Chin, Andrew (2013) ***The biology and ecology of the blacktip reef shark Carcharhinus melanopterus (Quoy & Gaimard, 1824) and implications for management.*** **PhD Thesis, James Cook University.**

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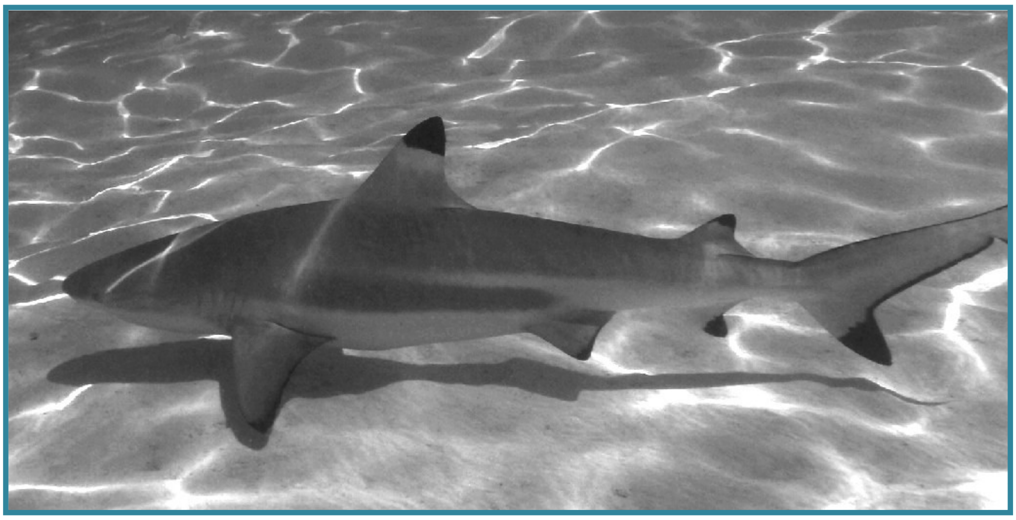

Thesis by

Andrew Chin B. Sc. (Hons)

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School of Earth and Environmental Sciences

James Cook University

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Contribution of others to this thesis

The Queensland Department of Education, Employment, Development and Innovation (DEEDI).

- Fisheries observer data from the Queensland commercial fisheries observer program (Chapter 2)
- Vertebrae samples and capture data from the Queensland Shark Control Program (Chapters 3 and 4)

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Cairns Marine

- Vertebrae samples from two blacktip reef sharks (Chapter 4)

Reef HQ

- Housing four blacktip reef sharks in aquaria for 15 months for age and growth studies (Chapter 4)
- Observations on mating in captive specimens (Chapters 3 and 4)

Daydream Island resort

- Observations on the growth and development of four neonate blacktip reef sharks born in captivity (Chapters 3 and 4)

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Statement of Ethics

The research presented and reported in this thesis was conducted in compliance with the National Health and Medical Research Council (NHMRC) Australian Code of Practice for the Care and Use of Animals for Scientific Purposes, 7th Edition, 2004, and the Qld Animal Care and Protection Act, 2001. The proposed research study received animal ethics approval from the JCU Animal Ethics Committee Approval Number A1566.

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(Chapter 4) Chin A, Simpfendorfer CA, Tobin AJ, Heupel MR (2013) Validated age, growth and reproductive biology of *Carcharhinus melanopterus*, a widely distributed and exploited reef shark. *Marine and Freshwater Research*.

(Chapter 3) Chin A, Tobin AJ, Heupel MR, Simpfendorfer CA (2013) Population structure and residency patterns of the blacktip reef shark *Carcharhinus melanopterus* in turbid coastal environments. *Journal of Fish Biology*, **82**: 1192-1210.

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Other publications (co-authored publications and publications not directly contributing to the thesis)

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Chin A, (2013) *Citizen science and the Great Barrier Reef: a scoping study for the eReefs project*. Great Barrier Reef Marine Park Authority and the Great Barrier Reef Foundation, 126p.

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Chin A, Sweatman H, Forbes S, Perks H, Walker R, Jones G, Williamson D, Evans R, Hartley F, Armstrong S, Malcolm H, Edgar G (2008) Status of coral reefs in Australia and Papua New Guinea. In: Wilkinson C (ed) *Status of the coral reefs of the world: 2008*. Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre, Townsville, pp296

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1. Introduction

The chondrichthyan fishes (sharks, rays and chimaeras) are a widely distributed group of fishes with representatives present in every marine region of the world except the Antarctic (Musick *et al.*, 2004). As a group, the chondrichthyan fishes are often regarded as top-level predators that can have significant effects on prey populations, and potentially on other components of the ecosystem (Heithaus, 2004, Stevens *et al.*, 2000). Sharks and rays are also important components of the global fisheries production (Clarke *et al.*, 2005, Vannuccini, 1999) and some species are especially important to tourism (Anderson, 2002, Clua *et al.*, 2011, Stoeckl *et al.*, 2010, Vianna *et al.*, 2012). Australia's Great Barrier Reef World Heritage Area (GBRWHA) has a diverse range of sharks and rays, indeed, northern Australia and Indonesia have amongst the world's highest levels of chondrichthyan fish diversity and endemism (Musick *et al.*, 2004, White & Kyne, 2010). The sharks and rays of the GBRWHA are also socially, culturally and economically important and may perform important ecological roles (Chin, 2005). However, as in many locations around the world, the chondrichthyan fishes of the GBRWHA are affected by numerous pressures and there is increasing concern over the conservation and management of these species (GBRMPA, 2009). This project focuses on the blacktip reef shark (*Carcharhinus melanopterus*), a widely distributed, medium sized reef shark that ranges from the western Indian Ocean to the central Pacific (Hawaii and French Polynesia). The blacktip reef shark is one of the most commonly encountered and recognised sharks by divers and fishers visiting coral reef habitats (Last & Stevens, 2009). While considered to be a reef species, the blacktip reef shark has also been recorded in non-reef habitats such as muddy foreshores and mangrove habitats. In spite of its wide distribution and iconic status, relatively little is known about its biology and life history (Heupel, 2005). This research project addresses these knowledge gaps, and provides information that will support the management and conservation of this species in the GBRWHA, and throughout the Pacific and Indian Oceans.

1.1 Biology of sharks and rays

The chondrichthyan fishes (sharks, rays and chimaeras – henceforth referred to as 'sharks and rays') – are a morphologically and ecologically diverse group of some 1,200 extant species (Fowler *et al.*, 2005). While being a diverse group of fishes, sharks and rays share many common biological and life history traits that affect both their ecology and vulnerability to impacts. All chondrichthyan fishes lack ossified (bony) bones and instead, have a skeleton comprised of lighter and more flexible cartilage. Additionally, while sharks and rays exhibit a range of reproductive strategies (Carrier *et al.*, 2004), their life history patterns are generally characterised by slow growth, late sexual maturity, long life span and gestation periods and relatively low fecundity compared to teleost (bony) fishes (Cortés, 2000). These traits typify the 'K-selected' life history traits of many sharks and rays (Cortés, 2004, Smith *et al.*, 1998), with examples of strongly K-selected species including the dusky shark (*Carcharhinus obscurus*) which grows to a large size, has slow growth, late age at maturity, large offspring size, small litter sizes, and prolonged reproductive cycles (Romine *et al.*, 2009, Simpfendorfer *et al.*, 2002b). Another example is the bull shark (*Carcharhinus leucas*) which is also a large-bodied, late maturing species that may have a life span of over 50 years (Wintner *et al.*, 2002). Deep water sharks and rays such as chimaeras (Chimaeridae), hardnose skates (Rajidae), dogfishes (Squalidae) and lanternsharks (Etmopteridae) have especially strong K-selected life history traits (Simpfendorfer & Kyne, 2009).

The K-selected life history traits of many sharks and rays have been widely reported to contribute to the vulnerability of some species to pressures such as fishing and habitat loss (Camhi *et al.*, 1998, Cortés, 2004, Dulvy *et al.*, 2008, Fowler *et al.*, 2005, Simpfendorfer *et al.*, 2011). For instance, fishing pressure on the common skate (*Raja batis*) led to its extirpation in parts of its range (Brander, 1981), and is suspected of driving declines in reef sharks such as the grey reef shark (*Carcharhinus amblyrhynchos*) and whitetip reef shark (*Triaenodon obesus*) in coral reef ecosystems (Friedlander & DeMartini, 2002, Graham *et al.*, 2010, Heupel *et al.*, 2009, Nadon *et al.*, 2012, Robbins *et al.*, 2006). Other examples of fisheries effects on sharks include declines in school shark populations (*Galeorhinus galeus*) in southern Australia (Punt & Walker, 1998) and the eastern Pacific (Ripley, 1946);

thresher sharks on the west coast of the United States (Holts, 1988); and declines in a range of coastal sharks and rays in southeast Asia (Blaber *et al.*, 2009, White & Kyne, 2010). There are also suspected declines in populations from other regions in the Pacific although there are few data on the status of these populations (Chin *et al.*, 2011). Additionally, strongly K-selected sharks and rays have a low capacity for population recovery which means that recovery from depletion may take decades, or even centuries (Simpfendorfer, 2000, Simpfendorfer & Kyne, 2009).

Declines in highly K-selected sharks and rays have also been caused by their incidental catch (or bycatch) in fisheries targeting other species, or as byproduct (unintended catch that is kept due to its commercial value). Bycatch has also contributed population declines in sawfishes (*Pristis spp.*) – the sawfishes' toothed rostra make them susceptible entanglement in nets and their life history traits reduce their ability to sustain fishing mortality (Simpfendorfer, 2000). In Australia, trawl fisheries targeting deepwater redfish (*Centroberyx affinis*), gemfish (*Rexea solandri*) and mirror dory (*Zenopsis nebulosus*) in New South Wales have driven severe declines in many deep water sharks such as gulper sharks (*Centrophorus spp.*) (Graham *et al.*, 2001, Graham & Daley, 2011).

While many sharks and rays are strongly K-selected species, it is important to consider that some of these life history traits vary between species, and that species conservation and fisheries management should be based on species-specific biology and life history information (Simpfendorfer *et al.*, 2011). Cortés (2000) found that while pelagic sharks generally grow to a large size and have a long life span, some species such as the blue shark (*Prionacea glauca*) also have large litter sizes. This increases their reproductive output which, combined with their wide distribution, reduces their vulnerability to fishing (Smith *et al.*, 1998). Furthermore, some coastal sharks such as the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*), Australian sharpnose shark (*Rhizoprionodon taylori*) and bonnethead shark (*Sphyrna tiburo*) are characterised by their short life spans, small to moderate body size, small-sized offspring and high growth rates (Cortés, 2000, Cortés, 2004, Harry *et al.*, 2010, Simpfendorfer, 1998, Smith *et al.*, 1998). These species also have higher rebound potential and are less susceptible to fishing pressure (Cortés, 2004, Smith *et al.*, 1998). With careful management and good information, these faster growing species can sustain viable commercial fisheries, with the gummy shark (*Mustelus antarcticus*) being a commonly cited example of a shark fishery showing stable catches over multiple decades (Prince, 2005, Walker, 1998). Even strongly K-selected species such as the dusky shark can sustain stable commercial harvests given appropriate management (McAuley *et al.*, 2007a). Consequently, the generalisation that all sharks and rays are highly vulnerable to anthropogenic pressures needs to be tempered with an understanding of their biology and life history.

