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Spatial ecology of mobile predators in a nearshore tropical environment and its implication for marine protected areas

Thesis submitted by
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Nearshore tropical environments provide important habitat for a range of shark species of different life stages including juvenile pigeye *Carcharhinus amboinensis* (top) and adult spottail *Carcharhinus sorrah* (bottom) sharks. *Photo credits: Fishing and Fisheries Research Centre and M. R. Heupel.*

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ABSTRACT

Nearshore environments are of high value and provide important habitat for a diverse assemblage of shark species. However, these regions are also highly dynamic, creating challenging conditions for inhabitants due to their shallow nature and close proximity to shore. This dissertation research defines the spatial ecology of sharks within a nearshore tropical environment to (1) provide a better understanding of the factors influencing species distribution, habitat use and movement patterns and (2) evaluate the effectiveness of marine protected areas (MPAs) for sheltering these mobile species from exploitation (e.g. fishing pressure).

Although shark species are highly diverse and occur in a wide range of habitats, limited effort has gone into understanding population level use of habitat. Theoretical models describing coastal shark populations have remained largely unchanged since the 1960s despite limitations in applicability to many species, with smaller-bodied species being poorly represented by the current models. Coastal shark populations have typically been described as using nearshore nursery areas as juveniles and then moving further offshore as adults. A new theoretical model is proposed in this dissertation to represent those species that spend most or all of their life within nearshore regions, but do not show use of discrete nursery areas. Description of this new model outlines the importance of nearshore regions to smaller-bodied species in particular.

Field work was conducted using passive acoustic monitoring to examine the presence and movements of two coastal shark species within a nearshore tropical environment. An array of fifty-seven acoustic receivers deployed throughout two MPA regions in Cleveland

Bay, north Queensland, Australia, passively tracked pigeye *Carcharhinus amboinensis* and spottail *Carcharhinus sorrah* sharks from 2008 to 2010. These species were selected to define differences in the use of nearshore habitat between sharks that have different life history and ecological characteristics, putting the results of the theoretical population models into context. *Carcharhinus amboinensis* individuals consisted of juveniles from three age classes (young-of-the-year, one-year-olds and two-year-olds), and *C*. *sorrah* individuals were adults.

Juvenile *C*. *amboinensis* were present in Cleveland Bay for long periods, ranging from 3 to 429 days (mean = 88). Individuals associated strongly with shallow turbid habitats, with core home ranges consistently remaining in areas adjacent to creek and river mouths. Significant differences in minimum convex polygon measures of home range revealed that older juveniles used larger areas and undertook movements from core ranges more frequently than younger juveniles. Movements of *C*. *amboinensis* were related to the tidal cycle, but changes in water depth associated with the tide had the strongest influence on the youngest juveniles. An ontogenetic shift in depth used was also evident, with young-of-the-year individuals restricting their movements to shallower depths (mean = 236 cm) than one- and two-year-old individuals (means = 261 and 269 cm, respectively).

Freshwater influences associated with the wet season played a role in habitat use of juvenile *C*. *amboinensis* in this nearshore region. Home ranges and distribution of *C*. *amboinensis* showed distinct changes across two consecutive wet seasons, with individuals moving away from creek mouths during times of high freshwater inflow. Although juvenile *C*. *amboinensis* moved in response to freshwater inflow, home range sizes remained stable, and the amount of space individuals used did not change in

relation to freshwater inflow. This result suggests that individuals use consistent amounts of space despite changes in location.

Adult *C. sorrah* were also present in Cleveland Bay for long periods, ranging from 8 to 408 days (mean = 190). Unlike *C. amboinensis*, however, this species used areas away from creek and river mouths and generally remained in deeper water habitats (mean = 421 cm). Analyses of home range revealed that individuals consistently used the same areas and similar amounts of space over time. A high level of spatial segregation occurred among *C. sorrah* within this nearshore region, with individuals using different types of habitat and showing high attachment to specific areas. In addition, the range of depths individuals used varied between sexes. Males tended to remain within a narrow depth range, whereas females displayed a seasonal shift in the range of depths used. Mean monthly depths varied by as much as 200 cm for females, with individuals using shallower habitats where water temperature was higher (up to 4º C) during the winter months.

Both species spent a large proportion of time inside the MPAs. The mean proportion of time *C. amboinensis* and *C. sorrah* spent inside MPAs was 0.22 and 0.32, respectively, and MPA use varied seasonally. Both species used large areas inside the MPAs, but individuals generally used only half of the available protected space. All individuals made excursions from the MPAs, however, both species exited and re-entered MPAs within consistent locations along the boundaries.

Long-term use of Cleveland Bay demonstrates that this region contains important habitat for both juvenile *C. amboinensis* and adult *C. sorrah*. However, differences in movement and habitat use suggest that this nearshore environment serves different functions for these species. Use of discrete, shallow areas is likely a refuging strategy for young *C.*

amboinensis, and an ontogenetic shift in depth used may be a mechanism to decrease competition between different juvenile age classes using the same area. For *C. sorrah*, the high level of spatial segregation among individuals may be a strategy to improve foraging success by increasing separation and using more areas. Although movement and habitat use patterns varied between species, both used MPA regions for a large proportion of time. Thus, coastal MPAs provide some protection and benefits for mobile species like sharks. By defining the spatial ecology of coastal sharks, this dissertation contributes to improving the conservation and management of their populations, and provides a framework for future research on the effectiveness of MPAs for mobile species within Australia and around the world.

TABLE OF CONTENTS

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

CHAPTER 6

Habitat Use and Movement of Adult *Carcharhinus sorrah*

CHAPTER 7

Evaluating the Effectiveness of Marine Protected Areas for Sharks

CHAPTER 8

General Discussion

LIST OF TABLES

CHAPTER 4

CHAPTER 5

CHAPTER 6

LIST OF FIGURES

CHAPTER 3

CHAPTER 4

CHAPTER 5

CHAPTER 6

CHAPTER 7

CHAPTER 1

General Introduction

Spatial ecology is a well studied theme in science that has been used to answer questions pertaining to animal behaviour and define relationships between wildlife and the surrounding environment (Tilman and Kareiva 1997). Identifying patterns in animal movement and use of space can help explain ecological drivers of behaviour. For example, analyses of species distributions, home range and habitat use have identified strategies that shape animal behaviour (e.g. Rettie and Messier 2000; Valeix *et al.* 2007; Carfagno and Weatherhead 2008; Fernando *et al.* 2008). Collecting this type of ecological information is important for understanding the mechanisms that affect species movement and use of space within dynamic and changing environments throughout the world. A steady advancement in technology is helping to develop increasingly comprehensive scientific studies, allowing for more difficult research questions to be tackled.

It has generally been challenging to study spatial ecology in the aquatic realm because animals are not as easily observed as they are in the terrestrial realm. However, innovative tracking technology has provided an opportunity to monitor the movements of fish and other marine species in environments where they cannot be seen. Specifically, acoustic telemetry can monitor and record the presence of acoustically tagged individuals, and a wide range of research designs can be applied depending on the question being asked (Voegeli *et al.* 2001; Heupel *et al.* 2006a). For example, studies can use passive acoustic monitoring to continuously track multiple individuals to obtain long-term and population level data (Heupel and Hueter 2001). Data from passive acoustic monitoring has been used to calculate home ranges (Heupel *et al.* 2004), identify species response to environmental factors (Heupel *et al.* 2003), define patterns in habitat use (Farrugia *et al.* 2011) and has provided useful information for the conservation and management of exploited species (Simpfendorfer *et al.* 2010). Thus, passive acoustic monitoring is a powerful tool that can be used to address numerous research questions. These techniques will help provide a better understanding of species behaviour and can be applied in a wide range of habitats within the marine environment.

Nearshore regions are one of the most productive and valuable areas within the marine environment (Constanza *et al.* 1997), which can be attributed to the general high abundance and rich diversity of species in these areas (Blaber *et al.* 1989; Heck *et al.* 1995). However, nearshore regions are also highly dynamic and create challenging conditions for inhabitants due to their shallow nature and close proximity to shore. These regions are becoming increasingly exposed to both environmental and anthropogenic impacts, which affect species survival and destroy habitat (Rodriguez *et al.* 1994; Jackson *et al.* 2001). Exploitation through fishing is one the most altering human activities impacting nearshore regions (Jackson *et al.* 2001) and has significantly affected the population status of many top predator species (Myers *et al.* 2007). Providing protection from exploitation and habitat degradation is difficult, and some agencies employ marine protected areas (MPAs) to help manage these regions. MPAs are designated regions where human activities (e.g. fishing) are placed under certain restrictions in an effort to protect and conserve habitat and species. It is therefore crucial to understand how species use dynamic nearshore environments to implement protective measures that are effective at sheltering their populations. Thus, acquiring information on species ecology (e.g. home range, habitat use, movement, etc.) will be essential for establishing protective measures like MPAs, particularly for top predators that are vulnerable to exploitation.

Sharks are a key component of nearshore environments because as top and mobile predators they use a high proportion of available energy (Cortés 1999), and help stabilise food webs by integrating energy sources over large spatial scales (Rooney *et al.* 2006). Previous studies have found that multiple shark species may inhabit the same nearshore regions, and overlaps in diet indicate that species use the same or similar resources (Castro 1993; Simpfendorfer and Milward 1993). Further research has demonstrated that different shark species using the same nearshore regions may share space by partitioning themselves temporally and/or by habitat type (White and Potter 2004). Thus, how sharks use space and habitat varies among the different species that inhabit nearshore environments, and is likely in part a reflection of the high diversity in their life histories and ecologies. However, since different behaviours will have varying implications for species success (see Chapter 2), it is important that differences in use of space and habitat are well defined.

Although nearshore regions are of high value and provide important habitat for many shark species, the following questions remain unanswered: (1) how do shark species use nearshore habitats, (2) what factors influence their distribution, habitat use and movement patterns and (3) can MPAs contribute to the effective management of their populations? To address these questions, this dissertation first reviews the distribution and habitat use of shark species in nearshore environments. This review evaluates a current population model and proposes a new model to encompass a wider range of shark populations. Second, using passive acoustic monitoring this dissertation characterises the spatial ecology of two shark species by defining their presence, distribution, home range and movement patterns in a nearshore region. By defining how sharks use space within a nearshore region, this research also determines how effective MPAs are at providing shelter from fishing pressure. The main hypotheses of this dissertation are: (1) shark species that use the same nearshore region will have similar home ranges and movement patterns, (2) shark species that use the same nearshore region will avoid overlap in their distribution, (3) movement and habitat use of sharks in nearshore regions will vary with season, age class and sex and (4) shark species will gain protection from fishing pressure in nearshore regions by remaining inside MPA boundaries. The progress of effective conservation and management in nearshore environments requires a clear understanding of how species use these areas and associated habitat. This dissertation provides important and novel information regarding nearshore habitat use of multiple shark species, and may serve as a model for other studies in nearshore regions worldwide.

CHAPTER 2

Sharks in Nearshore Environments

2.1 Introduction

Nearshore regions typically consist of shallow water with temporally varying characteristics and are commonly comprised of highly dynamic ecosystems supporting high biodiversity (Robertson and Duke 1987; Morin *et al*. 1992). Major fluctuations in salinity, temperature, depth, flow and turbidity occur in nearshore waters on a variety of temporal scales (from hours to seasons) due to changes in tidal level, freshwater flow, rainfall and seasonal weather patterns (Mann 2000; Masselink *et al*. 2008). Although variable conditions may create challenging environments for inhabitants, nearshore regions are highly productive and have a relatively high abundance and rich diversity of fish and invertebrate species (Blaber *et al*. 1989; Beck *et al*. 2001). As a result of high productivity, nearshore waters have considerable economic value supporting recreational, commercial and indigenous fisheries. Overall, nearshore regions contribute goods and services of high quantity and quality to both environment and economy, resulting in these areas being identified as significantly valuable ecosystems (Constanza *et al*. 1997).

Close proximity to land allows easy accessibility to nearshore regions, resulting in these areas to be susceptible to increased exploitation. Fishing is one of the major human impacts affecting nearshore waters and overfishing has resulted in the decline and/or collapse of some coastal ecosystems (Pauly *et al*. 1998; Jackson *et al*. 2001). Coastal development also has detrimental effects on nearshore regions through modification practices such as dredging, construction and deforestation, which can cause large-scale habitat degradation or loss (Suchanek 1994; Vitousek *et al*. 1997). The estimated proportion of the world's total human population living within 100 km of the coast is 60% (Vitousek *et al*. 1997), with this value projected to be 75% within 60 km of the coast by the year 2020 (DeMaster *et al*. 2001). Due to increasing human population in coastal areas, it is likely that human pressure in these regions will continue and potentially increase. With increased pressure, it will be progressively more important to understand how species and communities use nearshore waters so that effective conservation and management can be implemented. In addition to anthropogenic influences, environmental impacts such as weather events result in erosion, scouring, habitat destruction, sediment movement and increased turbidity in nearshore regions (Rodriguez *et al*. 1994; Masselink *et al*. 2008). Inter-annual climate anomalies (e.g. El Niño, La Niña, drought, etc.) can change the physical characteristics of nearshore environments, making conditions less favourable for inhabitants (Mol *et al*. 2000; Abel *et al*. 2007). Since nearshore regions are highly dynamic and variable, as well as vulnerable to exploitation, species that inhabit these waters must either cope with the changes they face, adapt accordingly or leave in order to survive.

Sharks are a key component of nearshore ecosystems, acting as top predators and using a high proportion of available energy (Cortés 1999). Since nearshore waters provide a wide variety of habitat characteristics, sharks can exploit regions with features that are optimal for survival. For example, young sharks may use shallow or low salinity environments to decrease predation risk (Simpfendorfer *et al*. 2005; Wetherbee *et al*. 2007), or forage in areas where food resources are most abundant (Simpfendorfer and Milward 1993). In addition, adults may exploit habitats to target high quality prey items for diet and growth (Heithaus *et al*. 2002). Nearshore regions are also used in different ways by different shark species, and the characteristics and habitat type of a region may influence species distribution and movement (White and Potter 2004; DeAngelis *et al*.

2008). Thus, habitat use by sharks within nearshore regions is likely to be influenced by a combination of ecological factors including environmental characteristics, resource abundance and distribution and/or presence of other competing species.

Common coastal shark species consist primarily of carcharhinids and sphyrnids in tropical and subtropical regions and triakids in temperate regions (Bigelow and Schroeder 1948; Compagno 1984; Last and Stevens 2009). Species from these groups tend to be well studied because they are encountered often in nearshore regions and are easily captured. These groups also form the basis of some important fisheries, which has further driven research (Grace and Henwood 1997; Francis 1998; Walker 1998; Pradervand *et al*. 2007). However, the diversity of sharks that occur in nearshore waters is much greater than these three families alone (e.g. scyliorhinids, orectolobids, ginglymostomatids, heterodontids, etc.). It is important to recognise the diversity of sharks using nearshore waters because different species behave in different ways (Bethea *et al*. 2004), have different life histories (Cortés 2000) and as top predators may have a large influence on nearshore community dynamics (Heithaus *et al*. 2008).

Although the species composition of sharks that occur in nearshore waters is diverse, descriptions of distribution and habitat use tend to be generalised. For example, a theoretical model proposed by Springer (1967) broadly outlined the geographic range and distribution of a hypothetical population of sharks. In this population, young are born in nearshore nursery areas in spring/summer, where they remain until they reach sexual maturity and join the adult population further offshore. Adults occur offshore, segregated from the young except when they move inshore to give birth and mate in spring/summer. However, not all populations of sharks that occur in nearshore regions fit this model. The strategy a species uses is shaped by both its life history characteristics (Branstetter 1990) and surrounding environment (Sims 2003) to maximise survival, which results in distribution and habitat use varying greatly between species. Opposed to Springer's hypothetical population, a combination of life stages may be present in nearshore regions, with species using patterns that will enhance population success.

Understanding differences in distribution and habitat use between shark species that use nearshore regions will help effectively conserve important habitats and the populations that use them. In this chapter I outline and discuss: (1) theoretical models of shark populations in nearshore regions, (2) how sharks use nearshore waters and (3) challenges and potential consequences sharks face by using nearshore waters. By discussing how shark species use nearshore regions and identifying differences in species behaviour, I will present a second population model and some exceptions to Springer's theoretical population. For the purpose of this chapter, discussion will be limited to sharks and will not include skate or ray species. In addition, the term 'nearshore' will refer to all waters immediately adjacent to the coast down to a depth of 20 m including intertidal areas, bays, lagoons and estuaries.

2.2 Theoretical models of shark populations in nearshore environments

The hypothetical population introduced by Springer (1967) represents the distribution and habitat use of some common carcharhinoid shark species including blacktip *Carcharhinus limbatus*, sandbar *Carcharhinus plumbeus*, scalloped hammerhead *Sphyrna lewini* and lemon *Negaprion brevirostris* sharks. Young of these species are usually found in warm, shallow nearshore waters during the spring and summer months, which many authors have attributed to nursery area use (e.g. Castro 1993; Heupel and Hueter 2001; Merson and Pratt 2001; Carlson 2002). Adults of these species are encountered much less frequently in nearshore regions but females may move inshore during the summer months when ready to give birth (e.g. Springer 1950, 1960; Klimley 1987; Castro 1996). Nursery areas for aquatic species have been defined as regions where juveniles occur in higher densities, receive increased protection from predators and grow at faster rates, all of which result in increased recruitment into the adult population (Beck *et al*. 2001). More specifically for shark species, nursery areas have been identified as not only where juveniles occur in higher densities, but also where juveniles inhabit for long periods of time and where females pup over many years (Heupel *et al*. 2007). For species representative of Springer's model population, juveniles remain within nursery areas for extended lengths of time while using restricted areas of space and displaying high degrees of site attachment to nearshore habitat (e.g. Morrissey and Gruber 1993a; Merson and Pratt 2001; Heupel *et al*. 2004; DeAngelis *et al*. 2008). Seasonal variation may occur in spatial distribution, and individuals of some species migrate to over-wintering grounds when water temperature begins to cool in the autumn months (Castro 1996; Conrath and Musick 2008). Although Springer's description is accurate, particularly for many large carcharhinoid species of the United States east coast, it only encompasses some coastal species. Species displaying Springer's hypothetical pattern generally reach a large maximum size, have slow growth rates and long life expectancies.

I propose a second theoretical model to encompass smaller-bodied species such as Atlantic sharpnose *Rhizoprionodon terraenovae*, Australian sharpnose *Rhizoprionodon taylori*, bonnethead *Sphyrna tiburo* and blacknose *Carcharhinus acronotus* sharks. These species occur in nearshore waters for the duration of their life span, with immature and mature individuals of both sexes using the same regions and habitats (e.g. Simpfendorfer and Milward 1993; Parsons and Hoffmayer 2005; Heupel *et al*. 2006b; Ulrich *et al*. 2007).

Species that fit this model are typically less reliant on specific areas and move farther distances throughout nearshore environments (e.g. *R*. *terraenovae*; Carlson *et al*. 2008). Early life stages of these species do not appear to use discreet nursery areas (Parsons and Hoffmayer 2005; Heupel *et al*. 2006b; Ulrich *et al*. 2007) but may roam considerable distances and use large amounts of space. For example, Carlson *et al*. (2008) reported that juvenile *R*. *terraenovae* had wide-ranging movements (e.g. 399 km), did not remain within any specific area for significant lengths of time and often moved through deep water. Young individuals of these species may display some site attachment and return to specific nearshore regions (Hueter *et al*. 2005), but such patterns are not as evident and are reported less often in these species than in those fitting Springer's model. Despite limited attachment to one particular area, species that represent this second population model may be more dependent on nearshore regions since they use these areas for their entire life cycle. However, because these species often appear less reliant on specific habitat and move widely throughout nearshore regions, they may be less vulnerable to localised impacts.

It is important to note that not all nearshore shark populations fit within the two population models above and exceptions can be found where different types of distribution and habitat use are used. For example, juveniles of some species occur further from shore and/or at greater depths than adults. Young *C*. *plumbeus* in Western Australia have been reported to inhabit deep water offshore, whereas adults occupied areas that were closer to shore (McAuley *et al*. 2007). This population, as well as a population of *C*. *plumbeus* in Hawaii, do not appear to use discreet nursery areas (McElroy *et al*. 2006; McAuley *et al*. 2007). This pattern is opposite to that displayed by *C*. *plumbeus* in the northwest Atlantic, where the smallest and youngest individuals inhabit shallow areas closest to shore as described by Springer. Some reef shark populations also demonstrate a lack of nearshore nursery area use. In Hawaii, juvenile Galapagos sharks *Carcharhinus galapagensis* do not use shallow nursery areas, and were reported to occur at greater depths than sub-adult and adult female individuals (Wetherbee *et al*. 1996). In Belize, the smallest Caribbean reef sharks *Carcharhinus perezi* were found to inhabit the deepest available habitat and did not use shallow regions (Pikitch *et al*. 2005). It has historically been assumed that shallow nearshore waters offer greatest protection from predators and provide increased survival for young sharks. However, different regions may require different strategies for a population to thrive, with the habitat type and/or physical characteristics of an environment influencing distribution and behaviour patterns. For example, the coastline in Western Australia lacks the major estuarine systems found in nearshore environments of the northwest Atlantic (e.g. Chesapeake and Delaware Bay in the United States), which young *C*. *plumbeus* in those regions use as nursery areas (Wetherbee *et al*. 2001; Grubbs *et al*. 2007). Thus, habitat and resource requirements for young *C*. *plumbeus* that can be obtained in nearshore environments in the northwest Atlantic may be located elsewhere in Western Australia (i.e. offshore). Therefore, distribution and habitat use by sharks in nearshore regions may be a function of the ecological characteristics specific to the environment, combined with resource needs and life history characteristics. Given variations in distribution and habitat use, the two proposed models cannot describe all shark species, but they do provide a generalised concept that will encompass many shark populations in nearshore waters.

Regional differences in distribution, habitat use and movement occur among shark species, and populations may show plasticity in behaviour to cope in different regions. Using *N*. *brevirostris* as an example, it is clear that differences exist among populations in different locations. Young *N*. *brevirostris* using nearshore nursery areas in the Bahamas displayed a preference for warm water (30° C; Morrissey and Gruber 1993b), while a nearshore nursery area in southeast United States showed the highest abundance of young *N*. *brevirostris* to occur in winter when water was cooler (18-22° C; Reyier *et al*. 2008). Inhabiting cooler water may act as a refuge by decreasing interspecific competition with other species that use warmer areas over the winter months. This may provide an advantage for the northwest Atlantic population of *N*. *brevirostris* that are faced with more competitors than those in the Bahamas, so this difference may be beneficial for foraging, growth and survival. In comparison, *N*. *brevirostris* at an offshore atoll in Brazil were reported to have faster growth rates than those in the Bahamas (Freitas *et al*. 2006). Since the atoll lacks protective cover from predators offered by mangrove habitat, young sharks could have adapted for faster growth in order to reach a size less vulnerable to predation more quickly (Freitas *et al*. 2006). However, differences in growth rates between regions could also be due to poor habitat quality or decreased resources in the Bahamas, resulting in slower growth. These examples show that the strategy and behaviour a species uses is in part based on its environment. Nearshore regions are not interchangeable but are unique and dynamic systems, which may explain the variety of strategies displayed among shark species.

In addition to shark populations that use nearshore regions frequently and regularly, there are also species that visit these areas on a more occasional basis. First, there are species that tend to have long ranging movements and roam far distances offshore, such as the salmon *Lamna ditropis* and tiger *Galeocerdo cuvier* shark. For example, in the northeast Pacific, *L*. *ditropis* moved throughout nearshore waters but also used large areas offshore and undertook long distance migrations (Weng *et al*. 2008). Similarly, in both Shark Bay, Western Australia and Hawaii *G*. *cuvier* used shallow nearshore waters but also displayed large home ranges and frequently moved to deep offshore waters (Holland *et al*. 1999; Heithaus *et al*. 2007; Meyer *et al*. 2009). When *G*. *cuvier* was using nearshore waters in

Hawaii, individuals undertook a ‘coastal patrolling’ behaviour and did not remain in one area for a long period of time (Meyer *et al*. 2009). Second, there are species that are typically found in deep water environments offshore such as the sixgill *Hexanchus griseus* and Greenland *Somniosus microcephalus* shark. However, Stokesbury *et al*. (2005) reported *S*. *microcephalus* using shallow nearshore bays in Canada during the spring and summer months. Similarly, in Puget Sound in the United States juvenile *H*. *griseus* were found to display short and localised movements close to shore (Andrews *et al*. 2007). Although these four species are examples of sharks that usually undertake long ranging movements and/or inhabit deep offshore waters, they also use nearshore regions, perhaps for the diverse range of functions and benefits these habitats offer.

2.3 How shark populations use nearshore environments

A variety of ecosystem functions are provided for inhabitants of nearshore regions. Although evidence is scarce, it has been suggested that adult females of some shark species give birth in shallow nearshore waters since neonate individuals are found inhabiting and using these regions (Castro 1993). Repeated use of nearshore regions for the purpose of parturition would suggest a successful strategy that increases survival of young. This behaviour promotes population survival and kin selection; adult females presumably expend energy migrating inshore to distinct areas for no other reason than to give birth and leave their pups in nearshore regions (e.g. Weng *et al*. 2008), receiving no direct physical benefit themselves. If giving birth in nearshore regions increases survival of young, this would in turn increase recruitment to the adult population and benefit the entire population, making the energetic investment worthwhile. For some species, nearshore regions may function as critical nursery and pupping habitat. Evidence of philopatry to specific natal nurseries for many years after birth, by both pupping females (Feldheim *et al*. 2004; Keeney *et al*. 2005; DiBattista *et al*. 2008) and juveniles (Hueter *et al*. 2005; Grubbs *et al*. 2007), reinforces the important function of nearshore habitat for these species.

Although nearshore nursery areas are used by and contain crucial habitat for some sharks (e.g. species of Springer's hypothetical population), not all species use nursery areas and not all nearshore habitats function as nurseries (Heupel *et al*. 2007). For example, smaller-sized species that represent the second population model (e.g. *R*. *terraenovae* and *C*. *acronotus*) have productive life histories with rapid growth, early maturity and annual reproduction (Cortés 2002), and do not use discreet nearshore nursery areas (Carlson 2002; Parsons and Hoffmayer 2005). Rather, smaller-sized species may use nearshore habitats to exploit prey resources and increase foraging success in order to reach sexual maturity more quickly. Since smaller-sized species often have productive life histories and high rates of reproduction, the potential cost of increased mortality in early life stages from lack of nursery use may be outweighed by the benefit of using more resources to promote fast growth. In addition, juveniles of small-sized species may be of a size where they do not receive the same level of protection from nearshore waters than juveniles of large-sized species. For juveniles of small species, predators may include those juveniles of large species using the same areas, so no sufficient protective benefit exists for them to show the same site attachment to specific nursery areas. Thus, nearshore regions may function mostly as productive feeding grounds for these smaller-sized species.

Productive nearshore waters provide a source of food that benefits inhabitants of these regions but can also be used in the short-term by sharks moving in from areas further offshore. As inhabitants, sharks make up a major proportion of predator biomass in nearshore regions, consuming a diverse range and high abundance of the prey available in these environments (Blaber *et al*. 1989; Stevens and McLoughlin 1991; Salini *et al*. 1992). Overlaps in diet have been reported between many of these species (Simpfendorfer and Milward 1993; Bethea *et al*. 2004), which suggests that nearshore regions have sufficient productivity to support multiple shark species using the same or similar resources. Ontogenetic shifts in diet have also been observed in some species, with adult life stages consuming larger and/or more diverse prey items (Lowe *et al*. 1996; Bethea *et al*. 2006; McElroy et al. 2006). Shifts in diet might be why adults of larger-sized species roam farther distances than juveniles, as they would need to expand their range to exploit additional habitats. Nearshore productivity can also be exploited by sharks that occur in these areas only occasionally, with some species moving into nearshore regions from areas further offshore to use nearshore habitats and feed on high quality prey (Heithaus *et al*. 2002). Diets of shark species vary with geographic location (McElroy *et al*. 2006), thus sharks take advantage of the diversity of resources available to them in the nearshore regions they are using.

In addition to parturition, nursery area use and foraging, nearshore regions provide habitat for a variety of other functions. Nearshore waters provide breeding grounds for some shark species, and mature females have also been found to use shallow areas as a refuge to avoid aggressive males and conserve energy during mating season (Pratt and Carrier 2001; Sims *et al*. 2001). In addition, for smaller-sized species representative of the second theoretical model, nearshore waters may offer increased protection from predation. For example, Carlson (2002) found a high level of segregation between small-sized species (e.g. *R. terraenovae*, *C. acronotus* and S. *tiburo*) and large-sized species (e.g. *C. limbatus* and *C. plumbeus*). Smaller-sized species may segregate from larger-sized species to increase shelter from predation and enhance survival. Shallow nearshore waters also appear to be used for thermoregulation and energy conservation, which is thought to increase metabolic rate, growth and embryonic development (Economakis and Lobel 1998; Hight and Lowe 2007). Overall, nearshore regions serve numerous functions and using nearshore habitats provides multiple advantages and benefits for species success.

2.4 Living in nearshore waters: challenges, adaptations and consequences

Nearshore environments are characterised by shallow depths with large fluctuations in physical parameters. Thus, there are challenges specific to nearshore waters to which inhabitants must adapt in order to remain in these regions. As mobile species, sharks can use conditions to their advantage. For example, juvenile *C*. *plumbeus* in the northwest Atlantic moved with tidal flow and showed straightest line movements during the strongest currents. This behaviour was presumed to minimise energetic costs associated with swimming in strong currents (Medved and Marshall 1983; Wetherbee and Rechisky 1999). Leopard sharks *Triakis semifasciata* in Tomales Bay, California also used tidal fluctuation by moving with incoming tides to exploit food resources in nearshore regions that could otherwise not be reached (Ackerman *et al*. 2000). In contrast, some changes may force individuals to leave regions. For example, along the west coast of Florida, *S*. *tiburo* and young bull sharks *Carcharhinus leucas* were reported to leave estuaries when salinity declined (Heupel and Simpfendorfer 2008; Ubeda *et al*. 2009). Temperature is another factor that affects the distribution of shark species and the exodus of individuals from nearshore regions has been related to decreasing water temperature (Grubbs *et al*. 2007; Heupel 2007). Since sharks are highly mobile, they are able to move in response to unfavourable changes in their physical environment, such as varying salinity or temperature. Although moving to another region when conditions become unfavourable may promote immediate survival, implications arise from relocation and species circumstances may not always be improved. For example, while young *C. leucas* leaving a nursery to move to an adjacent bay when salinity levels declined reduced the stress of living in a low salinity environment, it also exposed these individuals to potential predation outside the nursery (Simpfendorfer *et al*. 2005). Displacement from a species original and/or preferred habitat to other regions may have consequences, such as reduced habitat quality, decreased food availability, increased predation risk or increased competition with other species. However, there may also be consequences if species remain in regions of unfavourable conditions. For example, *C. leucas* have perished in shallow estuaries during winter months when water temperature has dropped severely (Snelson and Bradley 1978). Overall, shark species that inhabit dynamic nearshore regions are faced with many challenges but high use of these habitats suggests sharks have evolved to derive maximum benefit despite this. For example, Heithaus *et al*. (2009) found that it was not salinity that influenced the distribution of juvenile *C. leucas* in a Florida estuary, but rather dissolved oxygen concentrations. Thus, there may be different physical factors that affect species distribution and movement within different regions, and some species appear able to adapt and cope with variable physical conditions in these dynamic environments. However, shark species that are highly dependent on specific habitat and use restricted portions of nearshore regions are probably the most vulnerable when environmental conditions extend beyond their physical limitations.

In addition to seasonal (e.g. temperature) and regular (e.g. tidal) changes, nearshore regions are highly susceptible to sudden events such as storms and weather phenomena that can affect the structure and characteristics of these environments. Species that use nearshore waters may either perish in these events or adapt and alter their behaviour to deal with sudden changes. For example, when a tropical storm approached the west coast of Florida, *C*. *limbatus* moved from a shallow nursery to the deeper waters of Tampa Bay prior to the storm making landfall (Heupel *et al*. 2003). Analysis of this event suggested sharks used the corresponding drop in barometric pressure as a cue to leave the bay (Heupel *et al*. 2003). Presumably individuals moved to avoid storm surge or other adverse conditions produced by severe storm systems, and as such, moved to increase survival. However, when an El Niño event occurred off the coast of California, *T*. *semifasciata* in the region did not leave (Smith and Abramson 1990). The El Niño event resulted in warm, nutrient-poor water along the California coast, which probably decreased prey quality and availability. The result was a higher fishing mortality of *T*. *semifasciata* than expected (Smith and Abramson 1990). Thus, this population of *T*. *semifasciata* may have been more vulnerable to fishing pressure as a result of increased hunger (Stoner 2004). These examples illustrate some of the potential benefits and consequences of moving from, or remaining in, nearshore regions when conditions change.

The final, and potentially most significant, factor in nearshore systems is direct and continuous contact with humans. Close proximity between nearshore waters and humans results in three major anthropogenic impacts affecting these regions: (1) habitat degradation due to coastline development and destructive practices, (2) pollution via terrestrial runoff and (3) exploitation through fisheries.

Coastal development often employs practices such as dredging, construction and deforestation, all of which have detrimental effects on nearshore environments and can lead to large-scale habitat degradation (van Dolah *et al*. 1984; Bilkovic and Roggero 2008). For example, mangrove habitat has declined 35% worldwide over the past 25 years as a result of clearing, cutting and filling for lumber and development (Valiela *et al*. 2001). Destruction of important and productive habitat can hinder the survival and proliferation of species that use these regions. For example, Jennings *et al*. (2008) found a 23.5% decline in the survival rate of young *N*. *brevirostris* and a related 17.7% decline in seagrass habitat in the Bahamas, which was a result of increased coastal development. Moreover, other young sharks have appeared emaciated and to have lost weight while using nearshore regions (Lowe 2002; Reyier *et al*. 2008). Weight loss may be a result of small and inexperienced sharks having low foraging success and increased competition with other species using the same areas, or possibly a result of reduced liver mass as energy reserves are quickly used up after birth (Hussey *et al*. 2010). However, it is also likely that some nearshore habitats simply no longer contain adequate food sources for the shark species that use them, which may be a result of habitat degradation and resource decline due to anthropogenic impacts. Philopatric behaviour patterns may mean sharks continue to return to these regions despite declining conditions.

Increased terrestrial runoff reduces water quality by increasing sedimentation and pollutant levels in nearshore regions (Thrush *et al*. 2004; Smith *et al*. 2008). A major consequence of nearshore pollution is eutrophication (Nixon 1995), which reduces oxygen levels, causes declines in the health and overall condition of coastal communities and affects how species use these environments (Kemp *et al*. 2005). For example, *T*. *semifasciata* have been reported to leave nearshore regions during periods of anoxia (Carlisle and Starr 2009). Pollution has also been reported to lower productivity and damage prey populations within nearshore ecosystems (Thomas and Seibert 1977; Turley 1999), which may negatively impact the foraging success of sharks that use these areas. In addition, some pollutants can have specific implications for species by disrupting biological processes. For example, infertility in *S*. *tiburo* has been linked to organochlorines in nearshore waters (Gelsleichter *et al*. 2005). Thus, pollutants and other impacts to water quality may have severe consequences for coastal shark species.

Shark populations are exposed to commercial and recreational fisheries in nearshore regions, with individuals taken as both target species and bycatch. This presents additional challenges for species that use nearshore waters, as they must be productive enough to withstand fishing pressure. Variations in life history characteristics result in some species being more resilient to fishing pressure than others (Stevens *et al*. 2000a). Species with slow growth rates and small litter sizes, such as the species of Springer’s population model, are generally more vulnerable to fisheries than smaller and more productive species (Smith *et al*. 1998). Although small and productive species appear to be more resilient, they may still be vulnerable to fishing pressure to some degree. Since smaller-sized species typically reside in nearshore regions for the duration of their life span, they may encounter numerous coastal fisheries and be caught in higher abundance. For example, in 1995 and 1996, small-sized species made up 72% of total shark catch in fishing surveys conducted in the Gulf of Mexico and northwest Atlantic, with similar numbers being reported in commercial fishing activities (Grace and Henwood 1997). Moreover, young sharks that use discreet nursery areas and small core areas of space may be susceptible to a direct and localised fishery. In an example from a bay where fishing occurred, natural and fishing mortalities in a population of young *C*. *limbatus* were estimated to be 32 to 72% and 41 to 60%, respectively, resulting in a high total mortality of 61 to 91% (Heupel and Simpfendorfer 2002). In contrast, in regions where fishing was negligible, a population of young *N*. *brevirostris* was only affected by natural mortality, and mortality here was estimated to be just 44 to 61% (Manire and Gruber 1993). Fishing pressure is not a physical variable that sharks can respond to by leaving an area when conditions become unfavourable, such as how they might respond to changes in temperature or salinity. If a shark leaves an area where fishing occurs, it is likely that it will enter another. The consequence of fisheries in nearshore waters is that species living there have a greater chance of being overfished without careful management. Surviving exploitation from fishing pressure is a challenge for many species and is an additional impact on shark populations using easily accessed nearshore regions.

The newly proposed model for coastal shark populations remaining in nearshore regions through most of their life cycle has implications for understanding the effects of humans. Since all age classes of these populations may inhabit one specific nearshore region, an entire population will be highly vulnerable if a direct impact occurs there. Unlike the species that fit Springer's population model, there is no age refuge for these smaller-sized species. For example, it is possible for a coastal fishery (commercial and/or recreational) to land all age classes of smaller-sized shark species inhabiting one area, resulting in a higher negative effect on these populations compared to the populations whose juveniles only occur nearshore. However, implementation of certain management initiatives such as marine protected areas (MPAs) may be effective in protecting small-sized species that show site attachment and use restricted portions of nearshore regions. Although MPAs may be successful in protecting some of these small-sized species, they will probably be less effective for those that tend to have a roaming behaviour. It is important to identify these additional population models that address the differences in life history and behavioural characteristics of coastal shark species so this information can be included in conservation and management planning.

CHAPTER 3

General Methods

3.1 Study site

Cleveland Bay (19.20° S, 146.90° E) is a tropical, nearshore region located on the northeast coast of Queensland, Australia adjacent to Townsville (Fig. 3.1). Most of the bay is less than 10 m deep and maximum tidal range is 4.2 m. The bay covers an area of approximately 225 km^2 and is comprised of a diverse range of habitats. On the western side of the bay between Magnetic Island and the mainland there are patches of coral reefs and reef flats and the bottom type is mostly coral rubble and sand. In contrast, the eastern side of the bay consists of mangrove lined mud flats with patches of seagrass and the bottom type is mud and sand. There are three main freshwater river systems that flow into Cleveland Bay (i.e. Ross River, Alligator Creek and Crocodile Creek) and these enter the bay from the south. Water temperature in the study site ranged from 21 to 32º C (D. M. Knip, unpublished data). Salinity generally remained between 30 and 35 ppt but reached 37 ppt, and dropped as low as 8 ppt (surface) and 15.5 ppt (bottom) near the creek and river mouths (D. M. Knip, unpublished data).

