R, Baker R (2016) Use of mangroves by fish: new insights from in-forest videos. Marine Ecology Progress Series 549:167-182

Shepard ELC, Ahmed MZ, Southall EJ, Witt MJ, Metcalfe JD, Sims DW (2006) Diel and tidal rhythms in diving behaviour of pelagic sharks identified by signal processing of archival tagging data. Marine Ecology Progress Series 328:205-213

Shepherd TD, Myers RA (2005) Direct and indirect fishery effects on small coastal elasmobranchs in the northern Gulf of Mexico. Ecology Letters 8:1095-1104

Shipley ON, Brownscombe JW, Danylchuk AJ, Cooke SJ, O'Shea OR, Brooks EJ (2018) Fine-scale movement and activity patterns of Caribbean reef sharks (*Carcharhinus perezi*) in the Bahamas. Environmental Biology of Fishes 101:1097-1104

Simpfendorfer CA, Freitas GG, Wiley TR, Heupel MR (2005) Distribution and habitat partitioning of immature bull sharks (*Carcharhinus leucas*) in a southwest Florida estuary. Estuaries 28:78-85

Simpfendorfer CA, Heupel MR, Collins AB (2008) Variation in the performance of acoustic receivers and its implication for positioning algorithms in a riverine setting. Canadian Journal of Fisheries and Aquatic Sciences 65:482-492

Simpfendorfer CA, Heupel MR, Hueter RE (2002) Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. Canadian Journal of Fisheries and Aquatic Sciences 59:23-32

Simpfendorfer CA, Milward NE (1993) Utilisation of a tropical bay as a nursery area by sharks of the families Carcharhinidae and Sphyrnidae. Environmental Biology of Fishes 37:337-345

Simpfendorfer CA, Wiley TR, Yeiser BG (2010) Improving conservation planning for an endangered sawfish using data from acoustic telemetry. Biological Conservation 143:1460-1469

Simpfendorfer CA, Yeiser BG, Wiley TR, Poulakis GR, Stevens PW, Heupel MR (2011) Environmental influences on the spatial ecology of juvenile smalltooth sawfish (*Pristis pectinata*): results from acoustic monitoring. PLoS ONE 6:1-12

Sims D (2003) Tractable models for testing theories about natural strategies: foraging behaviour and habitat selection of free-ranging sharks. Journal of Fish Biology 63:53-73

Sims DW (2005) Differences in habitat selection and reproductive strategies of male and female sharks. In: Ruckstuhl KE, Neuhaus P (eds) Sexual segregation in vertebrates: ecology of the two sexes. Cambridge University Press, Cambridge

Sims DW, Nash JP, Morritt D (2001) Movements and activity of male and female dogfish in a tidal sea lough: alternative behavioural strategies and apparent sexual segregation. Marine Biology 139:1165-1175

Sims DW, Quayle VA (1998) Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. Nature 393:460-464

Sims DW, Wearmouth VJ, Southall EJ, Hill JM, Moore P, Rawlinson K, Hutchinson N, Budd GC, Righton D, Metcalfe J, Nash JP, Morritt D (2006) Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. Journal of Animal Ecology 75:176-190

Smith JW, Merriner JV (1985) Food habits and feeding behavior of the cownose ray, *Rhinoptera bonasus*, in lower Chesapeake Bay. Estuaries 8:305-310

Smith JW, Merriner JV (1987) Age and growth, movements and distribution of the cownose ray, *Rhinoptera bonasus*, in Chesapeake Bay. Estuaries 10:153-164

Smith TM, Hindell JS (2005) Assessing effects of diel period, gear selectivity and predation on patterns of microhabitat use by fish in a mangrove dominated system in SE Australia. Marine Ecology Progress Series 294:257-270

Smith TM, Hindell JS, Jenkins GP, Connolly RM (2008) Edge effects on fish associated with seagrass and sand patches. Marine Ecology Progress Series 359:203-213

Smith TM, Hindell JS, Jenkins GP, Connolly RM (2010) Seagrass patch size affects fish responses to edges. Journal of Animal Ecology 79:275-281