1.2 Ecology, behaviour and habitat use of sharks and rays

Sharks and rays are thought to play important ecological roles in marine systems through ‘top down’ control of prey populations, and thus, are reported to be important to maintaining healthy ecosystems (Heithaus, 2004). For example, ecosystem models have suggested that removal of tiger sharks from tropical reef systems could result in cascade effects that eventually cause the decline of fishes (Stevens *et al.*, 2000). The presence of sharks may also affect the habitat use of other species such as turtles and dugongs which play important roles in the ecology of coastal habitats such as seagrasses (Heithaus *et al.*, 2002, Wirsing *et al.*, 2007, Wirsing *et al.*, 2008). Top level predators can also affect species richness and the processes determining the development of fish communities (Chase *et al.*, 2009). Nevertheless, it is important to remember that while ecological theory and modeling suggest that these links exist, collecting this information in the field is extraordinarily difficult and as yet there is little empirical evidence to quantify the nature and strength of these ecosystem links (Heithaus, 2004).

As a group, sharks and rays show a diverse range of distribution, behaviour and habitat use patterns. They occur in a wide range of marine ecosystems ranging from shallow estuaries to bathyal habitats (Compagno, 1990), and range from tropical zones to the Arctic polar regions (Musick *et al.*, 2004). Some sharks and rays such as sawfishes (*Pristis* spp.) and bull sharks (*C. leucas*) also use freshwater systems (Compagno, 2002, Pillans *et al.*, 2005, Whitty *et al.*, 2009). Information on the spatial ecology of sharks and rays is plentiful with research conducted on numerous species and their movement, behaviour and habitat associations.

Research on the movement and habitat use of sharks and rays covers a wide range of topics such as the effects of environmental factors on behaviour and habitat use (e.g. Ackerman *et al.*, 2000, Heupel *et al.*, 2003, Hight & Lowe, 2007, Knip *et al.*, 2011b); interactions such as competition and predation within and between shark communities and their prey (e.g. Bethea *et al.*, 2004, Dill *et al.*, 2003, Heithaus *et al.*, 2002); spatial and temporal patterns in distribution and habitat use (e.g. Andrews *et al.*, 2010, Carlson *et al.*, 2008, Heupel *et al.*, 2006, Speed *et al.*, 2010, Taylor, 1996, Yeiser *et al.*, 2008); and the effects of human activities on these patterns (e.g. Clua *et al.*, 2010, Fitzpatrick *et al.*, 2011, Gaspar *et al.*, 2008). This research has revealed complex patterns of behaviour and habitat use that vary between species and locations, with numerous biological, ecological and environmental factors driving these patterns. The coastal zone is an area of particular interest in studies of shark and ray ecology, with interest in the roles these habitats may play in sustaining populations as well as the roles sharks and rays perform themselves in structuring and regulating these systems (Knip *et al.*, 2010, Simpfendorfer *et al.*, 2011).

While research on spatial ecology and critical habitat dependencies are certainly important for the conservation and management of some species (e.g. the gummy shark), further work is still needed. There is inconsistency in the literature about how critical habitats are defined and identified. As such, further research on the spatial ecology of sharks and rays will provide valuable information about the biology and ecology of a given species (e.g. ontogenetic changes in habitat use and the factors driving these patterns), and may contribute to the conservation and management of sharks and rays (e.g. identifying critical habitats, assessing the efficacy of marine protected areas, identifying the effects of habitat degradation on shark and ray populations) (Simpfendorfer *et al.*, 2011).

1.3 The social and economic significance of sharks and rays

As well as (potentially) being crucial to the functioning of marine ecosystems, sharks and rays are socially and economically important and are harvested for meat, fins, liver oil, leather, and a wide range of other products (Clarke *et al.*, 2005, Vannuccini, 1999). The United Nations Food and Agricultural Organisation (FAO) Fishstat Capture Production database has recorded an increase in global shark catches steadily rising from about 626,000 metric tonnes in 1985 to 899,771 tonnes in 2003, with reported catches subsequently declining to 180,000 tonnes in 2007 (Clarke *et al.*, 2005, Lack & Sant, 2009). While harvests have consistently increased since the 1950s, increasing demand for shark fins has driven a rapid increase in landings, especially since the 1980s (Camhi *et al.*, 1998, Clarke *et al.*, 2005). Sharks and rays are also taken in artisanal and subsistence fisheries and are important to local economies and food security in communities in Africa, Asia and SE Asia, and Oceania (Barnett, 1996a, Camhi *et al.*, 1998, Marshall, 1996a, Teh *et al.*, 2007, White & Kyne, 2010). Sharks and rays may also indirectly contribute to fisheries and income. In the Maldives, fishermen believe that if they remove all the pelagic sharks, catches of tuna will decline because the sharks cause the tuna to form schools close to the surface, making them accessible to fishers (Anderson & Hafiz, 2002). Similarly, these tuna fishers rely on small live baitfish collected from reefs, and believe that reef sharks drive baitfish to congregate in schools that are easy to catch (Anderson & Hafiz, 2002). These fishers have also complained that overfishing of reef sharks (and other reef predators) in the Maldives has reduced the availability of bait fish (Anderson & Hafiz, 2002).

Sharks and rays are also important for non-extractive use, particularly tourism. Shark tourism includes specialised operations focused on large charismatic species such as whale sharks (*Rhincodon typus*), white sharks (*Carcharodon carcharias*) and manta rays (*Manta spp.*), and in tropical coral reef systems, diving and snorkeling activities to view reef sharks and rays (Anderson, 2002, Clarke *et al.*, 2005, Clua *et al.*, 2011, Stoeckl *et al.*, 2010). In some developing countries, the income generated from shark associated tourism is considerable, and has prompted some island nations and territories in the Pacific such as Palau and French Polynesia to introduce nation-wide bans on shark fishing (Chin *et al.*, 2011, Vianna *et al.*, 2010, Vianna *et al.*, 2012).

1.4 The global status of sharks and rays

Globally, there has been increasing interest and concern in the conservation of sharks and rays (Simpfendorfer *et al.*, 2011). As previously described, sharks and rays are generally considered to be vulnerable to fishing pressure due to their slow growth, low reproductive output and longevity, and there are numerous examples of declining or depleted populations that may require decades to recover (Camhi *et al.* 1998; Dulvy *et al.* 2000; Simpfendorfer 2000). However, sharks and rays are also affected by other issues such as habitat loss and degradation (Stevens *et al.*, 2005, Walker, 2002) and global issues such as climate change (Chin *et al.*, 2010).

While numerous threats to sharks have been documented and numerous species have been assessed as being threatened with extinction, the status and trends in global shark populations is less certain. There are few long term datasets available on trends in shark populations, and these data are usually proxy data from fisheries records. The FAO collates fisheries data from member nations and compiles statistics in a database of global catches. Unfortunately, there is considerable uncertainty in FAO fisheries landings data and issues in reporting, species identification, compliance and Illegal, Unregulated and Unreported (IUU) fishing make it difficult to accurately assess status and trends (Clarke *et al.*, 2005). As historically sharks were low value products, relatively little attention has been paid to monitoring status and trends in shark catches and the difficulties in species identification compound reporting errors (Camhi *et al.*, 1998, Lack & Sant, 2009). Additionally, many sharks may be taken as incidental bycatch or byproduct and thus tend to be poorly recorded (Bonfil, 1994, Camhi *et al.*, 1998, Clarke *et al.*, 2005). Global trends in shark catch may also be masked by fishing mobility with fishers moving to new locations as exploited fishing grounds are depleted (Clarke *et al.*, 2005). Certainly there is evidence of regional declines in sharks in areas such as Indonesia, with fishers moving to new locations to target sharks and rays (Field *et al.*, 2009). The problems these issues create in estimating the global status and trends of sharks through catch data are clearly demonstrated in statistics for the trade of shark fins, where FAO estimates of global shark fin production, imports and exports in 2000 were significantly lower than imports of unprocessed fins entering Hong Kong in the same year (Clarke *et al.*, 2005, Clarke *et al.*, 2004). Rough estimates suggest that the actual catch of sharks and rays may be double the catch recorded in the FAO database, which would equate to approximately 82 million sharks and rays taken in 2000 (Clarke *et al.*, 2006), and potentially, up to 100 million sharks and rays in 2003. While accurate and precise estimates for the global catch of sharks and rays are not available, it is clear that many populations of sharks and rays have declined, and that pressures on sharks and rays are increasing (Stevens *et al.*, 2005, Walker, 2002). Altogether, some 20% of the sharks and rays that have been assessed by the World Conservation Union are listed as 'threatened' (IUCN, 2008b), but more information is needed to clarify the status and trends of regional populations which in turn, will help to clarify their global status.

1.5 The sharks and rays of Australia's Great Barrier Reef

Australia's Great Barrier Reef World Heritage Area (GBRWHA) region stretches for 2,300 km along the east coast of Queensland, and covers approximately 350,000 km^2. The GBRWHA ecosystem consists of a diverse range of interconnected habitats of which coral reefs only comprise between 5% and 7% by area (GBRMPA, 2009, Hutchings *et al.*, 2008). The coastal environs of the GBRWHA include habitats such as rivers, floodplains, mangroves, salt marshes and seagrass beds. Further offshore, lesser known deepwater sponge and soft coral habitats, algal beds, deep seagrass beds, rocky shoals and seabed habitats of the continental shelf (up to 200 m depth) account for over 60% of the region's area. A further 31% of the area is comprised of continental slope habitats (200 m to 1000 m depth) and deep oceanic waters (>1000 m depth) that are mostly unexplored (GBRMPA 2009). Altogether, some 70 distinct bioregions (areas of relatively uniform habitats, communities and physical characteristics) have been identified and represent great diversity (Hutchings *et al.* 2008; GBRMPA 2009). This diversity extends to sharks and rays with some 133 species from 41 families recorded from the GBRWHA, including a particularly high proportion of Australian endemics (Chin *et al.*, 2010, Kyne *et al.*, 2005, Last & Stevens, 2009).

The sharks and rays of the GBRWHA are morphologically and ecologically diverse, occurring in habitats ranging from freshwater river systems to pelagic waters and bathyal (deep water) habitats of the continental slope. They also exhibit complex patterns of habitat use, and sharks and rays may use specific habitats at various stages of their life cycle. For example, Simpfendorfer and Milwood (1993) proposed that Cleveland Bay in the central region of the GBRWHA may serve as a coastal nursery ground for a number of sharks and rays. The environmental conditions and characteristics of different habitats may also affect the distribution and composition of GBRWHA shark communities (Knip *et al.*, 2011b), as well as factors such as prey availability and predators (Kinney *et al.*, 2011).