3.2 Study species

The study species for this research were the pigeye *Carcharhinus amboinensis* and spottail *Carcharhinus sorrah* shark (Fig. 3.2). These species have an Indo-West Pacific distribution and range throughout northern Australia from Carnarvon in Western Australia to Brisbane (*C. amboinensis*) and Gladstone (*C. sorrah*) in Queensland (Compagno 1984;

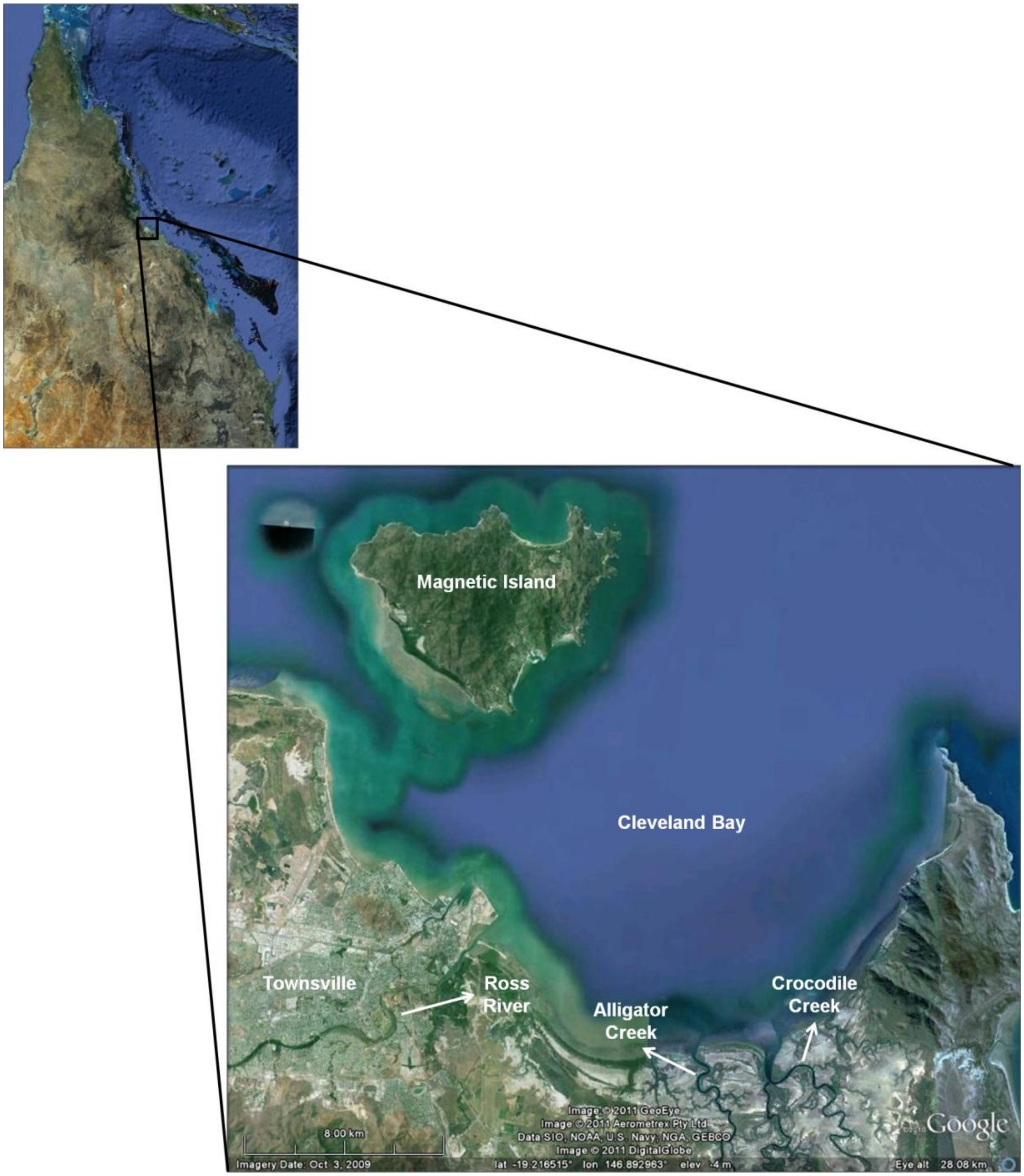

Fig. 3.1 Study site. Google Earth^{TM} aerial image of Cleveland Bay relative to its location along the Queensland coast.

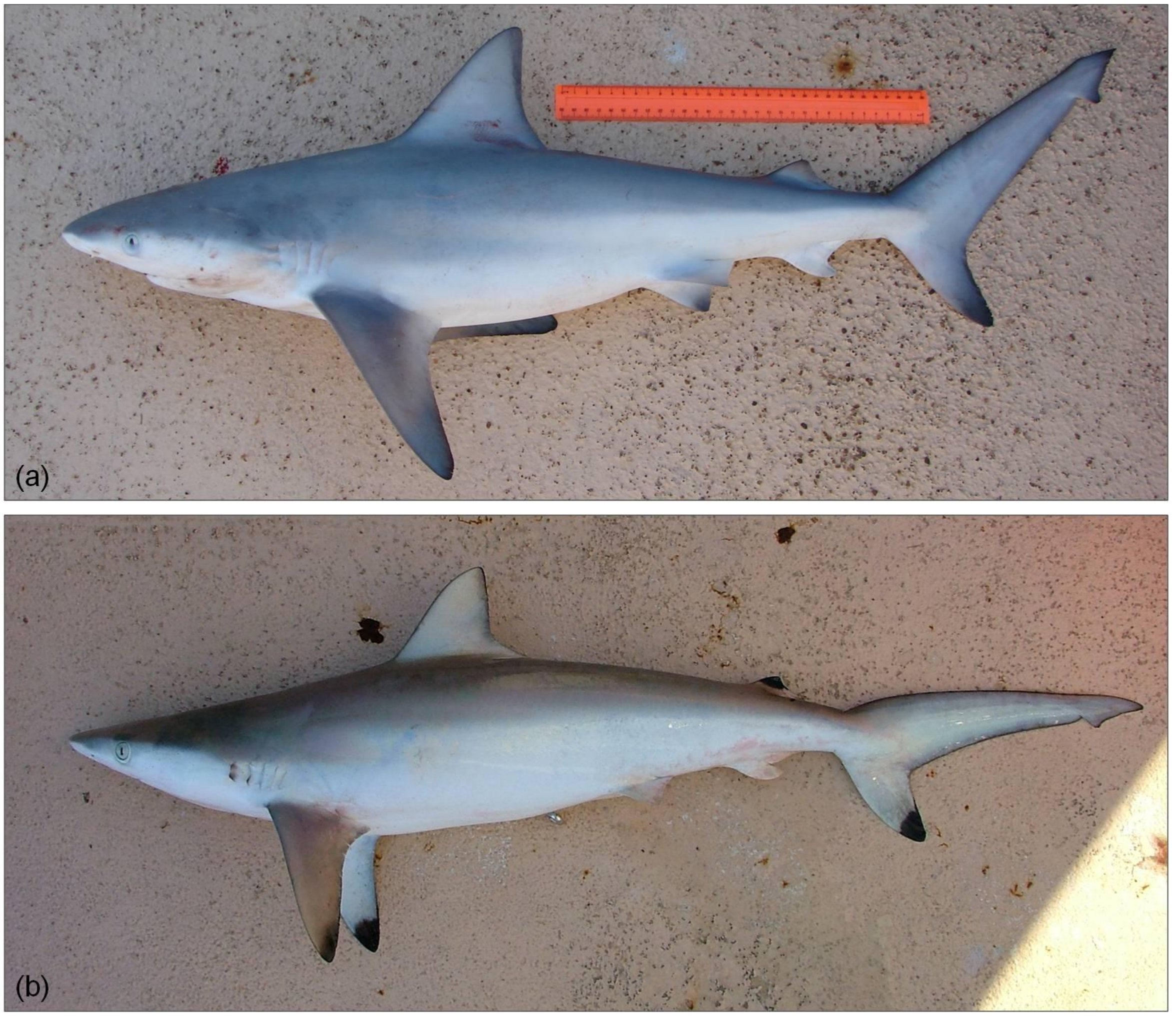

Fig. 3.2 Study species. Photos of a juvenile *C*. *amboinensis* (a) and an adult *C*. *sorrah* (b).
Photo credits: Fishing and Fisheries Research Centre

Last and Stevens 2009). Although both species use nearshore environments, they have different life history and ecological characteristics. *Carcharhinus amboinensis* is a slow growing, large-bodied shark; size at birth is 60 to 65 cm, individuals mature at just over 200 cm and reach a maximum size of approximately 280 cm (Last and Stevens 2009). Diet consists of teleosts, crustaceans, cephalopods and mollusks (Compagno 1984; Last and Stevens 2009). Throughout its range, *C*. *amboinensis* has been reported to inhabit warm turbid waters in close proximity to estuaries and river mouths and to occasionally enter brackish habitats (Cliff and Dudley 1991; Last and Stevens 2009). Similar to other large-bodied species, *C*. *amboinensis* may use nearshore regions as nursery habitat during early life stages (Heupel *et al*. 2007). Unlike *C*. *amboinensis*, *C*. *sorrah* is a fast growing, medium-bodied shark; size at birth is 50 cm, individuals mature at approximately 90 to 95 cm and attain a maximum size of 160 cm (Last and Stevens 2009). Diet consists predominantly of teleosts, and cephalopods and crustaceans to a lesser extent (Stevens and Wiley 1986). *Carcharhinus sorrah* has generally been found to associate with both muddy bottoms and coral reef habitat, and is also caught offshore to depths of approximately 80 m (Compagno 1984; Last and Stevens 2009). Previous research in northern Australia reported that *C*. *sorrah* had relatively localised movements (< 50 km) but were also capable of moving greater distances (> 1000 km) (Stevens *et al*. 2000b). In addition, *C*. *sorrah* is a commercially important species, and is one of the main components in the Australian gillnet fishery (Last and Stevens 2009). Little else is known about the movements of *C*. *amboinensis* or *C*. *sorrah* and how they use nearshore habitats, particularly in Queensland waters. As common inhabitants of tropical nearshore regions, understanding the movement and habitat use of these species will be crucial to defining their life history strategies and ecological roles within these systems.

3.3 Passive acoustic monitoring

Passive acoustic monitoring is a two component system that consists of acoustic receivers and acoustic transmitters (Fig. 3.3), allowing continuous and long-term tracking of multiple individuals simultaneously. The receiver is an omnidirectional hydrophone and data logger that remains moored in the water column to detect and record the presence of acoustically tagged individuals that swim within listening range. The transmitter is the signal device that remains fixed to the individual being monitored and emits a unique acoustic signal to identify each individual. Passive acoustic monitoring of the study species was conducted in Cleveland Bay using an array of fifty-seven VR2 or VR2W acoustic receivers (Vemco Ltd., Canada) (Fig. 3.4). Forty-seven receivers were initially deployed in November 2008, and nine receivers were added to the array in August 2009 to cover additional areas and habitat. As part of a separate study, one receiver was deployed in Ross River in January 2010. Most receivers were suspended in the middle of the water column, but twelve receivers in the intertidal zone along the eastern side of the bay were fixed to the bottom (Fig. 3.5). These twelve receivers were in shallower water than the rest of the receivers in the array and became exposed at low tides (at tidal stages < 80 cm). Receivers were not deployed throughout the middle section of Cleveland Bay, as that area is a designated shipping channel. The array of receivers included all representative habitats within the bay including reef, seagrass, sand, mud and river mouths. Coverage allowed study species to be monitored throughout all available habitat types. Data was downloaded from the receivers every 6 to 8 weeks and stored and organised in a database (VUE 1.8.1, Vemco Ltd., Canada). Detection range of acoustic receivers within the study site was approximately 900 m (M. R. Heupel, unpublished data).

Fig. 3.3 Components of passive acoustic monitoring. Vemco's VR2W acoustic receiver (a) and V16 acoustic transmitter (b). *Photo credits: Vemco Ltd.*

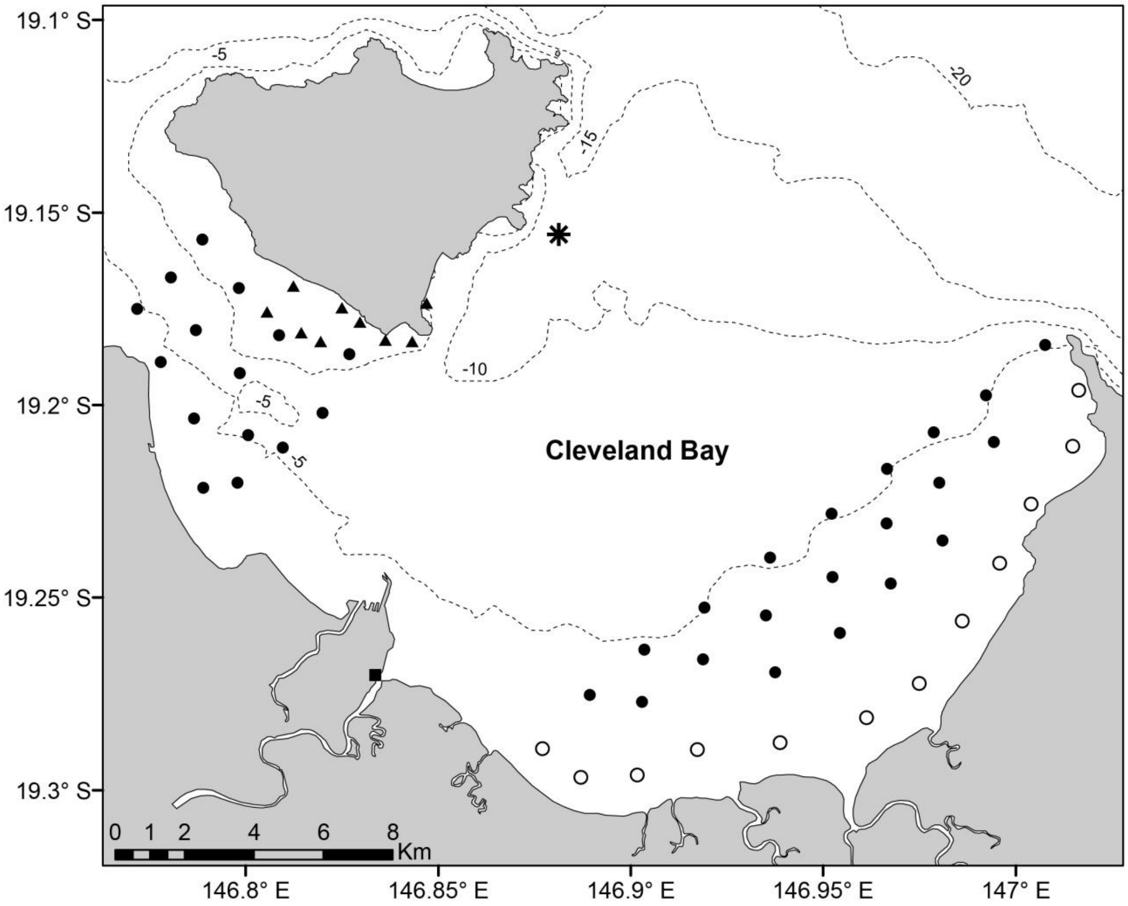

Fig. 3.4 Cleveland Bay. Symbols are locations of acoustic receivers deployed in November 2008 (● = mid-water deployments, ○ = fixed bottom deployments), August 2009 (▲) and January 2010 (■). Asterisk indicates location of a hydrographic station in the bay. Dashed lines indicate bathymetry.

Fig. 3.5 Acoustic receivers deployed in Cleveland Bay: mid-water deployment (a), fixed bottom deployment (b). *Photo credits: A. J. Tobin and the Fishing and Fisheries Research Centre.*

Sharks were captured on short long-lines (500 m bottom set mainline, 6 mm nylon rope) that were anchored at both ends and soaked for one hour. Gangions consisted of 1 m of 5 mm nylon cord and 1 m of wire leader. Size 14/0 Mustad tuna circle hooks were baited with frozen butterfly bream *Nemipterus* sp., mullet *Mugil cephalus*, blue threadfin *Eleutheronema tetradactylum* or fresh trevally *Caranx* spp. Sampling occurred on both sides of the bay within the receiver array and sharks were released at their capture location. All captured sharks were identified, measured to the nearest millimetre, sexed and tagged with a rototag in the first dorsal fin and a single-barb dart tag in the dorsal musculature for identification prior to release. Study species were also fitted with a V16 (16 x 65 mm) acoustic transmitter (Vemco Ltd., Canada), which was surgically implanted into the body cavity to ensure long-term retention (Fig. 3.6a,b). A small incision (3 to 4 cm) was made in the abdomen and the transmitter inserted. The wound was closed by suturing both the muscle and skin layers to ensure adequate wound closure and healing. Transmitters had a unique code to identify individual sharks, pulsed on a random repeat interval of 45-75 seconds at a frequency of 69 kHz and had a battery life of approximately eighteen months. Sharks were retained on board for approximately ten minutes during measuring and tagging procedures and were released in good condition (Fig. 3.6c).

3.4 Permits and ethics

All research activities were conducted under the Great Barrier Reef Marine Park Authority permit #G10/33315.1 and Queensland Department of Primary Industries and Fisheries permit #90911. Treatment of all animals was conducted under ethical guidelines approved by James Cook University animal ethics committee (ethics approval #A1566).

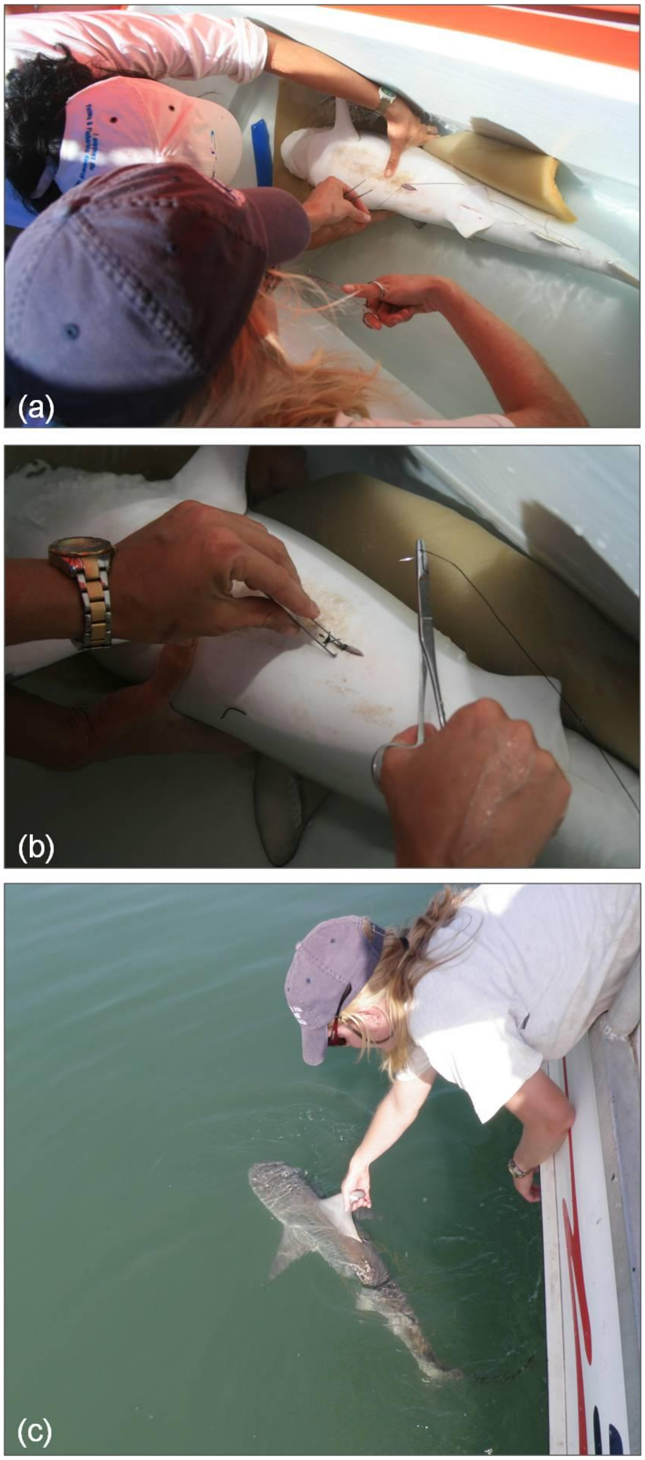

Fig. 3.6 Surgery and release procedures of study species. Field work assistant holding a *C*. *sorrah* while surgery is conducted (a), suturing the muscle and skin layers (b) and releasing a *C*. *amboinensis* in good condition (c). *Photos credits: F. Cardona and the Fishing and Fisheries Research Centre.*

CHAPTER 4

Habitat Use and Movement of Juvenile *Carcharhinus amboinensis*

4.1 Introduction

Nearshore regions are highly dynamic environments consisting of a network of habitats and areas that include rivers, estuaries, lagoons and bays. These regions are typically shallow and characteristically have large variations in physical parameters (e.g. salinity, temperature, depth, dissolved oxygen, flow and turbidity) over a range of temporal scales due to changes in tide, rainfall, freshwater inflow, season and weather (Walker 1981; Rodriguez *et al*. 1994). Although less extreme than large-scale changes associated with seasonal or weather events, fluctuations occurring on short temporal scales (i.e. hours) still have a considerable impact on nearshore communities. For example, diel changes and recurring changes in water depth due to the tidal cycle can influence the movement and habitat use of inhabitants over the course of a day. Species may move to select for certain habitats (Bellquist *et al*. 2008), avoid predators (Wetherbee *et al*. 2007) and exploit foraging opportunities (Ackerman *et al*. 2000).

Despite potentially taxing conditions, the high biodiversity and productivity of nearshore regions suggests that these areas contain important habitat for a wide range of species (Beck *et al*. 2001). In particular for sharks, nearshore regions provide habitat for many different functions including foraging and use of nursery areas (Castro 1993; Bethea *et al*. 2004; Heupel *et al*. 2007). Previous research has found that multiple shark species may inhabit the same nearshore region, with different species presumably using the same or similar resources (Castro 1993; Simpfendorfer and Milward 1993). Further studies have examined how different shark species share space within these environments and found that habitats are partitioned on both spatial and temporal scales (White and Potter 2004; Pikitch *et al*. 2005; DeAngelis *et al*. 2008). Although these interspecific differences in habitat use among sharks have been investigated, equivalent intraspecific differences have been given less consideration. For example, both small and large juvenile sharks commonly use nearshore regions but only a limited number of studies have examined differences in movement and habitat use between age classes of the same species (e.g. bull sharks *Carcharhinus leucas*; Simpfendorfer *et al*. 2005; Heupel and Simpfendorfer 2008). If individuals of different age classes use the same areas and resources there may be resulting implications, such as increased competition. With nearshore regions being used by a range of age classes of multiple shark species, individuals not only have to compete with other species but also amongst themselves, which likely has the greatest impact on the youngest and least experienced individuals.

In this chapter I examine how juvenile *C*. *amboinensis* use nearshore habitats to define factors that influence movement and to determine how movement and habitat use vary among age classes. Previous research has found that home ranges of young sharks increase in size over time (Heupel *et al*. 2004) and that segregation may occur between different age classes of juveniles (Simpfendorfer *et al*. 2005). Thus, I hypothesised that (1) younger juveniles will use shallower depths and have movements more strongly influenced by physical factors than older juveniles and (2) home range size and the range of depths juveniles use will increase with age class.

4.2. Data analyses

Data collected from acoustic receivers were used to analyse presence, home range and movement patterns of juvenile *C*. *amboinensis* in Cleveland Bay. Locations of monitored *C*. *amboinensis* in the study site were estimated every 30 minutes using a mean position algorithm that provided an individual's centre of activity (COA) (Simpfendorfer *et al*. 2002). COA locations represent an individual's mean position for the set time-step. For small sharks, the error of COA estimates in relation to real-time locations is approximately 225 m (Simpfendorfer *et al*. 2002).

4.2.1 Presence

Presence was examined daily, with individuals considered present if two or more detections were heard on any receiver in the study site on a given day. Plots were created to provide a daily timeline to indicate individual presence within the study site. Total number of days monitored (i.e. number of days from first to last detection), total number of days present and number of continuous days present were calculated for each individual to analyse patterns in presence. The ratio between the number of days an individual was present in the study site to the total number of days monitored was calculated to provide a residency index. Residency values range from 0 to 1, with values close to 0 indicating low residence and values close to 1 indicating high residence. Presence data were checked for normality with Quantile-Quantile plots and log(x+1) transformed, if required. Two-factor analysis of variance (ANOVA) was used to test for differences in total days monitored, total days present, continuous days present and residency index between age classes and years.

4.2.2 Home range

Home ranges of individual *C. amboinensis* were calculated based on COA estimates using 50% (e.g. core home range) and 95% (e.g. total home range) fixed kernel utilisation distributions (KUDs) and minimum convex polygons (MCPs) with the adehabitat package in R (Calenge 2006). MCPs define the extent of an individual's home range, while KUDs provide information regarding the use of space within an individual's home range. KUD estimates are probability density functions, with a smoothing factor controlling the amount of variation in each component of the estimate (Worton *et al*. 1989). For example, a small smoothing factor value will highlight the fine-scale detail of the KUD, while a large smoothing factor value will obscure all but its most prominent features (Worton *et al*. 1989). There are different methods that can be used to estimate the smoothing factor for a fixed KUD, such as the default ad-hoc method and the Least Square Cross Validation method, or the smoothing factor can also be given any numerical value (Worton *et al*. 1989; Seaman and Powell 1996). Therefore, to set the appropriate smoothing factor when estimating KUD home ranges, I examined KUD estimates using all smoothing factor methods. Manually selecting a numerical value for the smoothing factor produced the most reliable and accurate KUD estimates. Thus, I tested a range of smoothing factor values, examined the KUDs and selected the one value that provided the most sensible and consistent KUD estimates. Home ranges were calculated at monthly intervals to examine changes in distribution and habitat use over time and were plotted in ArcGIS 9.3.1 (Environmental Systems Research Institute, Redlands, United States) to show spatial and temporal distribution patterns of individual sharks. Home range data were examined for normality with Quantile-Quantile plots and log(x+1) transformed, if required. Three-factor ANOVA was used to test for differences in all measures of home range between age classes, months and years.

4.2.3 Movement

Detection data from acoustic receivers were examined to define patterns in movement of *C. amboinensis* based on time of day and tidal stage. Due to limited detections for individuals with short presence times, data were only analysed for individuals that were consistently present in the study site for longer than two weeks (n = 28). For time of day analysis, the number of detections was calculated per hour for each individual and summed across hours. χ^2 goodness-of-fit tests were used to test for differences in the number of detections with hour of the day. For tidal stage analysis, hourly tidal stages for the Townsville region were obtained from tide tables provided by Maritime Safety Queensland (Queensland Transport, Australia). Hourly tidal stages were summed into 20 cm bins, and then the hourly shark detections were placed into the corresponding tidal bins and summed for the entire duration each individual was monitored. χ^2 goodness-of-fit tests were used to compare the frequency of detections in each 20 cm tidal bin to the frequency of tidal stages in that bin.

To determine if individuals moved between shallow and deeper water areas with the tidal cycle, detection frequencies for the twelve fixed bottom receivers (hereafter referred to as the shallow water receivers) were examined separately to the mid-water receivers (hereafter referred to as the deep water receivers). The proportion of detections in each 20 cm tidal bin was plotted against the actual tidal stage distribution for each juvenile age class and group of receivers (shallow and deep). Detection data were examined for normality with Quantile-Quantile plots and met the assumptions for parametric testing. *t*-tests were used to test for differences in detections based on tidal stage between years and receiver groups for each age class.

Spectral analysis was conducted to identify regular signals in the detection data. Detections were summed by hour for each age class at both receiver locations (shallow and deep), providing six time series datasets. A fast Fourier transform with a Hamming window was applied to each time series and a spectral density function plotted. Cycles in the data were detected by peaks in spectral density and were equal to the inverse of the frequency. For example, since detections were based on an hourly time period, a daily signal would have a frequency of 0.042 (24^{-1}) and a tidal signal would have a frequency of 0.087 (11.5^{-1}). Spectral analysis was conducted in Statistica 8.0 (StatSoft 2007, Tulsa, USA).

4.2.4 Habitat use by depth

Depths used were analysed for the monitored individuals in the study site to further examine how water depth influences habitat use of *C. amboinensis*. Depth was estimated throughout the study site by calculating a mean depth at each receiver station by hour. To calculate mean hourly depths, depth and tidal stage were first recorded simultaneously at each receiver station. The hourly tidal stages were then subtracted from the depth values, providing an estimation of depth at each receiver by hour. Mean hourly depth used was calculated for each individual by averaging the depths at the receivers an individual was detected on in that hour. Depth data were examined for normality with Quantile-Quantile plots and met the assumptions for parametric testing. *t*-tests were conducted to test for differences in mean depths used between years.

Comparisons were made between depths individuals used and depths available within the study site to determine if *C. amboinensis* displayed electivity for or avoidance of specific depths using Chesson's α (Chesson 1978):

$$\alpha = (r_i / p_i) / \sum(r_i / p_i)$$

where r_i is the proportion of time an individual spent at depth i in the study site and p_i is the proportion of depth i available in the study site. Values of α can range from 0 to 1, with a value of 1/(number of categories) indicating no electivity or avoidance. Both the available depths in the study site and the depths used were tallied into 50 cm depth categories for all sharks. Tallies of depths that sharks used and those that were available in the study site were converted to proportions and the electivity for each depth category was calculated. Electivity was calculated separately for each age class. Since values of α varied between age classes, values were standardised by subtracting 1/(number of categories). All data analyses and statistical procedures were conducted in the 'R' environment (R Development Core Team 2009), unless otherwise stated.

4.3 Results

From 2008 to 2010, forty-three *C. amboinensis* were released with acoustic transmitters in Cleveland Bay. Young-of-the-year (YOY) individuals were released in January to February 2009 (n = 18; 6 female, 12 male) and December 2009 to May 2010 (n = 16; 6 female, 10 male). One-year-old (1YO) individuals were released in December 2008 (n = 2; 2 male) and December 2009 (n = 3; 1 female, 2 male). Two-year-old (2YO) individuals were only released in the second year of the study from October to December 2009 (n = 4; 4 female). Six individuals were either not detected or had limited detections, so were not included in the analyses. Remaining individuals (n = 37) were monitored in Cleveland Bay from December 2008 to August 2010 (Table 4.1). Size range was 690 to 820 mm stretch total length (STL) for YOY individuals, 925 to 1000 mm STL for 1YO individuals and 1200

Table 4.1 Tagging information for *C. amboinensis* monitored in Cleveland Bay from 2008 to 2010 including date tagged, age class, stretch total length, sex and total days monitored. *individuals still present at the end of the monitoring period (31/07/2010).

ID	Date tagged	Age class	Stretch total length (mm)	Sex	Total days monitored
579*	11/12/2008	1YO	990	M	586
563	18/12/2008	1YO	925	M	563
487	18/02/2009	YOY	740	M	128
490	18/02/2009	YOY	790	F	316
495	18/02/2009	YOY	785	M	13
562	18/02/2009	YOY	720	M	255
573	18/02/2009	YOY	770	M	58
574	18/02/2009	YOY	820	M	36
575	18/02/2009	YOY	770	F	9
577*	18/02/2009	YOY	770	F	524
3460*	18/02/2009	YOY	760	F	525
3461	19/02/2009	YOY	810	M	10
3462	19/02/2009	YOY	780	M	38
3463	19/02/2009	YOY	742	M	147
3464	19/02/2009	YOY	690	F	6
3466	19/02/2009	YOY	800	M	9
3467	19/02/2009	YOY	690	M	7
487a	02/10/2009	2YO	1260	F	299
3463a	02/10/2009	2YO	1230	F	91
63605*	03/12/2009	2YO	1290	F	239
63608	03/12/2009	2YO	1200	F	174
63606	03/12/2009	1YO	1000	M	37
63607*	03/12/2009	1YO	990	M	239
63610*	16/02/2010	YOY	705	M	139
63612*	16/02/2010	YOY	775	F	164
63614*	17/02/2010	YOY	770	F	160
63621	17/02/2010	YOY	770	M	22
63622*	17/02/2010	YOY	735	M	162
63615*	23/02/2010	YOY	790	F	133
63618*	23/02/2010	YOY	770	M	155
63619*	23/02/2010	YOY	760	F	125
63620	23/02/2010	YOY	790	M	4
63611*	03/03/2010	YOY	740	M	149
63613*	03/03/2010	YOY	775	M	149
63617	03/03/2010	YOY	740	F	7
63623*	03/03/2010	YOY	765	M	144
490a	11/05/2010	YOY	820	M	45

to 1290 mm STL for 2YO individuals. All *C*. *amboinensis* were sexually immature and YOY individuals were identified by an umbilical scar (either open or closed). 1YOs and 2YOs were determined by their body size (STL), with sizes compared to length-at-age data (Tillet et al. 2011). In 2009, 3 YOYs were removed from the study by recreational (n = 2) or commercial (n = 1) fishers. Two individuals were recaptured in Cleveland Bay and the other approximately 10 km north of the study site, with time at liberty ranging from 128 to 375 days.

4.3.1 Presence

Juvenile *C*. *amboinensis* were monitored for total periods of 4 to 586 days (mean = 159) and were present within the study site from 3 to 429 days (mean = 76) (Tables 4.1, 4.2). There was no significant difference in total days monitored based on year ($F_{1,32} = 0.21$, $p = 0.738$), age class ($F_{2,32} = 2.62$, $p = 0.088$) or the interaction of year and age class ($F_{1,32} = 2.32$, $p = 0.138$). For total days present, there was also no significant difference between years ($F_{1,32} = 0.03$, $p = 0.856$) but there was a significant difference based on age class ($F_{2,32} = 3.46$, $p = 0.047$) and the interaction of year and age class ($F_{1,32} = 3.02$, $p = 0.091$). However, no significant differences were evident in residency index (year: $F_{1,32} = 0.14$, $p = 0.714$; age class: $F_{2,32} = 0.15$, $p = 0.860$; year x age class: $F_{1,32} = 0.14$, $p = 0.714$), indicating that use of the study site was similar across years and age classes regardless of the number of days individuals were present. Residency index was variable, ranging from 0.17 to 0.97, but values were similar for each age class (Table 4.2). Continuous days present in the study site ranged from 1 to 73 days (mean = 4.4) (Table 4.2). There was no significant difference in continuous days present between years ($F_{1,625} = 0.40$, $p = 0.530$), but a significant difference between age classes was evident ($F_{2,625} = 4.26$, $p = 0.015$). 2YOs tended to be present for longer continuous periods of time (mean = 7.5 days) when compared to the two younger age classes (mean range = 3.5 to 4.8 days). There was also

Table 4.2 Presence of *C. amboinensis* in Cleveland Bay. Summary includes total days present, continuous days present and residency index by year and age class. Brackets are standard errors.

			Total Days Present			Continuous Days Present			Residency Index		
Year	Age class	n	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean
2008-2009	YOY	15	4	233	56 (18)	1	40	3.5 (0.3)	0.18	0.89	0.57 (0.06)
	1YO	2	208	429	319 (111)	1	28	4.5 (0.4)	0.35	0.76	0.76 (0.20)
2009-2010	YOY	14	3	133	58 (12)	1	73	4.8 (0.7)	0.17	0.89	0.53 (0.06)
	1YO	2	36	61	49 (13)	1	22	4.2 (1.0)	0.26	0.97	0.61 (0.36)
	2YO	4	55	142	103 (20)	1	51	7.5 (1.4)	0.18	0.95	0.62 (0.16)

a significant difference in continuous days present based on the interaction term of year and age class ($F_{1,625}$ = 5.46, p = 0.020), which may indicate that age classes behaved differently across years, or may be due to 2YOs only being released in the second year.

4.3.2 Home range

Most movements of *C. amboinensis* were confined to the eastern side of Cleveland Bay. Half of the monitored individuals made movements to the western side of the bay (Fig 4.1), which included 38% of the YOYs, 75% of the 1YOs and 75% of the 2YOs. These proportions indicate that older juveniles moved farther than younger juveniles, but the frequency and length of these movements varied between individuals. Two individuals (one YOY and one 1YO) were detected in Ross River, each on a single day (Fig. 4.1). Although the Ross River receiver was deployed for a shorter period of time (January to August 2010), lack of detections on this receiver suggests that *C. amboinensis* did not spend much time in the river.

For all *C. amboinensis* monitored, 50% monthly KUDs ranged from 2.58 to 25.01 km^2 (mean = 7.66 km^2) and 95% monthly KUDs ranged from 3.96 to 101.05 km^2 (mean = 37.86 km^2) (Fig. 4.2). There was no significant difference based on year or age class for 50% (year: $F_{1,156}$ = 1.95, p = 0.164; age class: $F_{2,156}$ = 1.00, p = 0.372) or 95% (year: $F_{1,156}$ = 0.16, p = 0.684; age class: $F_{2,156}$ = 2.67, p = 0.072) monthly KUDs. Month was a significant factor for both 50% and 95% KUDs (50%: $F_{19,156}$ = 6.82, $p < 0.001$; 95%: $F_{19,156}$ = 5.88, $p < 0.001$) and there was some fluctuation between home ranges across months, with largest home ranges generally occurring during summer wet season months (i.e. January to March) (Fig. 4.2). There was no significant difference between monthly MCPs based on year ($F_{1,156}$ = 0.25, p = 0.614) but a highly significant difference between age classes was present ($F_{2,156}$ = 10.58, $p < 0.001$). Monthly MCPs ranged from 0.01 to 180.53

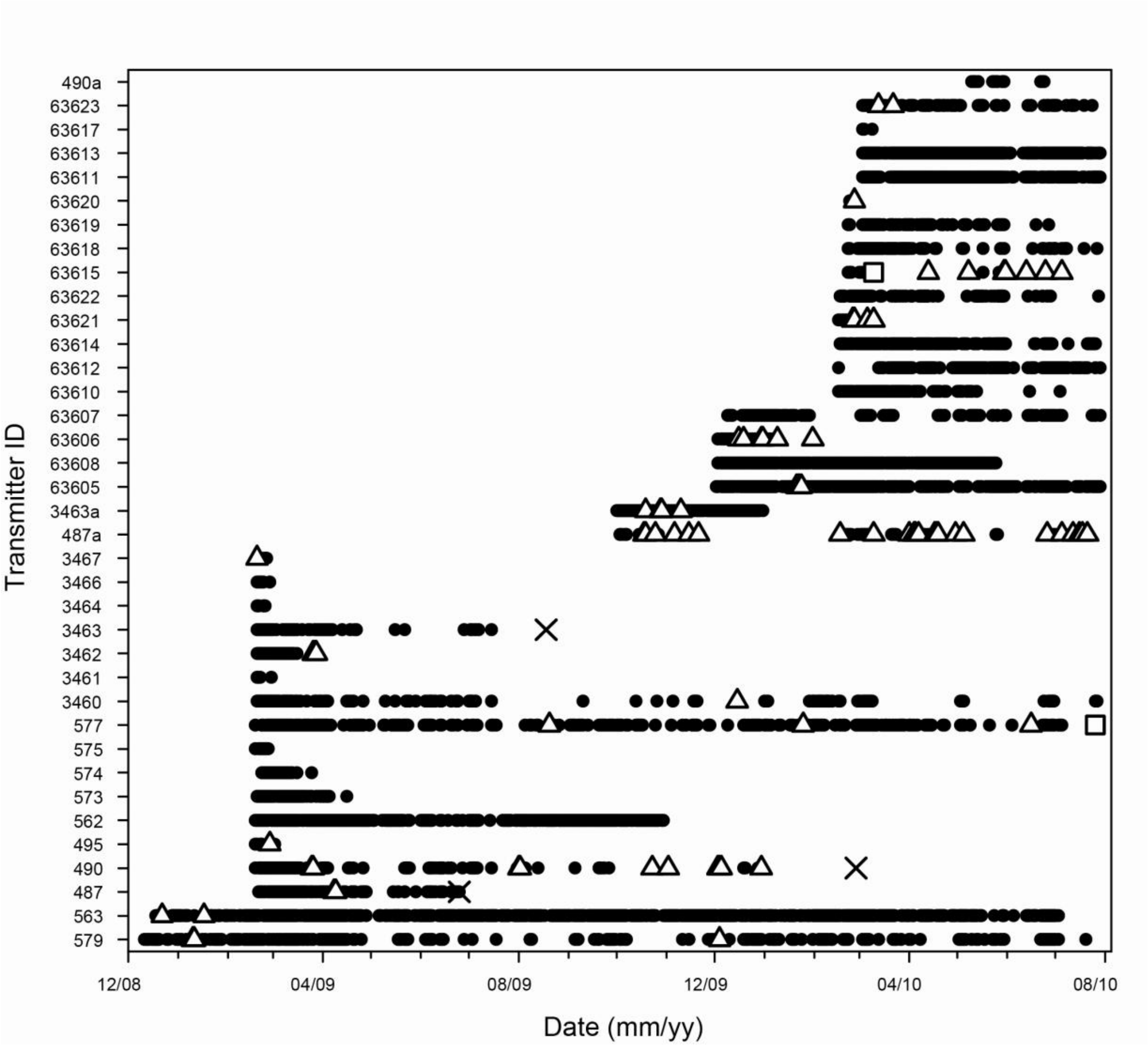

Fig. 4.1 Presence plot of *C. amboinensis* in Cleveland Bay by day. Symbols represent days detected on the eastern array (●), western array (Δ), Ross River receiver (□) and days when individuals were removed by fishers (X).