Snelson FF, Bradley WK (1978) Mortality of fishes due to cold on the east coast of Florida, January, 1977. Florida Scientist 41:1-12

Speed CW, Meekan MG, Field IC, McMahon CR, Abrantes K, Bradshaw CJA (2012a) Trophic ecology of reef sharks determined using stable isotopes and telemetry. Coral Reefs 31:357-367

Speed CW, Meekan MG, Field IC, McMahon CR, Bradshaw CJA (2012b) Heat-seeking sharks: support for behavioural thermoregulation in reef sharks. Marine Ecology Progress Series 463:231-244

Speed CW, Meekan MG, Field IC, McMahon CR, Harcourt RG, Stevens JD, Babcock RC, Pillans RD, Bradshaw CJA (2016) Reef shark movements relative to a coastal marine protected area. Regional Studies in Marine Science 3:58-66

Speed CW, Meekan MG, Field IC, McMahon CR, Stevens JD, McGregor F, Huveneers C, Berger Y, Bradshaw CJA (2011) Spatial and temporal movement patterns of a multi-species coastal reef shark aggregation. Marine Ecology Progress Series 429:261-275

Speers-Roesch B, Brauner CJ, Farrell AP, Hickey AJ, Renshaw GM, Wang YS, Richards JG (2012) Hypoxia tolerance in elasmobranchs. II. Cardiovascular function and tissue metabolic responses during progressive and relative hypoxia exposures. Journal of Experimental Biology 215:103-114

Stevens JD (1984) Life-history and ecology of sharks at Aldabra Atoll, Indian Ocean. Proceedings of the Royal Society of London Series B, Biological Sciences 222:79-106

Stevens JD, Bonfil R, Dulvy NK, Walker PA (2000) The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES Journal of Marine Science 57:476-494

Strickland BA, Massie JA, Viadero N, Santos R, Gastrich KR, Paz V, O'Donnell P, Kroetz AM, Ho DT, Rehage JS (2019) Movements of juvenile bull sharks in response to a major hurricane within a tropical estuarine nursery area. Estuaries and Coasts:1-14

Stump K, Crooks C, Fitchett M, Gruber S, Guttridge T (2017) Hunted hunters: an experimental test of the effects of predation risk on juvenile lemon shark habitat use. Marine Ecology Progress Series 574:85-95

Switzer PV (1993) Site fidelity in predictable and unpredictable habitats. Evolutionary Ecology 7:533-555

Tamburello N, Côté IM, Dulvy NK (2015) Energy and the scaling of animal space use. The American Naturalist 186:196-211

Tanner JE (2005) Edge effects on fauna in fragmented seagrass meadows. Austral Ecology 30:210-218

Thorson TB (1972) The status of the bull shark, *Carcharhinus leucas*, in the Amazon River. Copeia 3:601-605

Thorson TB (1974) Occurence of the sawfish, *Pristis perotteti*, in the Amazon River, with notes on *P. pectinatus*. Copeia 2:560-564

Thums M, Meekan M, Stevens J, Wilson S, Polovina J (2013) Evidence for behavioural thermoregulation by the world's largest fish. Journal of the Royal Society Interface 10:20120477

Tickler DM, Letessier TB, Koldewey HJ, Meeuwig JJ (2017) Drivers of abundance and spatial distribution of reef-associated sharks in an isolated atoll reef system. PLoS ONE 12:e0177374

Tobin AJ, Mapleston A, Harry AV, Espinoza M (2014) Big fish in shallow water; use of an intertidal surf-zone habitat by large-bodied teleosts and elasmobranchs in tropical northern Australia. Environmental Biology of Fishes 97:821-838

Torres LG, Heithaus MR, Delius B (2006) Influence of teleost abundance on the distribution and abundance of sharks in Florida Bay, USA. Hydrobiologia 569:449-455

Ubeda AJ, Simpfendorfer CA, Heupel MR (2009) Movements of bonnetheads, *Sphyrna tiburo*, as a response to salinity change in a Florida estuary. Environmental Biology of Fishes 84:293-303