1.5.1 The significance of sharks and rays in the GBRWHA

Sharks and rays are important components of the GBRWHA ecosystem. As previously described, sharks and rays are often reported to play important ecological roles in marine ecosystems, indeed, management authorities in the GBRWHA list these ecological roles as one of the attributes underpinning management concern for these species (GBRMPA, 2009). Sharks and rays are also important components of commercial fisheries in the GBRWHA which include the East Coast Inshore Finfish Fishery (ECIFF – henceforth referred to as the GBR net fishery) and the Great Barrier Reef (GBR) Coral Reef Finfish Fishery. The GBR net fishery is the largest and most diverse fishery on the Queensland east coast with fishers using nets and lines to target a wide range of finfish species (Queensland Department of Primary Industries and Fisheries, 2008). While many species are taken, sharks comprise the main component of the catch (by weight) taken by this fishery (Simpfendorfer *et al.*, 2007). The catch of sharks in GBR net fishery steadily increased between 1988 (when catch reporting began) and 2003, from 329 tonnes in 1988 to 1,202 tonnes in 2003 (Queensland Department of Primary Industries and Fisheries, 2011). Similarly, the value of sharks taken in GBR net fishery from GBRWHA waters has increased over time, rising from \$1.9 million in 1988 to a peak of \$7.2 million in 2003, before declining to $3.8 million in 2005 (Queensland Department of Primary Industries and Fisheries, 2011). This decline reflects a decline in shark catch, most likely driven by management changes and the re-adjustment of the fishery including license ‘buy-outs’ (Queensland Department of Primary Industries and Fisheries, 2008). Nevertheless, sharks remain a major component of GBR net fishery catch and value, comprising approximately 40% of the fishery’s Gross Value of Production (GVP) in 2005 ($3.8 million of a total fishery GVP of $9.3 million) (Queensland Department of Primary Industries and Fisheries, 2011). Sharks are also taken in the GBR Coral Reef Finfish Fishery (CRFF), with grey reef sharks (*Carcharhinus amblyrhynchos*), whitetip reef sharks (*Triaenodon obesus*) and blacktip reef sharks (*Carcharhinus melanopterus*) accounting for the vast majority of the CRFF shark catch (Heupel *et al.*, 2009). However, unlike GBR net fishery which includes specialist shark fishers, the sharks taken in the CRFF are largely caught as bycatch while targeting more valuable teleost fishes such as coral trout (*Plectropomus spp.*) (Gribble *et al.*, 2005, Heupel *et al.*, 2009). Nevertheless, sharks caught in the CRFF are often retained as byproduct for meat and fins and thus, provided supplementary fisheries products in the CRFF. In 2009, new management arrangements set restrictions on the number of sharks fishers in both the CRFF and GBR net fishery can retain (either as catch or bycatch) and currently, only specialist shark fishers with a ‘S’ symbol license can retain commercially significant quantities of sharks (Queensland Primary Industries and Fisheries, 2009).

Sharks are also valued by recreational users of the GBRWHA. Recreational fishing is a popular activity that occurs in a wide range of GBRWHA habitats, and fishers catch a range of shark and rays species. While species specific catch data are limited, recreational fishers appear to keep relatively few sharks compared to more highly valued species (Lyle *et al.*, 2003), and many recreational fishers place a high value on releasing sharks and rays alive and in good condition (Lynch *et al.*, 2010). Sharks are also valued by snorkellers and SCUBA divers, with SCUBA divers visiting the GBRWHA reporting positive experiences from interactions with sharks and rays (Whatmough *et al.*, 2011). Surveys of divers on multi-day dive expeditions in the GBRWHA revealed that divers placed a high value on seeing sharks and rays, and would pay more for guaranteed sightings of sharks and rays than they would for other reef species (Stoeckl *et al.*, 2010).

Aboriginal and Torres Strait Islander communities in the GBRWHA also value sharks and rays for their cultural significance as well as supplying an important source of protein for some communities. In some communities, rays are traditionally hunted at the start of the wet season following the first rains and the flowering of certain plants (Chin, 2005). While providing food, the act of hunting and gathering sharks and rays is also culturally important (Henry & Lyle, 2003, Saunders & Carne, 2010, Smith, 1987). A number of Traditional Owner groups in the GBRWHA also have spiritual connections with sharks and rays, with these species featuring in stories, oral histories and as symbols and totems (Chin, 2005).

1.5.2 The status of sharks and rays in the GBRWHA

In spite of the ecological, social and economic importance of sharks and rays in the GBRWHA, relatively little is known about the status of these species (Chin 2005). Similar to many other locations around the world, information about the population status of sharks and rays in the GBR is limited to data from fisheries records. While catch and effort data for fisheries in the GBRWHA are available from 1988, these data are compromised by the same problems evident in shark fisheries around the world: poor reporting of species specific information (catch has been recorded as "Shark – unspecified"); difficulties with species identification; and a lack of validation of reported catch and effort data (Chin, 2005, GBRMPA, 2007). Given the lack of species specific population trend data, the status of sharks and rays in the GBRWHA is often described in the context of risk assessments. The International Union for the Conservation and Nature (IUCN) Shark Specialist Group (SSG) assessed the conservation status of sharks in Australasia and found that the proportion of threatened sharks and rays in the Australasian region is similar to global trends, and assessed 16 species of sharks and rays in the GBRWHA as being either *Vulnerable*, *Endangered* or *Critically Endangered* (Cavanagh *et al.*, 2003). These species include sawfishes (*Pristis spp.*), several rays species and iconic species such as the whale shark (*R. typus*), white shark (*C. carcharias*) and grey nurse shark (*Carcharias taurus*) (Cavanagh *et al.*, 2003). Many of these species are protected under Commonwealth and Queensland State legislation (Chin, 2005).

Increasing interest and focus on sharks and rays in the GBRWHA in the last decade has resulted in recent research that is providing new information about the status of these species. Risk assessments have been completed using the information available on species-specific interactions with fisheries, and their biology and life history. Gribble *et al.* (2005) used limited fishery observer data available (4 observer trips) for GBR net fishery to identify the catch composition of the fishery and assess the risks to sharks and rays. This preliminary assessment identified a range of species as being “at risk” to fishing pressure. Additional information was collected and applied in a subsequent risk assessment (Salini *et al.*, 2007) for northern Australia, which also identified numerous species as potentially being at risk from fishing pressure. These assessments have been used by GBR net fishery Scientific Advisory Group to identify the risks to sharks and rays taken in the fishery. Sharks and rays assessed as being at ‘High risk’ include the sawfishes (*Pristis spp.*) and some reef sharks, while species at moderate risk include 11 whaler sharks (Carcharhinidae) (GBRMPA, 2007). Unfortunately, these assessments are somewhat compromised by their dependence on proxy biological and life history data collected on conspecifics in other regions. Comparative studies have documented that the biology and life history traits of sharks and rays can significantly vary between locations (Carlson *et al.*, 2006, Cope, 2006, Driggers *et al.*, 2004, Lombardi-Carlson *et al.*, 2003, Yamaguchi *et al.*, 2000) and consequently, using proxy data from a different region can compromise the accuracy of risk assessments.

The status of some sharks and rays in the GBRWHA has also been inferred from spatial and temporal comparisons. Studies on reef sharks suggest that populations have declined with significantly fewer sharks found in fished areas compared to areas where fishing pressure is reduced (Robbins *et al.* 2006; Heupel *et al.* 2009). However, these spatial and temporal comparisons are not available for other species. Nevertheless, increasing catches, reported declines, risk assessments and consideration of their potential vulnerability to fishing pressure contributed to the introduction of a range of new fisheries management arrangements for shark fisheries in 2009 (Queensland Primary Industries and Fisheries, 2006, Queensland Primary Industries and Fisheries, 2009).

The lack of information about the biology, ecology, life history, fisheries interactions and status of sharks and rays in the GBRWHA has complicated efforts to assess impacts from fishing, habitat loss and climate change on these populations (Chin, 2005, Chin *et al.*, 2010, GBRMPA, 2009). While declines in two reef shark species are evident, data about the status and trends of other species are equivocal. Furthermore, there is little information about how the two main management tools affecting sharks and rays; zoning in the Great Barrier Reef Marine Park and revised fisheries regulations, contribute to the long-term protection and sustainable use of these fishes. These knowledge gaps include species-specific and regionally appropriate information about the biology, life history and spatial ecology of these species, as well as their interactions with anthropogenic impacts (GBRMPA, 2010, Simpfendorfer *et al.*, 2011).

1.6 The blacktip reef shark: background and knowledge gaps

The blacktip reef shark *Carcharhinus melanopterus* (Quoy & Gaimard, 1824) is a medium-sized carcharhinid (whaler) shark that is widely distributed across the central and western tropical Indo-Pacific, and has invaded the eastern Mediterranean via the Suez Canal. In Australia, the species occurs across northern Australia from Moreton Bay (southern Queensland) on the east coast to Shark Bay on the west coast (Last & Stevens, 2009). However, records from Moreton Bay are from reported visual observations (P. Kyne pers comm.) and the species has not been observed by commercial fishers or divers in the region (S. Taylor pers comm.). It is possible that this was a misidentification as tropical coral reef habitats only extend to Bundaberg (several hundred kilometers to the north), and misidentifications of this species have occurred in other locations (Yano & Morrissey, 1999). Together with the whitetip reef shark and grey reef shark, the blacktip reef shark is one of the most commonly encountered sharks on coral reefs but it is also observed in other habitats including coastal mangroves and occasionally in brackish waters (Last &

Stevens, 2009). The species often occurs in water just a few metres deep and small specimens may be observed along beaches in depths of less than a metre (Papastamatiou *et al.*, 2009b, Stevens, 1984).

1.6.1 Biology and ecology of the blacktip reef shark

Studies in Australian waters suggest that blacktip reef sharks predominantly prey upon teleost fishes (Lyle, 1987) but also consume small numbers of molluscs and crustaceans. Interestingly, surveys in Darwin harbour demonstrated that the species also eats sea snakes (Lyle & Timms, 1987). They also appear to eat turtle hatchlings around coral cays (A. Chin pers obs). There are no accounts of ontogenetic shifts in diet between juveniles and adults. While being a widely distributed, recognisable and commonly encountered reef shark, surprisingly little is known about the species' biology and ecology. A literature review on ISI Web of Science retrieved 71 references regarding the blacktip reef shark, however, most of the literature focuses on anatomy and physiology, parasitology and animal husbandry with only 14 papers on biology and ecology. Of these publications, only three included life history and biology data from wild animals. Additionally, these studies have documented a range of values for life history parameters (Table 1.1) which vary between locations. Lastly, while some life history parameters have been investigated, several important biological parameters remain unknown including:

- Age at maturity
- Average reproductive age
- Rate of population increase
- Longevity
- Mortality rate
- Growth parameters (e.g. maximum size, growth rate)

The data that are available about the species have also been collected from a variety of locations. Intra-specific variation between populations in different locations has been documented in a number of sharks. Carlson *et al.* (2003) found differences in the length-at-maturity of finetooth sharks (*Carcharhinus isodon*) between stocks from South Carolina and those from the Gulf of Mexico, and growth rates and age at maturity of blacknose sharks (*Carcharhinus acronatus*) have been found to differ between the Atlantic and the Gulf of Mexico (Driggers *et al.*, 2004). The length and age at maturity, and growth rate of the bonnethead shark (*Sphyrna tiburo*) increases with increasing latitude (Lombardi-Carlson *et al.*, 2003), and latitudinal changes in other parameters have been recorded (Cope, 2006). Thus, while it is possible to use proxy data from other regions to define demographic parameters and construct risk assessments for the blacktip reef shark in the GBRWHA, this would introduce greater uncertainty and increase the likelihood of errors in such assessments.