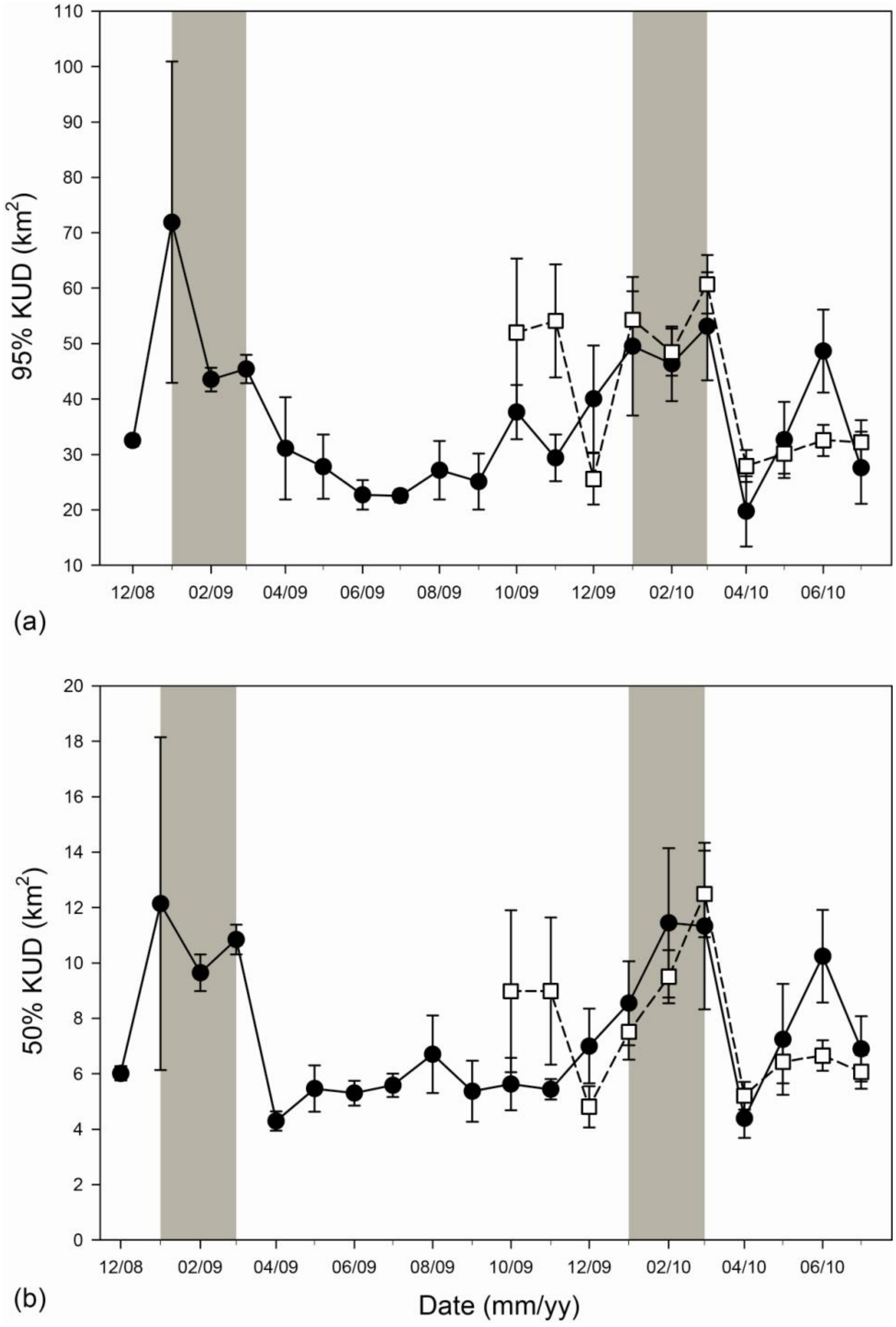

Fig. 4.2 Mean monthly home ranges with standard errors for *C. amboinensis* released in 2008-2009 (● and solid line) and 2009-2010 (□ and dashed line) calculated with 95% KUDs (a) and 50% KUDs (b). Grey shading indicates months that typically receive the most rainfall during the monsoonal wet season in the Townsville region.

km^2 for YOYs (mean = 35.78 km^2), 0.03 to 201.88 km^2 for 1YOs (mean = 24.79 km^2) and 3.09 to 212.52 km^2 for 2YOs (mean = 57.29 km^2). Monthly MCPs tended to increase with age class, indicating that older juveniles used more space than younger juveniles (Fig. 4.3). MCPs include all detection locations, while 95% KUD calculations are probability distributions based on 95% of locations and may exclude rare movements, such as use of additional areas (Fig. 4.3). Therefore, significant differences in MCPs between age classes suggest that larger individuals ranged more widely within Cleveland Bay than smaller individuals.

4.3.3 Movement

Examination of detection data by hour of the day revealed significant differences for all *C. amboinensis* (Table 4.3). Although detections were not evenly distributed across hours, there was no consistent pattern in behaviour. Six individuals were detected more often during the day, three were detected more often during the night and the remaining nineteen showed no daily patterns in detections. Overall, there was a large degree of individual variability in detections when analysed with time of day, and different behaviours resulted in some individuals being detected more often either during the day or night.

Similarly, analysis of detection data showed significant differences for all *C. amboinensis* in relation to tidal stage, indicating that individuals were detected more frequently during certain stages of the tide (Table 4.3). Analysing shallow and deep water receivers separately revealed that movements of *C. amboinensis* were strongly influenced by the tidal cycle (Fig. 4.4). Individuals moved into shallow intertidal habitat with the rising tide and were detected more frequently on shallow water receivers than deep water receivers during high tides. There was no significant difference in detections based on tidal stage between years (YOYs: $t_{12.03} = –0.03$, $p = 0.975$; 1YOs: $t_{1.00} = 0.36$, $p = 0.780$), so data

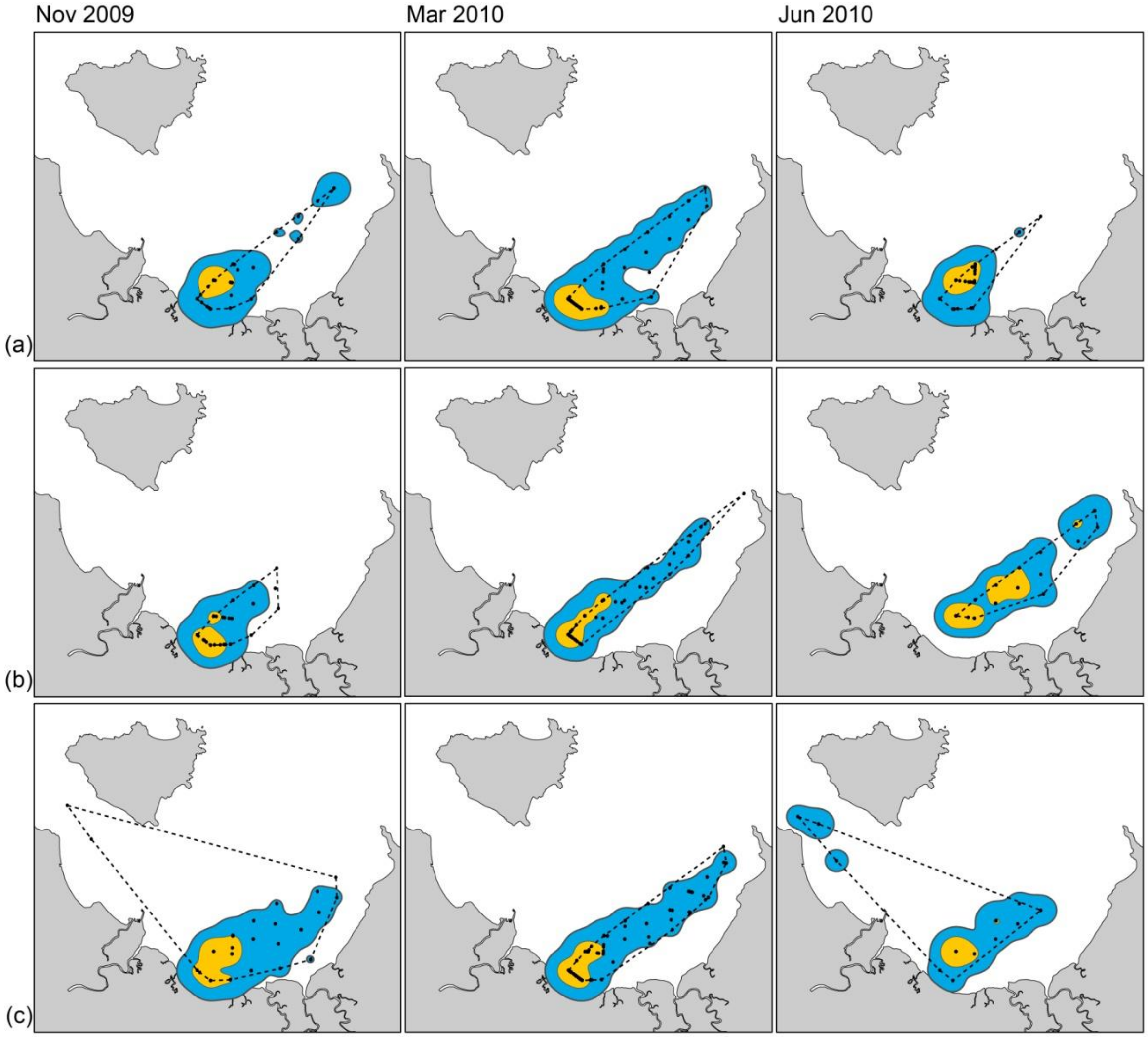

Fig. 4.3 Representative monthly home ranges of nine *C. amboinensis* for November 2009, March 2010 and June 2010. Panels include young-of-the-year (a), one-year-old (b) and two-year-old (c) individuals. Blue fill: 95% KUDs, yellow fill: 50% KUDs, dashed line: MCPs, black dots: COA locations used to calculate home ranges.

Table 4.3 Results of χ^2 goodness-of-fit tests for number of detections versus time of day and tidal stage for *C. amboinensis*. Data is listed by year and age class.

	Time of Day			Tidal Stage	
ID - *by year and age class*	χ^2 value	*p* value	most detections	χ^2 value	*p* value
2008-2009: YOYs					
487	1271.75	**< 0.001**	no pattern	2364.17	**< 0.001**
490	339.18	**< 0.001**	no pattern	618.18	**< 0.001**
562	2175.57	**< 0.001**	night	1775.16	**< 0.001**
573	609.27	**< 0.001**	no pattern	656.69	**< 0.001**
574	520.21	**< 0.001**	no pattern	831.65	**< 0.001**
577	1532.21	**< 0.001**	night	1260.71	**< 0.001**
3460	261.05	**< 0.001**	no pattern	798.15	**< 0.001**
3462	305.40	**< 0.001**	no pattern	343.86	**< 0.001**
3463	311.44	**< 0.001**	no pattern	978.48	**< 0.001**
2008-2009: 1YOs					
579	446.14	**< 0.001**	no pattern	434.51	**< 0.001**
563	1786.54	**< 0.001**	no pattern	1082.06	**< 0.001**
2009-2010: YOYs					
63610	308.64	**< 0.001**	no pattern	704.16	**< 0.001**
63612	1041.86	**< 0.001**	night	948.66	**< 0.001**
63614	461.10	**< 0.001**	no pattern	1207.25	**< 0.001**
63621	401.15	**< 0.001**	day	450.04	**< 0.001**
63622	795.64	**< 0.001**	no pattern	1816.77	**< 0.001**
63615	468.63	**< 0.001**	no pattern	707.87	**< 0.001**
63618	357.95	**< 0.001**	no pattern	549.76	**< 0.001**
63619	363.80	**< 0.001**	no pattern	925.40	**< 0.001**
63611	3587.38	**< 0.001**	night	5086.75	**< 0.001**
63613	4388.36	**< 0.001**	night	5257.17	**< 0.001**
63623	1610.24	**< 0.001**	night	1736.64	**< 0.001**
2009-2010: 1YOs					
63606	266.49	**< 0.001**	no pattern	381.2	**< 0.001**
63607	3755.13	**< 0.001**	day	1562.6	**< 0.001**
2009-2010: 2YOs					
487a	276.10	**< 0.001**	no pattern	1048.20	**< 0.001**
3463a	668.25	**< 0.001**	no pattern	195.66	**< 0.001**
63605	611.63	**< 0.001**	day	1222.14	**< 0.001**
63608	2952.28	**< 0.001**	no pattern	1265.82	**< 0.001**

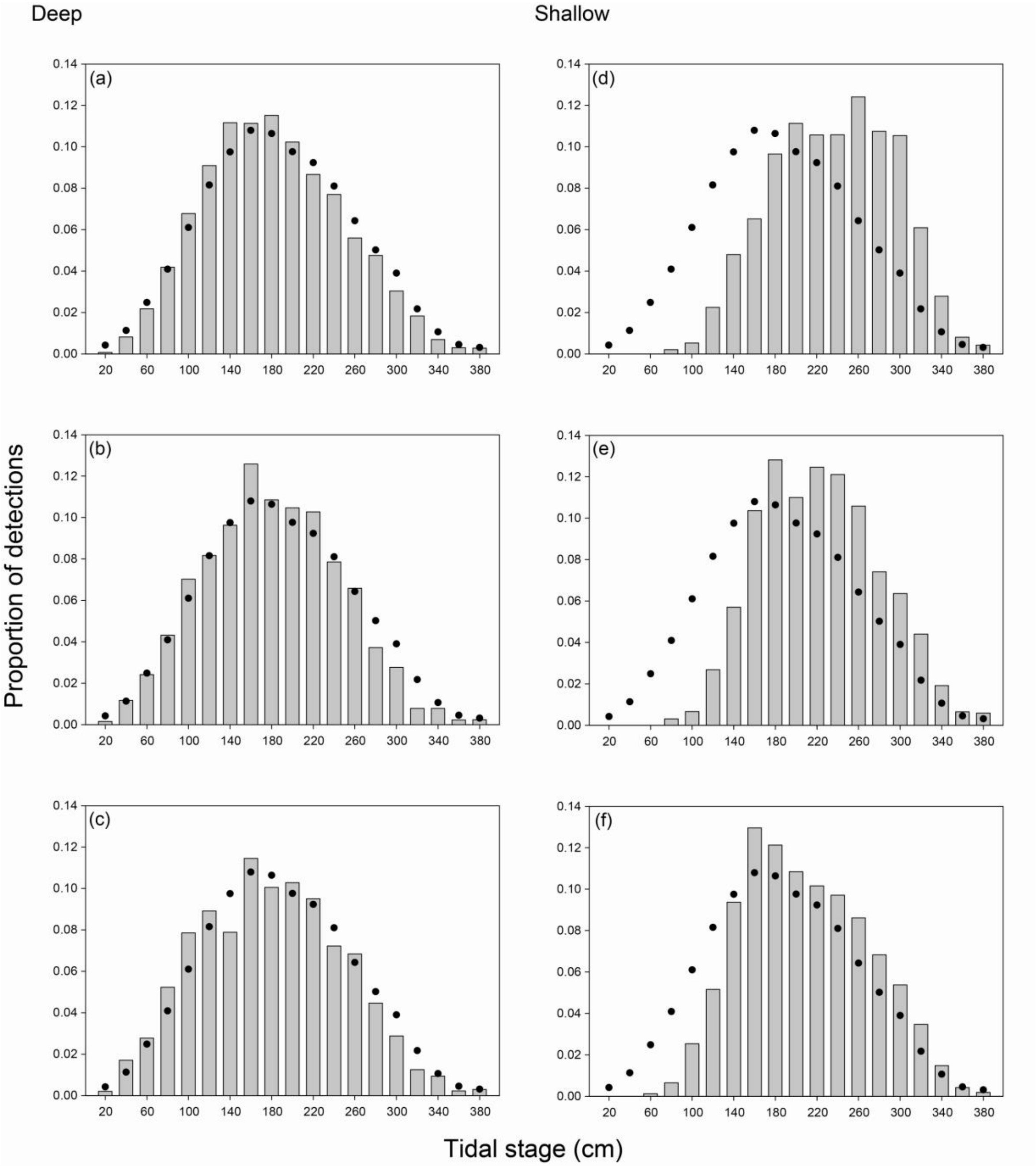

Fig. 4.4 Proportion of detections during each 20 cm tidal stage (grey bars) and actual tidal stage distribution (●) for *C. amboinensis*. Panels indicate detections on deep (a-c) and shallow (d-f) receivers for young-of-the-year (a,d), one-year-old (b,e) and two-year-old (c,f) age classes.

were pooled across years. All juvenile individuals moved with the tidal cycle but there was some variation in movement between age classes. For shallow water receivers, detections occurred during tidal stages ranging from 71 to 409 cm for YOYs (mean = 246 cm), 79 to 409 cm for 1YOs (mean = 232 cm) and 73 to 406 cm for 2YOs (mean = 218) (Fig. 4.5). For deep water receivers, detections occurred during tidal stages ranging from 22 to 397 cm for YOYs (mean = 192 cm), 29 to 410 cm for 1YOs (mean = 90 cm) and 29 to 397 cm for 2YOs (mean = 185 cm) (Fig. 4.5). Comparing detections based on tidal stage between shallow and deep receivers revealed significant differences among all age classes (YOYs: $t_{31.25} = 10.58$, $p < 0.001$; 1YOs: $t_{4.64} = 5.72$, $p = 0.002$; 2YOs: $t_{5.47} = 3.81$, $p = 0.011$).

Spectral analysis revealed up to 4 peaks in the time series detection data of *C. amboinensis* (Fig. 4.6). The initial peak at 0.000 was indicative of autocorrelation in the data. A peak at 0.042 reflected a daily pattern (24 hours), a peak at 0.087 reflected a tidal pattern (11.5 hours) and a peak at 0.125 corresponded to an 8 hour signal, which could be due to a tide lag in the movement response of *C. amboinensis*. The strength of these signals varied between receiver location (shallow and deep) based on age class. Relative to the initial peak in the data, YOYs and 1YOs had strong signals on the shallow receivers and either weak or no signals on the deep receivers. 2YOs had weaker signals on the shallow receivers when compared to the deep receivers, though the signals on the deep receivers were less defined with more variability (Fig. 4.6). This result demonstrates that daily changes in the environment (i.e. changes in water depth due to the tidal cycle) had the strongest influence on the movements of the youngest juveniles in shallow nearshore habitat. However, movements associated with daily and tidal patterns appeared to be an important behaviour for all age classes of *C. amboinensis* and older juveniles had similar movement patterns in deeper habitats, indicating a shift in habitat use with increasing age and/or size.

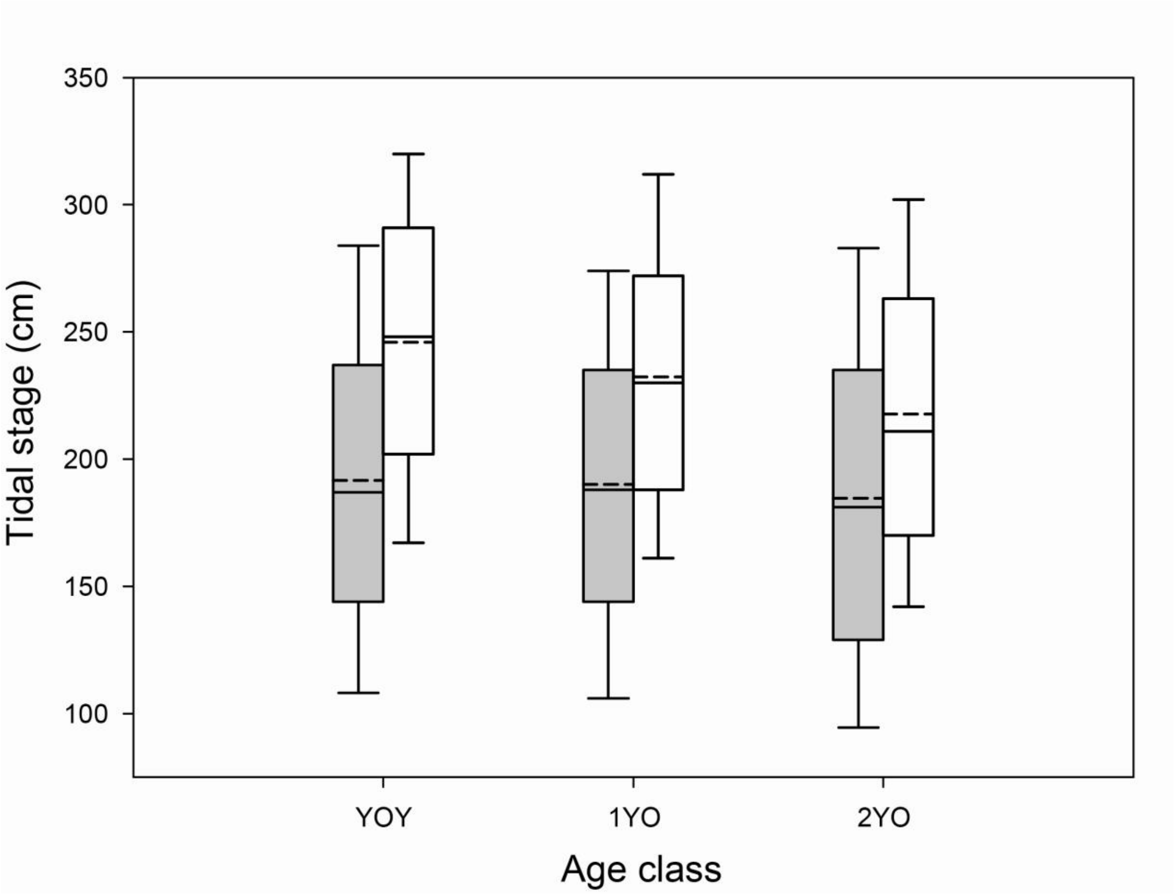

Fig. 4.5 Boxplots showing distribution of detections on deep receivers (grey) and shallow receivers (white) by tidal stage for each age class of *C. amboinensis*. Boxes are 10th and 90th percentiles (whiskers), 25th and 75th percentiles (boxes), mean (dashed line) and median (solid line).

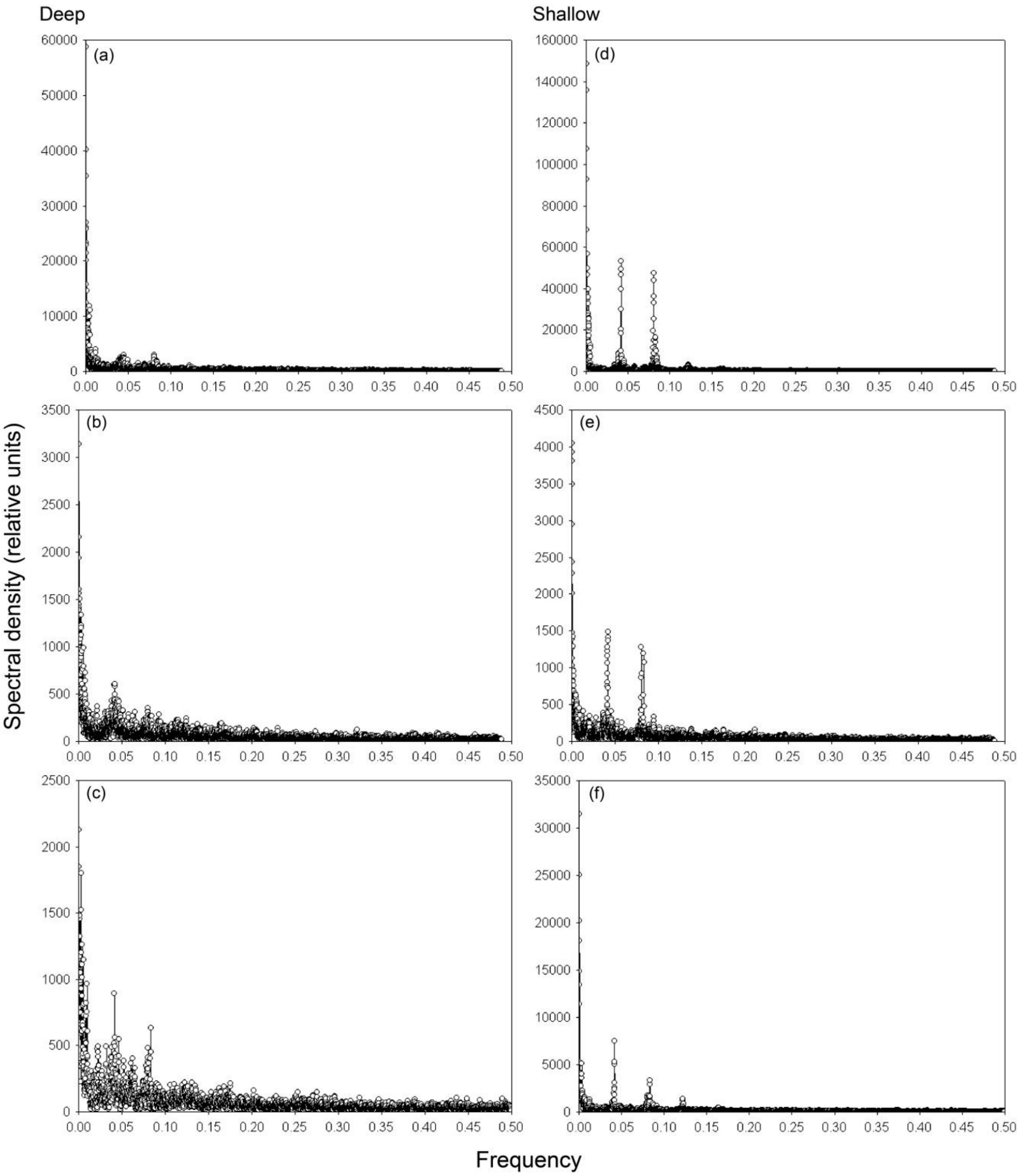

Fig. 4.6 Spectral density of hourly detections for *C. amboinensis* on deep (a-c) and shallow (d-f) receivers calculated separately for young-of-the-year (a,d), one-year-old (b,e) and two-year-old (c,f) age classes.

4.3.4 Habitat use by depth

There was no difference in mean depths used between years (YOYs: $t_{17.98} = -0.38$, $p = 0.710$; 1YOs: $t_{1.01} = 0.00$, $p = 0.998$), so data were pooled across years for depth analyses. Approximately 40% of the depth available in the study site was > 400 cm, but all age classes of *C*. *amboinensis* spent at least 80% of their time in depths < 400 cm (Fig. 4.7a). In addition, the amount of time individuals spent in < 200 cm of water, which consisted of only 24% of the depth available in the study site, was 41% for YOYs, 35% for 1YOs and 29% for 2YOs (Fig. 4.7a). Thus, juvenile *C*. *amboinensis* used depths disproportionately to what was available in the study site and there was variation among age classes, with YOYs typically using shallower depths (mean = 236 cm) than 1YOs (mean = 261 cm) and 2YOs (mean = 269 cm).

Electivity analysis revealed that *C*. *amboinensis* had affinities for different depths based on age class (Fig. 4.7b). Affinity of YOYs peaked around 200 cm and then decreased until 400 cm where avoidance for depths > 400 cm was evident. Affinity of 1YOs increased to a peak at 100 cm and declined until 250 cm before peaking again at approximately 300 cm. 2YOs showed greatest affinity for deeper depths of 300 to 400 cm. Both 1YOs and 2YOs displayed increasing avoidance of depths > 550 cm. Thus, depths used varied among age classes of juvenile *C*. *amboinensis*, with the youngest individuals having affinity for shallower depths than older individuals. In addition, 1YOs showed high affinity for both shallow (100 cm) and deeper (300 to 400 cm) depths, which may be an indication of these individuals expanding their movements into deeper habitats as they grow larger.

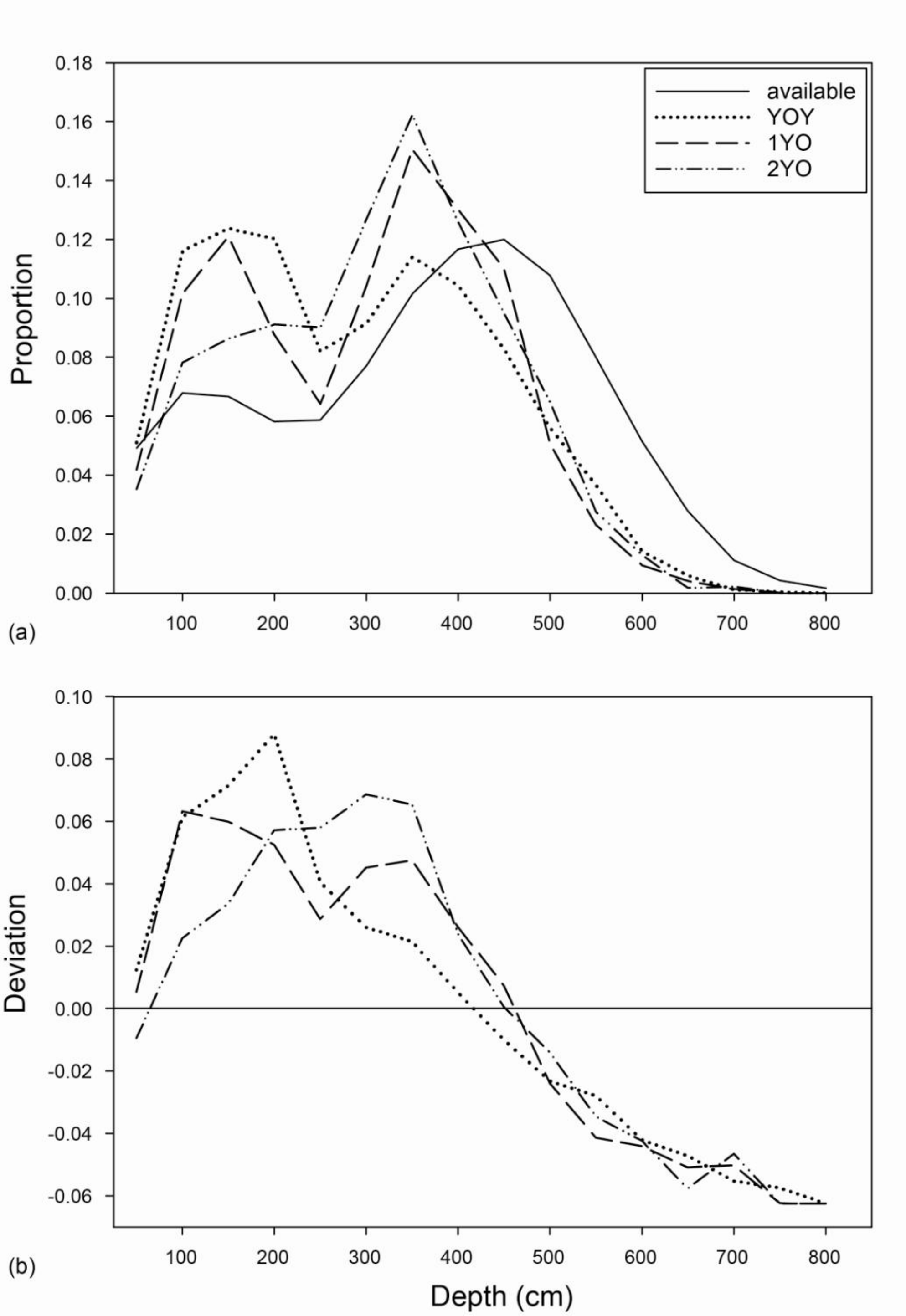

Fig. 4.7 Proportion of available depths in Cleveland Bay (solid line) and proportion of depths used by young-of-the-year (dotted line), one-year-old (dashed line) and two-year-old (dotted-dashed line) age classes of *C. amboinensis* (a). Electivity analysis of depth for young-of-the-year (dotted line), one-year-old (dashed line) and two-year-old (dotted-dashed line) age classes of *C. amboinensis*. Values above zero indicate affinity (b).

4.4. Discussion

Juvenile *C*. *amboinensis* were present in Cleveland Bay during all seasons throughout the year, with some individuals present for longer than 400 days. Long-term presence was common across years and age classes, although there were some individuals that left the study site after shorter periods of time. Similar long-term presence patterns have been documented in other coastal elasmobranch species including *C. leucas* (Heupel *et al*. 2010a), *S*. *lewini* (Duncan and Holland 2006) and the cownose ray *Rhinoptera bonasus* (Collins *et al*. 2008). Patterns in presence varied among age classes of *C*. *amboinensis*, with older juveniles continuously present for longer periods than younger juveniles. Older juveniles had more extensive movements than younger juveniles and likely used more areas within a day as a result, which would increase their chance of being detected within the receiver array over consecutive days.

Movements of *C*. *amboinensis* were generally restricted to the eastern side of Cleveland Bay, with individuals occasionally moving across the bay to the western side. Although all individuals monitored during this study were released on the eastern side of the bay, catch data verified that *C*. *amboinensis* were rarely found elsewhere in Cleveland Bay (D. M. Knip, unpublished data). Individuals that undertook movements across the bay did so in all months and there was no evident pattern or cue that triggered these movements. Moving 10 km across the bay appeared to be an occasional event for most individuals, indicating that juvenile *C*. *amboinensis* had relatively localised movements in this region. In addition, the three sharks removed from the study were all caught in close proximity to Cleveland Bay, with the individual recaptured approximately 10 km north of the study site at liberty for more than a year. Similar localised movements have been reported for *C*. *amboinensis* along the northern coast of Australia (Stevens *et al*. 2000b). The eastern side of Cleveland Bay has areas of strong tidal flow and high turbidity, due to the three main river systems that enter the bay along the southeast shore. The shallow, turbid habitat within this relatively localised area along the eastern side of Cleveland Bay may offer sufficient and/or preferred resources for *C. amboinensis*, which could result in their limited movement from this specific area.

Limited movements of *C. amboinensis* were also supported by home range analyses. Total home ranges of *C. amboinensis* sometimes included areas in both the northern and western portion of Cleveland Bay, but core home ranges consistently remained in the southern portion of the bay adjacent to the creek mouths, where individuals displayed a strong association with shallow, turbid habitats. This finding is similar to that of Cliff and Dudley (1991), who reported *C. amboinensis* in South African waters using turbid areas in close proximity to estuaries and rivers. However, limited detections of *C. amboinensis* on the Ross River receiver suggest that individuals rarely moved up or used the creeks and rivers. *Carcharhinus amboinensis* has been reported using brackish water, but unlike its close relative *C. leucas*, has not yet been found to penetrate freshwater systems (Last and Stevens 2009). Rather, juvenile *C. amboinensis* have been reported to move away from rivers at times of high freshwater inflow (see Chapter 5), so it is likely that this species does not have a tolerance for low salinities or high flows, which are characteristic of river environments. Other studies have suggested that competitive exclusion or habitat partitioning might occur between *C. amboinensis* and *C. leucas* (Bass et al. 1973; Compagno 1984). Competitive exclusion may be occurring to some degree in Cleveland Bay, as juvenile *C. leucas* are commonly caught in adjacent rivers and creeks, and juvenile *C. amboinensis* are not (A. J. Tobin, unpublished data). Thus, it is possibly a combination of habitat preference, physical limitation and resource partitioning that dictates the home range and habitat use of juvenile *C. amboinensis* in Cleveland Bay.

There were no differences in home range size between age classes of juvenile *C. amboinensis* based on KUDs, but significant differences were apparent between age classes using MCP measures. Although there were a lower number of older juveniles monitored, these individuals had larger MCPs than younger individuals, which may indicate an ontogenetic shift in the movement and home range behaviour of juvenile *C. amboinensis*. Home range size has been found to increase with increasing body size in other elasmobranch species including *R. bonasus* in a Florida estuary (Collins *et al*. 2007) and the lemon shark *Negaprion brevirostris* in the Bahamas (Morrissey and Gruber 1993a). Increasing MCP size with age class suggests that older *C. amboinensis* juveniles roamed more widely and had more extensive movements than younger juveniles. Imansyah *et al*. (2008) found a similar result with komodo dragons *Varanus komodoensis* in Indonesia, where the youngest hatchlings used smaller spaces than older juveniles. Likewise, Simpfendorfer *et al*. (2010) found that home range size increased with age class among juvenile smalltooth sawfish *Pristis pectinata* in Florida waters, but also that home range sizes remained consistent among individuals within the same age class. These authors hypothesised that the differences in space use were due to age classes being affected by different selective pressures. A similar situation may be occurring among age classes of juvenile *C. amboinensis*. Young juveniles may be more influenced by factors like predation risk and as such, consistently use smaller areas and do not move as far. Older juveniles may be more driven by resource acquisition and so increase their use of space to include additional habitats. To meet resource needs as a larger individual, older juveniles may roam farther to obtain larger-sized and a higher diversity of prey items. However, while they are younger, juveniles may have more restricted movements and use smaller spaces as a refuging strategy to increase survival. Movements and home ranges then increase as juveniles grow larger and become more successful competitors and less vulnerable to different risks. However, it is important to note that the small sample sizes of 1YO and 2YO sharks are a weakness in this data, and statistical comparisons should therefore be interpreted with caution.

Home range patterns of *C*. *amboinensis* remained consistent across years but varied significantly between months. In general, both 50% and 95% KUDs increased and became more variable in the months of January to March. These months coincide with the monsoonal wet season in the Townsville region, during which an increased, though highly variable, amount of rainfall occurs (Bureau of Meteorology, Australia). Juvenile *C*. *amboinensis* were found to shift their home ranges to more northern parts of Cleveland Bay during the wet season (see Chapter 5). Thus, larger monthly home ranges likely indicate times when individuals shifted their activity due to freshwater flow, resulting in larger overall home ranges during wet season months. However, an increase in monthly home ranges could indicate times when individuals made movements from their core home ranges, such as across the bay or north away from the creeks. Thus, variation in monthly home ranges could also be due to differences in movement, particularly by older juveniles who tended to move more sporadically and roam farther than younger juveniles.

Although diel movement patterns have been reported in other coastal shark species, this pattern was not evident in *C*. *amboinensis*. Some individuals were detected more often during the day or at night, but for most individuals, there was no pattern in detection frequency with hour of the day. This result is similar to that found with the bonnethead shark *Sphyrna tiburo* in a Florida estuary and the grey reef shark *Carcharhinus amblyrhynchos* within the Great Barrier Reef, where most individuals displayed no consistent pattern in movement with time of day (Heupel *et al*. 2006b, 2010b). Although there was no pattern found between detections and time of day for *C*. *amboinensis*, a large daily signal was evident in the spectral analysis for all age classes. A daily signal in the detection data could be a result of several factors including the strong tidal pattern in the data, as well as the nine individuals that had a higher detection frequency either during the day or night. In addition, daily physical (e.g. wind) and biological (e.g. crepuscular noise) patterns in the environment may have affected equipment performance, resulting in an hourly variation of detection frequency. Lack of a consistent pattern between detections and time of day for juvenile *C. amboinensis* suggests that factors other than diel changes have a more important role in their movements.

Carcharhinus amboinensis had movements strongly driven by the tidal cycle, with individuals of all age classes moving into the intertidal zone with the rising tide and back out to deeper areas with the falling tide. Cleveland Bay has a relatively high maximum tidal range (4.2 m), which allowed individuals to use the tide to their advantage and move onto the shallow mud flats that usually dry out at low tide. However, it is unclear what factors were driving these tidal movement patterns. *Carcharhinus amboinensis* may be moving into the intertidal zone at high tides to increase foraging opportunities by accessing additional habitats and prey items. Similar tidal movements have been documented in the leopard shark *Triakis semifasciata* in two California bays. Both Ackerman *et al*. (2000) and Carlisle and Starr (2010) found that *T. semifasciata* moved with the tide to maximise foraging area by using regions that could only be reached at high tide. Tidal fluctuations have also been found to influence the movements of several fish species, which in turn may affect the movements of predators foraging on those species (Sogard *et al*. 1989). Thus, juvenile *C. amboinensis* may be moving with the tide to follow and forage on moving prey items. Examination of tidal signals in the detection data indicated that movements of the youngest juveniles were the most influenced by the tide in shallow areas. Similarly, smallest *N. brevirostris* juveniles at an atoll in Brazil were found to be the most influenced by the tide and these individuals restricted their movements to the shallowest tide pools (Wetherbee *et al*. 2007). The authors believed these young individuals moved with the tide so they could remain in depths shallow enough to avoid predators using the same region. Large sharks are encountered often throughout Cleveland Bay (D. M. Knip, unpublished data) and presumably present a predatory threat to small *C*. *amboinensis*. Thus, moving with the tide to remain in shallower depths may also be a refuging strategy for juvenile *C*. *amboinensis*. Small individuals are likely the most vulnerable, which may be why tidal movement patterns were most evident among youngest juveniles in shallow habitats.

Perhaps not as important as predator avoidance (Steele 1998), differences in movement and habitat use among age classes of juvenile *C*. *amboinensis* may also act as a mechanism to reduce intraspecific competition. Remaining in shallower habitats would allow young juveniles to avoid older individuals using deeper waters, who would likely out-compete them for similar resources. Age class segregation has been reported in *C. leucas* in Florida waters, where the youngest juveniles remained up river while older juveniles used areas farther downstream towards the coast (Simpfendorfer *et al*. 2005). These authors suggested that younger juveniles used different habitat to that of older juveniles to decrease predation risk, but also to reduce competition associated with larger individuals. Being smaller in size, young juveniles are presumably weaker competitors, as well as less skilled at acquiring prey when compared to older juveniles. Spina (2000) found that age segregation occurred in the rainbow trout *Oncorhynchus mykiss*, with older individuals using deeper habitats. Although the ontogenetic shift in habitat use may have been due to size specific habitat requirements, it also reduced intraspecific competition (Spina 2000). Similarly, age segregation in *C*. *amboinensis* may be driven by size specific habitat requirements, with individuals shifting their habitat use behaviours as they grow. This in turn may reduce intraspecific competition between individuals of different sizes and ultimately increase population success.