Udyawer V, Chin A, Knip D, Simpfendorfer CA, Heupel MR (2013) Variable response of coastal sharks to severe tropical storms: environmental cues and changes in space use. Marine Ecology Progress Series 480:171-183

Udyawer V, Dwyer RG, Hoenner X, Babcock RC, Brodie S, Campbell HA, Harcourt RG, Huveneers C, Jaine FR, Simpfendorfer CA (2018) A standardised framework for analysing animal detections from automated tracking arrays. Animal Biotelemetry 6:17

Udyawer V, Read M, Hamann M, Simpfendorfer CA, Heupel MR (2015) Effects of environmental variables on the movement and space use of coastal sea snakes over multiple temporal scales. Journal of Experimental Marine Biology and Ecology 473:26-34

Valiela I, Bowen JL, York JK (2001) Mangrove forests: one of the world's threatened major tropical environments. Bioscience 51:807-815

Vaudo JJ, Heithaus MR (2009) Spatiotemporal variability in a sandflat elasmobranch fauna in Shark Bay, Australia. Marine Biology 156:2579-2590

Vaudo JJ, Heithaus MR (2012) Diel and seasonal variation in the use of a nearshore sandflat by a ray community in a near pristine system. Marine and Freshwater Research 63:1077-1084

Vaudo JJ, Wetherbee BM, Wood AD, Weng K, Howey-Jordan LA, Harvey GM, Shivji MS (2016) Vertical movements of shortfin mako sharks *Isurus oxyrinchus* in the western North Atlantic Ocean are strongly influenced by temperature. Marine Ecology Progress Series 547:163-175

Verweij M, Nagelkerken I, De Graaff D, Peeters M, Bakker E, Van der Velde G (2006) Structure, food and shade attract juvenile coral reef fish to mangrove and seagrass habitats: a field experiment. Marine Ecology Progress Series 306:257-268

Vianna GMS, Meekan MG, Meeuwig JJ, Speed CW (2013) Environmental influences on patterns of vertical movement and site fidelity of grey reef sharks (*Carcharhinus amblyrhynchos*) at aggregation sites. PLoS ONE 8:e60331

Vignaud T, Clua E, Mourier J, Maynard J, Planes S (2013) Microsatellite analyses of blacktip reef sharks (*Carcharhinus melanopterus*) in a fragmented environment show structured clusters. PLoS ONE 8:e61067

Vignaud TM, Mourier J, Maynard JA, Leblois R, Spaet JL, Clua E, Neglia V, Planes S (2014) Blacktip reef sharks, *Carcharhinus melanopterus*, have high genetic structure and varying demographic histories in their Indo-Pacific range. Molecular Ecology 23:5193-5207

Wallman HL, Bennett WA (2006) Effects of parturition and feeding on thermal preference of Atlantic stingray, *Dasyatis sabina* (Lesueur). Environmental Biology of Fishes 75:259-267

Wearmouth VJ, Sims DW (2008) Sexual segregation in marine fish, reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. In: Sims DW (ed) Advances in Marine Biology. Elsevier Academic Press Inc., San Diego, CA

Wearmouth VJ, Sims DW (2010) Sexual segregation in elasmobranchs. Biologia Marina Mediterranea 17:236-239

Webster PJ, Holland GJ, Curry JA, Chang HR (2005) Changes in tropical cyclone number, duration, and intensity in a warming environment. Science 309:1844-1846

Weideli OC, Bouyoucos IA, Papastamatiou YP, Mescam G, Rummer JL, Planes S (2019) Same species, different prerequisites: investigating body condition and foraging success in young reef sharks between an atoll and an island system. Scientific reports 9:1-11

Welsh JQ, Fox RJ, Webber DM, Bellwood DR (2012) Performance of remote acoustic receivers within a coral reef habitat: implications for array design. Coral Reefs 31:693-702

Werner EE, Gilliam JF, Hall DJ, Mittelbach GG (1983a) An experimental test of the effects of predation risk on habitat use in fish. Ecology 64:1540-1548