1.6.2. Spatial ecology of the blacktip reef shark

The movement and habitat use of blacktip reef sharks has been studied in several isolated coral atoll habitats. Stevens (1984) studied the movement patterns of blacktip reef sharks at Aldabra Atoll in the Indian Ocean by tag-recapture and visual tracking methods. The study found that blacktip reef sharks have small home ranges of only a few square kilometers and that most individuals remained in the lagoon throughout the tidal cycle, moving with the tide. There appeared to be little interchange between individuals from opposite ends of the lagoon (~34 km). Papastamatiou *et al.* (2009) studied the movement and habitat use of blacktip reef sharks at Palmyra Atoll in the northern Line Islands in the central Pacific. This study also found that blacktip reef sharks had small home ranges of <1 km^2 and showed strong site fidelity to shallow sand flats. Ontogenetic shifts in habitat use were also observed with adult sharks showing greater use of deeper reef ledge habitats compared with neonate and young of the year (YOY) animals only recorded in very shallow sand-flat habitats close to the shore, often in water <10 cm deep and these habitats may function as nursery grounds (Papastamatiou *et al.*, 2009a, Papastamatiou *et al.*, 2009b). Blacktip reef sharks have also been observed in non-reef habitats such as mangroves and coastal foreshores (Last & Stevens, 2009, Lyle & Timms, 1987), but their occurrence in and use of these habitats has not been studied and the significance of these habitats to the species is not known.

1.6.3. Threats, status and conservation

As a widely distributed species living in shallow coral reef habitats, the blacktip reef shark is exposed to a variety of human impacts. Blacktip reef sharks are taken for meat and fins in artisanal fisheries in Africa including countries such as Eritrea (Marshall, 1996b), Somalia (Marshall, 1996a), Tanzania and Zanzibar (Barnett, 1996b), and are also taken in inshore fisheries India and Thailand (Compagno, 1984). Blacktip reef sharks are also taken in coastal fisheries in South East Asian countries such as Malaysia and Indonesia (Teh *et al.*, 2007, White, 2007). In Australian waters, the blacktip reef shark is taken in coastal net fisheries and coral reef line fisheries from Western Australia, the Northern Territory and Queensland (Gribble *et al.*, 2005, Heupel *et al.*, 2009, Rose *et al.*, 2003, Salini *et al.*, 2007).

Use of coral reef and coastal habitats may also expose blacktip reef sharks to impacts from habitat loss and degradation which globally, pose significant pressure on sharks and rays (Stevens *et al.*, 2005, Walker, 2002). Coastal habitats and coral reefs are some of the most degraded and impacted marine habitats (Halpern *et al.*, 2008, Hughes *et al.*, 2003). For example, coastal development, sedimentation and pollution are universal issues affecting coral reefs throughout the world (Chin *et al.*, 2011, Hughes, 2009) including Queensland and the GBR (Brodie & Fabricius, 2009, GBRMPA, 2009). These pressures can translate to effects on sharks and rays using these habitats. For example, lemon sharks (*Negaprion brevirostris*) have been affected by coastal development in the Caribbean (Jennings *et al.*, 2008), and the impacts of climate change on coastal habitats and processes are predicted to affect sharks and rays in the GBRWHA (Chin *et al.*, 2010). In the GBRWHA, the coastal zone is where most of the GBR net fishery activity occurs (GBRMPA, 2009), but it is also the location of numerous marine park zoning arrangements that prohibit or restrict the types of net fishing activities that are most likely to catch blacktip reef sharks.

While several pressures are likely to affect the blacktip reef shark, the condition and trends of populations around the world (including the GBRWHA) are unknown. The IUCN Red List assessed the blacktip reef shark as being ‘Near Threatened’ and suggests that populations are declining globally (Heupel, 2005, Heupel, 2009), and noted that its distribution and use of shallow habitats make it accessible to artisanal fisheries. While it does not appear to be a major component of reported fisheries catches, what is known about the biology of the species suggests that it could be vulnerable to over-exploitation due to its potential accessibility to fishing and its apparently low reproductive output. In the GBRWHA, Gribble *et al.* (2005) noted that increases in fishing pressure would dramatically increase the sustainability risk for this species.

1.7 Project approach, aims and objectives

This project aimed to provide new information on the biology and ecology of the blacktip reef shark to address key knowledge gaps and provide information that informs the conservation and management of the blacktip reef shark.

This thesis uses a vulnerability assessment approach that has been applied in a variety of fisheries and natural resource management contexts. This approach has been taken because vulnerability assessments provide a useful framework for organising and integrating different types of information. Vulnerability frameworks have been used to assess a variety of fisheries related risks including the risks to bycatch species such as sea snakes and turtles (Griffiths *et al.*, 2006, Milton, 2001) and sharks and rays (Stobutzki *et al.*, 2002); the economic risks climate change poses to fisheries (Fletcher, 2005); sustainability and risks of targeted fishing for sharks and rays (Salini *et al.*, 2007, Walker, 2005a), and a wide range of other fisheries (see Hobday *et al.*, 2007 for review). Australian fisheries have used vulnerability frameworks which compare a species' susceptibility to the fishery against its productivity to describe sustainability (Gribble *et al.*, 2005, Hobday *et al.*, 2007, Salini *et al.*, 2007, Stobutzki *et al.*, 2001). Vulnerability frameworks are also used in assessing the vulnerability of species and systems to climate change (Chin *et al.*, 2010, Füssel & Klein, 2006, Johnson & Marshall, 2007).

In spite of the diversity of approaches, most vulnerability frameworks used to describe human-environment systems contain common conceptual elements (Adger, 2006): the **exposure** of the assessment entity (e.g. a species) to risk factors; the **sensitivity** of the assessment entity to the risks identified; and the **adaptive**

capacity of the species to cope with the risk factors (Adger, 2006). These three components (or ‘dimensions’) and their interactions describe the characteristics of the entity being assessed, the relationships between these characteristics and external factors, and integrate this information to estimate relative risk (Polsky *et al.*, 2007) (see Fig 1.1). In this project, a vulnerability framework is used to identify and contextualize information about the biology, life history and spatial ecology of the blacktip reef shark, to describe the species’ exposure to pressures from fishing and habitat degradation, and to describe the consequences of these interactions for the conservation and management of the species (Fig 1.1).

1.7.1 Specific project aims and thesis structure

Based on the previously identified knowledge gaps and the implications of these data for the conservation and management of the species, this project is has four discrete aims, each of which is designed to explore critical aspects of the blacktip reef shark’s biology, ecology and conservation.

Aim 1 (chapter 2): quantify the catch of blacktip reef sharks in the GBR net fishery and describe trends in catch locations and fate of captured sharks. This will document the interactions between the blacktip reef shark and the largest shark fishery operating in the GBRWHA. This information will describe the **exposure** of the species to fishing pressure which is currently believed to be the most significant pressure facing sharks and rays in the GBRWHA, and provide preliminary information about the blacktip reef shark’s occurrence amongst the various habitats of the GBRWHA.

Aim 2 (chapter 3): describe the population characteristics of blacktip reef sharks in the GBRWHA lagoon. The project will describe the structure of blacktip reef shark populations in the coastal and inshore regions of the GBRWHA and identify patterns in sex composition and sexual maturity of individuals in a population. The timing and location of critical life history events (e.g. mating, parturition) will also be identified, and population movements (immigration, emigration, dispersal, site fidelity) will be documents. Collectively, these data will help to determine the

exposure and **sensitivity** of the blacktip reef shark to anthropogenic factors such as fishing and habitat degradation.

Aim 3 (chapter 4): describe the biology and life history of the blacktip reef shark. The project will provide the first description of the age and growth parameters of the species, and will also provide regionally relevant and validated life history and reproductive parameters such as reproductive periodicity, litter size and size at maturity data. These data will help to assess the species **sensitivity** to pressures such as fishing and habitat loss.

Aim 4 (chapters 5 and 6): describe the movement and habitat use patterns of the blacktip reef shark in the GBRWHA lagoon. The project will document the species' movement and habitat use patterns at a variety of temporal scales to identify critical habitats and movement corridors. The behavior of the blacktip reef shark will also be examined, and the coverage provided by marine park zoning will also be explored. These data will provide information on the species' **exposure** to anthropogenic pressures, and **sensitivity** and **adaptive capacity** to these pressures.

The penultimate chapter of the thesis (chapter 7) will draw these elements together to discuss the significance of these data in advancing scientific understanding of the biology and ecology of the study species and the interactions between coastal habitats and sharks and rays, and through the vulnerability framework, provide a comprehensive account of the vulnerability of this species to fishing and habitat loss.