Ontogenetic shifts in depth among age classes of juvenile *C*. *amboinensis* showed that individuals used the shallowest depths while young, and expanded their use of habitats to include deeper depths as they grew. Similarly, studies that examined habitat use of *P*. *pectinata* in Florida waters and freshwater sawfish *Pristis microdon* in a Western Australia river reported differences in depths used among juvenile age classes, with the youngest individuals using shallower depths (Whitty *et al*. 2009; Simpfendorfer *et al*. 2010). These authors suggested that using shallow water was a predator avoidance mechanism for smaller juveniles. Small *C*. *amboinensis* may similarly be using shallow depths as a refuging strategy, but it is also likely that these young individuals were constrained to a narrower depth range due to their restricted movements. Since older juveniles typically had more extensive movements and expanded their use of space, they probably also used deeper depths as a result.

Changes in habitat use among age classes of juvenile *C*. *amboinensis* were also strongly supported by spectral analyses. The shift in tidal signal strength from shallow to deep water receivers with the 2YO age class suggests a transition occurred in the movement and habitat use behaviour of *C*. *amboinensis*. A tidal signal on the deep receivers indicates that older juveniles were using additional areas in deeper water but continued undertaking movements similar to those of their younger counterparts. In addition, a weaker tidal signal for older juveniles on the shallow receivers suggests that moving with the tide to remain in shallow depths was not as important for them as it was for younger juveniles. Similar ontogenetic shifts in habitat use have generally not been well documented in coastal elasmobranch species, but have been reported in some teleost fishes. For example, specific habitat preference of juvenile sparids *Diplodus* sp. in the Mediterranean Sea was found to decrease as individuals grew (Macpherson 1998), and habitat use of Roanoke logperch *Percina rex* in a river in the eastern United States was reported to change based on age class (Rosenberger and Angermeier 2003). Similarly, *C. amboinensis* showed the greatest preference for a specific habitat during the earliest life stages, where young juveniles restricted their movements to depths typically less than 2 m and only occasionally moved out of core home ranges adjacent to creek mouth habitat. When juvenile *C. amboinensis* reached around two years of age, they showed less preference to that specific habitat region and began using different behaviours and habitats, such as making more frequent movements from core ranges and using more space. This transitioning behaviour may be an ontogenetic strategy for this species, in which older juveniles prepare for eventually leaving shallow nearshore regions to use deeper habitats further offshore.

CHAPTER 5

Wet Season Effects on the Distribution of Juvenile *Carcharhinus amboinensis*

5.1 Introduction

Freshwater flow and flooding has a major impact on nearshore regions (e.g. bays, lagoons and estuaries) and can cause large fluctuations in the physical characteristics of an environment (Finlayson and McMahon 1988; Fraser 1997). Tropical regions are susceptible to increased amounts of freshwater impinging these systems due to extreme rainfall events that occur in wet season months (Balek 1983). Rainfall in the tropics is generally around 2,000 mm per year, with some regions experiencing up to 10,000 mm per year (Latrubesse *et al*. 2005). Such a significant input of freshwater causes high variability in the flows of tropical river systems, especially rivers in northern Australia, which are affected by annual monsoonal events (Balek 1983; Finlayson and McMahon 1988). Understanding the effects of extreme annual flow and flooding episodes on nearshore inhabitants is important, as freshwater flow influences species differently (Ter Morshuizen *et al*. 1996; Flannery *et al*. 2002) and may even cause mortality in some species (Whitfield and Paterson 1995).

Mobile fish species can modify their behaviour or physiology to cope with fluctuating environmental conditions, or may leave a region when conditions extend beyond their physiological limitations. For example, some teleost species have been reported to move from deep to shallow water in response to low dissolved oxygen concentrations (Pihl *et al*. 1991). Similar results have been found with sharks, with leopard sharks *Triakis semifasciata* leaving nearshore regions during anoxic periods (Carlisle and Starr 2009) and bonnethead sharks *Sphyrna tiburo* moving out of estuaries when salinity declines (Ubeda *et al*. 2009). Few studies, however, have investigated the specific response of individual animals (e.g. movement and distribution) to seasonal variation (e.g. freshwater inflow) in tropical nearshore regions. Studies have found a general decrease in the abundance and diversity of fish species in tropical nearshore regions during wet season events (Cyrus and Blaber 1992; Fraser 1997). One study specifically examined the movement and distribution of juvenile bull sharks *Carcharhinus leucas* in the estuarine portion of a Florida river and determined that individuals moved downriver with decreasing salinity and increasing freshwater flow rate (Heupel and Simpfendorfer 2008).

With altered climate scenarios becoming an increasing concern for tropical nearshore regions, a better understanding of species response to environmental and seasonal variability is needed. Thus, in this chapter I examine home range and distribution of juvenile *C*. *amboinensis* in relation to freshwater inflow to determine if high flow rates during the wet season affect species movement and habitat use. I hypothesised that juvenile *C*. *amboinensis* will respond to freshwater inflow by shifting their distribution away from sources of strong flows.

5.2 Townsville wet season

The wet season in northern Queensland is variable. Average annual rainfall in Townsville is around 1200 mm but has been higher over the past few years. Townsville received approximately 1830 mm of rainfall from December 2008 to April 2009 and 1460 mm of rainfall from December 2009 to April 2010 (Fig. 5.1). In 2009, 88% of total wet season rainfall occurred in February and March, whereas in 2010 only 64% of wet season rainfall

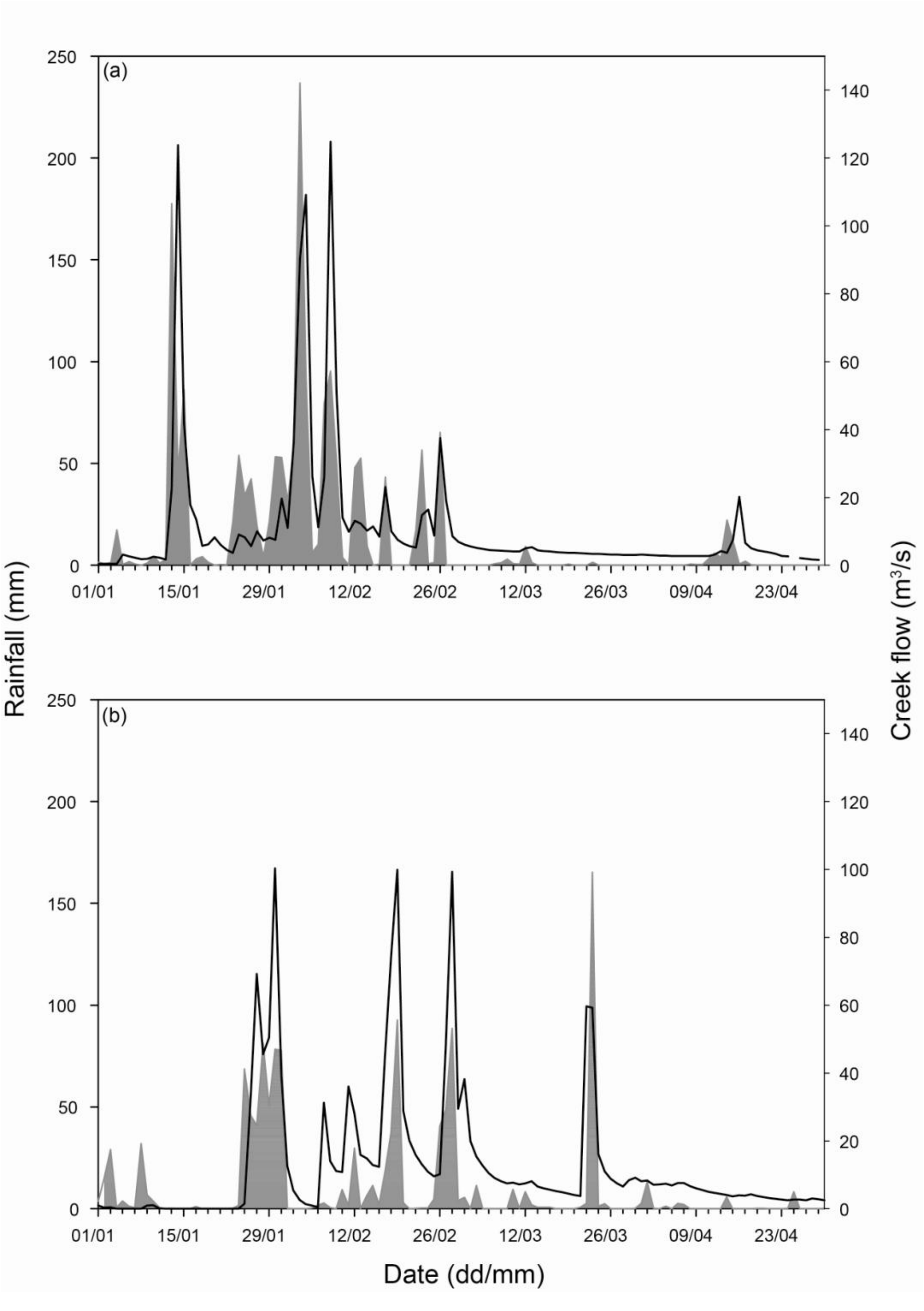

Fig. 5.1 Mean daily rainfall for the Townsville region (grey fill) and mean daily Alligator Creek flow (solid line) from January through April for 2009 (a) and 2010 (b).

occurred in those two months (Fig. 5.1). Freshwater inflow from creeks adjacent to Cleveland Bay is directly influenced by rainfall, with the largest flow rates occurring immediately after rainfall events (Fig. 5.1). Due to the variability in rainfall between these two years examined, the amount and pattern of freshwater inflow also varied. A major consequence of increased freshwater inflow during the wet season is decreased salinity in Cleveland Bay, and the lowest salinity levels have been recorded at times of highest freshwater inflow (Walker 1981).

5.3 Data analyses

5.3.1 Distribution and home range

Only data from acoustic receivers on the eastern side of the array were included in this analysis for two reasons. First, detections of *C. amboinensis* on the western array were rare and second, the western array did not cover areas of high freshwater inflow. To examine the effects of the tropical wet season on the movement of juvenile *C. amboinensis* and to remain consistent between years, data were analysed from December through April over two years (2008-2009 and 2009-2010). Locations of monitored *C. amboinensis* in the study site during this time frame were estimated every 30 minutes using a mean position algorithm that provided an individual's centre of activity (COA) (Simpfendorfer *et al*. 2002; see Chapter 4). COA locations represent an individual's mean position for the set time-step.

Home ranges of individual *C. amboinensis* were calculated based on COA estimates using 50% and 95% kernel utilisation distributions (KUDs) with the adehabitat package in R (Calenge 2006; see Chapter 4). Home ranges were calculated at both weekly and monthly intervals to examine changes in distribution and habitat use over time and were plotted in ArcGIS 9.3.1 (Environmental Systems Research Institute, Redlands, United States) to show spatial and temporal distribution patterns across wet season months.

5.3.2 Regression analysis

Freshwater inflows from creeks into Cleveland Bay are of similar magnitude and data from Alligator Creek were used as flow data available at this site were continuous (Queensland Department of Environment and Resource Management, Australia). The latitudes of COA locations of juvenile *C. amboinensis* were used to represent the distribution of animals in the bay relative to the mouths of the main sources of freshwater inflow, which were all on the southern boundary of the bay. Mean weekly latitude locations and weekly home range sizes of *C. amboinensis* were compared and correlated against creek flow.

The normality of the data (both latitude locations and home ranges) was checked by examination of Quantile-Quantile plots and satisfied the assumptions for parametric testing. Tests of regression analysis demonstrated that there was no significant difference between fitting linear, polynomial or segmented models to the data. The strength of each model was the same and a linear model was used for further statistical testing of the data. Analysis of covariance (ANCOVA) was used to test for significance of creek flow on latitude location and home range size of *C. amboinensis*, and to determine if differences were present between age classes and years. Analysis of variance (ANOVA) was used to test for differences in latitude locations of *C. amboinensis* across dry season weeks.

5.4 Results

Only young-of-the-year (YOY) and one-year-old (1YO) *C*. *amboinensis* were included in the wet season analyses because two-year-olds (2YOs) were not released with transmitters during the first year of the study. Thirty-two individuals were monitored for 2 to 101 days during the wet seasons and two YOYs released in 2009 were present in the study site in 2010, and so were included in the 1YO age class for the second year (Table 5.1).

5.4.1 Distribution and freshwater inflow

Distributional shifts of juvenile *C*. *amboinensis* during wet season months occurred at times of greatest freshwater inflow from Alligator Creek (Fig. 5.2). During periods of high freshwater inflow, *C*. *amboinensis* responded by moving north away from the creek mouths (Fig. 5.2). As freshwater inflow decreased following the wet season, *C*. *amboinensis* responded by returning to the southern portion of the bay (Fig. 5.2). Regression analysis showed that creek flow strongly influenced latitude location of sharks in the bay ($r^2 = 0.44$, $p < 0.001$) (Fig. 5.3). Although the residuals appeared non-uniform with regression analysis, the assumption of linearity was met ($F_{3,58} = 14.53$, $p < 0.001$). There was no significant difference in mean weekly latitude location between age classes in either year (2008-2009: $F_{1,28} = 0.04$, $p = 0.843$; 2009-2010: $F_{1,26} = 0.14$, $p = 0.717$) and freshwater inflow did not affect mean weekly latitude location of age classes differently (2008-2009: F1,28 = 3.57, p = 0.069; 2009–2010: F1,26 = 0.69, p = 0.414), indicating that freshwater inflow affected YOY and 1YO individuals in the same manner. However, it is important to note that the sample size of the 1YOs was much smaller than the YOYs, thus statistical comparisons should be interpreted with caution. Although the relationship between freshwater inflow and latitude location was stronger in 2008-2009, freshwater

Table 5.1 Tagging information for *C. amboinensis* monitored in Cleveland Bay during two wet seasons including date tagged, date of last detection, number of days monitored during wet season period and age class. Date last detected indicates the last detection during monitoring period analysed (December-April). *individuals monitored in both years.

ID	Date tagged	Date last detected	Days monitored	Age class
579	11/12/2008	25/04/2009	92	1YO
563	18/12/2008	30/04/2009	101	1YO
487	18/02/2009	28/04/2009	51	YOY
490	18/02/2009	26/04/2009	40	YOY
495	18/02/2009	02/032009	7	YOY
562	18/02/2009	30/04/2009	69	YOY
573	18/02/2009	20/04/2009	55	YOY
574	18/02/2009	25/03/2009	22	YOY
575	18/02/2009	26/02/2009	8	YOY
577*	18/02/2009	22/04/2010	50,70	YOY
3460*	18/02/2009	25/03/2010	37,24	YOY
3461	19/02/2009	28/02/2009	4	YOY
3462	19/02/2009	28/03/2009	37	YOY
3463	19/02/2009	22/04/2009	41	YOY
3464	19/02/2009	24/02/2009	4	YOY
3466	19/02/2009	27/02/2009	6	YOY
3467	19/02/2009	25/02/2009	6	YOY
63606	03/12/2009	31/01/2010	55	1YO
63607	03/12/2009	21/04/2010	57	1YO
63610	16/02/2010	20/04/2010	53	YOY
63612	16/02/2010	20/04/2010	31	YOY
63614	17/02/2010	22/4/2010	43	YOY
63621	17/02/2010	10/03/2010	12	YOY
63622	17/02/2010	19/04/2010	37	YOY
63615	23/02/2010	08/03/2010	10	YOY
63618	23/02/2010	18/04/2010	39	YOY
63619	23/02/2010	22/04/2010	36	YOY
63620	23/02/2010	24/02/2010	2	YOY
63611	03/03/2010	22/04/2010	46	YOY
63613	03/03/2010	22/04/2010	49	YOY
63617	03/03/2010	09/03/2010	3	YOY
63623	03/03/2010	22/04/2010	30	YOY

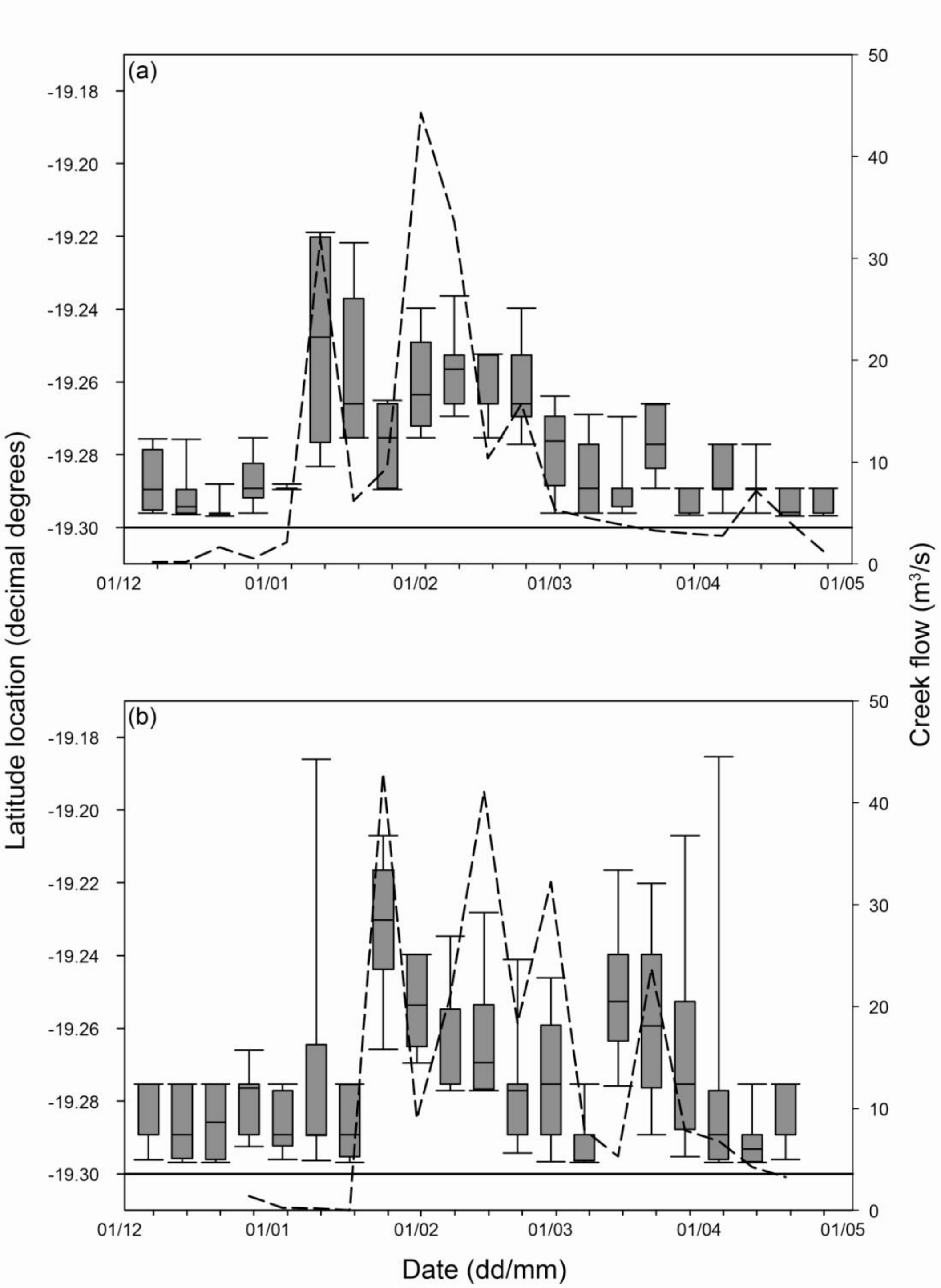

Fig. 5.2 Boxplots showing range of latitude locations of *C. amboinensis* in Cleveland Bay by week in relation to mean weekly flow from Alligator Creek (dashed line) and the location of the mouth of Alligator Creek (solid line). Weeks include December through April for 2008-2009 (a) and 2009-2010 (b). Boxes are 10th and 90th percentiles (whiskers), 25th and 75th percentiles (boxes) and median (solid line).

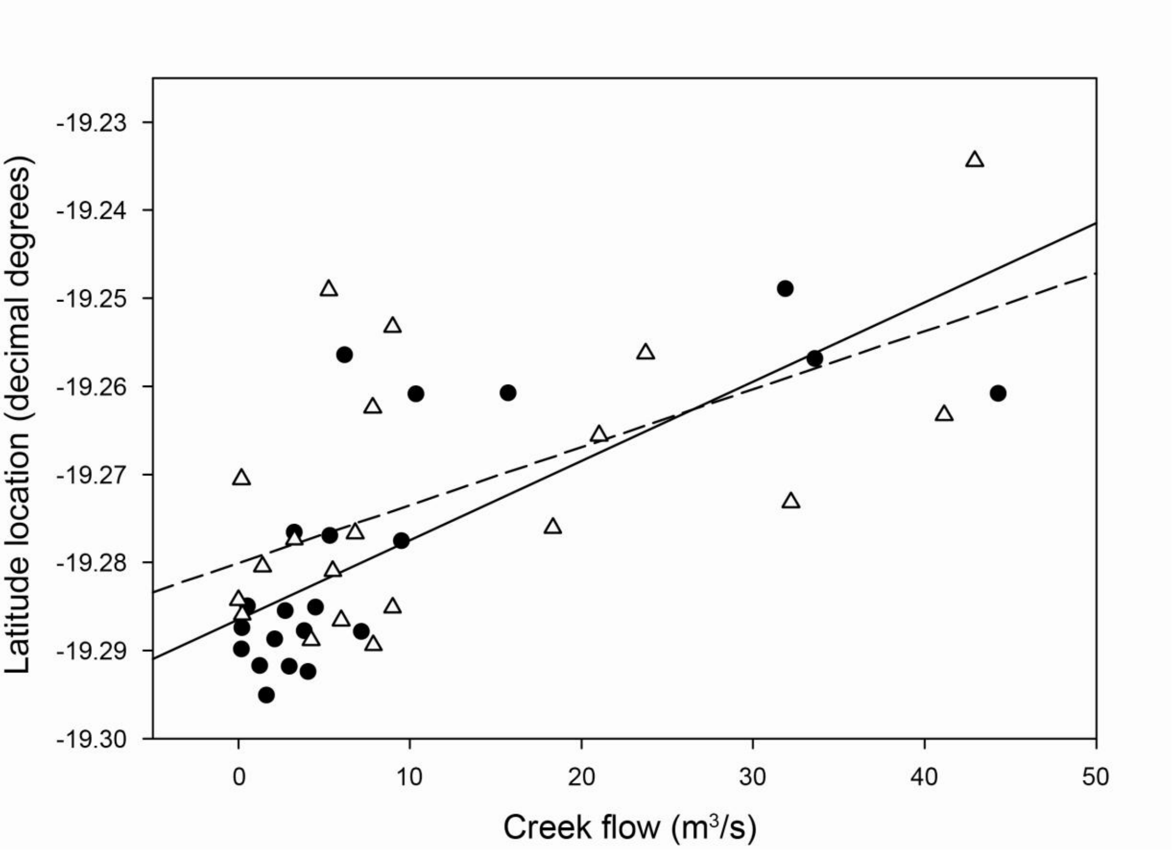

Fig. 5.3 Regression lines of mean weekly latitude location of *C. amboinensis* and mean weekly flow of Alligator Creek for 2008-2009 (● and solid line) and 2009-2010 (Δ and dashed line).

inflow was a significant factor influencing the location of *C*. *amboinensis* in Cleveland Bay in both years (2008-2009: $F_{1,19} = 26.19$, $p < 0.001$; 2009-2010: $F_{1,18} = 9.19$,$p = 0.007$). There was no significant difference in the effect of freshwater inflow on latitude location of *C*. *amboinensis* between years ($F_{1,37} = 1.18$, $p = 0.285$).

5.4.2 Home range

Home ranges of juvenile *C*. *amboinensis* typically encompassed areas in the southern portion of Cleveland Bay adjacent to the creek mouths (Fig. 5.4). During February (the peak of the wet season), however, core home ranges (i.e. 50% KUDs) shifted away from the creek mouths and total home ranges (i.e. 95% KUDs) included more area in the northern portion of the bay (Fig. 5.4). After the wet season (April), home range analysis indicated that *C*. *amboinensis* remained in the southern portion of the bay (Fig. 5.4). Home range location also did not change outside wet season weeks. Juvenile *C*. *amboinensis* remained in the southern portion of the bay and there was no significant difference in latitude location between dry season weeks ($F_{9,9} = 1.06$, $p = 0.468$).

Although *C*. *amboinensis* shifted location in response to freshwater inflow, total weekly home range size remained stable (mean = 29.05 km^2). Regression analysis revealed no relationship between mean weekly home range size and creek flow ($r^2 = 0.01$, $p = 0.249$) (Fig. 5.5). There was no significant difference in mean weekly home range size between age classes in either year (2008-2009: $F_{1,28} = 0.13$, $p = 0.726$; 2009-2010: $F_{1,26} = 1.15$, $p = 0.294$), indicating that age classes used similar amounts of space. Freshwater inflow also did not affect home range size of age classes differently (2008-2009: $F_{1,28} = 2.11$, $p = 0.158$; 2009-2010: $F_{1,26} = 1.38$, $p = 0.250$). Freshwater inflow did not significantly influence home range size of *C*. *amboinensis* in Cleveland Bay, with mean weekly home range size (i.e. 95% KUD) in the wet season (31.56 km^2) similar to that in the dry season (26.15 km^2)

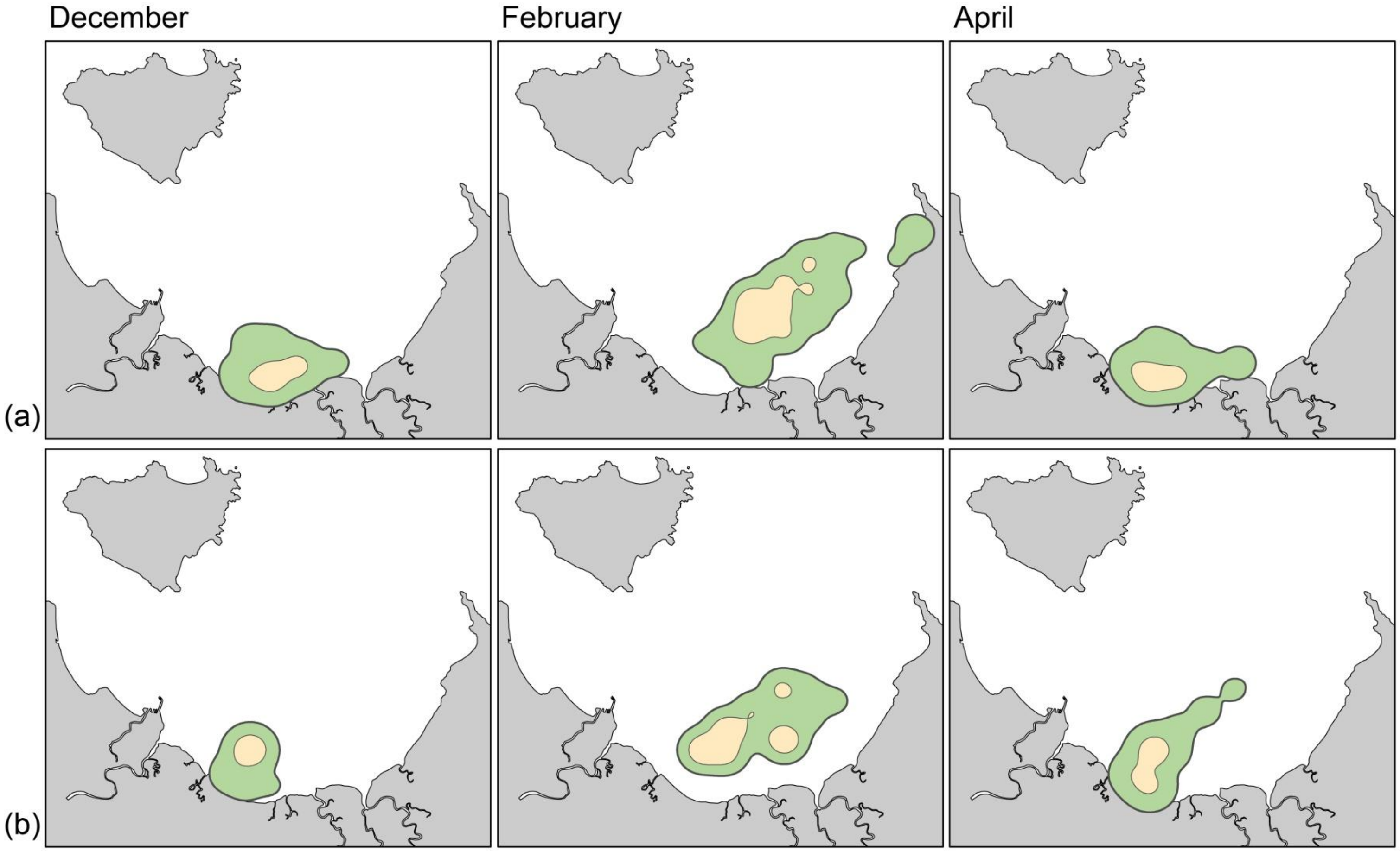

Fig. 5.4 Representative monthly home ranges of two *C. amboinensis* over two consecutive wet seasons including the months of December (start of wet season), February (peak of wet season) and April (end of wet season) for 2008-2009 (a) and 2009-2010 (b). Green fill: 95% KUDs, beige fill: 50% KUDs.

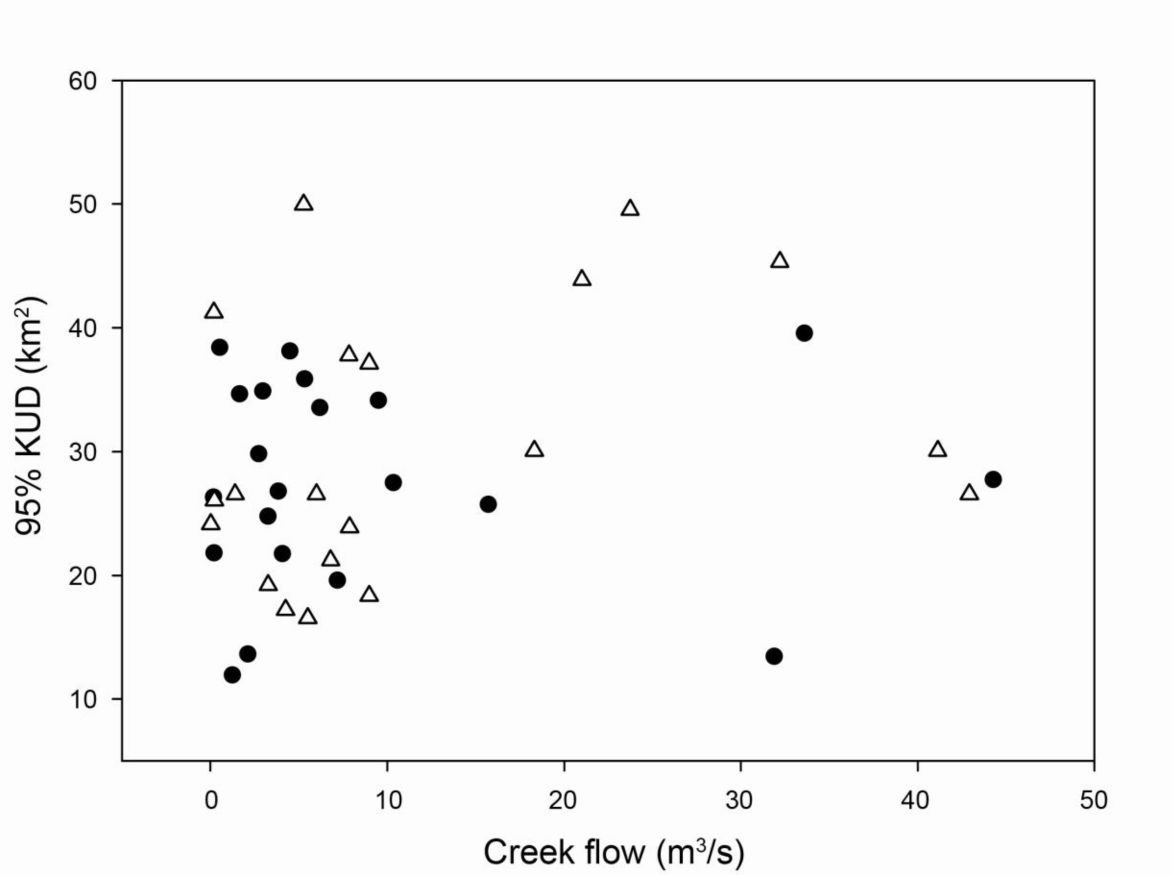

Fig. 5.5 Regression of mean weekly home ranges (95% KUDs) of *C*. *amboinensis* and mean weekly flow of Alligator Creek for 2008-2009 (●) and 2009-2010 (Δ).

(2008-2009: $F_{1,19} = 0.39$, $p = 0.54$; 2009-2010: $F_{1,18} = 3.43$, $p = 0.080$). Thus, individuals used the same amount of space regardless of freshwater inflow.

5.5 Discussion

These results strongly suggest that juvenile *C. amboinensis* responded to wet season freshwater flows by changing the way they used Cleveland Bay. Although the same amount of space was used, their location within this nearshore habitat showed a distinct seasonal change. This response to freshwater inflow is similar to that reported for other shark species, such as *S. tiburo* in central Florida (Ubeda *et al*. 2009). The response of sharks to these changing conditions suggests a lack of tolerance for lower salinity levels, a preference for alternative conditions or some other ecological factor.

Increased freshwater inflow may cause decreased salinity levels in nearshore environments and in Cleveland Bay a strong inverse relationship has been reported between freshwater inflow and salinity (Walker 1981). During this study, salinity levels in Cleveland Bay generally remained between 30 and 35 ppt but in the wet season salinity dropped as low as 8 ppt (surface) and 15.5 ppt (bottom) near the creek mouths (D. M. Knip, unpublished data). Thus, it is possible that the distribution of *C. amboinensis* was in part influenced by the low salinity levels that occurred during wet season months. However, the closely related *C. leucas* is a euryhaline species, with juveniles showing an affinity for low salinities ranging from 7 to 17 ppt within estuarine environments (Simpfendorfer *et al*. 2005; Heupel and Simpfendorfer 2008). Being close relatives, it could be presumed that *C. amboinensis* has similar physiological capabilities and behavioural characteristics to *C. leucas*. Although previous studies have reported *C.*

amboinensis using brackish water and turbid areas adjacent to creek and river mouths (Cliff and Dudley 1991), this species has not been found to penetrate freshwater. Also unlike *C*. *leucas*, juvenile *C*. *amboinensis* avoided creeks and rivers during times of high freshwater inflow. For example, juvenile *C*. *leucas* moved down river in a Florida estuary with increasing freshwater flow, but individuals continued using estuarine habitat during times of high flow (> 113 m^3/s) (Heupel and Simpfendorfer 2008). At similar flow rates, juvenile *C*. *amboinensis* moved away from creek mouths and used deeper marine areas. Further, in February 2009 when juvenile *C*. *amboinensis* were spatially displaced within Cleveland Bay, juvenile *C*. *leucas* were captured in fishing nets in both Alligator and Crocodile Creeks (A. J. Tobin, unpublished data). Therefore, these results suggest that *C*. *amboinensis* is less tolerant of high freshwater inflow than *C*. *leucas* and provide evidence that low salinity levels (e.g. 7-17 ppt) may be beyond the physiological limits of *C*. *amboinensis*.

Variation in rainfall resulted in different freshwater inflow patterns between years. The total amount of freshwater inflow was similar in both years, with maximum flow occurring in February, but in 2010 high freshwater inflow continued throughout March. The movement response of juvenile *C*. *amboinensis* may not only depend on the total amount of freshwater inflow, but the rate of inflow as well. A large volume of freshwater inflow concentrated in a shorter time period (i.e. 2009) resulted in a stronger movement response from juvenile *C*. *amboinensis*. In 2009, there were only two large peaks of freshwater inflow in a short period of time and the response of *C*. *amboinensis* was strong, with individuals moving away from the southern portion of the bay until high freshwater inflow ceased. Since there were, however, multiple peaks of freshwater inflow over a longer period of time in 2010, the relationship between flow and distribution of *C*. *amboinensis* was weaker. Individuals still moved away from creek mouths during times of highest freshwater inflow, but distribution remained spread out over a longer period and some individuals continued using northern portions of the bay into the month of April. In both years, however, individuals displayed a strong association with creek mouth habitat and consistently returned to and remained in the southern part of the bay after times of high freshwater inflow.

Moving in response to strong currents and flows has been reported in other shark species. For example, juvenile sandbar sharks *Carcharhinus plumbeus* inhabiting estuaries in the northwest Atlantic moved with tidal flow and showed greatest straight line movement when currents were strongest (Medved and Marshall 1983; Wetherbee and Rechisky 1999). In a southwest Florida estuary, juvenile blacktip sharks *Carcharhinus limbatus* also moved with tidal flow (Steiner and Michel 2007) and was considered to be a possible strategy to minimise energetic costs associated with swimming in strong currents. It is possible that juvenile *C. amboinensis* moved away from creek mouths during times of high freshwater inflow to avoid strong currents and preserve energy. Unlike *C. amboinensis* and these other examples, juvenile *C. leucas* were not found to swim with tidal flow and movements of young individuals were random and not influenced by strong currents (Steiner and Michel 2007). These examples suggest that the behaviour of juvenile *C. amboinensis* is more similar to other young carcharhinid sharks than to the closely related *C. leucas.*

The greatest northward movement of *C. amboinensis* away from creek mouth habitat in both years occurred during the first peak of freshwater inflow. In tropical environments, the wet season occurs during summer, which is when water temperature is highest. Increased water temperature results in increased biological productivity (i.e. algal blooms), which in turn decreases dissolved oxygen concentrations and may even cause anoxic conditions in creeks, rivers and estuaries (NOAA 1998; Perna and Burrows 2005). It is likely that the first flooding event of a wet season pushes low quality water with low dissolved oxygen concentrations into nearshore regions. Thus, the first freshwater flow probably had the largest impact on the physical environment of Cleveland Bay, explaining why *C. amboinensis* had the greatest movement response with the first peak of freshwater inflow. Dissolved oxygen has been found to influence the movement and distribution of other shark species. For example, juvenile *C. leucas* using an estuarine habitat were caught in higher abundances in areas of high dissolved oxygen (Heithaus *et al*. 2009) and low dissolved oxygen caused the exodus of *T. semifasciata* from shallow nearshore environments (Carlisle and Starr 2009). It is possible that lower dissolved oxygen concentrations during times of increased freshwater inflow may in part influence the movement of juvenile *C. amboinensis* away from shallow nearshore waters adjacent to creek habitats.

High freshwater flow rates can be a disturbance for some inhabitants of rivers, creeks and estuaries. It is common for the community structure of these nearshore environments to vary seasonally and mobile fish species may respond by leaving areas at times of high flow (Rayner *et al*. 2008). Fish generally leave an area of high flow to seek refuge from high flow rates or to target prey items that have also left the high flow environment (Winemiller and Jepsen 1998). Thus, it is possible that the increased freshwater inflow that occurred during this study moved fish species from adjacent creeks into Cleveland Bay. *Carcharhinus amboinensis* may have moved away from the creeks at times of high freshwater inflow to follow target prey species that also left the creek habitat at that time. Changes in the movement of predators in relation to prey distribution as a result of wet season events have been documented with other tropical species, such as the water python *Liasus fuscus* (Madsen and Shine 1996). Thus, predator species may change their behaviour in relation to prey distribution and sharks have been reported to show an association with habitats where prey is most abundant (e.g. Heithaus *et al*. 2002).

Although *C*. *amboinensis* moved in response to increased freshwater inflow and used areas outside of creek mouth habitat during the wet season, the amount of space individuals used remained consistent. Some predatory fish species have been documented to move greater distances and use more space at times of high freshwater flow (de Morais and Raffray 1999; Scruton *et al*. 2005). Increased movement and home range expansion during the wet season have been attributed to more space being available for use due to rising water levels, and also to individuals needing to move greater distances to locate adequate prey. The fact that habitat is similar throughout the eastern side of Cleveland Bay and space use of *C*. *amboinensis* did not differ between wet and dry seasons suggests that this region provides adequate food resources for this species in both seasons, even when individuals are using areas outside of creek mouth habitat.

Tropical nearshore regions are highly dynamic environments with fluctuating conditions, and are predicted to experience further changes and become more variable owing to factors associated with climate change. In northern Australia, nearshore regions are most vulnerable to changes in rainfall patterns and freshwater inflow, which will alter the habitats, productivity and physical characteristics of these environments (Chin *et al*. 2010). Since *C*. *amboinensis* responds strongly to changes in freshwater inflow, it is likely highly exposed to the effects of altered rainfall and changing salinity levels. Specifically, intensified rainfall and periods of flooding in tropical nearshore regions may result in this species having more sporadic and extreme movements (Chin *et al*. 2010). Uncertainty in future projections of rainfall in tropical nearshore regions presents a concern for species vulnerable to the effects of a changing climate. Defining the response of *C. amboinensis* to highly variable freshwater flow events will help provide a better understanding of species behaviour and responses within a dynamic and changing environment. Thus, these results provide information that will be useful for both river regulation and control in tropical regions and predicting responses in species behaviour as a result of changing climate scenarios.