Werner EE, Mittelbach GG, Hall DJ, Gilliam JF (1983b) Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. Ecology 64:1525-1539

Werry JM, Lee SY, Lemckert CJ, Otway NM (2012) Natural or artificial? Habitat-use by the bull shark, *Carcharhinus leucas*. PLoS ONE 7:e49796

Wetherbee BM, Cortés E, Bizzarro JJ (2004) Food consumption and feeding habits. In: Carrier J, Musick J, Heithaus M (eds) Biology of Sharks and Their Relatives. CRC Press LLC, Florida

Wetherbee BM, Gruber S, Cortes E (1990) Diet, feeding habits, digestion and consumption in sharks, with special reference to the lemon shark, *Negrapion brevirostris*. In: Pratt Jr. HL, Gruber SH, Taniuchi T (eds) Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries. NOAA Technical Report 90, Seattle

Wetherbee BM, Gruber SH, Rosa RS (2007) Movement patterns of juvenile lemon sharks *Negaprion brevirostris* within Atol das Rocas, Brazil: a nursery characterized by tidal extremes. Marine Ecology Progress Series 343:283-293

Wetherbee BM, Rechisky EL (2000) Movement patterns of juvenile sandbar sharks on their nursery grounds in Delaware Bay. In: Eiler JH, Alcorn DJ, Neuman MR (eds) Biotelemetry 15: Proc of the 15th Int Symp on Biotelemetry. International Society on Biotelemetry, Wagenigen

White WT, Potter IC (2004) Habitat partitioning among four elasmobranch species in nearshore, shallow waters of a subtropical embayment in Western Australia. Marine Biology 145:1023-1032

Whitney NM, Papastamatiou YP, Holland KN, Lowe CG (2007) Use of an acceleration data logger to measure diel activity patterns in captive whitetip reef sharks, *Triaenodon obesus*. Aquatic Living Resources 20:299-305

Whitney NM, Pyle RL, Holland KN, Barcz JT (2012) Movements, reproductive seasonality, and fisheries interactions in the whitetip reef shark (*Triaenodon obesus*) from community-contributed photographs. Environmental Biology of Fishes 93:121-136

Whitty JM, Morgan DL, Peverell SC, Thorburn DC, Beatty SJ (2009) Ontogenetic depth partitioning by juvenile freshwater sawfish (*Pristis microdon*: Pristidae) in a riverine environment. Marine and Freshwater Research 60:306-316

Wiley TR, Simpfendorfer CA (2007) The ecology of elasmobranchs occurring in the Everglades National Park, Florida: implications for conservation and management. Bulletin of Marine Science 80:171-189

Williams DM, Hatcher AI (1983) Structure of fish communities on outer slopes of inshore, mid-shelf and outer shelf reefs of the Great Barrier Reef. Marine Ecology Progress Series 10:239-250

Wise G, Mulvey JM, Renshaw GMC (1998) Hypoxia tolerance in the epaulette shark (*Hemiscyllium ocellatum*). Journal of Experimental Zoology 281:1-5

Wismer S, Hoey AS, Bellwood DR (2009) Cross-shelf benthic community structure on the Great Barrier Reef: relationships between macroalgal cover and herbivore biomass. Marine Ecology Progress Series 376:45-54

Wolanski E, Jones M (1981) Physical properties of Great Barrier Reef lagoon waters near Townsville. I. Effects of Burdekin River floods. Marine and Freshwater Research 32:305-319

Wood SN (2004) Stable and efficient multiple smoothing parameter estimation for generalized additive models. Journal of the American Statistical Association 99:673-686

Wooldridge S, Brodie J, Furnas M (2006) Exposure of inner-shelf reefs to nutrient enriched runoff entering the Great Barrier Reef Lagoon: Post-European changes and the design of water quality targets. Marine Pollution Bulletin 52:1467-1479

Yates PM, Heupel MR, Tobin AJ, Moore SK, Simpfendorfer CA (2015) Diversity in immature-shark communities along a tropical coastline. Marine and Freshwater Research 66:399-410