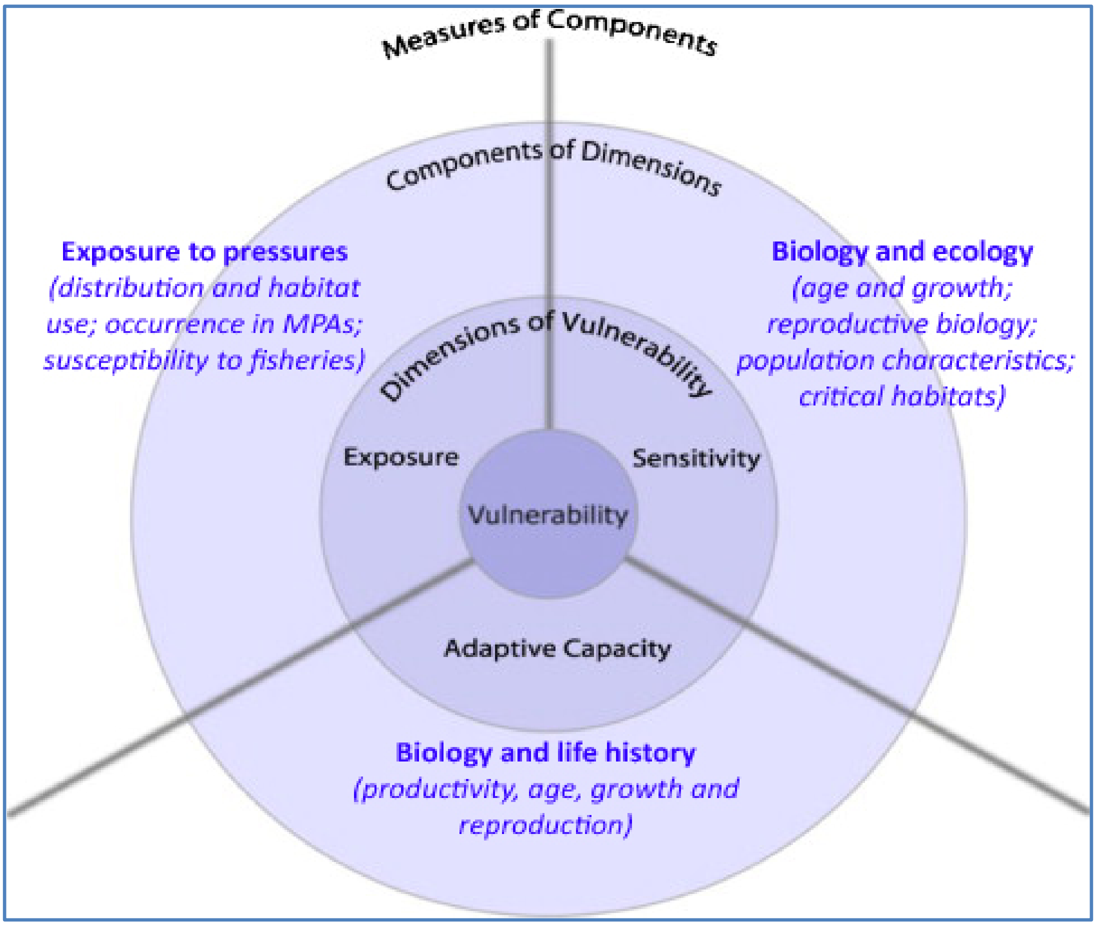


Figure 1**.** The vulnerability framework used in this thesis to organise and present information about the biology and ecology of the blacktip reef shark (adapted from Polsky *et al.*, 2007).

Source	Location	Mating (m), Ovulation (o) parturition (p)	Reprod. Cycle	Gestation period	No. of pups	Size at birth (TL)	Male length (TL) at maturity (bold) and sizes	Female length (TL) at maturity (bold) and sizes	Diet	Comments
(1) Goahar & Mazhar 1964 (2) Melouk 1957	Red Sea	(p) Jan and Jun[1]	Biannual	16 months[2]	–	–	–	–	–	Cited in Lyle 1987
Fourmanoir 1961	Madagascar	–	Biannual		–	–	–	–	–	Cited in Lyle 1987
Johnson 1978	French Polynesia	–	Biannual	–	–	–	–	–	–	Cited in Lyle 1987
(Stevens, 1984)	Indian Ocean	(o & m) Oct to Nov (p) Oct	Biannual	10 - 11 months	4	50cm	**105 cm** (max size 130 cm)	**110 cm** (max size 140 cm)	Teleosts, crustaceans, molluscs, cephalopods	Growth rate 3.5cm y^{-1}, movement restricted to small distances with the atoll
(Lyle, 1987, Lyle & Timms, 1987)	Nth Australia	(m) Jan to Mar (o) Feb to Mar (p) Oct to Nov	Annual	7 - 9 months	3-4	46 - 48cm	**93 – 95 cm** (max size 125cm)	**91 – 97 cm** (max size 125cm)	Teleosts, sea snakes, molluscs, crustaceans	135 specimens examined
(Taylor & Wisner, 1989)	Commercial aquaria	–	–	–	–	–	–	–	–	Growth rate 0.33mm.day^{-1} to 0.57mm.day^{-1}. Proportional to food ration
(Porcher, 2005)	French Polynesia	(m) Nov to Mar (p) Sept to Jan	Annual	9 - 10 months	–	–	–	–	–	Observational data from divers. Females mating 1.5 to 2.5 months after birth
(White, 2007)	Indonesia	(p) Aug to Sept	–	–	3	50.0 - 54.0cm	**108 cm** (size range 50-131 cm)	**>120cm** (size range 52-142 cm)	–	59 samples, only 2 mature females
(Papastamatiou *et al.* 2009a)	Palmyra Atoll (Central Pacific)		–	–	–		**94-102 cm** (size range 34-119 cm)	(size range 37-137 cm)	Teleosts, seabirds, rats	125 male and 129 females measured, bimodal population structure (no sub-adults), Growth rat 50 mm yr^{-1}

Table 1: Published life history data on the blacktip reef shark showing a range of size and maturity values between different locations. There are no published data on the age and growth of the blacktip reef shark.

2. Reef sharks and inshore habitats of the Great Barrier Reef: fisheries interactions, distribution and vulnerability

2.1 Introduction

The world's coral reefs support a diverse group of chondrichthyan fishes (henceforth referred to as reef sharks), ranging from large, mobile species up to 3 m in length (e.g. the lemon shark *Negaprion acutidens*), to small, cryptic reef species (e.g. the epaulette shark, *Hemiscyllium ocellatum*). Reef sharks are generally considered to be high order predators in reef ecosystems where they may exert 'top down' control of food webs (Heithaus *et al.*, 2008, Stevens *et al.*, 2000). In economic terms, reef sharks are an important source of income as a living attraction for dive tourism (Anderson, 2002, Clua *et al.*, 2011, Fitzpatrick *et al.*, 2011), and contribute to subsistence and commercial fisheries throughout the tropics (Barnett, 1996a, Teh *et al.*, 2007, White & Kyne, 2010). However, many sharks are long-lived, slow growing animals with relatively low reproductive rates (Cortés, 2000) and there are numerous examples of shark populations that have experienced over-exploitation and collapse due to fishing (Dulvy *et al.*, 2008, Fowler *et al.*, 2005, Graham *et al.*, 2001, Simpfendorfer, 2000, White & Kyne, 2010). There is also growing concern over the status of sharks on coral reefs (Jackson *et al.*, 2001, Pandolfi *et al.*, 2003), with recent studies suggesting reef shark declines in the main Hawaiian Islands and the Line Islands in the Pacific (Friedlander & DeMartini, 2002, Nadon *et al.*, 2012, Stevenson *et al.*, 2007), the Indian Ocean (Graham *et al.*, 2010), and the Great Barrier Reef (GBR) (Heupel *et al.*, 2009, Robbins, 2006). There are also anecdotal reports of declines in reef shark populations on coral reefs around numerous Pacific islands (Chin *et al.*, 2011). These concerns have given rise to numerous shark risk assessments ranging from global (Fowler *et al.*, 2005) to topical assessments for specific fisheries (Salini *et al.*, 2007, Tobin *et al.*, 2010) and climate change (Chin *et al.*, 2010).

Reef shark distribution and habitat use patterns need to be considered in conservation risk assessments, in planning conservation and management responses, and in sampling design for reef shark studies. Many tropical elasmobranchs, including reef sharks, have complex movement patterns across a range of spatial and temporal scales, which may include use of a range of habitat types and seasonal aggregations (White & Sommerville, 2010). These spatial use patterns affect the vulnerability of reef sharks to pressures such as fisheries and climate change (Chin *et al.*, 2010). Complex habitat use patterns may also produce skewed data in studies that do not consider these issues. For example, population structuring of blacktip reef sharks (*Carcharhinus melanopterus*) as evident in some locations (Papastamatiou *et al.*, 2009a), could lead to sampling bias in studies that only sampled those areas. Habitat use patterns are also important in risk assessments when defining groups or species assemblages. For example, previous studies have defined reef sharks as those species thought to depend on coral reef environments (Chin *et al.*, 2010), or those listed as occurring in coral reef habitats according to species lists and catalogues (Ward-Paige *et al.*, 2010b).

Relatively little is known about the habitat use of reef sharks, and the current understanding of reef shark habitat use may be limited by constraints such as the limits of SCUBA based surveys (Ward-Paige *et al.*, 2010a), and difficulties in tracking large, highly mobile species over extended periods. Research using long-term automated acoustic telemetry has revealed complex patterns of habitat use for some other shark species (Simpfendorfer & Heupel, 2004). However, such studies on reef sharks are few and have only recently begun (e.g. Field *et al.*, 2011, Fitzpatrick *et al.*, 2011, Heupel *et al.*, 2010, Papastamatiou *et al.*, 2010). These studies reveal that some reef sharks exhibit highly complex patterns of habitat use, and that some species also utilise non-reef environments such as sandy and muddy foreshores, mangroves and estuaries (DeAngelis *et al.*, 2008), and may traverse deep water habitats between reefs (Chapman *et al.*, 2005, Heupel *et al.*, 2010).

In the GBRWHA, 19 elasmobranchs have been categorised as reef sharks (Chin *et al.*, 2010) (supplementary material S1). While the GBR is arguably best recognised for its coral reef habitats, these comprise only 5% to 6% of the GBRWHA (GBRMPA, 2009, Pitcher *et al.*, 2009). Much of the remaining area is referred to as the GBR 'lagoon', an area comprised of the shallow waters of the continental shelf between the Queensland coast and the offshore barrier reefs (Pitcher *et al.*, 2009). This lagoon contains a wide range of 'inshore habitats', so called because they lie inshore of the midshelf and outer reefs that form the barrier reef. This mosaic of interconnected habitats includes mangroves, seagrasses, inshore reefs and shoals, and open water with a range of sediment types (Pitcher *et al.*, 2009). Some reef sharks have been recorded in a range of inshore habitat types across the GBRWHA (Salini *et al.*, 2007) suggesting movements beyond coral reef environments.

Reef sharks in the GBRWHA face a number of pressures including habitat degradation and fishing (GBRMPA 2009). The degradation of coral reef habitats through pressures such as climate change may have significant effects on GBR reef sharks (Chin *et al.*, 2010), and the GBR Coral Reef Line Fishery has recorded significant take of reef sharks, leading to declines of some species (Heupel *et al.*, 2009, Robbins *et al.*, 2006). Additionally, some reef sharks are also taken in inshore and coastal net fisheries (Harry *et al.*, 2011, Salini *et al.*, 2007). Within the GBRWHA, the largest take of sharks and rays occurs in the northern component of the GBR net fishery (Simpfendorfer *et al.*, 2007) which operates along over 2000 km of the Queensland east coast from Baffle Creek (~24.29^{o}S) near Bundaberg, to the tip of Cape York (Fig. 2.1). The GBR net fishery takes the majority of sharks in the GBRWHA, accounting for >90% of the annual harvest of sharks in the region (Queensland Department of Primary Industries and Fisheries, 2011). The most recent fishery data available indicate that there were approximately 465 mesh net licences and some 330 net boats operating in the GBR net fishery, of which approximately half operate in the GBRWHA (GBRMPA, 2009, Queensland Department of Primary Industries and Fisheries, 2008, Queensland Primary Industries and Fisheries, 2009). This fishery is extremely variable with boats ranging from small dinghies (4-5 m in length) crewed by a single fisher to larger vessels up to 16 m length with several crew. Fishing activity is widely dispersed throughout this region although commercial catches are highest near coastal population centres between Cairns and Gladstone, with relatively little catch between Cairns and the tip of Cape York (Fig. 2.1). While larger vessels may be berthed in ports, smaller vessels access the GBR from hundreds of small boat ramps located along the coast. Furthermore, individual fishing operations also vary greatly, and fishers may change location, target species, fishing gear and effort throughout the year. Fishers may set nets in rivers and estuaries, in coastal foreshores or in deeper offshore waters up to 50 m depth depending on target species, season and gear type. While net fishers generally avoid coral reef habitats, reef sharks are caught by net fishers but there are few data about species taken and catch rates. Additionally, fisheries legislation prohibits net fishers from keeping coral reef fish species such as coral trout as these species can only be taken by fishers licensed to operate in the Coral Reef Finfish Fishery (Queensland Primary Industries and Fisheries, 2009).