CHAPTER 6

Habitat Use and Movement of Adult *Carcharhinus sorrah*

6.1 Introduction

Nearshore regions (e.g. bays, lagoons and estuaries) are highly productive environments, supporting a high abundance and rich diversity of species (Blaber *et al*. 1989). Some species use nearshore regions consistently and may occupy specific areas year-round, indicating that these regions provide important habitat for species. For example, consistent presence and use of nearshore regions has been reported in both sharks (e.g. milk shark *Rhizoprionodon acutus*; Simpfendorfer and Milward 1993) and teleosts (e.g. barramundi *Lates calcarifer*; Blaber *et al*. 1989). Long-term and continuous use of nearshore regions demonstrates that species are highly dependent on habitat in these areas. To date, research in nearshore environments has largely been focused on the importance of habitat for aquatic organisms in early life stages and the function of nursery areas for young individuals (e.g. Blaber *et al*. 1995; Beck *et al*. 2001). However, nearshore regions have a range of functions for individuals of a variety of life stages including adults, such as providing foraging grounds and/or breeding habitat (Brewer *et al*. 1995; Pratt and Carrier 2001).

Many shark species, particularly those of smaller-sizes (e.g. Atlantic sharpnose *Rhizoprionodon terraenovae* and bonnethead *Sphyrna tiburo* shark), inhabit nearshore regions for the duration of their life span (see Chapter 2). Unlike larger-bodied species that consistently use nearshore regions as juveniles (e.g. sandbar shark *Carcharhinus plumbeus*), both adult and juvenile individuals of smaller-bodied species are dependent on nearshore habitat (e.g. Heupel *et al*. 2006b). Although some smaller-bodied species are consistent inhabitants of nearshore regions, how they use nearshore habitat remains relatively unclear, particularly for adult individuals. For sharks in adult life stages, habitat use patterns may vary between sexes due to different needs and behavioural strategies when they attain sexual maturity (Sims *et al*. 2001). For example, female leopard sharks *Triakis semifasciata* were found to use warm, shallow habitats for optimising reproductive processes (Hight and Lowe 2007), while male lesser spotted dogfish *Scyliorhinus canicula* were found to use colder, deeper habitats for increasing energetic efficiency (Sims *et al*. 2006). Thus, nearshore regions may serve numerous functions for inhabitants, and understanding how sharks in adult life stages use these environments will be crucial for defining the importance of nearshore habitat for their species.

In this chapter I examine how adult *C*. *sorrah* use nearshore habitats to define their movements within nearshore systems and to determine if differential behaviour occurs between sexes. Based on previous research on *C*. *sorrah* and other smaller-sized coastal shark species (e.g. Stevens *et al*. 2000b; Hight and Lowe 2007), I hypothesised that (1) adult individuals will spend little time in specific areas but will move widely throughout nearshore environments and (2) sexes will use nearshore habitats differently.

6.2 Data analyses

Data collected from acoustic receivers were used to analyse presence, home range and movement patterns of adult *C*. *sorrah* in Cleveland Bay. Locations of monitored *C*. *sorrah* in the study site were estimated every 30 minutes using a mean position algorithm that provided an individual’s centre of activity (COA) (Simpfendorfer *et al*. 2002; see Chapter 4). COA locations represent an individual’s mean position for the set time-step.

6.2.1 Presence

Presence was examined daily, with individuals considered present if two or more detections were heard on any receiver in the study site on a given day. Plots were created to provide a daily timeline to indicate individual presence within the study site. Total number of days monitored (i.e. number of days from first to last detection), total number of days present, number of continuous days present and number of continuous days absent were calculated for each individual to analyse patterns in presence. The ratio between the number of days an individual was present in the study site to the total number of days monitored was calculated to provide a residency index. Residency values range from 0 to 1, with values close to 0 indicating low residence and values close to 1 indicating high residence. Presence data were checked for normality with Quantile-Quantile plots and log(x+1) transformed, if required. One-factor analysis of variance (ANOVA) was used to test for differences in total days monitored, total days present, continuous days present, continuous days absent and residency index between sexes.

6.2.2 Home range

Home ranges of individual *C*. *sorrah* were calculated based on COA estimates using 50% and 95% kernel utilisation distributions (KUDs) with the adehabitat package in R (Calenge 2006; see Chapter 4). Home ranges were calculated at monthly intervals to examine changes in distribution and habitat use over time and were plotted in ArcGIS 9.3.1 (Environmental Systems Research Institute, Redlands, United States) to show spatial and temporal distribution patterns of individual sharks. Home range data were examined for normality with Quantile-Quantile plots and log(x+1) transformed, if required. Three-factor

ANOVA was used to test for differences in 50% and 95% KUDs between sexes, months and sides of the study site individuals used (i.e. east or west). Movements made across the bay (defined as the number of days individuals were detected on both sides of the bay) were also calculated, and a χ^2 goodness-of-fit-test was used to test for differences in the frequency of cross bay movements between sexes.

6.2.3 Habitat use by depth

Depths used were analysed for the monitored individuals in the study site to examine how water depth influenced habitat use of *C. sorrah*. Depth was estimated throughout the study site by calculating a mean depth at each receiver station by hour (See Chapter 4). To calculate mean hourly depths, depth and tidal stage were first recorded simultaneously at each receiver station. The hourly tidal stages were then subtracted from the depth values, providing an estimation of depth at each receiver by hour. Mean hourly depth used was calculated for each individual by averaging the depths at the receivers an individual was detected on in that hour. Depth data were examined for normality with Quantile-Quantile plots and met the assumptions for parametric testing.

Comparisons were made between depths individuals used and depths available within the study site to determine if *C. sorrah* displayed electivity for or avoidance of specific depths using Chesson's α (Chesson 1978):

$$\alpha = (r_i / p_i) / \sum(r_i / p_i)$$

where r_i is the proportion of time an individual spent at depth i in the study site and p_i is the proportion of depth i available in the study site. Values of α can range from 0 to 1, with a value of 1/(number of categories) indicating no electivity or avoidance. Both the available depths in the study site and the depths used were tallied into 50 cm depth categories for all sharks. Tallies of depths that sharks used and those that were available in the study site were converted to proportions and the electivity for each depth category was calculated. Electivity was calculated separately for each sex. Since values of α varied between sexes, values were standardised by subtracting 1/(number of categories).

Summary statistics of the depths used were plotted by month for each sex to investigate temporal patterns in habitat use for *C*. *sorrah*. The ranges of depths used were compared against mean water temperature for each month. Water temperature data for Cleveland Bay was obtained from an Australian Institute of Marine Science hydrographic station (see Chapter 3 Fig. 3.3). To define factors that influenced the depth of habitats used by *C*. *sorrah*, a mixed-effects model was developed using sex and month as factors and individual as a repeated measure. Since females were released on both sides of the study site, the model was run separately for females to test for differences in depths used between individuals using different sides of the study site.

6.3 Results

Twenty-nine *C*. *sorrah* were released with acoustic transmitters in Cleveland Bay from 2009 to 2010. Individuals were released on both sides of the study site in two groups: January to June 2009 (n = 14; 10 female, 4 male) and October 2009 to August 2010 (n = 15; 6 female, 9 male). Nine individuals were either not heard from or had limited detections, and thus were not included in analyses. All remaining individuals (n = 20; 12 female, 8 male) were greater than 950 mm STL and considered sexually mature (Last and

Stevens 2009) (Table 6.1). Size range was 970 to 1270 mm STL for females (mean = 1100 mm) and 950 to 1060 mm STL for males (mean = 1010 mm). *Carcharhinus sorrah* were monitored from March 2009 to November 2010. In 2009, one mortality occurred within the study site as a result of collection in fisheries independent sampling conducted by the James Cook University Fishing and Fisheries Research Centre. This individual was at liberty for 210 days.

6.3.1 Presence

Adult *C. sorrah* were monitored for total periods of 28 to 566 days (mean = 281) and were present within the study site from 8 to 408 days (mean = 185) (Tables 6.1, 6.2). Although long-term presence in the study site was common, residency index was variable ranging from 0.08 to 0.96 (mean = 0.64). Males generally had a lower residency index than females (Table 6.2), indicating that they were out of detection range or used areas outside of the study site more often. However, there were no significant differences in residency index ($F_{1,18} = 3.78$, $p = 0.068$), total days present ($F_{1,18} = 0.87$, $p = 0.363$) or total days monitored ($F_{1,18} = 0.36$, $p = 0.557$) by sex. Continuous days present in the study site ranged from 1 to 121 days (mean = 8.9) and when individuals left the study site they were absent for 1 to 73 continuous days (mean = 4.6) before returning (Table 6.2). There were no significant differences in continuous days present between sexes ($F_{1,424} = 0.07$, $p = 0.788$), however, there were differences in continuous days absent ($F_{1,401} = 14.01$, $p < 0.001$). When males left the study site they remained absent for a longer period of time (mean = 5.8 days) when compared to females (mean = 3.9 days).

6.3.2. Home range

Analyses of home range revealed that most adult *C. sorrah* tended to use only one side of Cleveland Bay (Fig. 6.1), which was the side of the bay they were captured and released

Table 6.1 Tagging information for *C. sorrah* monitored in Cleveland Bay from 2009 to 2010 including date tagged, side of the bay individuals were captured/released on, stretch total length, sex and total days monitored. *individuals still present at the end of the monitoring period (31/10/2010).

ID	Date tagged	Side of release	Stretch total length (mm)	Sex	Total days monitored
3397	08/01/2009	east	1100	F	468
3455	31/03/2009	east	1050	F	185
3459	02/04/2009	east	970	F	437
3396*	14/04/2009	west	1040	F	566
3439	14/04/2009	west	1070	F	316
3458	24/04/2009	east	1060	M	347
56292	24/04/2009	east	1050	M	144
56295*	24/04/2009	east	1070	F	556
56293	20/05/2009	east	980	F	507
56294*	23/06/2009	east	1060	M	483
56305*	27/10/2009	east	1040	M	369
56307	27/10/2009	east	950	M	33
56308*	27/10/2009	east	1050	M	370
3455a	16/02/2010	east	950	M	28
56301*	09/04/2010	east	1020	M	206
56303*	21/05/2010	east	1150	F	164
56297*	21/05/2010	east	1260	F	164
56306*	25/05/2010	west	1150	F	136
63636*	24/08/2010	west	970	F	69
56296*	24/08/2010	west	1270	F	68

Table 6.2 Presence of *C. sorrah* in Cleveland Bay. Summary includes total days present, continuous days present, continuous days absent and residency index by sex. Brackets are standard errors.

		Total Days Present			Continuous Days Present			Continuous Days Absent			Residency Index		
Sex	n	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean
F	12	27	408	207 (36)	1	121	9.0 (0.9)	1	73	3.9 (0.4)	0.39	0.95	0.72 (0.06)
M	8	8	326	153 (46)	1	102	8.6 (1.2)	1	48	5.8 (0.7)	0.08	0.90	0.52 (0.10)

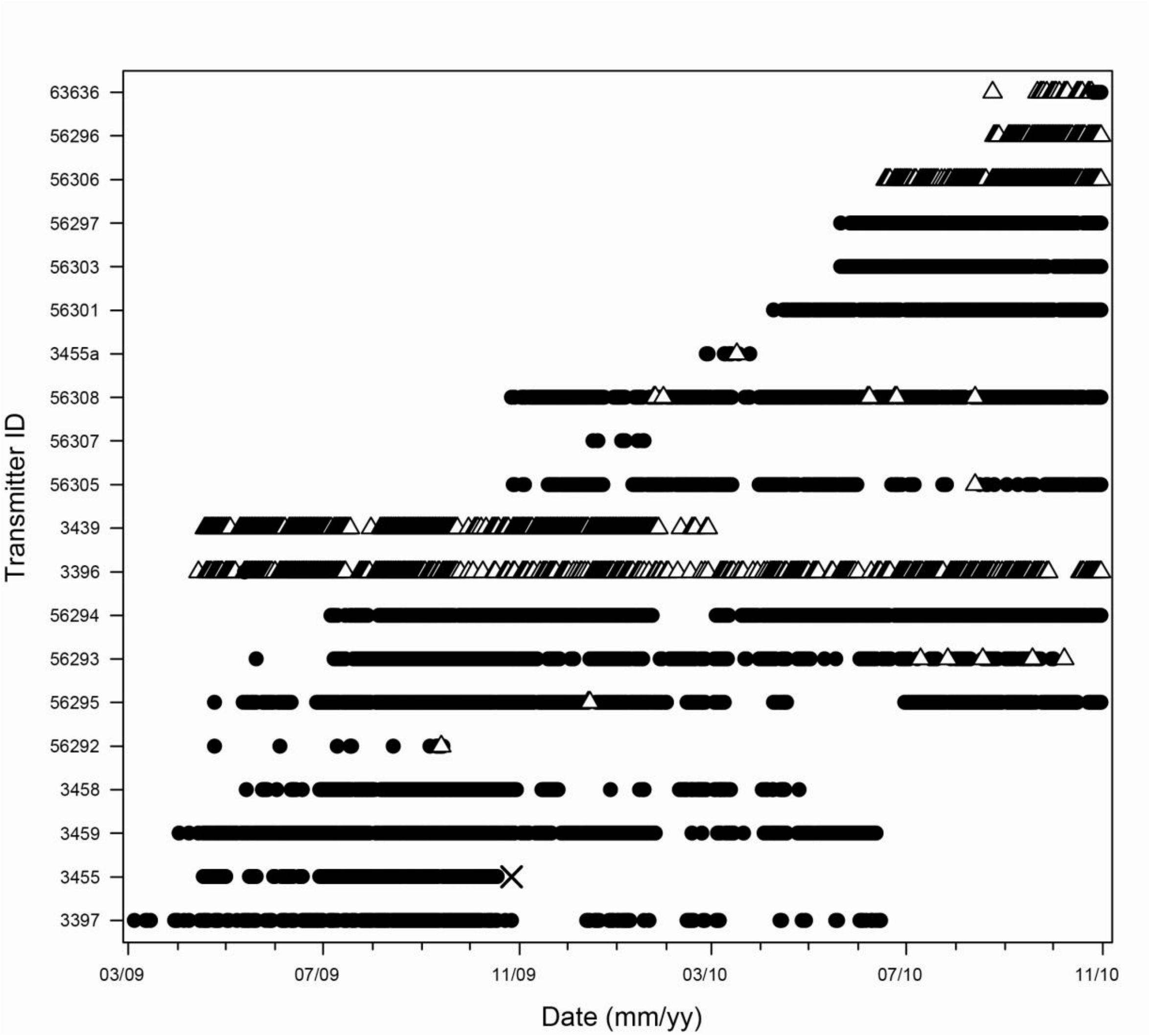

Fig. 6.1 Presence plot of *C. sorrah* in Cleveland Bay by day. Symbols represent days detected on the eastern array (●), western array (Δ) and days when individuals were removed by fishers (X).

on. Less than half of the monitored individuals (40%) undertook movements across the bay, of which 62.5% were males and 37.5% were females. There was a significant difference in the number of cross bay movements between sexes ($\chi^2 = 6.25$, $p = 0.012$), with males moving across more commonly than females. However, cross bay movements were rare and short in duration for all individuals. Home ranges of *C. sorrah* remained consistent in Cleveland Bay, with individuals using the same areas across consecutive months (Fig. 6.2). However, a high degree of segregation occurred between individuals due to use of different sides of the bay. This spatial segregation and use of different areas resulted in variation in the types of habitat used.

Monthly 50% KUDs ranged from 0.01 to 20.43 km^2 (mean = 9.08 km^2) and monthly 95% KUDs ranged from 0.01 to 78.02 km^2 (mean = 39.83 km^2) (Fig. 6.3). There were no significant differences based on sex for 50% ($F_{1,131} = 2.17$, $p = 0.143$) or 95% ($F_{1,131} = 2.35$, $p = 0.128$) KUDs. Month was also not a significant factor for either 50% or 95% KUDs (50%: $F_{19,131} = 0.97$, $p = 0.500$; 95%: $F_{19,131} = 1.09$, $p = 0.367$), however, a significant difference between sides of the study site was present for both KUD measures (50%: $F_{1,131} = 4.65$, $p = 0.033$; 95%: $F_{1,131} = 10.42$, $p = 0.002$). Individuals using the eastern side of the bay had larger home ranges than those using the western side (Fig. 6.3). Mean monthly 95% KUDs ranged from 30.66 to 51.20 km^2 (mean = 42.36 km^2) for the eastern side of the bay and 19.64 to 40.69 km^2 (mean = 31.93 km^2) for the western side. Mean monthly 50% KUDs were also typically larger on the eastern side of the bay and ranged from 6.77 to 11.67 km^2 (mean = 9.58 km^2) when compared to those on the western side that ranged from 3.65 to 11.23 km^2 (mean = 7.61 km^2).

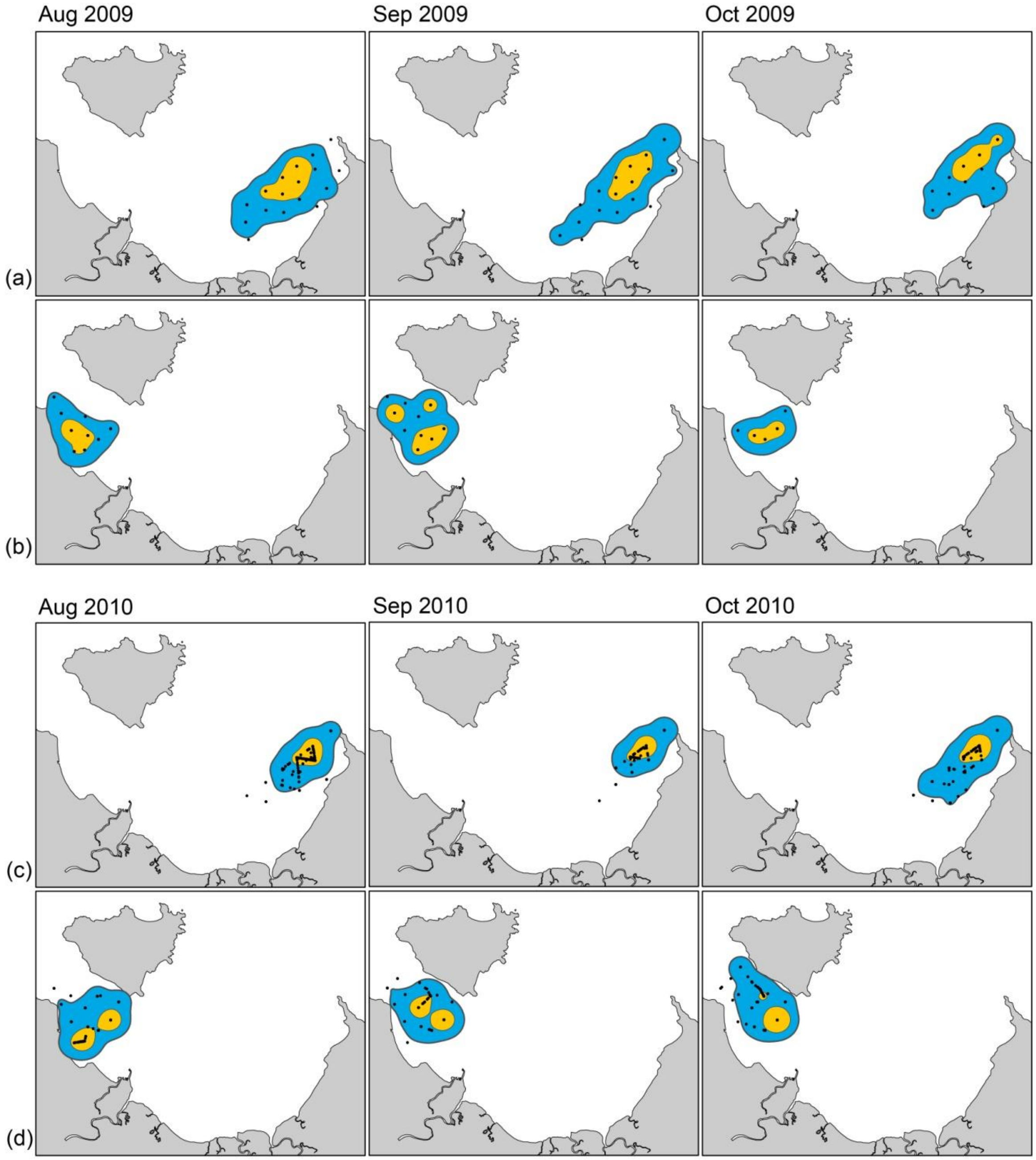

Fig. 6.2 Representative monthly home ranges of four *C. sorrah* over three consecutive months of August, September and October. Panels include two individuals released in 2009 (a,b) and two individuals released in 2010 (c,d). Blue fill: 95% KUDs, yellow fill: 50% KUDs, black dots: COA locations used to calculate home ranges.

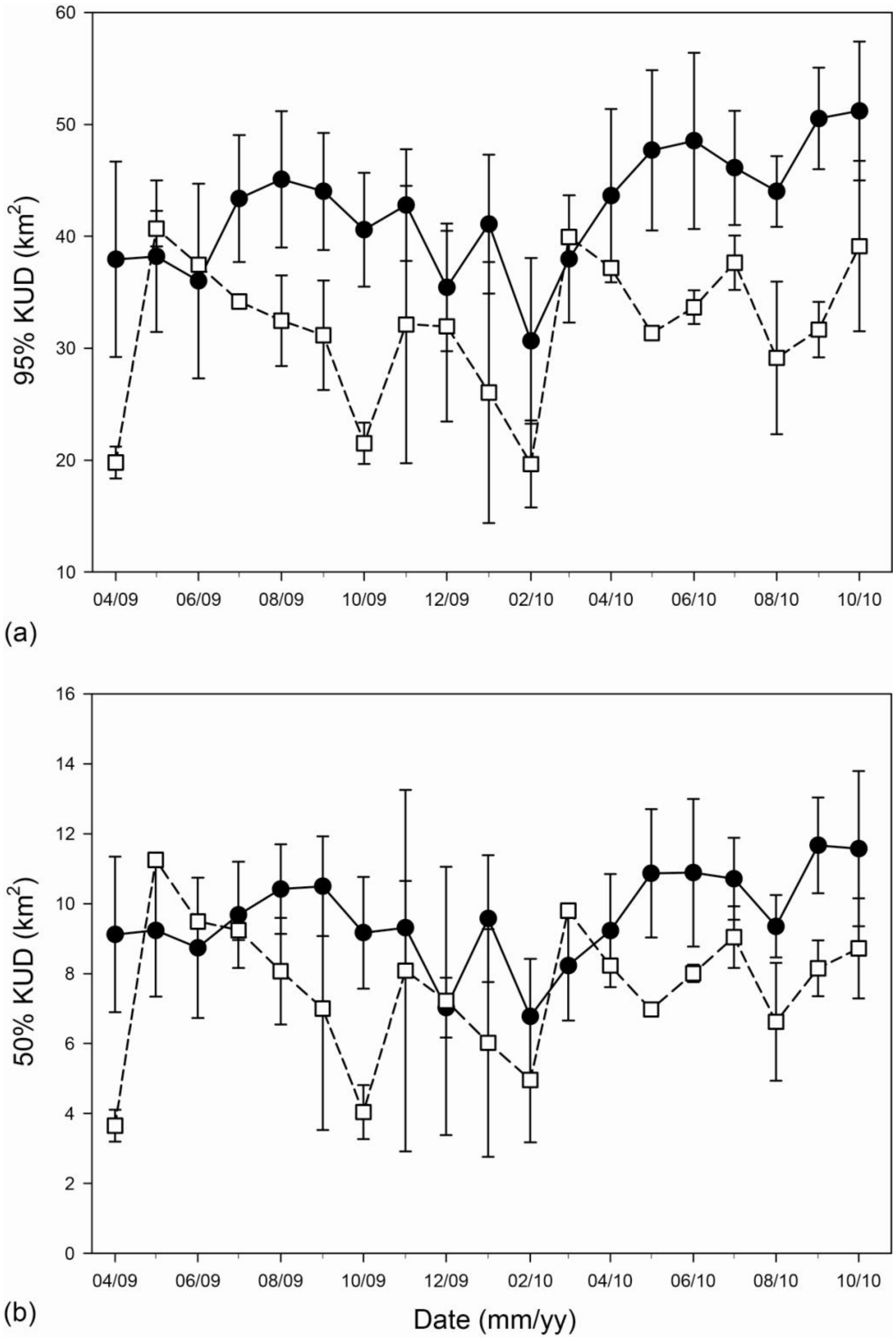

Fig. 6.3 Mean monthly home ranges with standard errors for *C. sorrah* using the eastern side of the bay (● and solid line) and western side of the bay (□ and dashed line) calculated with 95% KUDs (a) and 50% KUDs (b).

6.3.3 Habitat use by depth

Approximately 40% of the depth available in the study site was between 350 and 550 cm but *C*. *sorrah* used available depths disproportionately, with both males and females heavily using this range for 70% and 50% of their time, respectively (Fig. 6.4a). Females tended to use shallower depths more often than males and each sex spent about 20% and 5% of their time, respectively, in depths less than 300 cm. There was no significant difference in depths used based on side of the study site for females ($F_{1,10}$ = 3.55, p = 0.089), so all females were pooled for depth analyses. Electivity analysis confirmed that *C*. *sorrah* had affinities for different depths based on sex (Fig. 6.4b). Affinity of females increased quickly until 200 cm, peaked around 550 cm but remained on a plateau between 450 and 700 cm. Affinity of males, however, did not begin to increase until 250 cm, peaked at 450 cm and decreased until about 680 cm at which point individuals displayed an avoidance of deeper depths. Thus, depths used by *C*. *sorrah* varied among sexes, with males having an affinity for a narrower overall depth range than females.

Further analysis of habitat use by depth revealed different patterns across months by sex. Females inhabited shallower depths during the winter months when water temperature was coldest and deeper depths during warmer summer months (Fig. 6.5a). Males did not show any seasonal pattern and consistently remained within a narrow depth range regardless of month or changes in water temperature (Fig. 6.5b). Results of a repeated measures mixed-effects model showed that the range of depths used was not significantly different based on sex ($F_{1,18}$ = 1.39, p = 0.254), however, there was a significant difference based on month ($F_{16,34782}$ = 88.89, p < 0.001) and a significant interaction between sex and month ($F_{16,34782}$ = 23.44, p < 0.001). The interaction between sex and month revealed that mean monthly depths were shallower for females than males during all months, except January to March (summer) when females moved to deeper water (Fig. 6.6). Mean

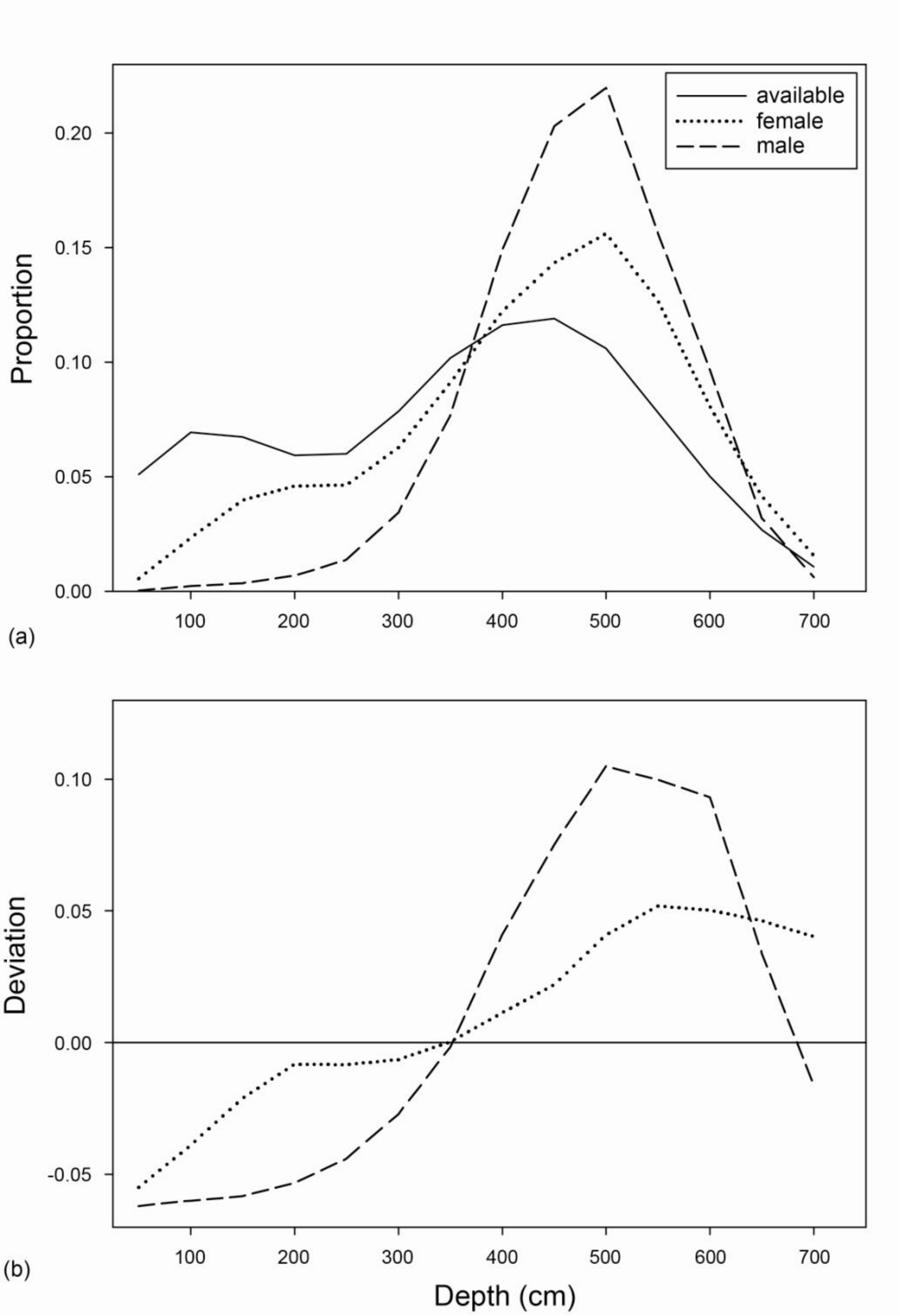

Fig. 6.4 Proportion of available depths in Cleveland Bay (solid line) and proportion of depths used by female (dotted line) and male (dashed line) *C. sorrah* (a). Electivity analysis of depth for female (dotted line) and male (dashed line) *C. sorrah*. Values above zero indicate affinity (b).

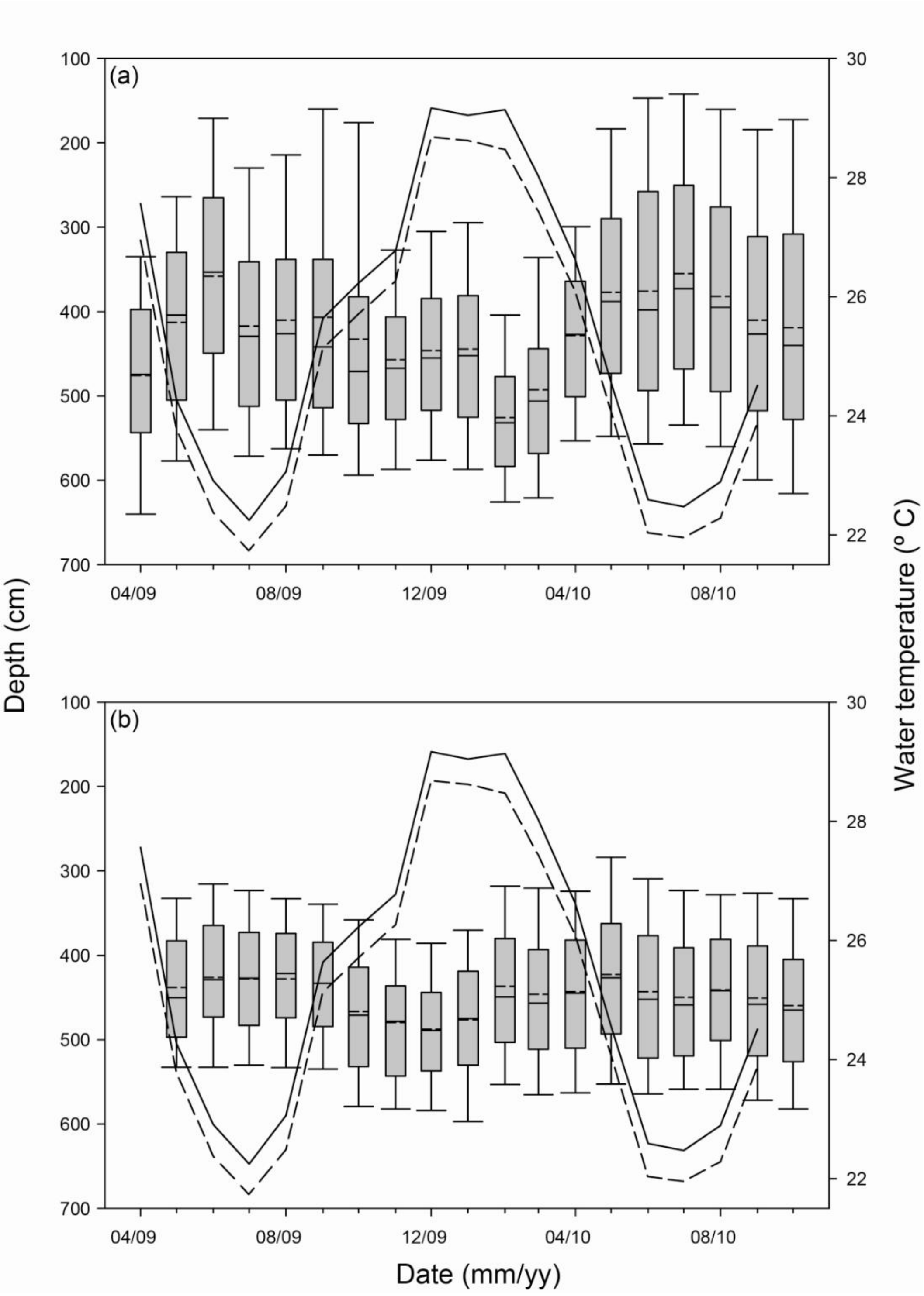

Fig 6.5 Boxplots showing range of depths used by female (a) and male (b) *C. sorrah* in Cleveland Bay by month in relation to water temperature at two depth strata (solid line: 190 cm, dashed line: 850 cm). Boxes are 10th and 90th percentiles (whiskers), 25th and 75th percentiles (boxes), mean (dashed line) and median (solid line).

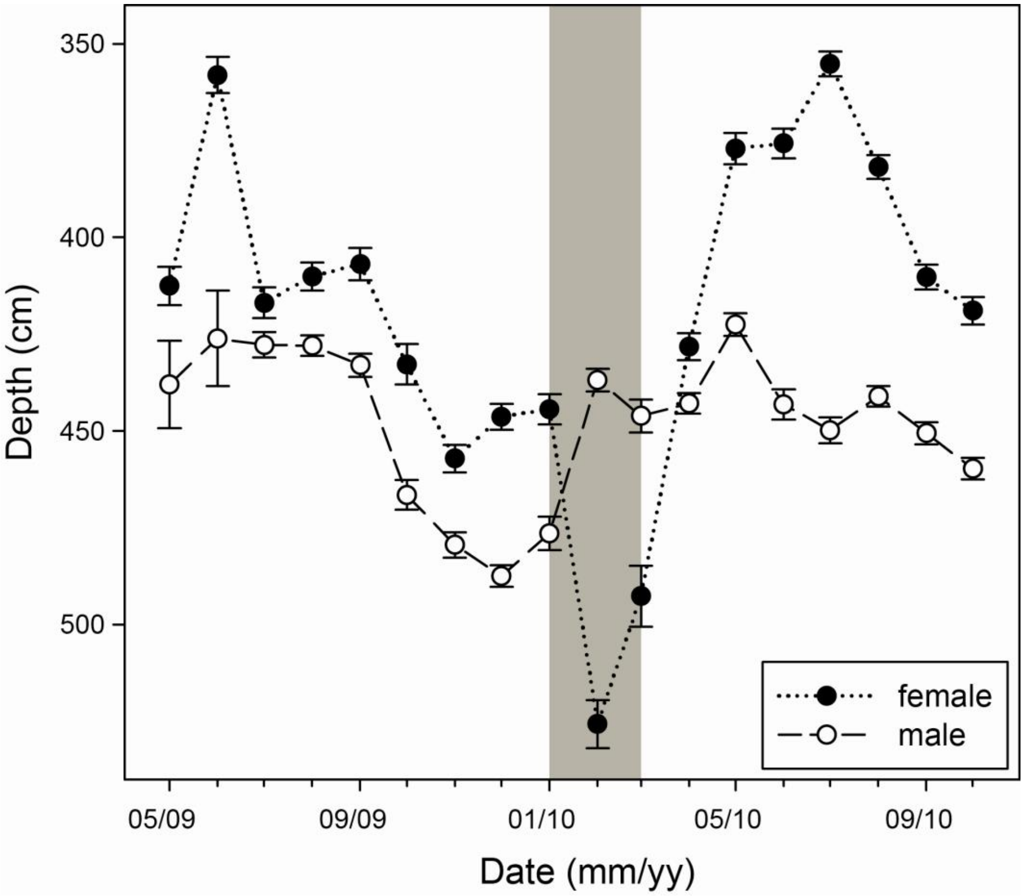

Fig. 6.6 Interaction plot with standard errors of mean monthly depths used by female (● and dotted line) and male (○ and dashed line) *C. sorrah*. Grey shading indicates months when females used deeper depths than males.

monthly depths used varied by as much as 200 cm between summer and winter months for females. In contrast, mean monthly depths used by males varied by just 50 cm between months. Data showed that water temperature varied by as much as 4º C between shallow (190 cm) and deeper (850 cm) habitats in Cleveland Bay, suggesting that water temperature may be a factor influencing the location of female *C*. *sorrah*.

6.4 Discussion

Adult *C*. *sorrah* had high levels of residency in Cleveland Bay, with individuals displaying long-term presence in the study site over the two year monitoring period. Individuals remained in the study site for as long as 121 consecutive days, with both sexes present for long periods and some individuals remaining in the region for more than 18 months. Long-term presence and consistent use of this nearshore environment was unexpected as smaller-bodied shark species have generally been reported to move widely and show limited attachment to specific nearshore areas (see Chapter 2). For example, *R*. *terraenovae* had wide-ranging movements and spent short periods within a nearshore environment, often moving throughout deeper water habitats (Carlson *et al*. 2008). Since smaller-bodied species have relatively productive life history strategies (e.g. early maturity, annual reproduction, etc.), moving widely and using additional habitats may benefit these species by increasing foraging success and promoting fast growth (see Chapter 2). Although not as common, long-term use of a nearshore region has been reported in adult individuals of some other smaller-bodied shark species. For example, adult female *T*. *semifasciata* remained in a California estuary for up to 229 days (Carlisle and Starr 2009). The authors attributed this high residency in part to foraging due to the high productivity of that region (Carlisle and Starr 2009). Long-term presence of adult *C*.

sorrah in Cleveland Bay suggests that these individuals acquire sufficient resources, and perhaps additional benefits (e.g. shelter from larger predators), by remaining in this nearshore region.

Although many *C*. *sorrah* showed a high degree of residency in Cleveland Bay, there was variation in presence among individuals. For example, some individuals used the region intermittently or irregularly, remaining in the study site for shorter periods (i.e. 8 days) or leaving for longer consecutive periods (i.e. 73 days). Shorter periods of presence may represent individuals with a more transient movement behaviour. These *C*. *sorrah* may be moving between different regions to use additional habitats, acquire mates and/or exploit prey resources. Variation in presence and residency among *C*. *sorrah* individuals in this study supports previous research that found there was sufficient movement of *C*. *sorrah* between regions to prevent genetically distinct populations (Lavery and Shaklee 1989). Similar variability in presence and residency has been reported in both shark and teleost species, such as the white stumpnose *Rhabdosargus globiceps* (Kerwath *et al*. 2009) and *R*. *terraenovae* (Carlson *et al*. 2008), with individuals spending different periods of time in nearshore regions.

Movements of *C*. *sorrah* were generally restricted to one side of Cleveland Bay, which was the side they were captured and released on, with few individuals making movements across the bay. The majority of individuals that moved across the bay were male, suggesting that males may move more widely than females. Adult males may have wider ranging movements to acquire additional mates, whereas females may use more discrete areas to remain in regions where they give birth (e.g. Keeney *et al*. 2005; DiBattista *et al*. 2008). However, for both sexes, extended movements across the bay were typically rare. A tagging study in northern Australia reported similar localised movements for *C*. *sorrah*, with half of recaptured individuals caught within 50 km of the original release location (Stevens *et al*. 2000b). Localised movements within a consistent area of Cleveland Bay resulted in a high level of segregation among individuals. In addition, habitat type between the two sides of Cleveland Bay varied, with the western side consisting of reef flats and sand and the eastern side of mud flats and seagrass. *Carcharhinus sorrah* is a species associated with muddy substrates, as well as with coral reefs (Last and Stevens 2009), and Cleveland Bay provides both of these habitats types. However, by using restricted areas individuals associated with only one of these habitat types within Cleveland Bay. Habitat use has been explored in other shark species, but unlike *C*. *sorrah*, most species have generally been found to associate strongly with one type of habitat. For example, tiger sharks *Galeocerdo cuvier* preferred shallow seagrass habitat in a nearshore region where their prey was most abundant (Heithaus *et al*. 2002) and juvenile lemon sharks *Negaprion brevirostris* preferentially used shallow areas with rock and sand substrates to avoid predators (Morrissey and Gruber 1993b). Variation in habitat use has been reported in some teleosts, with species associating with coral reef habitat, as well as seagrass and sand habitat (Jenkins and Wheatley 1998; Gomelyuk, 2009).

There is no diet information available for *C*. *sorrah* in this region, but research in northern Australia found that this species feeds predominantly on teleost fish, and cephalopods and crustaceans to a lesser extent (Stevens and Wiley 1986). Although it is possible that prey distribution varied between the two sides of Cleveland Bay, *C*. *sorrah* likely received adequate resources in both habitats due to the extensive use and high levels of attachment displayed on each side of the bay. Thus, spatial segregation and variation in habitat use may be a strategy to access additional resources, reduce overlap between individuals and decrease intraspecific competition. Although within species segregation is not commonly reported, habitat partitioning has been found to occur between species using the same nearshore regions in both sharks (White and Potter 2004) and teleosts (Malavasi *et al*. 2007), presumably to decrease competition. Since *C*. *sorrah* were not restricted by habitat type, individuals were able to distribute themselves across larger overall areas in Cleveland Bay. Being attached to one specific area and having localised movements thus reduced overlap between individuals, which may increase foraging efficiency and species success in this nearshore environment.

Home range sizes of *C*. *sorrah* were consistent, with little variation between months, indicating that individuals used the same amount of space over time. This result is unlike that found in juvenile *C*. *amboinensis* monitored in the same region (see Chapter 4). Home ranges of these individuals fluctuated between months (see Chapter 4) based on changes in freshwater inflow during the monsoonal wet season (see Chapter 5). Unlike *C*. *amboinensis*, *C*. *sorrah* used areas away from river habitat, so they were likely less influenced by freshwater flow dynamics. There was, however, a significant difference in home range sizes between *C*. *sorrah* using different sides of Cleveland Bay, with individuals on the western side generally having smaller core and total home ranges than individuals on the eastern side. This was in part due to the different sizes of the arrays. Since a smaller area was monitored on the western side of the bay, individuals may have used additional area outside of that array. In addition, individuals using the western side of the bay were more spatially restricted than individuals using the eastern side as their movements were limited by both Magnetic Island and the mainland. Thus, space limitations may have restricted home range sizes of *C*. *sorrah*, resulting in individuals on the western side of the bay using smaller spaces overall. However, home range sizes of *C*. *sorrah* were comparable to those reported for other coastal sharks of similar body sizes, such as *S*. *tiburo* (0.042-96.88 km^2; Heupel *et al*. 2006b) and *C*. *amboinensis* (3.96-101.05 km^2: see Chapter 4).

The depth of habitat *C. sorrah* used was disproportionate to that available in the study site, with individuals showing greatest affinity for deeper depths (i.e. > 400 cm). Cleveland Bay is used by multiple shark species including juveniles that inhabit shallow water habitats as refuge and nursery areas (Simpfendorfer and Milward 1993), as well as larger adults (Simpfendorfer 1993). Thus, using a deeper depth range within this nearshore environment may be a strategy among adult *C. sorrah* to reduce competition with those species that use shallower areas. For example, juvenile *C. amboinensis* restricted their movements to shallow water habitats in Cleveland Bay and showed greatest affinity for depths less than 300 cm (see Chapter 4). Juvenile *C. sorrah* also inhabit Cleveland Bay, however, their distribution is more variable and young individuals are encountered in both shallow and deeper water regions (D. M Knip, unpublished data). However, by using deeper water adult *C. sorrah* may decrease competition with juvenile conspecifics that use shallower habitats, which may increase survival of young individuals. Prey distribution may also be a factor affecting the depth of habitat used by *C. sorrah*, and prey has been found to influence the depth of habitat used in other smaller-bodied sharks. For example, in some areas along the California coast *T. semifasciata* used deeper habitats more often than all other available habitats due to prey distribution (Carlisle and Starr 2009). Thus, it may be a combination of competition and prey distribution that influences the depth of habitat adult *C. sorrah* use in Cleveland Bay.

Examining habitat use of adult *C. sorrah* over time revealed seasonal patterns in the range of depths used and differential behaviour based on sex. Females used shallow water habitats more often than males and also displayed an affinity for a larger overall depth range. Specifically, the range of depths females used shifted, with individuals using shallower water in the winter and deeper water in the summer. Using shallow areas may be a mechanism among females to reduce overlap with males inhabiting the same region, as reported for the nurse shark *Ginglymostoma cirratum* (Pratt and Carrier 2001) and *S. canicula* (Sims *et al*. 2001). In these studies, females used shallow habitats as a strategy for avoiding aggressive males during the mating season and/or limiting multiple matings to conserve energy (Pratt and Carrier 2001; Sims *et al*. 2001). *Carcharhinus sorrah* has annual reproduction (Last and Stevens 2009) and in Queensland females pup in the summer (around December), mate immediately afterward and are pregnant again by March (A. V. Harry, personal communication). Since the mating season for *C. sorrah* coincided with the time females used deeper habitats, it is unlikely that their use of shallow habitats was to avoid mating with males. Rather, it is possible that using shallow habitats played another role for these females, such as decreasing competition with males and/or optimising physiological processes.

The temperature in aquatic environments is generally higher in shallow water than in deeper water, and in Cleveland Bay temperature was as much as 4º C higher in shallow (190 cm) than in deeper (850 cm) areas. Since females moved into shallow water habitats in the winter, they were using areas where water temperature was highest during the coldest months of the year. Thus, this shift in depth used may be evidence for behavioural thermoregulation in this species. Preferential use of shallow habitats where water temperature is higher may be a strategy among sexually mature female *C. sorrah* to optimise physiological processes, such as increasing body temperature to speed gestation. Changes in body temperature can alter the rate of many physiological processes (Johnston and Bennett 1996) and Wallman and Bennett (2006) found that a 1º C increase in pregnant female Atlantic stingrays *Dasyatis sabina* reduced gestation time by as much as ten days. The fact that adult male *C. sorrah* did not demonstrate the same shift in depth provides further support for females using behavioural thermoregulation as a gestation strategy. Behavioural thermoregulation has also been identified as a potential strategy for facilitating growth rates (Ward *et al*. 2010). In many shark species, fecundity of females increases with body size (Cortés 2000). Litter sizes of *C*. *sorrah* range from 3 to 8 pups (Last and Stevens 2009) and in the Queensland region the largest females produce the most pups (A. V. Harry, personal communication). Evidence for behavioural thermoregulation has been reported in sexually mature females of other shark species including *T*. *semifasciata* (Hight and Lowe 2007) and the grey reef shark *Carcharhinus amblyrhynchos* (Economakis and Lobel 1998). Both species used warm, shallow water habitats to increase body temperature, which the authors suggested as a strategy to increase growth and/or embryonic development (Economakis and Lobel 1998; Hight and Lowe 2007). However, there are also implications associated with using warmer water, such as increased metabolic costs and energetic losses. A trade-off exists, with individuals using warm, shallow water increasing physiological processes and those using cooler, deeper water conserving energy (e.g. Sims *et al*. 2006). These results indicate that it is beneficial for female *C*. *sorrah* to use shallow water during the winter, but that it is likely too costly during the summer when water temperature is highest. Female *C*. *sorrah* may move into deeper water in the summer for other functions (e.g. mating or foraging) but they may also move to reduce metabolic costs and increase survival. For species like *C*. *sorrah* that have annual reproduction, using strategies to speed gestation would be highly advantageous as it would allow more time and energy for other functions, such as feeding and growth.

Use of discrete areas in shallow nearshore environments has most commonly been reported for sharks in early life stages (e.g. Wetherbee *et al*. 2001; Heupel *et al*. 2004), generally as a species strategy to increase survival of young (Branstetter 1990). Documenting sexually mature male and female *C*. *sorrah* using discrete areas in a coastal bay for long periods demonstrates that nearshore regions also play an important role for sharks in adult life stages. Consistency in home ranges and high attachment to core areas suggest that nearshore environments provide crucial habitat for adult *C*. *sorrah*. However, high site attachment also implies that individuals do not disperse or undertake extensive movements to different regions, which would make this species susceptible to depletion within localised areas. Although further research is needed to ascertain whether *C*. *sorrah* have similar habitat use patterns in other nearshore regions, these results indicate that this species may benefit from local management approaches, which would prevent population level depletion. Defining use of nearshore habitats and movement patterns of *C*. *sorrah* therefore provides useful information for the effective management of their populations.

CHAPTER 7

Evaluating the Effectiveness of Marine Protected Areas for Sharks

7.1 Introduction

Sharks are among the most threatened groups of species in the world (Myers *et al.* 2007) and are at risk due to fisheries and increasingly the loss and degradation of coastal habitats (Stevens *et al*. 2000a; Jackson *et al*. 2001). Global declines in shark populations have created uncertainty in the future status of many of these species (Baum *et al*. 2003). Conservation is needed, but due to the broad distribution, high mobility and migratory nature of sharks it is often difficult to define an effective approach. Understanding how protective measures can be implemented for sharks will be crucial for the persistence of their populations, and to date most effort has been focused on creating and improving existing fisheries management frameworks (e.g. Musick *et al*. 2000; Barker and Schluessel 2005).

Over the years, marine protected areas (MPAs) have been strongly advocated and widely used as both conservation and management tools for sheltering vulnerable species and habitat from exploitation (Agardy 1997; Sobel and Dahlgren 2004). Although the full potential of MPAs is still far from completely understood, there is overwhelming evidence of the benefits they provide to the marine environment (e.g. Shears *et al*. 2006; Russ and Alcala 2011). MPAs are an effective tool in fisheries management by increasing the yield of targeted species through spillover from protected areas to fished areas (Russ and Alcala 1996; Roberts *et al.* 2001; Hilborn *et al.* 2004). There are also fisheries benefits associated with MPAs established for conservation purposes (Gell and Roberts 2003) and many non-target species benefit from protection through restoration of important habitat and reduction in bycatch (Dayton *et al.* 1995; Allison *et al.* 1998). Due to the urgent need for protection in exploited marine environments, many MPAs have been implemented opportunistically without prior knowledge or insight into how they will function (Roberts 2000). However, evaluating the effectiveness of MPAs is essential for increasing and maximising their conservation potential (McNeill 1994).

MPAs have generally been thought to be most effective at protecting sedentary and sessile species, as any benefits resulting from protection will diminish once animals move outside MPA boundaries (DeMartini 1993; Bonfil 1999; Sale *et al.* 2005). However, recent studies have revealed that mobile species with large ranges can benefit from MPAs. For example, Kerwath *et al*. (2009) determined that a small coastal MPA provided a mobile teleost species some protection from fishing pressure, and Claudet *et al*. (2010) found that MPA protection was similar for mobile and sedentary species. Designing MPAs to specifically benefit mobile species requires sound knowledge of their biology, movement and habitat use to understand how behaviour will affect MPA function (Kramer and Chapman 1999; Roberts 2000). Strategically placing MPAs in areas that mobile species use consistently (e.g. spawning grounds or nursery areas) may offer protection to populations and reduce fishing mortality (Heupel and Simpfendorfer 2005; Meyer *et al.* 2007), but research to this effect is limited. The goal to increase global coverage of the world's MPAs by at least six-fold over the next few years (Wood *et al.* 2008) presents an opportunity to implement protection for exploited species, but it is unclear how increased MPA regions will benefit mobile species.

Conservation initiatives have employed the use of MPAs worldwide to protect exploited species and habitat, but knowledge of the conservation benefits they provide for shark populations remains limited. In this chapter I assess the effectiveness of MPAs for protecting sharks by defining the movements of *C*. *amboinensis* and *C*. *sorrah* within MPA regions. The main objective was to quantify the level of MPA protection afforded to sharks by determining the amount of time individuals spend inside MPAs and the number of times boundaries are crossed. I hypothesised that although mobile, sharks will receive protection from exploitation (e.g. fishing pressure) by remaining inside MPA boundaries, and thus gain conservation benefits from MPAs.

7.2 MPA study site and shark species

The Great Barrier Reef Marine Park (GBRMP) was rezoned in 2003 for the purpose of protecting a wider range of habitat regions, with no prior knowledge of how the zoning scheme would benefit inhabitants of these regions (Fernandes *et al*. 2005). Thus, Cleveland Bay provides an ideal system for evaluating the effectiveness of recently implemented protection zones within one of the largest networks of MPAs in the world. There are two Conservation Park (CP) zones in Cleveland Bay (Fig. 7.1). These CP zones cover an area of about 140 km^2 and there are strict fishing restrictions in these regions. Trawling and netting (bait netting excluded) are prohibited and line fishing is limited to one line per person and one hook per line. Although some line fishing occurs in these zones, fishers do not target sharks and if captured > 95% are released alive (Lynch *et al*. 2010). Thus, CP zones were considered as MPAs for shark species. Fifty-five acoustic receivers deployed throughout the two CP zones in Cleveland Bay monitored sharks inside MPAs.

From December 2008 to November 2010, data was collected from 37 *C*. *amboinensis* (2009 = 17, 2010 = 20) and 20 *C*. *sorrah* (2009 = 10, 2010 = 10) (see Chapters 4 and 6).

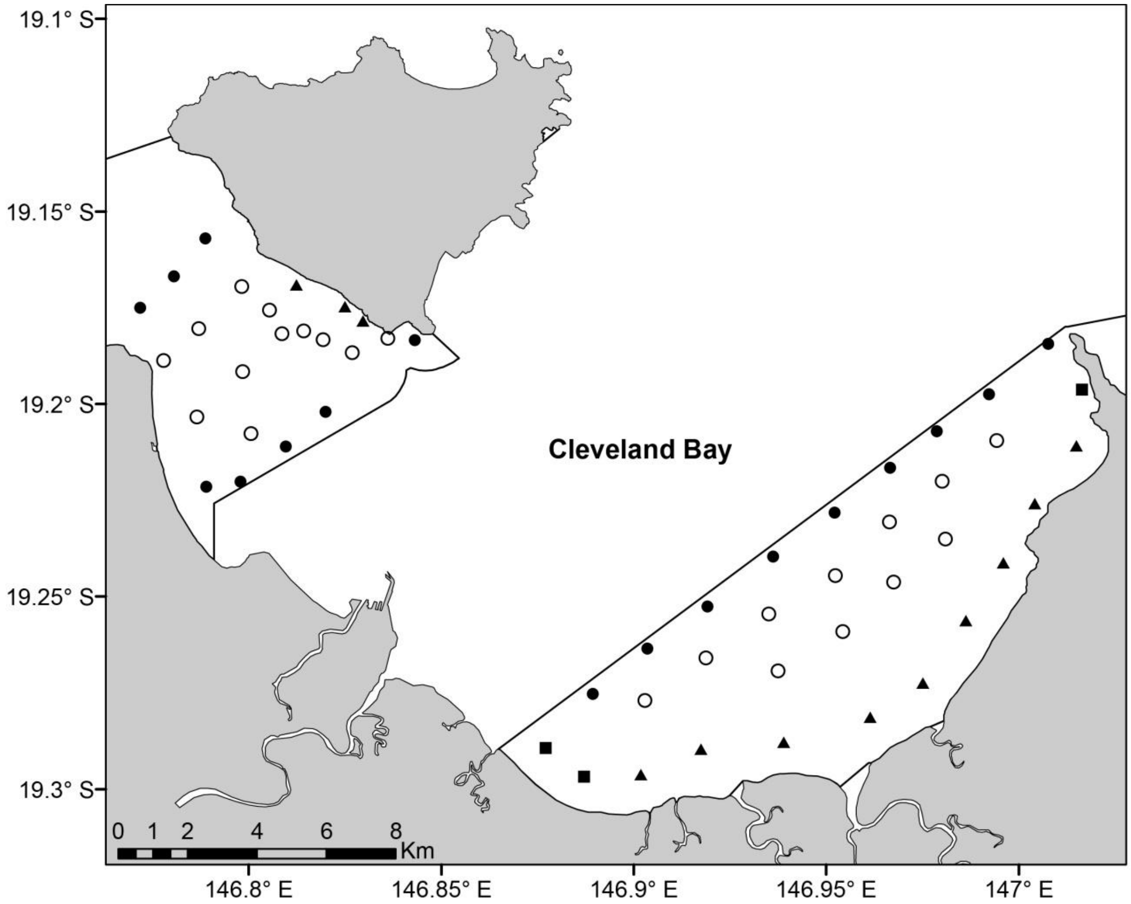

Fig. 7.1 Cleveland Bay. Solid lines indicate boundaries of Conservation Park zones. Symbols are locations of acoustic receivers deployed inside MPAs and classified as edge deep (●), edge shallow (■), inner deep (○) and inner shallow (▲).

Carcharhinus amboinensis consisted of juveniles from three age classes (i.e. young-of-the-year, one-year-olds and two-year-olds) and individuals ranged from 690 to 1290 mm stretch total length (STL). *Carcharhinus sorrah* were all adult individuals, with sizes ranging from 970 to 1270 mm STL for females and 950 to 1060 mm STL for males.

7.3 Data analyses

Detection data from the acoustic receivers were analysed to define when sharks were inside or outside the CP zones (hereafter referred to as MPAs). However, since all acoustic receivers were placed in the MPAs, detections only indicated when sharks were inside MPAs. Therefore, a method was developed for estimating when sharks exited the MPAs. A two-step approach was used: (1) a maximum period of non-detection was calculated from the detection data to estimate the time when sharks were determined to have exited the MPAs (referred to as ‘exit time’) and (2) the exit time was then applied to the entire detection data set to identify when sharks were outside the MPAs.

To estimate the exit time (i.e. the period of non-detection that indicated an individual had exited the MPA), the interval between all detections was calculated for each shark. These intervals defined the amount of time it took for a shark to depart one receiver and be detected by another. The longer the interval between detections, the more likely the shark had exited the MPA. Next, the receivers were given a classification depending on their location in the MPAs. Receivers along the outer boundaries were classified as ‘edge deep’ or ‘edge shallow’ and receivers along the inside of the edge lines were classified as ‘inner deep’ or ‘inner shallow’ (Fig. 7.1). Deep receivers were located where they remained submerged at all tidal stages, while shallow receivers were in the intertidal zone and dried at < 80 cm tidal height. Using this receiver classification a subset was taken from the detection data, which included the intervals between detections when sharks departed inner deep receivers. Thus, these intervals were the amount of time it took a shark to depart an inner deep receiver and be detected by any other receiver. Only data from the inner deep receivers were used to estimate the exit time, as a long non-detection period after a shark departed an edge receiver meant it had probably exited. In addition, a long non-detection period after a shark departed a shallow receiver meant it could still be inside the MPA, but using shallow water out of receiver detection range. Thus, the inner deep receivers provided the most reliable interval between detections. The 95th percentile of the detection data subset was used as the exit time for each shark. A mean exit time, weighted by the number of data points of each individual, was calculated for each species and MPA (i.e. east or west).

To define when sharks were outside MPAs, the exit time was applied to the entire detection data set for each individual shark. Specifically, each time a shark departed a receiver it was defined as either inside or outside the MPAs by comparing the exit time to both the period between detections and receiver classification. For edge deep receivers, individuals were defined as outside when the period between detections was greater than the exit time. However, it was also possible for individuals to depart the MPA without being detected on the boundary receivers. Thus, for edge shallow and inner deep receivers, individuals were defined as outside when the period between detections was greater than twice the exit time. In all other instances, individuals were considered to be inside the MPAs.

For the following data analyses, differences between sexes were tested for in *C. sorrah* as all individuals were sexually mature. In addition, since *C. sorrah* used both MPAs (i.e. east and west), differences between MPAs were tested for in this species to determine if the two MPAs performed differently.

7.3.1 Time spent inside MPAs

To calculate the total amount of time spent inside MPAs, the intervals when sharks were classified as inside the MPAs were summed. For each individual shark, the time spent inside was divided by the total time monitored (first detection to last) to determine the proportion of time spent in MPAs. Proportion of time inside was also calculated by month for each species to define seasonal changes in MPA use. Proportion of time was examined for normality with Quantile-Quantile plots and $\sin^{-1}\sqrt{x}$ transformed. A *t*-test was used to test for a difference in the proportion of time spent inside MPAs between species. For each species, analysis of covariance (ANCOVA) was used to test for differences in the proportion of time spent inside MPAs by year, month, size, sex and MPA (i.e. east or west).

7.3.2 Excursions from MPAs

Excursions from MPAs (defined as an individual crossing out of an MPA) were calculated by tallying the number of times sharks were classified as outside the MPAs. Since sharks were detected for varying lengths of time (e.g. days to years), the number of daily excursions was calculated by dividing the total number of excursions an individual made by the total number of days it was detected. To determine how long sharks were outside the MPAs during an excursion, mean excursion duration was calculated by dividing the total amount of time an individual spent outside the MPAs by its number of excursions. Excursion data were examined for normality with Quantile-Quantile plots and $\log(x+1)$ transformed. *t*-tests were used to test for differences in the number of daily excursions and mean excursion duration between species. For each species, ANCOVA was used to test for differences in the number of daily excursions and mean excursion duration by year, size, sex and MPA.

To determine where along the boundary of the MPAs sharks were crossing, detections on edge receivers were tallied each time an individual made an excursion from and returned to the MPAs. The number of detections on each edge receiver was divided by total edge receiver detections to calculate the proportion of detections occurring along the edge receivers. Proportions were calculated separately for both excursion and return events to establish if sharks returned at the same location as their exit.

7.3.3 Space use inside MPAs

To define the amount of space sharks used inside MPAs, minimum convex polygons (MCPs) were calculated for each individual. MCPs were calculated with the adehabitat package in R (Calenge 2006) and plotted to show the spatial distribution of individuals inside MPAs. MCP area was divided by total MPA area to determine the proportion of MPA space used by individuals. Proportion of space was examined for normality with Quantile-Quantile plots and $\sin^{-1}\sqrt{x}$ transformed. A *t*-test was used to test for a difference in the proportion of MPA space used between species. For each species, ANCOVA was used to test for differences in the proportion of MPA space used by year, size, sex and MPA.

7.4 Results

MPA use varied among the two species, with many individuals detected for long periods. Juvenile *C*. *amboinensis* were monitored for 4 to 676 days (mean = 190) and adult *C*.

sorrah were monitored for 28 to 566 days (mean = 281). Individuals of both species used only one of the two MPAs in Cleveland Bay (i.e. east or west) and were rarely detected on both sides of the bay. Specifically, *C. amboinensis* used the eastern MPA and *C. sorrah* tended to use either the eastern or the western MPA, but not both.

7.4.1 Time spent inside MPAs

The proportion of time spent inside MPAs was highly variable among individuals of both species. Proportion of time inside ranged from 0.02 to 0.67 for *C. amboinensis* (mean = 0.23) and 0.00 to 0.67 for *C. sorrah* (mean = 0.32). Although on average *C. sorrah* spent approximately 10% longer in MPAs than *C. amboinensis*, there was no significant difference in proportion of time inside between species ($t_{38.3} = -1.54$, $p = 0.132$). Most *C. amboinensis* spent less than 30% of time in MPAs, whereas a higher proportion of *C. sorrah* spent 30 to 60% of time in MPA regions (Fig. 7.2). For *C. sorrah*, proportion of time spent inside MPAs was significantly different between sexes ($F_{1,77} = 10.60$, $p = 0.002$), with females spending more time inside than males (means = 0.38 and 0.21, respectively) (Fig. 7.2). There was no significant difference in the proportion of time spent inside MPAs based on size for either species (*C. amboinensis*: $F_{1,189} = 2.22$, $p = 0.138$; *C. sorrah*: $F_{1,77} = 0.00$, $p = 0.985$), or MPA for *C. sorrah* ($F_{1,77} = 0.91$, $p = 0.342$).

Proportion of time inside MPAs was consistent between years, with no significant difference evident for either species (*C. amboinensis*: $F_{1,189} = 0.19$, $p = 0.667$; *C. sorrah*: $F_{1,77} = 0.92$, $p = 0.340$). However, proportion of time inside varied between months for both species (Fig. 7.3). *Carcharhinus amboinensis* spent twice as long in the MPAs in summer (i.e. November-April) than winter (i.e. May-October) (means = 0.28 and 0.14, respectively). However, the opposite pattern was evident among *C. sorrah*, with individuals spending a higher proportion of time in the MPAs in winter (mean = 0.40) than

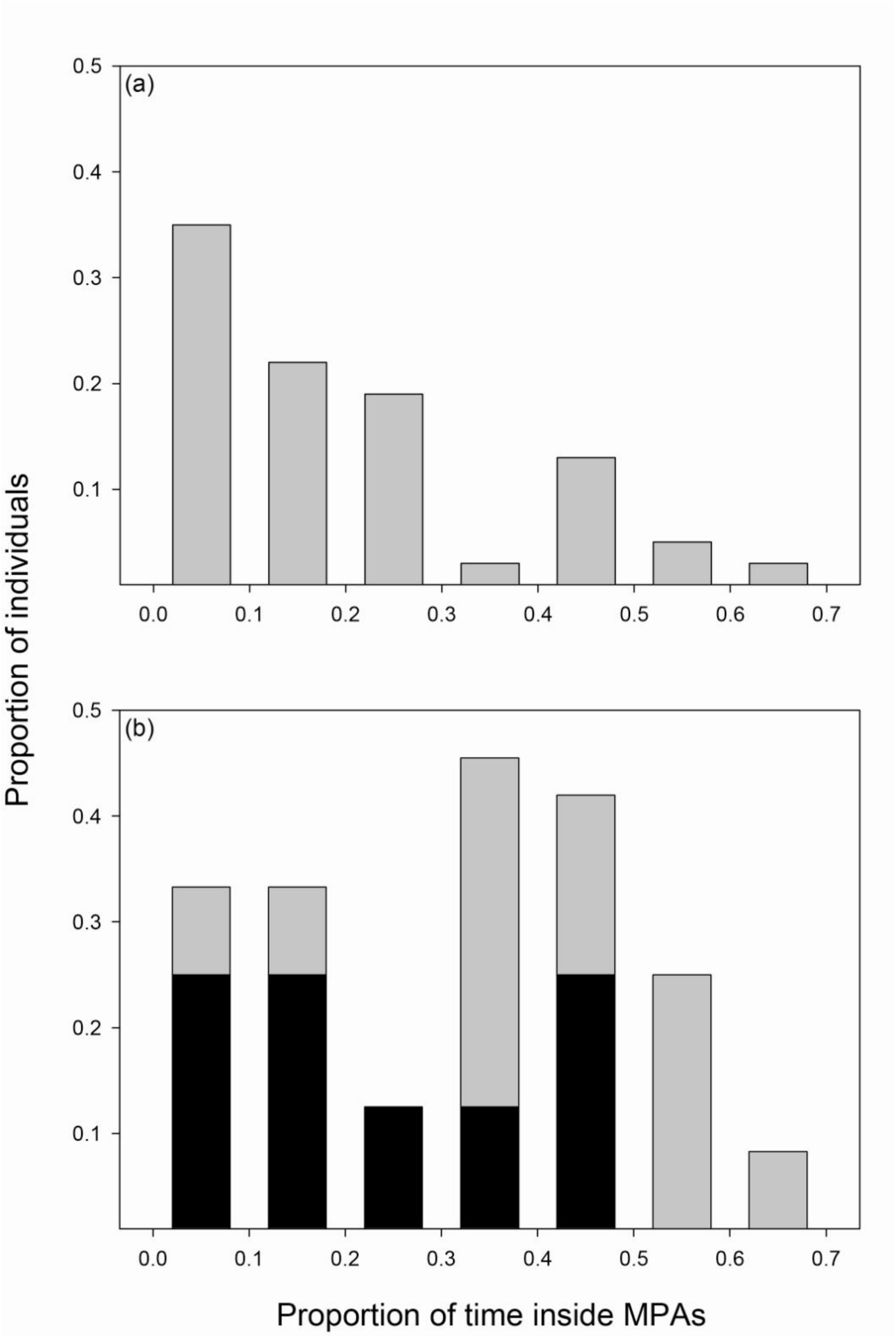

Fig. 7.2 Frequency histograms of the proportion of time individuals spent inside MPAs for *C. amboinensis* (a) and male (black) and female (grey) *C. sorrah* (b).

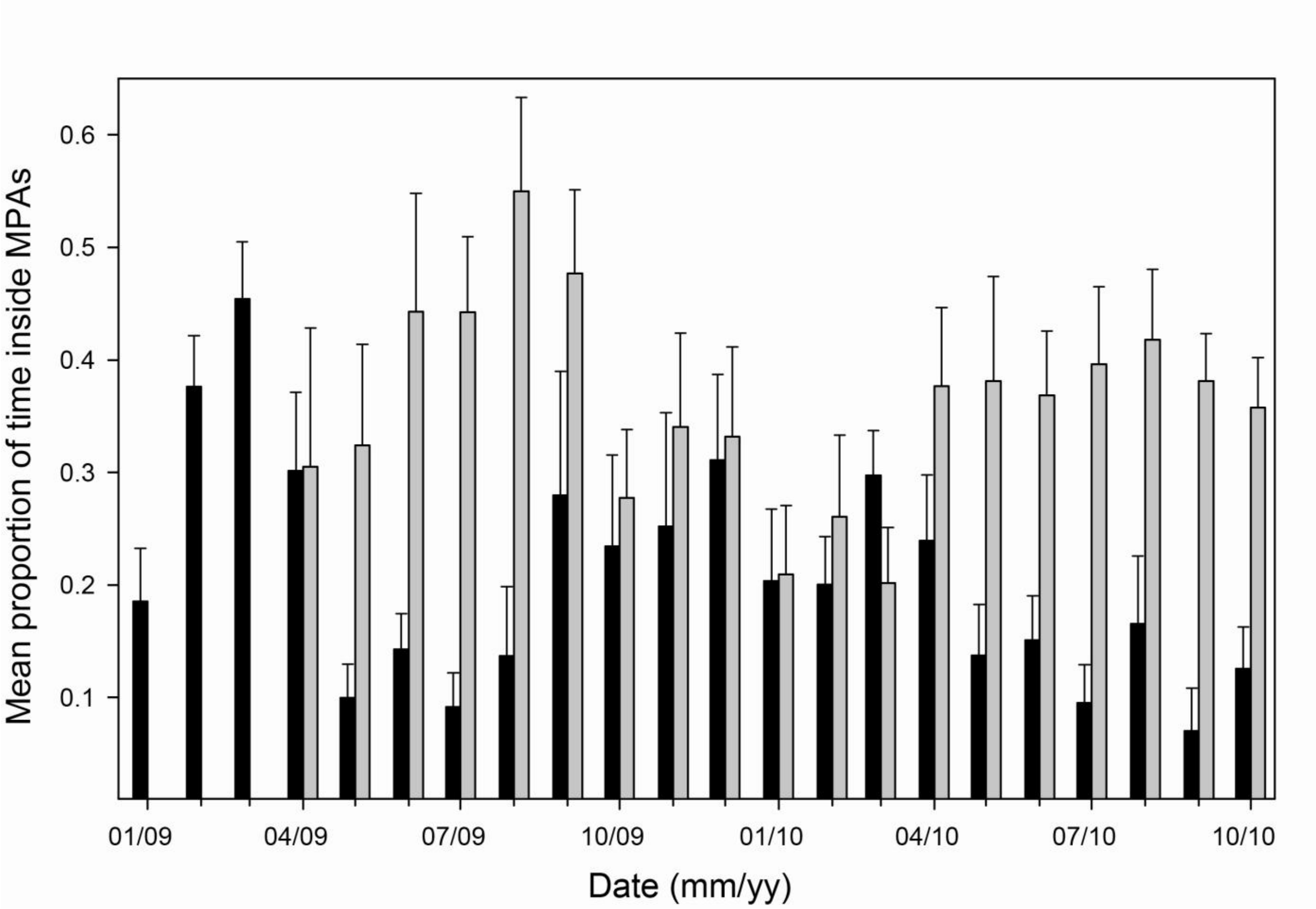

Fig. 7.3 Mean proportion of time individuals spent inside MPAs by month for *C. amboinensis* (black) and *C. sorrah* (grey).

summer (mean = 0.29). The difference in proportion of time inside MPAs between months ranged up to 0.38 for *C. amboinensis* and 0.35 for *C. sorrah*. Although the proportion of time spent inside MPAs varied between months for both species, the difference was only significant for *C. amboinensis* (*C. amboinensis*: $F_{11,189} = 5.50$, $p < 0.001$; *C. sorrah*: $F_{11,77} = 1.77$, $p = 0.075$). There was no significant interaction between year and month for either species (*C. amboinensis*: $F_{11,189} = 1.46$, $p = 0.149$; *C. sorrah*: $F_{11,77} = 1.16$, $p = 0.328$), indicating that individuals spent similar amounts of time inside MPAs during the same months across years.

7.4.2 Excursions from MPAs

All individuals made excursions from MPAs and the number and duration of excursions varied among individuals of both species. The number of excursions per day ranged from 0.33 to 2.84 for *C. amboinensis* (mean = 0.90) and 0.20 to 4.17 for *C. sorrah* (mean = 1.68). There was no significant difference in the number of daily excursions between species ($t_{24.7} = -1.02$, $p = 0.317$). For both species, most individuals made two or less excursions from the MPAs per day (Fig. 7.4a,b). Mean excursion duration ranged from 0.4 to 206.4 hours for *C. amboinensis* (mean = 43.1) and 4.0 to 214.0 hours for *C. sorrah* (mean = 48.5). There was no significant difference in mean excursion duration between species ($t_{36.4} = 0.22$, $p = 0.826$) and mean excursion duration was less than 80 hours for most individuals (Fig. 7.4c,d). For *C. amboinensis*, there was a significant difference in the number of daily excursions between years ($F_{1,33} = 16.61$, $p < 0.001$), with individuals in the first year crossing MPA boundaries less frequently than individuals in the second year (means = 0.90 and 1.47, respectively). There was, however, no significant difference in mean excursion duration between years for *C. amboinensis* ($F_{1,33} = 1.69$, $p = 0.203$). For *C. sorrah*, there was no significant difference between years in either the number of daily excursions ($F_{1,9} = 3.19$, $p = 0.108$) or mean excursion duration ($F_{1,9} = 4.75$, $p = 0.057$), but

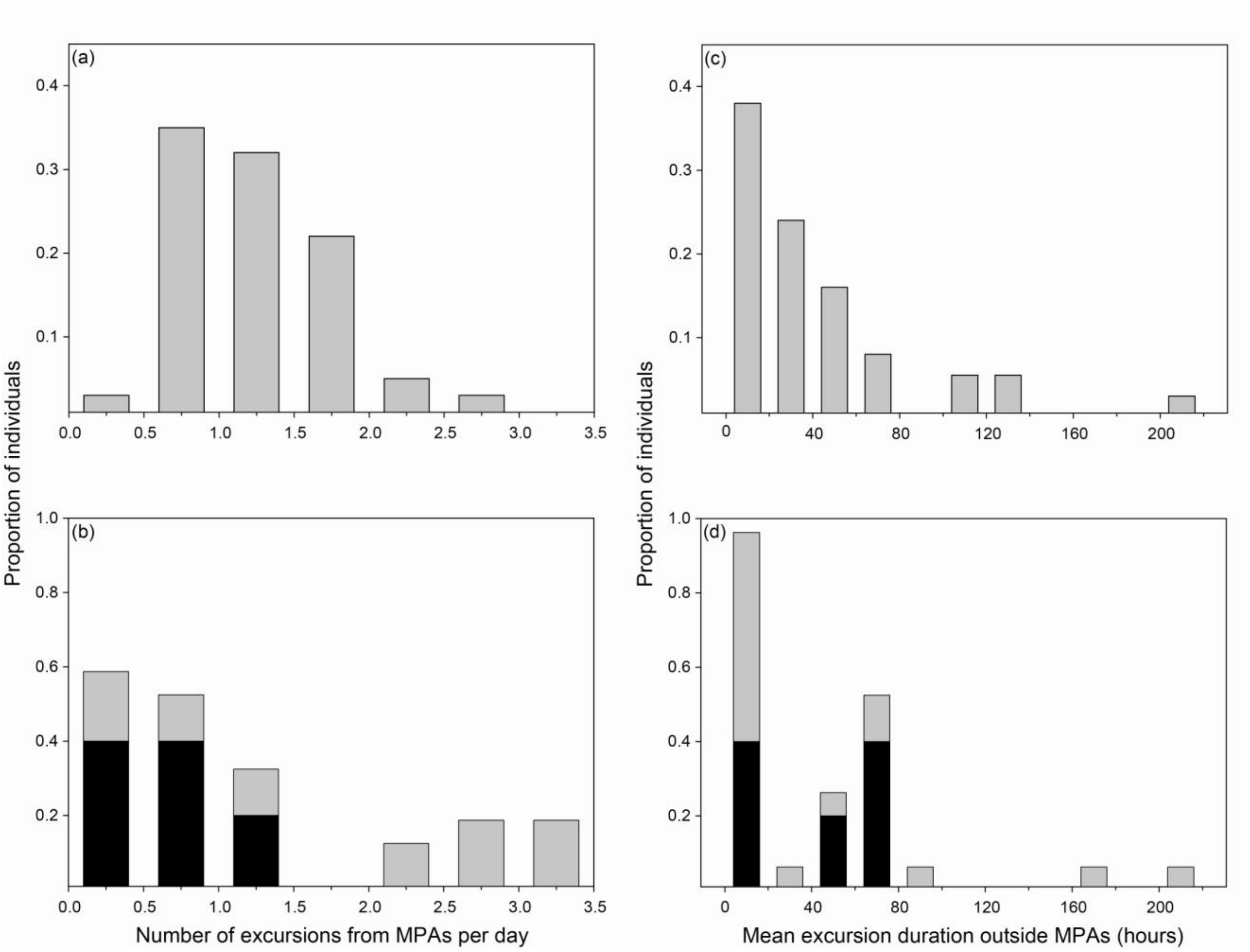

Fig. 7.4 Frequency histograms of number of daily excursions individuals made from MPAs and mean excursion duration in hours for *C. amboinensis* (a,c) and *C. sorrah* using the western (black) and eastern (grey) MPAs (b,d). Note differences in scale on y-axes.

there was a significant difference between MPAs (number of excursions: $F_{1,9} = 6.17$, $p = 0.035$; excursion duration: $F_{1,9} = 6.64$, $p = 0.030$). Specifically, individuals using the western MPA crossed boundaries less frequently than individuals using the eastern MPA (means = 0.73 and 1.98, respectively), and individuals using the western MPA also undertook shorter excursions (mean = 45.2) (Fig. 7.4b,d). For both species, there was no significant difference in either the number of daily excursions (*C. amboinensis*: $F_{1,33} = 0.01$, $p = 0.913$; *C. sorrah*: $F_{1,9} = 0.02$, $p = 0.886$) or mean excursion duration (*C. amboinensis*: $F_{1,33} = 0.18$, $p = 0.677$; *C. sorrah*: $F_{1,9} = 1.41$, $p = 0.265$) by size. There was also no significant difference between sexes for *C. sorrah* (number of excursions: $F_{1,9} = 0.11$, $p = 0.750$; excursion duration: $F_{1,9} = 4.34$, $p = 0.067$).

When sharks made excursions from the MPAs they typically exited and entered at the same location along the boundaries (Fig. 7.5). However, there was high variation in location of boundary crossings for each species and MPA used. In the eastern MPA, *C. amboinensis* exited and entered the MPA in the southern portion of the bay within the 5 m isobath more than 60% of the time (Fig. 7.5a,c). In contrast, most *C. sorrah* crossed the boundary in the northern part of the bay just outside the 5 m isobath (Fig. 7.5b,d). In the western MPA, *C. sorrah* exited and entered at one receiver along the eastern boundary outside the 5 m isobath more than 50% of the time, and less than 5% of crossings occurred along the western boundary, indicating that individuals rarely crossed the boundary on the western side of this MPA (Fig. 7.5b,d).

7.4.3 Space use inside MPAs

The proportion of space used inside MPAs ranged widely for both species, with some individuals using large areas (Fig. 7.6). Proportion of MPA space used ranged from 0.17 to 0.93 for *C. amboinensis* (mean = 0.50) and 0.06 to 0.83 for *C. sorrah* (mean = 0.55).