Managers in the GBR have expressed increasing concern about GBR sharks, citing evidence of reef shark declines, increasing threats from fishing and habitat loss and degradation, and concern over the potential ecological impacts of declines of top predators on GBR reefs (GBRMPA, 2009). Here we analysed fishery observer data from the GBR net fishery to quantify the catch of reef sharks in the largest shark fishery in the GBRWHA. These data were used to: (1) examine the distribution of reef sharks across a range of habitats in the GBR lagoon; (2) investigate the exposure of reef sharks to different risks such as fisheries throughout the GBR; and (3) explore the implications of these patterns of distribution, habitat use and risk exposure for research and management of reef sharks.

2.2 Materials and methods

2.2.1 Study area and observer data

This study used fishery observer data from the GBR net fishery to investigate the catch and occurrence of reef sharks within the GBR lagoon. This region included all tidal waters along the Queensland east coast stretching eastward of 142º09’E near Crab Island (approx. 11.0ºS Lat.) southwards to Baffle Creek (~24º29’S Lat) (Fig. 2.1). Fishing activity and resulting catch was recorded *in situ* by independent observers, with each deployment of a net comprising an independent sample. Nets used in foreshore and offshore waters were mostly monofilament mesh ranging from 115-165 mm mesh size to target both teleosts and sharks, and 300 m to 600 m in length. For each net sample, observers recorded the catch of each species, fate of captured individuals, length and sex. Observers also recorded the location of each net sample using GPS.

Participation by commercial fishers was voluntary with 28 boats participating, ranging from small dinghies (< 5 m in length) with hand hauled nets to larger vessels (up to 16 m long) with hydraulic net hauling apparatus. This represented a cross section of the type of fishing operations in the fishery, extending across all seasons and a variety of habitats between 2006 and 2009. A detailed account of the observer program and operational characteristics of the fishery is described in (Harry *et al.*, 2011).

2.2.2 Occurrence of reef sharks amongst GBR lagoon habitats

Observer data were examined to quantify the occurrence of reef sharks in net samples (n=1,188). In this study, ‘reef sharks’ were considered as any of the 19 sharks and rays identified as reef sharks in Chin *et al.* (2010) which classified reef sharks as species that primarily occurred in reef habitats and had an implied dependency on coral reefs. The GBR lagoon included all areas and inshore habitats lying between the Queensland coast and the mid-shelf reefs of the barrier reef. The distribution of reef sharks amongst the different inshore habitats of the GBR lagoon was analysed by examining presence/absence of reef sharks in a restricted set of net samples (n=328). The restricted set included every sample that recorded the presence of a reef shark, and all adjacent samples within a 40 km radius of these sample points. The 40 km radius reflected the distance between the coast and the barrier reef in the central GBR region, and including all samples within this radius ensured that presence/absence data for reef sharks was collected from all available samples across all habitat types. This restricted dataset included many samples where reef sharks were not caught (zero data) and thus, facilitated comparison of presence and absence between different habitat types. Samples in the restricted dataset fell into two cross shelf transects that corresponded to some of the highest shark catch areas in the GBR net fishery (Fig. 2.1). The first transect covered 10,443 km^2 of inshore habitat with the northern boundary stretching from Stephens Island (17° 43.625'S; 146° 9.916'E) to Ellison Reef (17° 44.432'S; 146° 22.590'E), and a southern boundary stretching from the Haughton River mouth (19° 23.971'S; 147° 7.973'E) to Keeper Reef (18° 45.162'S; 147° 15.769'E) (Fig. 1). The second transect covered 8,871 km^2 of inshore habitat with a northern boundary stretching from Cape Edgecombe (19° 58.349'S; 148° 15.654'E) to Gould Reef No. 3 (19° 31.861'S; 148° 44.167'E), and a southern boundary stretching from South Repulse Reef (20° 37.074'S; 148° 52.332'E) to Round Reef (19° 58.073'S; 149° 37.182'E). No reef sharks were recorded outside these transects.

To investigate the effect of *in situ* habitat type on the occurrence of reef sharks, the habitat type of each of the 328 samples was assigned using a range of spatial data and mapping tools. The position of each sample was plotted on Google Earth™ (WGS84 datum), and mapping accuracy was determined as being within 10 m through validation using 11 ground control points, including a fixed geo-reference site established by Geosciences Australia. Once plotted, the habitat type of each sample was qualitatively determined by assessing information from satellite imagery (QuickBird and Google Earth™); spatial datasets and maps from the Great Barrier Reef Marine Park Authority and the Queensland Government's Coastal Habitat Resources Information System; bathymetry; local expert knowledge from commercial fishers; and substrate composition data compiled from 135 sampling locations from the Seabed Biodiversity Project (Pitcher *et al.*, 2009). This process identified six habitat types which were used to assign a habitat type for each net sample (Table 2.1).

The presence of biological features in the vicinity of the sample location may also influence the occurrence of reef sharks in a sample. To account for these effects, the proximity of each net sample to three key biological features was recorded: (1) inshore reefs, (2) mangroves and (3) seagrass meadows. Proximity was defined as a sample being located within 2 km of one or more of these biological features. The 2 km criterion was based on information about reef shark movement distances recorded on coral reef atolls (Papastamatiou *et al.*, 2009a, Papastamatiou *et al.*, 2009b, Stevens, 1984). The spatial data sources previously mentioned were used to identify the presence of these biological features and distance to net samples. Additional data used for this analysis included seagrass distribution models (Coles *et al.*, 2009, Grech & Coles, 2010), seagrass monitoring data from Seagrass Watch (Mellors *et al.*, 2008), and reef extent data from the Great Barrier Reef Marine Park Authority. Seagrasses, reefs and mangroves were selected *a priori* as key biological features as they are significant features for a number of species including reef sharks (Knip *et al.*, 2010, Stevens, 1984, White & Potter, 2004, White & Sommerville, 2010) and could be mapped using the data available.

2.2.3 Habitat type and reef shark distribution

Once in situ habitat type and proximity data were collated, the effect of habitat type and proximity to key biological features on the probability of capturing a reef shark in a net sample (encounter probability) was explored using Logistic Regression Generalised Linear Models (GLM). This approach is well suited to modeling uneven, zero-inflated datasets (data with a high proportion of zero data) which violate many of the assumptions of normal statistical tests and modeling approaches (Mayer *et al.*, 2005). In this study, logistic GLMs were used to examine the relationship between the presence/absence of reef sharks (the outcome variable) and in situ habitat type and proximity to biological features (predictor variables). Specifically, logistic GLMs tested the effects of four factors: (1) in situ habitat type, (2) proximity to inshore reefs, (3) proximity to mangroves; and (4) proximity to seagrasses. Models were run to explore trends for any reef sharks (data pooled for all reef shark species), and for individual species to investigate species-specific patterns of occurrence. However, only the blacktip reef shark had sufficient data to explore species specific patterns. In both cases, models were run for each of the 16 possible combinations of these four factors and for a ‘null model’ which modeled reef shark presence/absence without any of these factors. Akaike Information Criteria (AIC weights) (Burnham & Anderson, 2002) was used to select the best models, indicating the combinations of predictor variables (habitat types and proximity to key biological features) that best explained the presence of reef sharks.

The coefficients of the best models were used to derive odds ratios which described the relative probabilities of encountering a reef shark between habitat types and key biological features. Models were run in Program R (R Development Core Team, 2012).

2.3 Results

2.3.1 Interactions between reef sharks and the GBR net fishery

A variety of reef shark species were encountered in this study (Table 2.2). Of the 19 reef shark species reported from the GBR by Chin *et al.* (2010), 6 were encountered in this study. These species included the blacktip reef shark (*C. melanopterus*) which represented the majority (60.2%) of the reef shark catch, with less frequently encountered reef sharks including (in descending order) the lemon shark (*N. acutidens*), zebra shark (*Stegostoma fasciatum*), grey reef shark (*Carcharhinus amblyrhynchos*), grey carpet shark (*Chiloscyllium punctatum*), and whitetip reef shark (*Triaenodon obesus*) (Fig. 2.2). Reef sharks comprised only a small component of the total shark catch in the GBR net fishery, with the combined catch of these six species (n=123) equalling 1.8% of the total number of sharks and rays recorded in the observed catch (n=6828). Size data for the blacktip reef shark showed that the majority of sharks captured were juvenile sharks of both sexes (Fig. 2.3).

2.3.2 Occurrence of reef sharks amongst inshore habitats

Reef sharks were captured in 38 of the 328 samples in the restricted data set, with 7 of these samples capturing 2 reef shark species. Sampling data show that reef sharks were encountered in a variety of habitats, and suggest some inter-specific differences in habitat use. Grey reef and whitetip reef sharks were only observed in samples where the *in situ* habitat type was reef, while observations of other species occurred predominantly in non-reef habitats (Table 2.2). However, most reefs sharks were caught within 2 km of a reef, suggesting that reef proximity was an important factor in encountering reef sharks. The only exception was the zebra shark which was mostly captured in locations >2 km away from the nearest reef (Table 2.2).

Logistic GLMs revealed that *in situ* habitat type and proximity to reefs significantly affected the probability of encountering a reef shark. Of all the models tested, the two factor GLM that modelled the factors '*in situ* habitat type' + 'proximity to reefs' had the highest AIC weight (0.36), meaning that this was the best supported model (Table 2.3) and that these two factors best explained the observed distribution of reef sharks. The two next best models which received moderate support from the data included the factors proximity to mangroves or proximity to seagrass (i.e. three factor models) (Table 2.3). The odds ratios for the best supported model indicated that reef sharks were most likely to be encountered in reef and shore habitats (Table 2.4.) compared to other habitat types, and especially when reefs were located close by. Compared to the modelled reference point - river/estuary (automatically selected by R during the analysis), reef sharks were 361% more likely to be encountered in a location within 2 km of a reef, 14% more likely to be encountered in shore habitats, and 7% more likely to be encountered in open water – muddy substrate habitats. The significance of open water - muddy substrate habitats may be driven by the zebra shark as this species was most often encountered in these habitats (Table 2.2). Proximity to mangroves and seagrasses also appeared to increase the probability of encountering a reef shark, as models that included these factors in addition to habitat type and proximity to reefs were the next two best models according to AIC weights (Table 2.3).