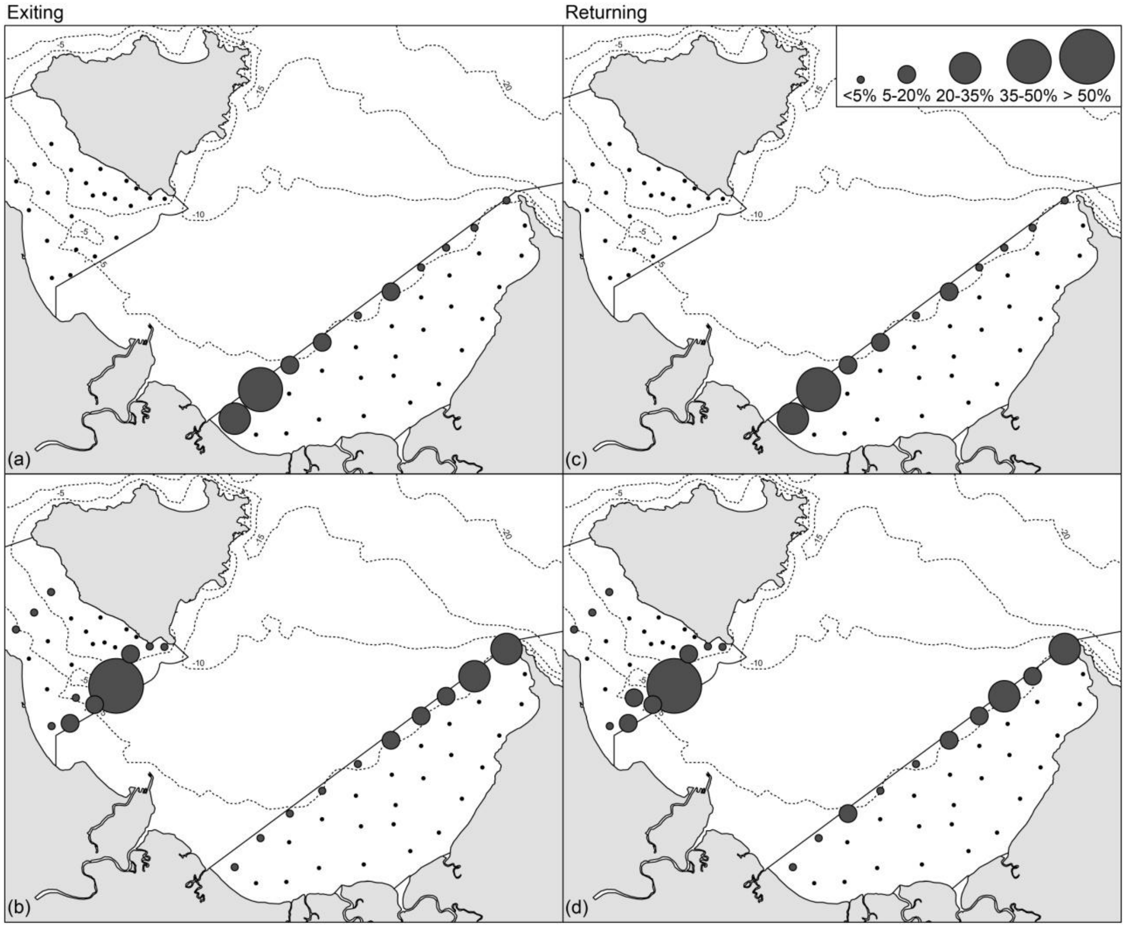

Fig. 7.5 Mean proportion of detections on edge receivers when individuals exited and returned to MPAs: *C. amboinensis* (a,c), *C. sorrah* using the eastern and western MPAs (b,d). Dashed lines indicate bathymetry.

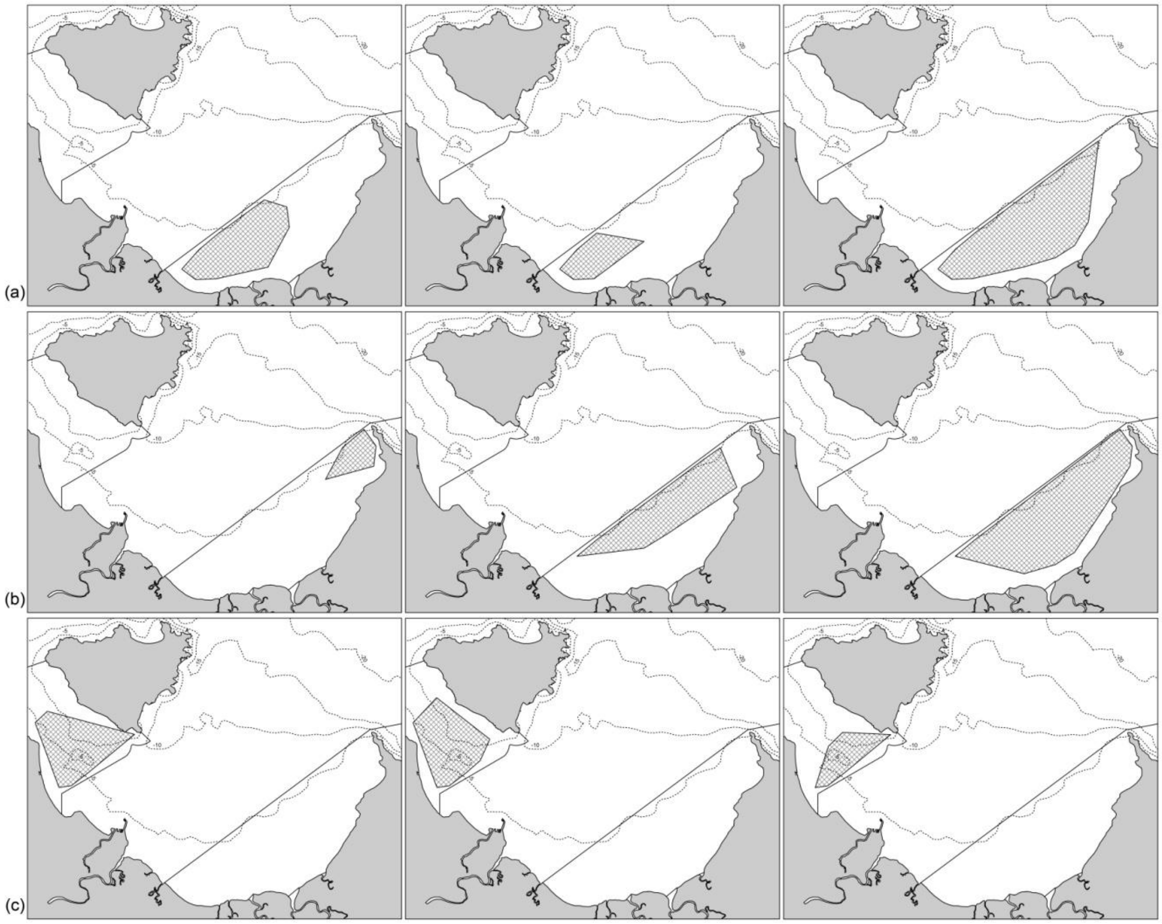

Fig. 7.6 Representative maps of minimum convex polygon home ranges (filled cross hatch) for nine individuals: *C. amboinensis* (a), *C. sorrah* using the eastern MPA (b), *C. sorrah* using the western MPA (c). Dashed lines indicate bathymetry.

Most *C. amboinensis* used 50 to 60% of the MPA area, whereas most *C. sorrah* used 70 to 80% (Fig. 7.7). There was no significant difference in the proportion of space used inside MPAs between species ($t_{40.9} = -0.82$, $p = 0.419$). For both species, there was no significant difference in proportion of space used inside MPAs between years (*C. amboinensis*: $F_{1,33} = 3.14$, $p = 0.086$; *C. sorrah*: $F_{1,9} = 0.02$, $p = 0.904$) or sizes (*C. amboinensis*: $F_{1,33} = 0.13$, $p = 0.724$; *C. sorrah*: $F_{1,9} = 0.01$, $p = 0.930$). There was also no significant difference based on sex or MPA for *C. sorrah* (sex: $F_{1,9} = 0.24$, $p = 0.636$; MPA: $F_{1,9} = 0.28$, $p = 0.609$).

7.5 Discussion

Using long-term movement data this study showed that two shark species of different life stages spend a high proportion of time within the protection of two MPAs in a highly variable coastal habitat. This empirical demonstration indicates that coastal MPAs can encompass a significant proportion of the spatial distribution of mobile and wide ranging shark species. The fact that a high proportion of sharks spent long periods of time inside MPAs suggests that spatial closures may have significant benefits for conservation and fisheries management. For example, commercially important species, such as *C. sorrah* (Harry *et al*. 2011), will gain shelter from fishing pressure via individuals remaining inside MPA boundaries. Thus, MPAs that have been designed to protect biodiversity and habitat regions like in the Great Barrier Reef Marine Park (GBRMP) (Fernandes *et al*. 2005) have additional functions, such as providing conservation benefits for shark populations.

Variation in species behaviour will result in variation in MPA use, and hence the level of protection derived. The amount of time sharks spent inside MPAs was variable for both *C.*

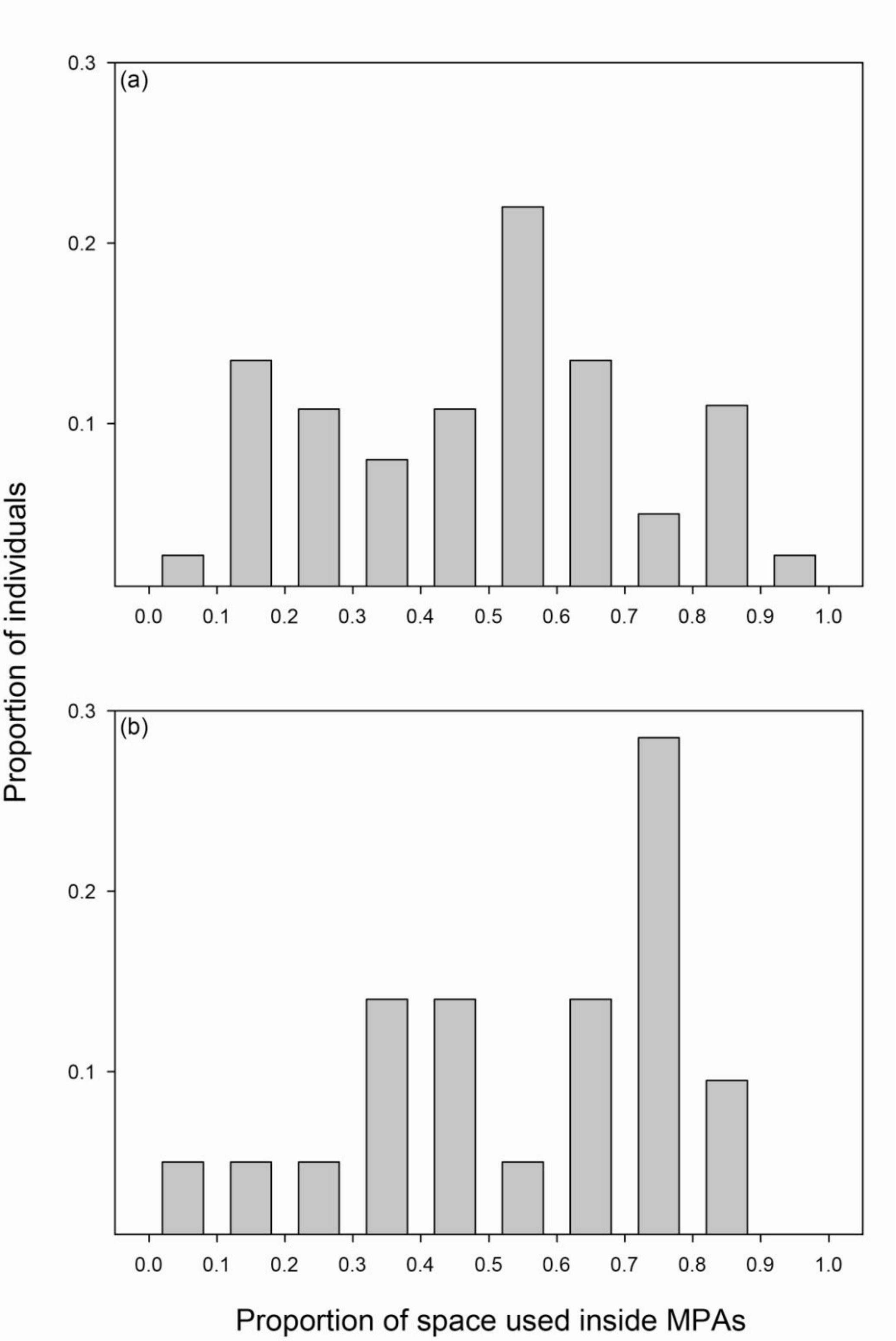

Fig. 7.7 Frequency histograms of proportion of space individuals used inside MPAs for *C. amboinensis* (a) and *C. sorrah* (b).

amboinensis and *C*. *sorrah*, with some individuals spending up to 70% of their time inside and others close to no time at all. A similar degree of variation was reported for the white stumpnose *Rhabdosargus globiceps* in a coastal MPA in South Africa, where individuals spent between 4 and 96% of time inside the MPA (mean = 50%) (Kerwath *et al*. 2009). The authors suggested that the high level of individual variation was a function of behaviour, with individual behaviour type (e.g. station keeping, migrating, etc.) affecting the amount of time spent inside the MPA (Kerwath *et al*. 2009). The proportion of time *C*. *amboinensis* and *C*. *sorrah* spent inside MPAs during this study was also likely in part a reflection of behaviour. Movement patterns of both species were variable, with some individuals displaying high degrees of site attachment while others moved more widely (see Chapters 4, 6). Individual variation in behaviour has been reported among other taxa (Willis *et al*. 2003; Afonso *et al*. 2009), and creates challenges when implementing protection for a population. Sheltering more resident portions of a population may be an effective approach for mobile and wide ranging species, and even partial protection may generate benefits for elasmobranchs. For example, Wiegand *et al*. (2011) found that a three-season spatial closure was enough protection to ensure the recovery of the thornback ray *Raja clavata* in the Thames Estuary. However, it is also important to recognize the limitations of MPAs for protecting mobile species like sharks. Animal populations typically consist of a combination of individuals that exhibit resident and nomadic behaviours (e.g. Swingland and Lessels 1979). Thus, it is likely that MPAs will primarily select for the most resident characteristics and not protect the full genetic diversity of targeted populations. Therefore, there may be a risk of losing genetic diversity in populations if MPAs are only effective at protecting the most resident behavioural phenotypes.

Life history strategies of sharks vary considerably between species, potentially affecting the benefits species derive from MPAs. Since *C*. *amboinensis* and *C*. *sorrah* used MPAs during different life stages, it is likely that MPAs played a different role for each species. For example, *C*. *amboinensis* used MPAs as young juveniles and remained in these regions until at least three years of age. Protecting juvenile life stages will benefit species like *C*. *amboinensis* through increased survival of young. However, once individuals leave MPA regions the benefits resulting from protection will diminish. Thus, older juvenile and adult *C*. *amboinensis* are likely a portion of the population more vulnerable to exploitation. In contrast, *C*. *sorrah* used MPAs as adults, and catch data showed that young juveniles also frequented the same areas (D. M. Knip, unpublished data). Thus, *C*. *sorrah* received protection from MPAs as adults and also possibly as juveniles, and protecting adult life stages will benefit populations through increased survival of the breeding stock. Specifically, protecting breeding stocks may increase the number and size of reproducing females, which will increase litter sizes (Cortés 2000) and enhance recruitment into the adult population. Although first year survival is important for population persistence, the demography of shark populations indicates that protecting older life stages is most important for maintaining a positive intrinsic rate of population increase (Kinney and Simpfendorfer 2008). Thus, population level benefits are likely greater for species like *C*. *sorrah* that use MPAs throughout their entire life span and receive protection during adult life stages. These relatively small-sized MPAs, however, provided protection to sharks in both juvenile and adult life stages, and examination of space use confirmed that MPAs do not need to be large to be effective for mobile species (e.g. Holland *et al*. 1996; Heupel and Simpfendorfer 2005).

There was no difference in the amount of time sharks spent inside MPAs on the basis of body size, which was unexpected, particularly for *C*. *amboinensis*, as ontogenetic shifts in movement and home range have been reported among juveniles of this species (see Chapter 4) and are known from other large-bodied carcharhinids (e.g. Morrissey and Gruber 1993a). Presumably, an MPA would be more effective at protecting young individuals that have restricted movements and use smaller areas of space. Since MPAs were used similarly across the size range of *C. amboinensis* monitored (i.e. 690 to 1290 mm STL), they likely provided similar protection for the youngest juveniles as for those a few years old. Thus, MPAs provide protection for a range of juvenile size classes, and a network of MPAs (e.g. the GBRMP) may offer increased protection for these larger-bodied shark species that expand their movements as they grow larger. There was also no difference in the amount of time spent inside MPAs on the basis of body size for *C. sorrah*, but there was a significant difference between sexes. Females spent more time inside MPAs than males, which was likely due to females using shallower habitats closer to shore (see Chapter 6). Thus, for adult sharks using nearshore regions, MPAs may benefit one sex more than the other depending on the location of the MPA and the type of available habitat inside. Since movement and habitat use affect species availability to fishing pressure, sex-biased MPA effectiveness will have significant implications for conservation and fisheries management (Mucientes *et al*. 2009).

MPAs should contain habitat types that are used most extensively to help encompass the movements of mobile and wide ranging species (Smith *et al*. 1996; Loyn *et al*. 2001; Simpfendorfer *et al*. 2010). A suggested strategy for MPA placement has been to set boundaries along non-contiguous habitat, or where there is a natural boundary impeding movement out of the MPA (Barrett 1995; Kramer and Chapman 1999; Lowe *et al*. 2003). In this study, all individuals made excursions from the MPAs, but both species consistently crossed boundaries at the same locations, both where they exited and where they returned. Although the boundary along the eastern MPA was close to 20 km long, most crossings of *C*. *amboinensis* occurred within a small area (ca. 4 km) inside the 5 m isobath in the southern part of the bay. The habitat in this area is non-complex and continuous, with the intertidal zone consisting of shallow mudflats. Juvenile *C*. *amboinensis* associate strongly with this shallow habitat (see Chapter 4), and detections on a temporary line of receivers covering 2 km of the intertidal zone outside the eastern MPA confirmed that individuals also used this non-protected area (D. M. Knip, unpublished data). Thus, an MPA that included more of the intertidal zone in this area or was bordered along a break in habitat may be more effective at encompassing the movements of *C*. *amboinensis*. *Carcharhinus sorrah* using the eastern MPA similarly crossed the boundary in consistent locations, but over a broader area (ca. 11 km). This species used deeper habitats, and thus crossed the boundary outside the 5 m isobath, which covered a larger overall distance. In the western MPA, *C*. *sorrah* also crossed boundaries consistently in deeper water outside the 5 m isobath. However, this deeper habitat covered a smaller distance on the western side of the bay, resulting in a relatively restricted area of boundary crossing (ca. 2 km). Understanding where individuals cross MPA boundaries is important for defining species exposure to exploitation (e.g. fishing pressure) outside MPAs (Heupel and Simpfendorfer 2005; Kerwath *et al.* 2009). For example, although *C*. *amboinensis* and *C*. *sorrah* used the same MPAs and spent similar amounts of time inside, differences in location of boundary crossings affected their susceptibility to fishing pressure. Most fishing effort in this region occurs in the intertidal zone, and since *C*. *amboinensis* crossed the MPA boundaries within this shallower area, it would be a more exposed species. Effects of fishing pressure were evident, with 21% of *C*. *amboinensis* removed by fishers in this region and no captures of *C*. *sorrah*.

The effects of fishing pressure emphasise the importance of understanding the activities that occur outside MPA boundaries. As shown here, the location and intensity of fishing pressure play a role in determining the outcome of MPA boundary crossings by targeted species. For example, if the area adjacent to an MPA boundary is heavily fished, the risk of capture for an individual will remain high even if it spends most of its time inside the MPA. The empirical data presented in this study show that despite many individuals spending a large proportion of time inside MPAs, sharks are frequent boundary crossers, with most individuals exiting the MPAs every day or two on average. Thus, if netters intensively fish areas adjacent to MPA boundaries, they may catch a substantial proportion of MPA resident individuals. This concern may justify an ‘onion-ring’ type approach to MPA design, where core protected areas are buffered by outer zones that exclude potentially high impact fisheries.

The question of how MPAs can be used to protect sharks was first addressed over a decade ago (Bonfil 1999) and since then little has been done to further examine the benefits this group of species gain from protection. This study is only one of few that have evaluated the effectiveness of MPAs for sharks worldwide (Chapman *et al*. 2004; Heupel and Simpfendorfer 2005; Garla *et al*. 2006; Barnett *et al*. 2011) and is among the first to assess how sharks benefit from MPAs within the GBRMP (Heupel *et al*. 2010b). With uncertainty surrounding the future status of many shark populations, it is essential that conservation strategies are investigated so effective action can be taken. Consistent patterns in MPA use documented in this study provide certainty that MPAs offer protection and conservation benefits for coastal shark populations. However, defining movement and habitat use of juveniles and adults is equally important for understanding MPA function for mobile species (Grüss *et al*. 2011) and the results of this study highlight the need for understanding the role of life history in MPA design. MPAs within the GBRMP and most others around the world have not been designed to provide protection for sharks. Thus, our understanding of the benefits sharks and other mobile species gain from protection will remain variable and unpredictable until data on movement and distribution are obtained. The greater our knowledge of shark biology and life history, the more confidence there will be in the design and effectiveness of MPAs for these species.

CHAPTER 8

General Discussion

8.1 Comparison of *C. amboinensis* and *C. sorrah* spatial ecology in Cleveland Bay

Nearshore environments provide many advantages for inhabitants, with sharks using these regions as nursery areas (Heupel *et al.* 2007), refuges from predators (Wetherbee *et al.* 2007), foraging areas (Bethea *et al.* 2004) and mating grounds (Pratt and Carrier 2001). Thus, since nearshore environments serve a magnitude of functions, multiple shark species from a range of life stages may inhabit these regions. A theoretical population model introduced in the 1960s defined the distribution and behaviour of coastal sharks (Springer 1967), and that description fits some species well. These are generally larger-bodied species that use restricted areas during early life stages, which suggests that nearshore regions contain important habitat and act as nurseries for the young of these species. However, there is high diversity among sharks using nearshore regions, and a second, alternative population model was proposed in this dissertation to represent species that are typically smaller-sized (see Chapter 2). Individuals of these species inhabit nearshore regions for their entire life cycle, indicating that they may be more dependent on nearshore habitat than larger-bodied species. Although *C*. *amboinensis* and *C*. *sorrah* species used the same nearshore environment, they are likely best described by different population models because they used this region during different life stages. For example, *C*. *amboinensis* used nearshore regions primarily as juveniles, while *C*. *sorrah* used the same environment as adults, which is similar to results reported previously for these species (Stevens and Wiley 1986; Cliff and Dudley 1991). Thus, the model defined by Springer (1967) most accurately describes *C*. *amboinensis* because individuals of this species used Cleveland Bay for long periods as juveniles. *Carcharhinus sorrah* is better defined by the alternative population model proposed in Chapter 2, as individuals of this species used Cleveland Bay during the adult life stage. However, it is important to acknowledge the limitations and difficulties in making comparisons between juvenile *C*. *amboinensis* and adult *C*. *sorrah* in this study because of the difference in their life stages. Adult *C*. *amboinensis* were captured only occasionally in Cleveland Bay (D. M. Knip, unpublished data). Juvenile *C*. *sorrah* were encountered throughout the bay, but unlike their adult conspecifics, they had a more variable and unpredictable distribution (M. J. Kinney, unpublished data; D. M. Knip, unpublished data). Thus, It remains to be seen how adult *C*. *amboinensis* behave in relation to adult *C*. *sorrah*, and how juvenile *C*. *sorrah* behave in relation to juvenile *C*. *amboinensis*. Interspecies comparisons should therefore be interpreted with caution.

Prior to this dissertation, the life history of *C*. *amboinensis* and *C*. *sorrah* had been investigated (Stevens and Wiley 1986; Cliff and Dudley 1991) but knowledge of their movement and habitat use remained scarce. Limited movement information obtained from a mark-recapture study in northern Australia found that *C*. *amboinensis* and *C*. *sorrah* tended to move short distances (e.g. < 50 km) and use localised areas in nearshore regions (Stevens *et al.* 2000b). Results from Cleveland Bay confirm and support this previous finding by demonstrating that both *C*. *amboinensis* and *C*. *sorrah* used nearshore habitat extensively, with many individuals undertaking short distance movements and using consistent areas. The fact that *C*. *amboinensis* showed a high level of attachment to nearshore habitat was expected, as juveniles of species fitting Springer's model tend to use restricted areas for long periods. However, *C*. *sorrah* displaying the same long-term presence and high attachment to specific nearshore habitat was unanticipated. Although smaller-bodied species like *C*. *sorrah* use nearshore regions for the duration of their life span, they generally have wider ranging movements and use large areas of space (e.g. *R*. *terraenova*; Carlson *et al*. 2008). Moving widely throughout nearshore waters is thought to be beneficial for smaller-bodied species, as accessing additional habitats may increase foraging success and promote fast growth (see Chapter 2). In addition, juveniles of smaller-bodied species may be too small to receive the same level of protection from using discrete nearshore nursery areas as larger-bodied species. However, for a species like *C*. *sorrah*, adult individuals are of similar sizes to some juveniles of large-bodied species, and so may be large enough to receive protective benefits from using discrete areas in nearshore regions. Perhaps some smaller-bodied sharks have wide ranging movements to exploit additional resources and promote fast growth as juveniles, and use consistent areas when they are less vulnerable as larger adults. Thus, there may yet be another population model that better describes the distribution and behaviour of species like *C*. *sorrah* that use restricted areas of nearshore regions as adults. The two current theoretical population models therefore do not encompass all species, and it is likely that additional models exist.

It is common for nearshore environments to be inhabited by multiple shark species (e.g. Castro 1993; Simpfendorfer and Milward 1993) and movement and habitat use may vary between species (White and Potter 2004). Differences in habitat use are complex and difficult to explain, but could be based in part on species life history stage or strategy. For example, *C*. *amboinensis* associated strongly with shallow (< 300 cm), turbid habitats adjacent to creek and river mouths (see Chapter 4), while *C*. *sorrah* generally used deeper (> 300 cm) water away from creek mouth habitat (see Chapter 6). *Carcharhinus amboinensis* may have used shallow habitats closer to shore because as juveniles, using shallow water may be a strategy for avoiding larger predators and increasing survival (e.g. Wetherbee *et al.* 2007). In addition, an ontogenetic shift in habitat use occurred among juvenile *C*. *amboinensis*, with individuals remaining in shallowest habitats while young and moving into deeper habitats as they grew larger. A similar result was found among juvenile *C*. *leucas*, which was thought to be a strategy for decreasing intraspecific competition between different age classes using the same region (Simpfendorfer *et al*. 2005). Youngest juveniles are likely among the most vulnerable to mortality (Heupel and Simpfendorfer 2002) and will require a suitable strategy to survive. *Carcharhinus sorrah* were of similar sizes to some juvenile *C*. *amboinensis*, but this species used deeper habitats. As adult individuals, they may be more experienced at avoiding predators in deeper habitats and/or mortality risk may be less costly for *C*. *sorrah* populations due to their higher productivity (see Chapter 2). Thus, although *C*. *amboinensis* and *C*. *sorrah* inhabited the same nearshore environment, both life history strategy and habitat use varied greatly between these two species.

Using different habitats could act as a mechanism for decreasing competition between species that inhabit the same nearshore environment. For example, in a nearshore environment in Western Australia, White and Potter (2004) concluded that multiple shark species partitioned space and food resources to reduce the potential for competition. Thus, use of different habitats may be a strategy to partition resources and increase survival among different species that access the same nearshore regions, such as *C*. *amboinensis* and *C*. *sorrah* in Cleveland Bay. However, differences in habitat use could also be attributed to diet and prey distribution, with *C*. *amboinensis* and *C*. *sorrah* using different areas because they prefer and target different prey items. The diet of *C*. *amboinensis* has been reported to consist mainly of benthic species including teleosts, crustaceans and mollusks, whereas *C*. *sorrah* has been found to primarily prey on teleosts and cephalopods (Compagno 1984; Stevens and Wiley 1986). There was no specific diet information available from individuals in Cleveland Bay, but it is possible that *C*.

amboinensis used shallow habitats adjacent to creek mouths to forage for prey along the bottom and *C*. *sorrah* used deeper habitats to target prey in the water column farther from shore. These differences in diet would increase the separation between *C*. *amboinensis* and *C*. *sorrah* within Cleveland Bay.

8.2 Implications for the broader spatial ecology of sharks in nearshore environments

Nearshore waters are susceptible to environmental fluctuations and seasonal variation due to their shallow nature and close proximity to land. Thus, these regions present an environment with dynamic conditions that continually challenges inhabitants. High use of nearshore regions implies that sharks are relatively tolerant of these variable environments, but to survive species must cope, adapt accordingly or leave when conditions become unfavourable. For example, *C*. *amboinensis* was highly influenced by changes in freshwater inflow, which was due to juvenile individuals strongly associating with shallow creek mouth habitat (see Chapter 5). Specifically, increased rainfall during the wet season resulted in high levels of freshwater inflow, and juvenile individuals responded by moving away from creek mouths at these times. Since *C*. *sorrah* used deeper water away from creek mouth habitat, this species was less exposed to changes in freshwater inflow and did not display the same movement response. Moving in response to increased freshwater inflow could be due to a range of factors including high flow rates, or changes in salinity (Ubeda *et al.* 2009), dissolved oxygen (Heithaus *et al.* 2009) and prey distribution (Winemiller and Jepsen 1998). Due to their mobility, sharks can use areas as needed and move or leave if conditions deteriorate. However, moving does not always guarantee survival and other costs may arise from moving to different, and possibly less optimal, habitat.

Tropical nearshore regions are becoming increasingly vulnerable to changes in rainfall patterns and freshwater inflow (Chin *et al*. 2010), which will have varying and/or adverse effects on inhabitants. Species like *C*. *amboinensis,* and those using similar habitats (e.g. smalltooth sawfish *Pristis pectinata*; Simpfendorfer *et al*. 2011a), will likely be among the most exposed to the effects of altered rainfall and changing levels of freshwater inflow. Thus, defining how seasonal and environmental fluctuation influences coastal sharks will be crucial for understanding species exposure and vulnerability to dynamic and changing climate scenarios.

Although nearshore environments are characteristic of having highly variable conditions, some shark species may use these fluctuations to their advantage. For example, changes in water temperature affected the location of female *C*. *sorrah* in Cleveland Bay. Specifically, decreased water temperature during the winter months resulted in these individuals to move into shallower water habitats where water temperature was higher. Using habitats with higher water temperatures may provide advantages to shark species by optimising physiological processes, such as speeding embryonic development in sexually mature females (e.g. Economakis and Lobel 1998; Hight and Lowe 2007). However, using warm water habitats may also provide challenges, such as increasing metabolic and energetic demands. Using deeper habitats where water temperature is cooler may be more energetically efficient for species (e.g. Sims *et al*. 2006) but severe drops in water temperature have also been reported to be the cause of mortality in some sharks (Snelson and Bradley 1978). Thus, nearshore environments provide both advantages and disadvantages for inhabitants, and sharks will need to move or adapt in order to remain in environments that are within their physiological limitations.

In addition to being highly exposed to environmental changes, nearshore regions are becoming increasingly susceptible to anthropogenic impacts and habitat loss. Degradation of nearshore environments and significant declines of important habitat (e.g. mangroves and seagrass) have been documented worldwide (Short and Wyllie-Echeverria 1996; Valiela *et al*. 2001). Thus, there may be implications for multiple shark species using shared environments, particularly if resources become limiting in those regions. For example, decreased habitat availability may increase competition, and species that are out-competed will be required to move in order to locate sufficient resources. Thus, strategies that increase spatial and temporal habitat partitioning will be highly beneficial for sharks using a shared environment, especially for species using the same or similar resources. However, species that show high degrees of attachment to specific habitat (e.g. *C*. *sorrah*) or use restricted areas during vulnerable life stages (e.g. *C*. *amboinensis*) will be among the most vulnerable to habitat degradation and loss.

Due to the high and frequent impacts occurring in nearshore environments, effective conservation and management measures are crucial for protecting and sustaining exploited species and habitat. Marine protected areas (MPAs) are becoming widely used conservation and management tools worldwide (Halpern and Warner 2003) but it remains unclear how effective they are at protecting mobile species. This research defined the capacity of MPAs for sheltering shark species from exploitation (e.g. gillnet fishing pressure), and revealed an interesting discrepancy between the theoretical population models and the observed use of MPAs. Since the alternative population model proposed in this dissertation specified no use of specific nursery areas, it could be predicted that MPAs would not be effective for those particular species. However, MPAs appeared to be quite effective for both juvenile *C*. *amboinensis* and adult *C*. *sorrah*. These MPAs still likely played a different role for these two species due to the different life stages being protected. For example, *C*. *amboinensis* received protection as juveniles, which would benefit their population through increased survival of young. Although protecting individuals during a vulnerable life stage may decrease mortality rates (Heupel and Simpfendorfer 2005), protective benefits will diminish once these individuals move away from nearshore environments as older juveniles and adults. In contrast, *C*. *sorrah* received protection as adults, which would be highly beneficial for their population by increasing survival of reproductive individuals. Sub-adult and adult individuals are important for population persistence; if adults remain sheltered from fishing pressure they may attain larger maximum sizes, produce more young and ultimately increase recruitment into their populations. Although *C*. *amboinensis* and *C*. *sorrah* received a similar degree of protection from MPAs, population level benefits will vary depending on the life stage being protected. Thus, it is important to understand spatial ecology across all life stages of shark species to define the conservation potential of MPAs for their populations. The effectiveness of an MPA will not only depend on the species being encompassed by its boundaries, but also on the location and intensity of fishing pressure. There are also additional implications for mobile species, such that MPAs may primarily select for individuals with resident characteristics and fail to protect the full genetic diversity of targeted populations. Spatial data can be used to help indentify when MPAs may be an effective conservation strategy for elasmobranch populations (Simpfendorfer *et al*. 2011b), and when other approaches (e.g. size limits in fisheries) may be more feasible (Wiegand *et al*. 2011).

8.3 Directions for future research

Although this dissertation research fills many knowledge gaps regarding the spatial ecology of *C*. *amboinensis* and *C*. *sorrah*, further work is needed to gain additional knowledge of their use of nearshore environments. Future work should include biological studies, such as defining how foraging behaviour or diet may shift with seasonal changes (e.g. wet vs. dry seasons) or vary among individuals using different habitats (e.g. *C*. *sorrah* using different areas of Cleveland Bay). For *C*. *amboinensis*, it would be useful to examine movement and habitat use in relation to different physical factors, such as salinity and dissolved oxygen, to determine the physiological limitations of this species. For *C*. *sorrah*, monitoring individuals within different nearshore regions would help determine if, and where, other highly resident populations occur along the Queensland coast. There is much more research that would contribute to our understanding of *C*. *amboinensis* and *C*. *sorrah*, as well as other coastal sharks, and the suggestions listed here are just some examples.

Understanding the distribution and behaviour of species across all life stages will be necessary for implementing appropriate conservation and management strategies for their populations (Bowen *et al*. 2005). It would therefore be useful to study older juvenile and sub-adult *C*. *amboinensis* to determine at what size/age individuals move to deeper, offshore waters and how far these individuals move when they leave nearshore regions. It would be equally beneficial to gain an understanding of how *C*. *sorrah* use nearshore environments as juveniles to compare juvenile behaviour to that of adults. By defining the spatial ecology of different shark species during specific life stages, this research provides an important piece of the knowledge needed for improving our understanding of shark populations.

Shark populations in the Great Barrier Reef Marine Park (Chin *et al*. 2010) and around the world (Stevens *et al*. 2000a) have become a major source of conservation concern, but protecting these species is difficult due to their high mobility and broad distribution. This research demonstrated that individual MPAs generate conservation benefits for multiple shark species and do not need to follow a species specific initiative. Rather, establishing MPAs to fulfil numerous objectives may be an efficient and effective conservation strategy for sharks and other mobile species in nearshore regions. Thus, further work is required to gather information across a wider spectrum of species, particularly those under the most threat, to increase and maximise the conservation potential of MPAs. Quantifying movements is essential for understanding the benefits MPAs provide sharks and other mobile species, and collecting information on shark movement and habitat use has been acknowledged as a conservation priority (Heupel and Simpfendorfer 2010; Simpfendorfer *et al*. 2011b). By being among one of the first studies to assess the effectiveness of MPAs for sharks species worldwide, this dissertation may ultimately serve as a model for the facilitation of future MPA research.

REFERENCES

Abel, D. C., Young, R. F., Garwood, J. A., Travaline, M. J., and Yednock, B. K. (2007). Survey of the shark fauna in two South Carolina estuaries and the impact of salinity structure. In 'Shark Nursery Grounds of the Gulf of Mexico and the East Coast Waters of the United States'. (Eds. C. T. McCandless, N. E. Kohler and H. L. Pratt Jr.) pp. 109-124. (American Fisheries Society: Bethesda, USA.)

Ackerman, J. T., Kondratieff, M. C., Matern, S. A., and Cech, J. J. Jr. (2000). Tidal influence on spatial dynamics of leopard sharks, *Triakis semifasciata*, in Tomales Bay, California. *Environmental Biology of Fishes* **58**, 33-43.

Afonso, P., Fontes, J., Holland, K. N., and Santos, R. S. (2009). Multi-scale patterns of habitat use in a highly mobile reef fish, the white trevally *Pseudocaranx dentex*, and their implications for marine reserve design. *Marine Ecology Progress Series* **381**, 273-286.

Agardy, T. S. (1997). ‘Marine Protected Areas and Ocean Conservation’. (Academic Press: San Diego, USA.)

Allison, G. W., Lubchenco, J., and Carr, M. H. (1998). Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications* **8**, S79-S92.

Andrews, K. S., Levin, P. S., Katz, S. L., Farrer, D., Gallucci, V. F., *et al*. (2007). Acoustic monitoring of sixgill shark movements in Puget Sound: evidence for localized movement. *Canadian Journal of Zoology* **85**, 1136-1142.

Balek, J. (1983). 'Hydrology and Water Resources in Tropical Regions’. (Elsevier: Amsterdam, The Netherlands.)

Barker, M. J., and Schluessel, V. (2005). Managing global shark fisheries: suggestions for prioritizing management strategies. *Aquatic Conservation: Marine and Freshwater Ecosystems* **15**, 325-347.

Barnett, A., Abrantes, K. G., Stevens, J. D., and Semmens, J. M. (2011). Site fidelity and sex-specific migration in a mobile apex predator: implications for conservation and ecosystem dynamics. *Animal Behaviour* **81**, 1039-1048.

Barrett, N. S. (1995). Short-term and long-term movement patterns of 6 temperate reef fishes (families labridae and monacanthidae). *Marine and Freshwater Research* **46**, 853-860.

Bass, A. J., D'Aubrey, J. D., and Kistnasamy, N. (1973). Sharks of the east coast of southern Africa. I. The genus *Carcharhinus* (Carcharhinidae). *Investigational Report* **33**, 1-168. (Oceanographic Research Institute: Durban, South Africa.)

Baum, J. K., Myers, R. A., Kehler, D. G., Worm, B., Harley, S. J., *et al*. (2003). Collapse and conservation of shark populations in the northwest Atlantic. *Science* **229**, 389-392.

Beck, M. W., Heck, K. L. Jr., Able, K. W., Childers, D. L., Eggleston, D. B., *et al*. (2001). The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience* **51**, 633-641.

Bellquist, L. F., Lowe, C. G., and Caselle, J. E. (2008). Fine-scale movement patterns, site fidelity, and habitat selection of ocean whitefish (*Caulolatilus princeps*). *Fisheries Research* **91**, 325-335.

Bethea, D. M., Buckel, J. A., and Carlson, J. K. (2004). Foraging ecology of the early life stages of four sympatric shark species. *Marine Ecology Progress Series* **268**, 245-264.

Bethea, D. M., Carlson, J. K., Buckel, J. A., and Satterwhite, M. (2006). Ontogenetic and site-related trends in the diet of the Atlantic sharpnose shark *Rhizoprionodon terraenovae* from the northeast Gulf of Mexico. *Bulletin of Marine Science* **78**, 287-307.

Bigelow, H. B., and Schroeder, W. C. (1948). Sharks. In ‘Fishes of the Western North Atlantic, Part 1’. pp. 59-546. (Memoir Sears Foundation for Marine Research: New Haven, USA.)

Bilkovic, D. M., and Roggero, M. M. (2008). Effects of coastal development on nearshore estuarine nekton communities. *Marine Ecology Progress Series* **358**, 27-39.

Blaber, S. J. M., Brewer, D. T., and Salini, J. P. (1989). Species composition and biomasses of fishes in different habitats of a tropical northern Australian estuary: their occurrence in the adjoining sea and estuarine dependence. *Estuarine, Coastal and Shelf Science* **29**, 509-531.