2.3.3 Occurrence of the blacktip reef shark amongst inshore habitats

Only the blacktip reef shark had a sufficient number of capture events to examine species-specific spatial patterns. Similar to the analysis for all reef shark data combined, GLM models for the blacktip reef sharks showed the importance of habitat type and proximity to reefs in capturing blacktip reef sharks. The two factor GLM that modelled the factors '*in situ* habitat type' and 'proximity to reefs' had the largest support from the data (AIC weight = 0.44), while the models that also included mangrove proximity or seagrass proximity also had moderate support

(Table 3). The odds ratios for the best supported model indicated that compared to the reference point (river/estuary) blacktip reef sharks were 27 times more likely to be found in locations within 2 km of a reef (Table 2.4). The odds ratios also suggested that compared to the reference point, samples set in locations where the *in situ* habitat type was 'shore' or 'reef' were over a million times more likely to result in capture of blacktip reef sharks. However, these predictor variables had high standard errors (Table 2.4) and thus need to be treated with caution. Similar to the data for all reef sharks combined, the presence of mangroves and seagrasses within 2 km of a sample may also increase the probability of capturing a blacktip reef shark.

2.4 Discussion

This study reveals that several reef sharks species are found in a variety of inshore habitats in the GBR lagoon; particularly shallow inter-tidal and sub-tidal shore habitats and for species such as the zebra shark, open water – muddy substrate habitats. The proximity of mangroves and seagrasses also increase reef shark encounter probabilities. These findings add to previous accounts of habitat associations or classification systems where species such as the zebra shark and blacktip reef sharks were classified as 'reef sharks' because they primarily inhabit coral reefs (e.g. Chin *et al.*, 2010, White & Sommerville, 2010). While these sharks should still be regarded as 'reef sharks', especially since encounter probability rises within 2 km of reefs, this study illustrates that some of these species may have broader patterns of habitat use and on occasion, occur in habitats several kilometres away from the nearest reef. Some reef sharks may occur in these habitats when moving between different reefs, as has been demonstrated for grey reef sharks (Heupel *et al.*, 2010). Other reef sharks may use non-reef environments for extended periods, such as the lemon shark (*Negaprion brevirostris*) (DeAngelis *et al.*, 2008, Pikitch *et al.*, 2005). Further exploration of the residency and movement patterns of these species, and how they use different habitats, could help to redefine the habitat associations or these species, and thus, their vulnerability to pressures as well as their ecological roles.

Patterns of habitat use can affect the vulnerability of reef sharks and other mobile species to human pressures and other factors. Temporary-transitory movements or extended use of a range of habitats may expose the species to wider suite of risks, with the frequency of movement and the time spent in different habitats affecting the level of exposure to risks. Coastal habitats are under significant pressure around the world from fishing, pollution and habitat degradation, with severe impacts reported from several locations (Jackson *et al.*, 2001, Lotze *et al.*, 2006). Use of inshore habitats such as coastal foreshores, mangroves and seagrass beds, exposes these reef sharks to direct threats from fisheries and disturbance, as well as indirect effects of habitat loss and degradation. These pressures also affect coral reefs which are under pressure worldwide by pollution, habitat degradation, over-harvesting and climate change (Burke *et al.*, 2011, Hughes *et al.*, 2003). Thus, the occurrence of reef sharks in coral reef and coastal and inshore environments increases their exposure to multiple fisheries, and to multiple natural and anthropogenic impacts such as habitat degradation, pollution and disturbance.

The use of multiple habitats could also give rise to cumulative impacts, and can magnify impacts when multiple life stages are exposed to pressures. For example, fishing of adult sandbar sharks (*Carcharhinus plumbeus*) in northern Western Australia (WA) between 2000 and 2005 jeopardised a hitherto sustainable fishery that harvested juvenile sandbar sharks off south-western Australia (McAuley *et al.*, 2007a), and required prompt management intervention to significantly reduce the catch on the northern WA coast (Stobutski & McLoughlin, 2008). In the GBR, the number of reef sharks taken in the GBR net fishery is low compared to other shark species. Nevertheless, mortality from net fishing on, or near, inshore reefs could exacerbate the pressure on species such as the whitetip reef shark and grey reef shark which are already experiencing declines in the GBR (Heupel *et al.*, 2009, Robbins, 2006). Cumulative impacts may also be a concern for species such as the blacktip reef shark. This species is the third most commonly caught reef shark in the GBR coral reef line fishery, a fishery that has reportedly driven declines in other reef sharks (Heupel *et al.*, 2009, Robbins *et al.*, 2006). Catch composition data from Heupel *et al.* (2009) and commercial logbook catch data suggest that between 9,230 kg and 9,243 kg of blacktip reef sharks were captured in this fishery during peak landings between 2002 and 2003. The blacktip reef shark's use of shore habitats also exposes it to net fisheries which target these habitats for coastal species such as the high value barramundi (*Lates calcarifer*). The catch composition data presented in this study and commercial fisheries landings data suggest that the GBR net fishery caught more blacktip reef sharks than the line fishery over the 2002-2003 period, with catches between 10,857 kg and 13,222 kg respectively. However, the two fisheries are licensed separately, and the potential cumulative impact from exposure to both fisheries has not been explicitly considered in fisheries management arrangements. Furthermore, the long-term effect on the GBRWHA population of this level of catch of juvenile blacktip reef sharks is not known.

While the use of multiple habitats by reef sharks could increase their exposure to threats and cumulative pressures, it may also reduce their vulnerability through functional redundancy. Specialisation to particular ecological niches or habitat types may increase the vulnerability of species and ecosystems such as forests (Davies *et al.*, 2004), reef fishes (Munday, 2004) and birds (Julliard *et al.*, 2004). It follows that 'generalist' reef sharks which use multiple habitat types could be less vulnerable to pressures affecting coral reefs than coral reef specialists. However, this is only valid if these alternative habitat types can provide the same biological and ecological services that coral reefs provided for all life stages of these species. If coral reefs, or any other habitat used, provide unique and critical functions for any of a reef shark's life history stages, then loss of that habitat would negate the potential benefits gained from utilising multiple habitat types. Consequently, whether habitat generalisation reduces vulnerability depends on how reliant the species is in each of the habitats it uses, as well as its exposure to pressures while it is present in each habitat type.

Understanding patterns of occurrence can help to inform management and conservation priorities. In this study, the whitetip reef shark and grey reef shark only occurred in coral reef habitats and thus, are likely to be most vulnerable to reef associated pressures that can affect the quality and availability of coral reef habitats, such as anthropogenic impacts (Burke *et al.*, 2011, Hughes, 2009), climate change (Hoegh-Guldberg *et al.*, 2007b, Veron, 2008), and reef-based fisheries which are suspected of driving reef shark declines in the GBR (Heupel *et al.*, 2009, Robbins *et al.*, 2006). In contrast, their absence from other coastal and inshore environments reduces their exposure to the GBR net fishery as net fishing rarely occurs in coral reef habitats. In contrast, management and conservation for more widely occurring species (e.g. the blacktip reef shark) should consider preservation of coastal habitats as well as interactions with coastal net fisheries and cumulative impacts from coral reef based fisheries.

The use of a range of inshore and coastal habitats by reef sharks also prompts questions about the ecological roles these habitats play in sustaining reef shark populations. Habitats such as mangroves and lagoons have been proposed as important nursery grounds for a range of coral reef species (Adams *et al.*, 2006, Mumby *et al.*, 2004, Nagelkerken *et al.*, 2008b). Similarly, many coastal sharks use habitats such as seagrasses, mangroves and intertidal shore habitats for variety of purposes such as nursery areas, foraging grounds, or mating or pupping (Heithaus *et al.*, 2002, Knip *et al.*, 2010, Simpfendorfer & Heupel, 2004). Shallow sand flats have been suggested as nursery areas for reef sharks such as lemon sharks and blacktip reef sharks (Feldheim *et al.*, 2002, Papastamatiou *et al.*, 2009b, Wetherbee *et al.*, 2007, White & Potter, 2004). It is possible that reef sharks in the GBR are using these habitats for similar purposes which would further raise the importance of these habitats in sustaining intact coral reef ecosystems.

Certain factors need to be considered in interpreting the results of this study. Firstly, the presence of fishery observers may affect fisher behaviour which could affect data about the species caught, habitats fished and the fate of catch (Karp, 2005). The use of gill nets to sample sharks in the GBR lagoon may also affect species composition due to the gear selecting for species of specific shape and size (Harry *et al.*, 2011). This may account for low catches of species such as zebra sharks and rays which are less easily entangled in mesh nets, ultimately underestimating the occurrence of these species in non-reef habitats. Additionally, fishing patterns affected the spatial analysis. The observer programs were designed to collect data about normal fishing operations, so sampling effort was not evenly distributed amongst different combinations of habitat types in a fixed experimental design. This resulted in large standard errors in GLM outputs for some factor combinations due to low sample sizes. Furthermore, some factors are confounded where two or more factors naturally co-exist or were mutually exclusive. However, these issues do not alter the overall conclusion that reef shark encounter probabilities are relatively high in a range of inshore habitat types.

Distribution and habitat use patterns need to be carefully considered when studying mobile reef organisms and conducting risk assessments for these species. While previous work has classified reef sharks as those species listed as inhabiting coral reefs (Chin *et al.*, 2010, Ward-Paige *et al.*, 2010b), such classifications may be too simplistic. Chin *et al.* (2010) did not include the blacktip reef sharks or lemon sharks as species that occur in coastal and inshore habitats and thus, the vulnerability assessment for this species in incomplete. Ward-Paige (2010b) used SCUBA based counts to infer trends in reef shark abundance, but many of the species considered commonly occur in non-reef environments that were not sampled by divers. In both instances, considering the occurrence of reef sharks in a wider range of habitat types would provide more complete accounts of vulnerability and trends.

With increasing concern about the status of reef sharks and the potential effects reef shark declines could have on reef ecosystems, there is a need to better understand how these species move between and use habitats. This study has shown that habitat use should be carefully considered in reef shark management and research, especially for reefs sharks that spend extended periods in, and have ecological dependencies on, non-reef habitats. Future studies using tagging and acoustic telemetry data, and those that integrate multiple data sources from different habitat types, would help to clarify the habitat use patterns and dependencies of reef sharks, and help to ensure appropriate sample design, accurate interpretation of survey data, and more complete risk assessments to support the conservation and management of these species.