Blaber, S. J. M., Brewer, D. T., and Salini, J. P. (1995). Fish communities and the nursery role of the shallow inshore waters of a tropical bay in the Gulf of Carpentaria, Australia. *Estuarine, Coastal and Shelf Science* **40**, 177-193.

Bonfil, R. (1999). Marine Protected Areas as a shark fisheries management tool. In 'Proceedings of the 5th Indo-Pacific Fish Conference Nouméa, 1997’. (Eds. B. Seret and J. Y. Sire.) pp. 217-230. (Societe Francaise d’Ichtyologie and Institut de Recherche pour le Developpement: Paris, France.)

Bowen, B. W., Bass, A. L., Soares, L., and Toonen, R. J. (2005). Conservation implications of complex population structure: lessons from the loggerhead turtle (*Caretta caretta*). *Molecular Ecology* **14**, 2389-2402.

Branstetter, S. (1990). Early life-history implications of selected Carcharhinoid and Lamnoid sharks of the northwest Atlantic. *NOAA Technical Report, NMFS* **90**, 17-28.

Brewer, D. T., Blaber, S. J. M., Salini, J. P., and Farmer, M. J. (1995). Feeding ecology of predatory fishes from Groote Eylandt in the Gulf of Carpentaria, Australia, with special reference to predation on Penaeid prawns. *Estuarine, Coastal and Shelf Science* **40**, 577-600.

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.

Carfagno, G. L. F., and Weatherhead, P. J. (2008). Energetics and space use: intraspecific and interspecific comparisons of movements and home ranges of two Colubrid snakes. *Journal of Animal Ecology* **77**, 416-424.

Carlisle, A. B., and Starr, R. M. (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, A. B., and Starr, R. M. (2010). Tidal movements of female leopard sharks (*Triakis semifasciata*) in Elkhorn Slough, California. *Environmental Biology of Fishes* **89**, 31-45.

Carlson, J. K. (2002). Shark nurseries in the northeastern Gulf of Mexico. In 'Shark Nursery Grounds of the Gulf of Mexico and East Coast Waters of the United States: an Overview’. (Eds. C. T. McCandless, H. L. Pratt Jr. and N. E. Kohler.) pp. 165-182. An internal report to NOAA's Highly Migratory Species Office. (NOAA Fisheries: Narragansett, USA.)

Carlson, J. K., Heupel, M. R., Bethea, D. M., and Hollensead, L. D. (2008). Coastal habitat use and residency of juvenile Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*). *Estuaries and Coasts* **31**, 931-940.

Castro, J. I. (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.

Castro, J. I. (1996). Biology of the blacktip shark, *Carcharhinus limbatus*, off the southeastern United States. *Bulletin of Marine Science* **59**, 508-522.

Chapman, D. D., Pikitch, E. K., Babcock, E., and Shivji, M. S. (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.

Chesson, J. (1978). Measuring preference in selective predation. *Ecology* **59**, 211-215.

Chin, A., Kyne, P. M., Walker, T. I., and McAuley, R. B. (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.

Claudet, J., Osenberg, C. W., Domenici, P., Badalamenti, F., Milazzo, M.. *et al.* (2010). Marine reserves: fish life history and ecological traits matter. *Ecological Applications* **20**, 830-839.

Cliff, G., and Dudley, S. F. J. (1991). Sharks caught in the protective gill nets off Natal, South Africa. 5. The java shark *Carcharhinus amboinensis* (Muller and Henle). *South African Journal of Marine Science* **11**, 443–453.

Collins, A. B., Heupel, M. R., and Motta, P. J. (2007). Residence and movement patterns of cownose rays *Rhinoptera bonasus* within a south-west Florida estuary. *Journal of Fish Biology* **71**, 1159-1178.

Collins, A. B., Heupel, M. R., and Simpfendorfer, C. A. (2008). Spatial distribution and long-term movement patterns of cownose rays *Rhinoptera bonasus* within an estuarine river. *Estuaries and Coasts* **31**, 1174-1183.

Compagno, L. J. V. (1984). FAO species catalogue, Volume 4. Sharks of the world; an annotated and illustrated catalogue of shark species known to date, Part 2. Carcharhiniformes. *FAO Fisheries Synopsis* **125**, 461–463.

Conrath, C. L., and Musick, J. A. (2008). Investigations into depth and temperature habitat utilization and overwintering grounds of juvenile sandbar sharks, *Carcharhinus plumbeus*: the importance of near shore North Carolina waters. *Environmental Biology of Fishes* **82**, 123-131.

Constanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., et al. (1997). The value of the world's ecosystem services and natural capital. *Nature* **387**, 253-260.

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

Cortés, E. (2000). Life history patterns and correlations in sharks. *Reviews in Fisheries Science* **8**, 299-344.

Cortés, E. (2002). Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. *Conservation Biology* **16**, 1048-1062.

Cyrus, D. P., and Blaber, S. J. M. (1992). Turbidity and salinity in a tropical northern Australian estuary and their influence on fish distribution. *Estuarine, Coastal and Shelf Science* **35**, 545-563.

Dayton, P. K., Thrush, S. F., Agardy, M. T., and Hofman, R. J. (1995). Environmental effects of marine fishing. *Aquatic Conservation: Marine and Freshwater Ecosystems* **5**, 205-232.

de Morais, L. T., and Raffray, J. (1999). Movements of *Hoplias aimara* during the filling phase of the Petit-Saut dam, French Guyana. *Journal of Fish Biology* **54**, 627-635.

DeAngelis, B. M., McCandless, C. T., Kohler, N. E., Recksiek, C. W., and Skomal, G. B. (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.

DeMartini, E. E. (1993). Modeling the potential of fishery reserves for managing Pacific coral-reef fishes. *Fishery Bulletin* **91**, 414-427.

DeMaster, D. P., Fowler, C. W., Perry, S. L., and Richlen, M. E. (2001). Predation and competition: the impact of fisheries on marine-mammal populations over the next one hundred years. *Journal of Mammalogy* **82**, 641-651.

DiBattista, J. D., Feldheim, K. A., Thibert-Plante, X., Gruber, S. H., and Hendry, A. P. (2008). A genetic assessment of polyandry and breeding-site fidelity in lemon sharks. *Molecular Ecology* **17**, 3337-3351.

Duncan, K. M., and Holland, K. N. (2006). Habitat use, growth rates and dispersal patterns of juvenile scalloped hammerhead sharks *Sphyrna lewini* in a nursery habitat. *Marine Ecology Progress Series* **312**, 211-221.

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

Farrugia, T., Espinoza, M., and Lowe, C. (2011). Abundance, habitat use and movement patterns of the shovelnose guitarfish (*Rhinobatos productus*) in a restored southern California estuary. *Marine and Freshwater Research* **62**, 648-657.

Feldheim, K. A., Gruber, S. H., and Ashley, M. V. (2004). Reconstruction of parental microsatellite genotypes reveals female polyandry and philopatry in the lemon shark, *Negaprion brevirostris*. *Evolution* **58**, 2332-2342.

Fernandes, L., Day, J., Lewis, A., Slegers, S., Kerrigan, B., *et al.* (2005). Establishing representative no-take areas in the Great Barrier Reef: large-scale implementation of theory on Marine Protected Areas. *Conservation Biology* **19**, 1733-1744.

Fernando, P., Wikrarnanayake, E. D., Janaka, H. K., Jayasinghe, L. K. A., Gunawardena, M., *et al*. (2008). Ranging behavior of the Asian elephant in Sri Lanka. *Mammalian Biology* **73**, 2-13.

Finlayson, B. L., and McMahon, T. A. (1988). Australia vs the world: a comparative analysis of streamflow characteristics. In 'Fluvial Geomorphology of Australia'. (Ed. R. F. Warner.) pp. 17-40. (Academic Press: Sydney, Australia.)

Flannery, M. S., Peebles, E. B., and Montgomery, R. T. (2002). A percent-of-flow approach for managing reductions of freshwater inflows from unimpounded rivers to Southwest Florida estuaries. *Estuaries* **25**, 1318-1332.

Francis, M. P. (1998). New Zealand shark fisheries: development, size and management. *Marine and Freshwater Research* **49**, 579-591.

Fraser, T. H. (1997). Abundance, seasonality, community indices, trends and relationships with physicochemical factors of trawled fish in upper Charlotte Harbor, Florida. *Bulletin of Marine Science* **60**, 739-763.

Freitas, R. H. A., Rosa, R. S., Gruber, S. H., and Wetherbee, B. M. (2006). Early growth and juvenile population structure of lemon sharks *Negaprion brevirostris* in the Atol das Rocas Biological Reserve, off north-east Brazil. *Journal of Fish Biology* **68**, 1319-1332.

Garla, R. C., Chapman, D. D., Wetherbee, B. M., and Shivji, M. (2006). Movement patterns of young Caribbean 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.

Gell, F. R., and Roberts, C. M. (2003). Benefits beyond boundaries: the fishery effects of marine reserves. *Trends in Ecology & Evolution* **18**, 448-455.

Gelsleichter, J., Manire, C. A., Szabo, N. J., Cortés, E., Carlson, J., *et al*. (2005). Organochlorine concentrations in bonnethead sharks (*Sphyrna tiburo*) from four Florida estuaries. *Archives of Environmental Contamination and Toxicology* **48**, 474-483.

Gomelyuk, V. E. (2009). Fish assemblages composition and structure in three shallow habitats in north Australian tropical bay, Garig Gunak Barlu National Park, Northern Territory, Australia. *Journal of the Marine Biological Association of the United Kingdom* **89**, 449-460.

Grace, M., and Henwood, T. (1997). Assessment of the distribution and abundance of coastal sharks in the U.S. Gulf of Mexico and Eastern Seaboard, 1995 and 1996. *Marine Fisheries Review* **59**, 23-32.

Grubbs, R. D., Musick, J. A., Conrath, C. L., and Romine, J. G. (2007). Long-term movements, migration and temporal delineation of a summer nursery for juvenile sandbar sharks in the Chesapeake Bay region. In 'Shark Nursery Grounds of the Gulf of Mexico and the East Coast Waters of the United States'. (Eds. C. T. McCandless, N. E. Kohler and H. L. Pratt Jr.) pp. 87-107. (American Fisheries Society: Bethesda, USA.)

Grüss, A., Kaplan, D. M., Guénette, S., Roberts, C. M., and Botsford, L. W. (2011). Consequences of adult and juvenile movement for marine protected areas. *Biological Conservation* **144**, 692-702.

Halpern, B. S., and Warner, R. R. (2003). Matching marine reserve design to reserve objectives. *Proceedings of the Royal Society of London Series B-Biological Sciences* **270**, 1871-1878.

Harry, A. V., Tobin, A. J., Simpfendorfer, C. A., David, J. W., Mapleston, A., White, J., Williams, A. J., and Stapley, J. (2011). Evaluating catch and mitigating risk in a multispecies, tropical, inshore shark fishery within the Great Barrier Reef World Heritage Area. *Marine and Freshwater Research* **62**, 710-721.

Heck, K. L. Jr., Able, K. W., Roman, C. T., and Fahay, M. P. (1995). Composition, abundance, biomass, and production of macrofauna in a New England estuary - comparisons among eelgrass meadows and other nursery habitats. *Estuaries* **18**, 379-389.

Heithaus, M. R., Dill, L. M., Marshall, G. J., and Buhleier, B. M. (2002). Habitat use and foraging behaviour of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. *Marine Biology* **140**, 237-248.

Heithaus, M. R., Wirsing, A. J., Dill, L. M., and Heithaus, L. I. (2007). Long-term movements of tiger sharks satellite-tagged in Shark Bay, Western Australia. *Marine Biology* **151**, 1455-1461.

Heithaus, M. R., Frid, A., Wirsing, A. J., and Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution* **23**, 202-210.

Heithaus, M. R., Delius, B. K., Wirsing, A. J., and Dunphy-Daly, M. M. (2009). Physical factors influencing the distribution of a top predator in a subtropical oligotrophic estuary. *Limnology and Oceanography* **54**, 472-482.

Heupel, M. R. (2007). Exiting Terra Ceia Bay: an examination of cues stimulating migration from a summer nursery area. In 'Shark Nursery Grounds of the Gulf of Mexico and the East Coast Waters of the United States'. (Eds. C. T. McCandless, N. E. Kohler and H. L. Pratt Jr.) pp. 265-280. (American Fisheries Society: Bethesda, USA.)

Heupel, M. R., and Hueter, R. E. (2001). Use of an automated acoustic telemetry system to passively track juvenile blacktip shark movements. In ‘Electronic Tagging and Tracking in Marine Fisheries’. (Eds J. R. Sibert and J. L. Nielsen.) pp. 217-236. (Kluwer Academic Publishers: Dordrecht, The Netherlands.)

Heupel, M. R., and Simpfendorfer, C. A. (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, M. R., and Simpfendorfer, C. A. (2005). Using acoustic monitoring to evaluate MPAs for shark nursery areas: the importance of long-term data. *Marine Technology Society Journal* **39**, 10-18.

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

Heupel, M. R., and Simpfendorfer, C. A. (2010). Science of slaughter: need for lethal sampling of sharks. *Conservation Biology* **24**, 1212-1218.

Heupel, M. R., Simpfendorfer, C. A., and Hueter, R. E. (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, M. R., Simpfendorfer, C. A., and Hueter, R. E. (2004). Estimation of shark home ranges using passive monitoring techniques. *Environmental Biology of Fishes* **71**, 135-142.

Heupel, M. R., Semmens, J. M., and Hobday, A. J. (2006a). Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. *Marine and Freshwater Research* **57**, 1-13.

Heupel, M. R., Simpfendorfer, C. A., Collins, A. B., and Tyminski, J. P. (2006b). Residency and movement patterns of bonnethead sharks, *Sphyrna tiburo*, in a large Florida estuary. *Environmental Biology of Fishes* **76**, 47-67.

Heupel, M. R., Carlson, J. K., and Simpfendorfer, C. A. (2007). Shark nursery areas: concepts, definition, characterization and assumptions. *Marine Ecology Progress Series* **337**, 287-297.

Heupel, M. R., Yeiser, B. G., Collins, A. B., Ortega, L., and Simpfendorfer, C. A. (2010a). Long-term presence and movement patterns of juvenile bull sharks, *Carcharhinus leucas*, in an estuarine river system. *Marine and Freshwater Research* **60**, 1-10.

Heupel, M. R., Simpfendorfer, C. A., and Fitzpatrick, R. (2010b). Large-scale movement and reef fidelity of grey reef sharks. *PLoS ONE* **5**, e9650.

Hight, B. V., and Lowe, C. G. (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.

Hilborn, R., Stokes, K., Maguire, J. J., Smith, T., Botsford, L. W., *et al.* (2004). When can marine reserves improve fisheries management? *Ocean & Coastal Management* **47**, 197-205.

Holland, K. N., Lowe, C. G., and Wetherbee, B. M. (1996). Movements and dispersal patterns of blue trevally (*Caranx melampygus*) in a fisheries conservation zone. *Fisheries Research* **25**, 279-292.

Holland, K. N., Wetherbee, B. M., Lowe, C. G., and Meyer, C. G. (1999). Movements of tiger sharks (*Galeocerdo cuvier*) in coastal Hawaiian waters. *Marine Biology* **134**, 665-673.

Hueter, R. E., Heupel, M. R., Heist, E. J., and Keeney, D. B. (2005). Evidence of philopatry in sharks and implications for the management of shark fisheries. *Journal of Northwest Atlantic Fishery Science* **35**, 239-247.

Hussey, N. E., Wintner, S. P., Dudley, S. F. J., Cliff, G., Cocks, D. T., *et al*. (2010). Maternal investment and size-specific reproductive output in carcharhinid sharks. *Journal of Animal Ecology* **79**, 184-193.

Imansyah, M. J., Jessop, T. S., Ciofi, C., and Akbar, Z. (2008). Ontogenetic differences in the spatial ecology of immature Komodo dragons. *Journal of Zoology* **274**, 107-115.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., *et al.* (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**, 629-638.

Jenkins, G. P., and Wheatley, M. J. (1998). The influence of habitat structure on nearshore fish assemblages in a southern Australian embayment: Comparison of shallow seagrass, reef-algal and unvegetated sand habitats, with emphasis on their importance to recruitment. *Journal of Experimental Marine Biology and Ecology* **221**, 147-172.

Jennings, D. E., Gruber, S. H., Franks, B. R., Kessel, S. T., and Robertson, A. L. (2008). Effects of large-scale anthropogenic development on juvenile lemon shark (*Negaprion brevirostris*) populations of Bimini, Bahamas. *Environmental Biology of Fishes* **83**, 369-377.

Johnston, I. A., and Bennett, A. F. (1996). 'Animals and Temperature: Phenotypic and Evolutionary Adaptation'. (Cambridge University Press: Cambridge, Great Britain.)

Keeney, D. B., Heupel, M. R., Hueter, R. E., and Heist, E. J. (2005). Microsatellite and mitochondrial DNA analyses of the genetic structure of blacktip shark (*Carcharhinus limbatus*) nurseries in the northwestern Atlantic, Gulf of Mexico, and Caribbean Sea. *Molecular Ecology* **14**, 1911-1923.

Kemp, W. M., Boynton, W. R., Adolf, J. E., Boesch, D. F., Boicourt, W. C., *et al.* (2005). Eutrophication of Chesapeake Bay: historical trends and ecological interactions. *Marine Ecology Progress Series* **303**, 1-29.

Kerwath, S. E., Thorstad, E. B., Naesje, T. F., Cowley, P. D., Okland, F., *et al*. (2009). Crossing invisible boundaries: the effectiveness of the Langebaan Lagoon Marine Protected Area as a harvest refuge for a migratory fish species in South Africa. *Conservation Biology* **23**, 653-661.

Kinney, M. J., and Simpfendorfer, C. A. (2008). Reassessing the value of nursery areas to shark conservation and management. *Conservation Letters* **2**, 1-8.

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

Kramer, D. L., and Chapman, M. R. (1999). Implications of fish home range size and relocation for marine reserve function. *Environmental Biology of Fishes* **55**, 65-79.

Last, P. R., and Stevens, J. D. (2009). 'Sharks and Rays of Australia'. 2nd edition. (CSIRO Publishing: Melbourne, Australia.)

Latrubesse, E. M., Stevaux, J. C., and Sinha, R. (2005). Tropical rivers. *Geomorphology* **70**, 187-206.

Lavery, S., and Shaklee, J. B. (1989). Population genetics of two tropical sharks, *Carcharhinus tilstoni* and *C. sorrah*, in Northern Australia. *Australian Journal of Marine and Freshwater Research* **40**, 541-547.

Lowe, C. G. (2002). Bioenergetics of free-ranging juvenile scalloped hammerhead sharks (*Sphyrna lewini*) in Kāne'ohe Bay, Ō'ahu, HI. *Journal of Experimental Marine Biology and Ecology* **278**, 141-156.

Lowe, C. G., Wetherbee, B. M., Crow, G. L., and Tester, A. L. (1996). Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. *Environmental Biology of Fishes* **47**, 203-211.

Lowe, C. G., Topping, D. T., Cartamil, D. P., and Papastamatiou, Y. P. (2003) Movement patterns, home range, and habitat utilization of adult kelp bass *Paralabrax clathratus* in a temperate no-take marine reserve. *Marine Ecology Progress Series* **256**, 205-216.

Loyn, R. H., McNabb, E. G., Volodina, L., and Willig, R. (2001). Modelling landscape distributions of large forest owls as applied to managing forests in north-east Victoria, Australia. *Biological Conservation* **97**, 361-376.

Lynch, A. M. J., Sutton, S. G., and Simpfendorfer, C. A. (2010). Implications of recreational fishing for elasmobranch conservation in the Great Barrier Reef Marine Park. *Aquatic Conservation: Marine and Freshwater Ecosystems* **20**, 312-318.

Macpherson, E. (1998). Ontogenetic shifts in habitat use and aggregation in juvenile sparid fishes. *Journal of Experimental Marine Biology and Ecology* **220**, 127-150.

Madsen, T., and Shine, R. (1996). Seasonal migration of predators and prey - a study of pythons and rats in tropical Australia. *Ecology* **77**, 149-156.

Malavasi, S., Franco, A., Riccato, F., Valerio, C., Torricelli, P., and Franzoi, P. (2007). Habitat selection and spatial segregation in three pipefish species. *Estuarine, Coastal and Shelf Science* **75**, 143-150.

Manire, C. A., and Gruber, S. H. (1993). A preliminary estimate of natural mortality of age-0 lemon sharks, *Negaprion brevirostris*. *NOAA Technical Report, NMFS* **115**, 65-71.

Mann, K. H. (2000). ‘Ecology of Coastal Waters with Implications for Management.’ (Blackwell Publishing: Malden, USA.)

Masselink, G., Austin, M., Tinker, J., O'Hare, T., and Russell, P. (2008). Cross-shore sediment transport and morphological response on a macrotidal beach with intertidal bar morphology, Truc Vert, France. *Marine Geology* **251**, 141-155.

McAuley, R. B., Simpfendorfer, C. A., Hyndes, G. A., and Lenanton, R. C. J. (2007). Distribution and reproductive biology of the sandbar shark, *Carcharhinus plumbeus* (Nardo), in Western Australian waters. *Marine and Freshwater Research* **58**, 116-126.

McElroy, W. D., Wetherbee, B. M., Mostello, C. S., Lowe, C. G., Crow. G. L., *et al*. (2006). Food habits and ontogenetic changes in the diet of the sandbar shark, *Carcharhinus plumbeus*, in Hawaii. *Environmental Biology of Fishes* **76**, 81-92.

McNeill, S. E. (1994). The selection and design of marine protected areas: Australia as a case study. *Biodiversity and Conservation* **3**, 586-605.

Medved, R. J., and Marshall, J. A. (1983). Short term movements of young sandbar sharks, *Carcharhinus plumbeus* (Pisces, Carcharhinidae). *Bulletin of Marine Science* **33**, 87-93.

Merson, R. R., and Pratt, H. L. Jr. (2001). Distribution, movements and growth of young sandbar sharks, *Carcharhinus plumbeus*, in the nursery grounds of Delaware Bay. *Environmental Biology of Fishes* **61**, 13-24.

Meyer, C. G., Holland, K. N., and Papastamatiou, Y. P. (2007). Seasonal and diel movements of giant trevally *Caranx ignobilis* at remote Hawaiian atolls: implications for the design of Marine Protected Areas. *Marine Ecology Progress Series* **333**, 13-25.

Meyer, C. G., Clark, T. B., Papastamatiou, Y. P., Whitney, N. M., and Holland, K. N. (2009). Long-term movement patterns of tiger sharks *Galeocerdo cuvier* in Hawaii. *Marine Ecology Progress Series* **381**, 223-235.

Mol, J. H., Resida, D., Ramlal, J. S., and Becker, C. R. (2000). Effects of El Niño-related drought on freshwater and brackish-water fishes in Suriname, South America. *Environmental Biology of Fishes* **59**, 429-440.

Morin, B., Hudon, C., and Whoriskey, F. G. (1992). Environmental influences on seasonal distribution of coastal and estuarine fish assemblages at Wemindji, eastern James Bay. *Environmental Biology of Fishes* **35**, 219-229.

Morrissey, J. F., and Gruber, S. H. (1993a). Home range of juvenile lemon sharks, *Negaprion brevirostris*. *Copeia* **1993**, 425-434.

Morrissey, J. F., and Gruber, S. H. (1993b). Habitat selection by juvenile lemon sharks, *Negaprion brevirostris*. *Environmental Biology of Fishes* **38**, 311-319.

Mucientes, G. R., Queiroz, N., Sousa, L. L., Tarroso, P., and Sims, D. W. (2009). Sexual segregation of pelagic sharks and the potential threat from fisheries. *Biology Letters* **5**, 156-159.

Musick, J. A., Burgess, G., Cailliet, G., Camhi, M., and Fordham, S. (2000). Management of sharks and their relatives (Elasmobranchii). *Fisheries* **25**, 9-13.

Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P., and Peterson, C. H. (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* **315**, 1846-1850.

National Oceanic and Atmospheric Administration (NOAA). (1998). Oxygen depletion in coastal waters. In 'NOAA's State of the Coast Report'. (Ed. N. N. Rabalais.) pp. 1-16. (NOAA: Silver Spring, USA.) Available at http://oceanservice.noaa.gov/websites/retiredsites/sotc_pdf/HYP.PDF [Verified 4 November 2010].

Nixon, S. W. (1995). Coastal marine eutrophication - a definition, social causes, and future concerns. *Ophelia* **41**, 199-219.

Parsons, G. R., and Hoffmayer, E. R. (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.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. (1998). Fishing down marine food webs. *Science* **279**, 860-863.

Perna, C., and Burrows, D. (2005). Improved dissolved oxygen status following removal of exotic weed mats in important fish habitat lagoons of the tropical Burdekin River floodplain, Australia. *Marine Pollution Bulletin* **51**, 138-148.

Pihl, L., Baden, S. P., and Diaz, R. J. (1991). Effects of periodic hypoxia on distribution of demersal fish and crustaceans. *Marine Biology* **108**, 349-360.

Pikitch, E. K., Chapman, D. D., Babcock, E. A., and Shivji, M. S. (2005). Habitat use and demographic population structure of elasmobranchs at a Caribbean atoll (Glover's Reef, Belize). *Marine Ecology Progress Series* **302**, 187-197.

Pradervand, F., Mann, B. Q., and Bellis, M. F. (2007). Long-term trends in the competitive shore fishery along the KwaZulu-Natal coast, South Africa. *African Zoology* **42**, 216-236.

Pratt, H. L. Jr., and Carrier, J. C. (2001). A review of elasmobranch reproductive behavior with a case study on the nurse shark, *Ginglymostoma cirratum*. *Environmental Biology of Fishes* **60**, 157-188.

R Development Core Team (2009). 'R: A Language and Environment for Statistical Computing'. (R Foundation for Statistical Computing: Vienna, Austria.)

Rayner, T. S., Pusey, B. J., and Pearson, R. G. (2008). Seasonal flooding, instream habitat structure and fish assemblages in the Mulgrave River, northeast Queensland: towards a new conceptual framework for understanding fish-habitat dynamics in small tropical rivers. *Marine and Freshwater Research* **59**, 97-116.

Rettie, W. J., and Messier, F. (2000). Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* **23**, 466-478.

Reyier, E. A., Adams, D. H., and Lowers, R. H. (2008). First evidence of a high density nursery ground for the lemon shark, *Negaprion brevirostris*, near Cape Canaveral, Florida. *Florida Scientist* **71**, 134-148.

Roberts, C. M. (2000). Selecting marine reserve locations: optimality versus opportunism. *Bulletin of Marine Science* **66**, 581-592.

Roberts, C. M., Bohnsack, J. A., Gell, F., Hawkins, J. P., and Goodridge, R. (2001) Effects of marine reserves on adjacent fisheries. *Science* **294**, 1920-1923.

Robertson, A. I., and Duke, N. C. (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.

Rodriguez, R. W., Webb, R. M. T., and Bush, D. M. (1994). Another look at the impact of hurricane Hugo on the shelf and coastal resources of Puerto Rico, USA. *Journal of Coastal Research* **10**, 278-296.

Rooney, N., McCann, K., Gellner, G., and Moore, J. C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature* **442**, 265-269.

Rosenberger, A., and Angermeier, P. L. (2003). Ontogenetic shifts in habitat use by the endangered Roanoke logperch (*Percina rex*). *Freshwater Biology* **48**, 1563-1577.

Russ, G. R., and Alcala, A. C. (1996). Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Marine Ecology Progress Series* **132**, 1-9.

Russ, G. R., and Alcala, A. C. (2011). Enhanced biodiversity beyond marine reserve boundaries: The cup spillith over. *Ecological Applications* **21**, 241-250.

Sale, P. F., Cowen, R. K., Danilowicz, B. S., Jones, G. P., Kritzer, J. P., *et al.* (2005). Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology & Evolution* **20**, 74-80.

Salini, J. P., Blaber, S. J. M., and Brewer, D. T. (1992). Diets of sharks from estuaries and adjacent waters of the northeastern Gulf of Carpentaria, Australia. *Australian Journal of Marine and Freshwater Research* **43**, 87-96.

Scruton, D. A., Pennell, C. J., Robertson, M. J., Ollerhead, L. M. N., Clarke, K. D., *et al*. (2005). Seasonal response of juvenile Atlantic salmon to experimental hydropeaking power generation in Newfoundland, Canada. *North American Journal of Fisheries Management* **25**, 964-974.

Seaman, D. E., and Powell, R. A. (1996). An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* **77**, 2075-2085.

Shears, N. T., Grace, R. V., Usmar, N. R., Kerr, V., and Babcock, R. C. (2006). Long-term trends in lobster populations in a partially protected vs. no-take Marine Park. *Biological Conservation* **132**, 222-231.

Short, F. T., and Wyllie-Echeverria, S. (1996). Natural and human-induced disturbance of seagrasses. *Environmental Conservation* **23**, 17-27.

Simpfendorfer, C. (1993). The Queensland shark meshing program: analysis of the results from Townsville, north Queensland. In ‘Shark Conservation. Proceedings of an International Workshop on the Conservation of Elasmobranchs held at Taronga Zoo, Sydney, Australia, 24 February 1991’. (Eds. J. G. Pepperell, J. West and P. Woon.) pp. 71-85. (Zoological Parks Boards of NSW: Mosman, Australia.)

Simpfendorfer, C. A., and Milward, N. E. (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, C. A., Heupel, M. R., and Hueter, R. E. (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, C. A., Freitas, G. F., Wiley, T. R., and Heupel, M. R. (2005). Distribution and habitat partitioning of immature bull sharks (*Carcharhinus leucas*) in a Southwest Florida Estuary. *Estuaries* **28**, 78-85.

Simpfendorfer, C. A., Wiley, T. R., and Yeiser, B. G. (2010). Improving conservation planning for an endangered sawfish using data from acoustic telemetry. *Biological Conservation* **143**, 1460-1469.

Simpfendorfer, C. A., Yeiser, B. G., Wiley, T. R., Poulakis, G. R., Stevens, P. W., *et al*. (2011a). Environmental influences on the spatial ecology of juvenile smalltooth sawfish (*Pristis pectinata*): results from acoustic monitoring. *PLoS ONE* **6**, e16918.

Simpfendorfer, C. A., Heupel, M. R., White, W. T., and Dulvy, N. K. (2011b). The importance of research and public opinion to conservation management of sharks and rays: a synthesis. *Marine and Freshwater Research* **62**, 518-527.

Sims, D. W. (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, D. W., Nash, J. P., and 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, D. W., Wearmouth, V. J., Southall, E. J., Hill, J. M., Moore, P., *et al.* (2006). Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. *Journal of Animal Ecology* **75**, 176-190.

Smith, G. R. T., Learner, M. A., Slater, F. M., and Foster, J. (1996). Habitat features important for the conservation of the native crayfish *Austropotamobius pallipes* in Britain. *Biological Conservation* **75**, 239-246.

Smith, S. D. A., Rule, M. J., Harrison, M., and Dalton, S. J. (2008). Monitoring the sea change: preliminary assessment of the conservation value of nearshore reefs, and existing impacts, in a high-growth, coastal region of subtropical eastern Australia. *Marine Pollution Bulletin* **56**, 525-534.

Smith, S. E., and Abramson, N. J. (1990). Leopard shark *Triakis semifasciata* distribution, mortality rate, yield, and stock replenishment estimates based on a tagging study in San Francisco Bay. *Fisheries Bulletin* **88**, 371-381.

Smith, S. E., Au, D. W., and Show, C. (1998). Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine and Freshwater Research* **49**, 663-678.

Snelson, F. F., and Bradley, W. K. (1978). Mortality of fishes due to cold on the east coast of Florida, January, 1977. *Florida Scientist* **41**, 1-12.

Sobel, J., and Dahlgren, C. (2004). 'Marine Reserves: a Guide to Science, Design, and Use'. (Island Press: Washington DC, USA.)

Sogard, S. M., Powell, G. V. N., and Holmquist, J. G. (1989). Utilization by fishes of shallow, seagrass-covered banks in Florida Bay 2: Diel and tidal patterns. *Environmental Biology of Fishes* **24**, 81-92.

Spina, A. P. (2000). Habitat partitioning in a patchy environment: considering the role of intraspecific competition. *Environmental Biology of Fishes* **57**, 393-400.

Springer, S. (1950). Natural history notes on the lemon shark, *Negaprion brevirostris*. *Texas Journal of Science* **2**, 349-359.

Springer, S. (1960). Natural history of the sandbar shark, *Eulamia milberti*. *Fisheries Bulletin* **61**, 1-38.

Springer, S. (1967). Social organisation of shark populations. In 'Sharks, Skates and Rays'. (Eds P. W. Gilbert, R. F. Matheson and D. P. Rall.) pp. 149-174. (John Hopkins Press: Baltimore, USA.)

Steele, M. A. (1998). The relative importance of predation and competition in two reef fishes. *Oecologia* **115**, 222-232.

Steiner, P. A., and Michel, M. (2007). Effects of tidal current on the movement patterns of juvenile bull sharks and blacktip sharks. In 'Shark Nursery Grounds of the Gulf of Mexico and the East Coast Waters of the United States'. (Eds. C. T. McCandless, N. E. Kohler and H. L. Pratt Jr.) pp. 251-264. (American Fisheries Society: Bethesda, USA.)

Stevens, J. D., and Wiley, P. D. (1986). Biology of two commercially important Carcharhinid sharks from Northern Australia. *Australian Journal of Marine and Freshwater Research* **37**, 671-688.

Stevens, J. D., and McLoughlin, K. J. (1991). Distribution, size and sex composition, reproductive biology and diet of sharks from Northern Australia. *Australian Journal of Marine and Freshwater Research* **42**, 151-199.

Stevens, J. D., Bonfil, R., Dulvy, N. K., and Walker, P. A. (2000a). The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* **57**, 476-494.

Stevens, J. D., West, G. J., and McLoughlin, K. J. (2000b). Movements, recapture patterns, and factors affecting the return rate of Carcharhinid and other sharks tagged off Northern Australia. *Marine and Freshwater Research* **51**, 127-141.

Stokesbury, M. J. W., Harvey-Clark, C., Gallant, J., Block, B. A., and Myers, R. A. (2005). Movement and environmental preferences of Greenland sharks (*Somniosus microcephalus*) electronically tagged in the St. Lawrence Estuary, Canada. *Marine Biology* **148**, 159-165.

Stoner, A. W. (2004). Effects of environmental variables on fish feeding ecology: implications for the performance of baited fishing gear and stock assessment. *Journal of Fish Biology* **65**, 1445-1471.

Suchanek, T. H. (1994). Temperate coastal marine communities: biodiversity and threats. *American Zoologist* **34**, 100-114.

Swingland, I. R., and Lessells, C. M. (1979). Natural regulation of giant tortoise populations on Aldabra Atoll. Movement polymorphism, reproductive success and mortality. *Journal of Animal Ecology* **48**, 639-654.

Ter Morshuizen, L. D., Whitfield, A. K., and Paterson, W. (1996). Influence of freshwater flow regime on fish assemblages in the Great Fish River and estuary. *South African Journal of Aquatic Science* **22**, 52-61.

Thomas, W. H., and Seibert, D. L. R. (1977). Effects of copper on dominance and diversity of algae - controlled ecosystem pollution experiment. *Bulletin of Marine Science* **27**, 23-33.

Thrush, S. F., Hewitt, J. E., Cummings, V., Ellis, J. I., Hatton, C., *et al*. (2004). Muddy waters: elevating sediment input to coastal and estuarine habitats. *Frontiers in Ecology and the Environment* **2**, 299-306.

Tillett, B. J., Meekan, M. G., Field, I. C., Hua, Q., and Bradshaw, C. J. A. (2011). Similar life history traits in bull (*Carcharhinus leucas*) and pig-eye (*C. amboinensis*) sharks. *Marine and Freshwater Research* **62**, 850-860.

Tilman, D., and Kareiva, P. (1997). ‘Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions’. (Princeton University Press: Princeton, New Jersey.)

Turley, C. M. (1999). The changing Mediterranean Sea - a sensitive ecosystem? *Progress in Oceanography* **44**, 387-400.

Ubeda, A. J., Simpfendorfer, C. A., and Heupel, M. R. (2009). Movements of bonnetheads, *Sphyrna tiburo*, as a response to salinity change in a Florida estuary. *Environmental Biology of Fishes* **84**, 293-303.

Ulrich, G. F., Jones, C. M., Driggers, W. B. III., Drymon, J. M., Oakley, D., *et al*. (2007). Habitat utilization, relative abundance, and seasonality of sharks in the estuarine and nearshore waters of South Carolina. In 'Shark Nursery Grounds of the Gulf of Mexico and the East Coast Waters of the United States'. (Eds. C. T. McCandless, N. E. Kohler and H. L. Pratt Jr.) pp. 125-139. (American Fisheries Society: Bethesda, USA.)

Valeix, M., Chamaille-Jammes, S., and Fritz, H. (2007). Interference competition and temporal niche shifts: elephants and herbivore communities at waterholes. *Oecologia* **153**, 739-748.

Valiela, I., Bowen, J. L., and York, J. K. (2001). Mangrove forests: one of the world's threatened major tropical environments. *BioScience* **51**, 807-815.

van Dolah, R. F., Calder, D. R., and Knott, D. M. (1984). Effects of dredging and open water disposal on benthic macroinvertebrates in a South Carolina estuary. *Estuaries* **7**, 28-37.

Vitousek, P. M., Mooney, H. A., Lubchenco, J., and Melillo, J. M. (1997). Human domination of earth's ecosystems. *Science* **277**, 494-499.

Voegeli, F. A., Smale, M. J., Webber, D. M., Andrade, Y., and O'Dor, R. K. (2001). Ultrasonic telemetry, tracking and automated monitoring technology for sharks. *Environmental Biology of Fishes* **60**, 267-281.

Walker, T. (1981). Seasonal salinity variations in Cleveland Bay, northern Queensland. *Australian Journal of Marine and Freshwater Research* **32**, 143-149.

Walker, T. I. (1998) Can shark resources be harvested sustainably? A question revisited with a review of shark fisheries. *Marine and Freshwater Research* **49**, 553-572.

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

Ward, A. J. W., Hensor, E. M. A., Webster, M. M., and Hart, P. J. B. (2010). Behavioural thermoregulation in two freshwater fish species. *Journal of Fish Biology* **76**, 2287-2298.

Weng, K. C., Foley, D. G., Ganong, J. E., Perle, C., Shillinger, G. L., *et al*. (2008). Migration of an upper trophic level predator, the salmon shark *Lamna ditropis*, between distant ecoregions. *Marine Ecology Progress Series* **372**, 253-264.

Wetherbee, B. M., and Rechisky, E. L. (1999). Movement patterns of juvenile sandbar sharks on their nursery grounds in Delaware Bay. In 'Biotelemetry 15: Proceedings of the 15th International Symposium on Biotelemetry'. (Eds. J. H. Eiler, D. J. Alcorn and M. R. Neuman.) pp. 91-98. (International Society on Biotelemetry: Wageningen, The Netherlands.)

Wetherbee, B. M., Crow, G. L., and Lowe, C. G. (1996). Biology of the Galapagos shark, *Carcharhinus galapagensis*, in Hawai'i. *Marine Biology* **45**, 299-310.

Wetherbee, B. M., Rechisky, E. L., Pratt, H. L. Jr., and McCandless, C. T. (2001). Use of telemetry in fisheries management: juvenile sandbar sharks in Delaware Bay. In 'Electronic Tagging and Tracking in Marine Fisheries'. (Eds. J. R. Sibert and J. L. Nielsen.) pp. 249-262. (Kluwer Academic Publishers: Dordrecht, The Netherlands.)

Wetherbee, B. M., Gruber, S. H., and Rosa, R. S. (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.

White, W. T., and Potter, I. C. (2004). Habitat partitioning among four elasmobranch species in nearshore, shallow waters of a subtropical embayment in Western Australia. *Marine Biology* **145**, 1023-1032.

Whitfield, A. K., and Paterson, A. W. (1995). Flood-associated mass mortality of fishes in the Sundays Estuary. *Water Sa* **21**, 385-389.

Whitty, J. M., Morgan, D. L., Peverell, S. C., Thorburn, D. C., and Beatty, S. J. (2009). Ontogenetic depth partitioning by juvenile freshwater sawfish (*Pristis microdon*: Pristidae) in a riverine environment. *Marine and Freshwater Research* **60**, 306-316.

Wiegand, J., Hunter, E., and Dulvy, N. K. (2011). Are spatial closures better than size limits for halting the decline of the North Sea thornback ray, *Raja clavata*? *Marine and Freshwater Research* **62**, 722-733.

Willis, T. J., Millar, R. B., and Babcock, R. C. (2003). Protection of exploited fish in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. *Journal of Applied Ecology* **40**, 214-227.

Winemiller, K. O., and Jepsen, D. B. (1998). Effects of seasonality and fish movement on tropical river food webs. *Journal of Fish Biology* **53**, 267-296.

Wood, L. J., Fish, L., Laughren, J., and Pauly, D. (2008) Assessing progress towards global marine protection targets: shortfalls in information and action. *Oryx* **42**, 340-351.

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**, 164-168.