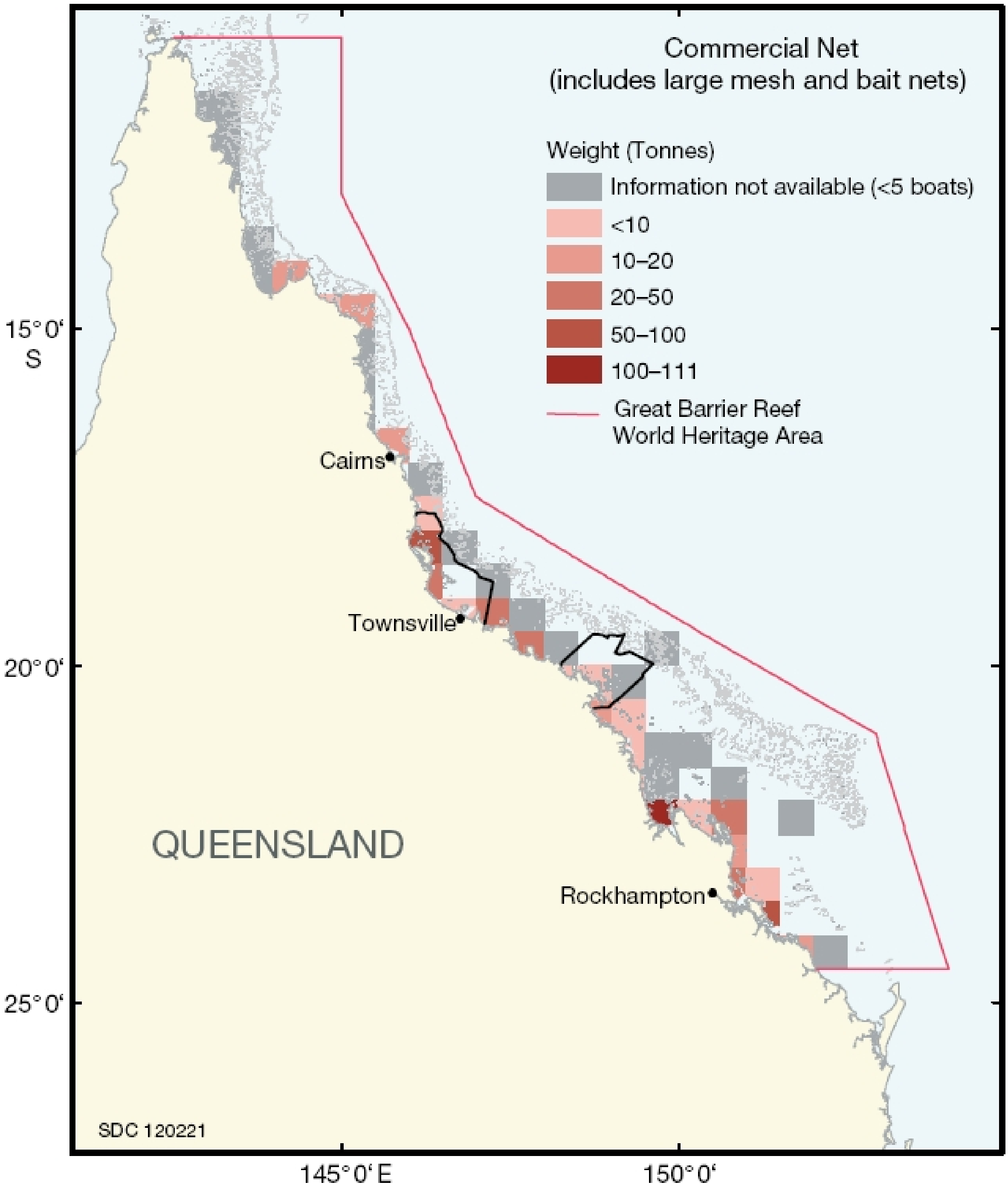


Figure 2.1: Delineation of the GBRWHA showing areas of peak shark catch in the GBR net fishery. Black lines indicate the two areas used for spatial analysis of reef shark occurrence amongst different inshore habitats.

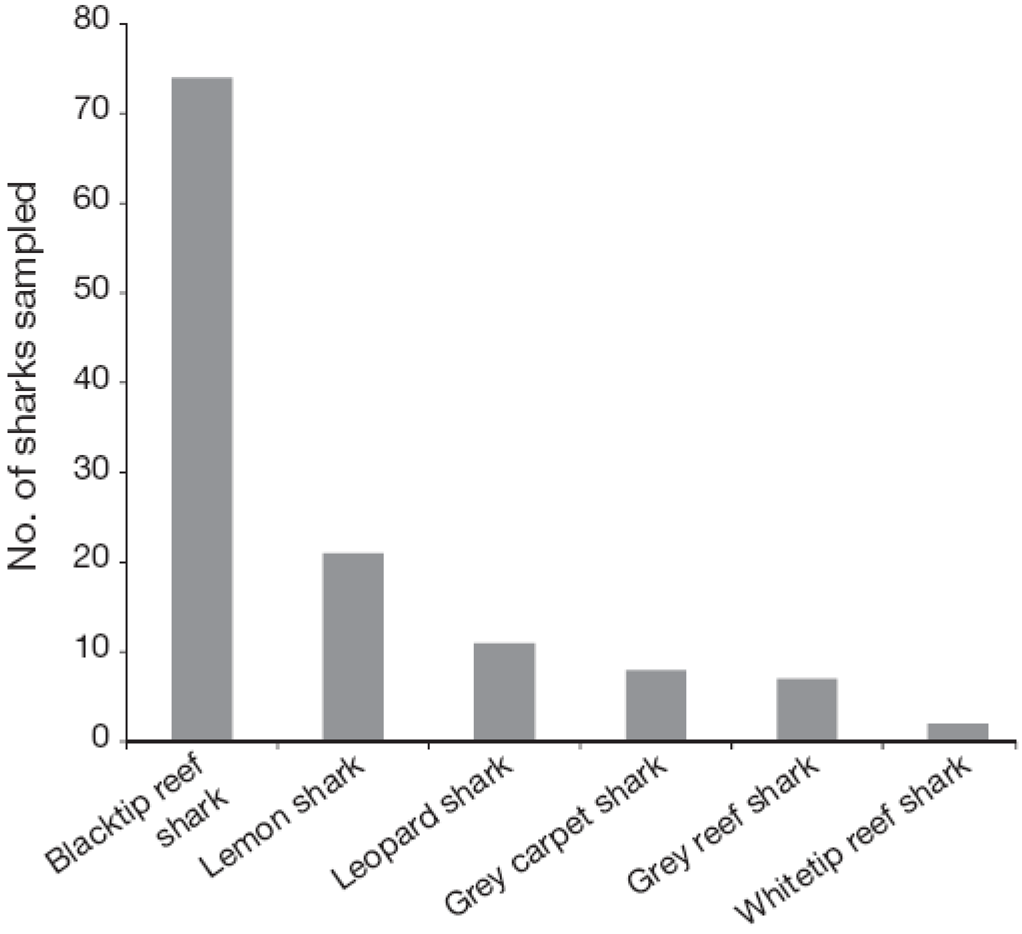
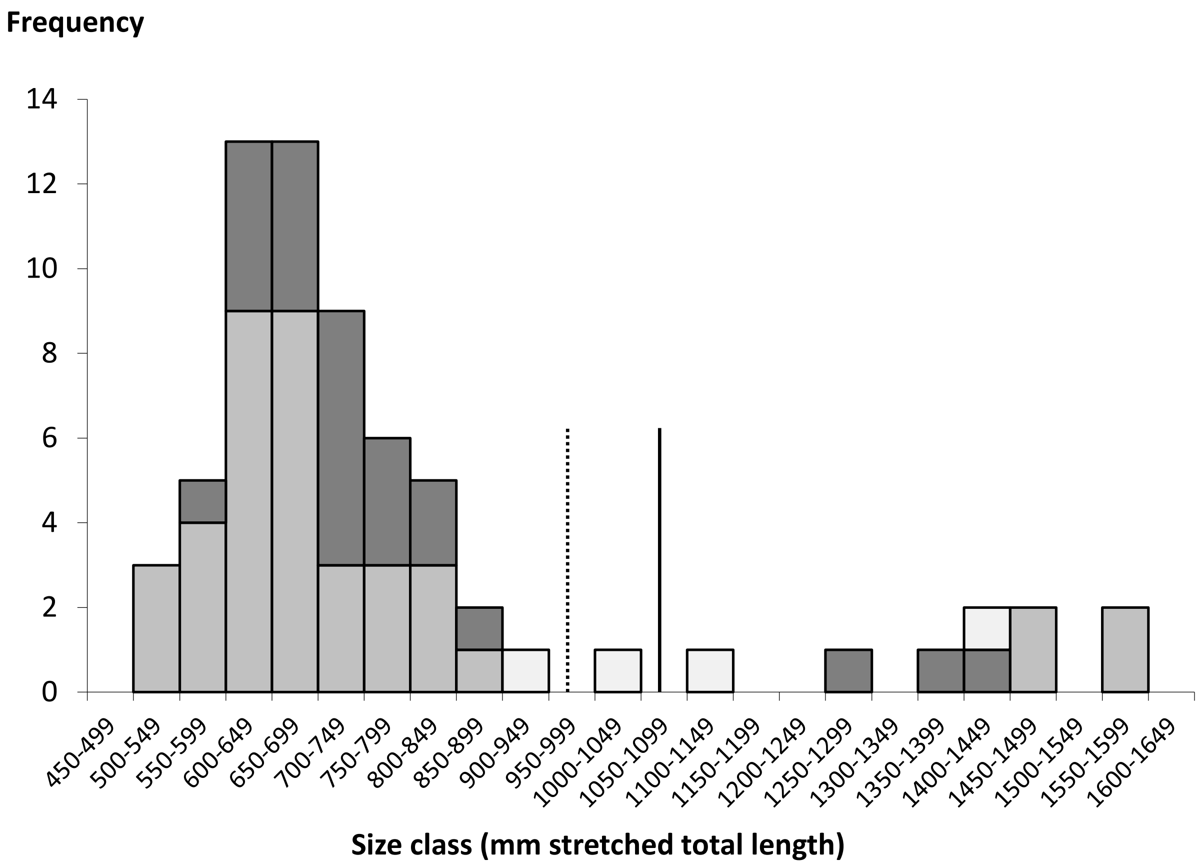


Figure 2.2: Composition of the reef shark catch taken in the GBR net fishery in inshore regions of the GBRWHA (n=128).



* Chin unpublished data, # (Lyle, 1987)

Figure 2.3: Size frequency distribution of male (white), female (light grey) and unsexed (dark grey) blacktip reef sharks (n=67) observed from the GBR net fishery. Size at maturity for males* (dashed line) and females# (solid line) shown.

Habitat types	**Description**	**No. of net samples per habitat type (total 328)**
River/estuary	Habitats within coastal rivers and estuaries that remain submerged at low the tide	6
Shore	Inter-tidal and sub-tidal habitats including sandy, muddy and rocky substrates along beaches and coastal foreshores	173
Reef	Inshore coral reefs and shoals with living hard and soft corals	12
Muddy open	Deeper water habitats >2m depth (low water) with mud or silt substrate	123
Sandy open	Deeper water habitats >2m depth (low water) with sandy to gravel and rock substrate	3
Rocky open	Deeper water habitats >2m depth (low water) with gravel to rocky substrate	11

Table 2.1: Information from the Seabed Biodiversity Project, maps, on-line datasets, satellite imagery and expert knowledge revealed six broad habitat categories ranging from estuaries to deeper water habitats of varying substrate types.

	Blacktip reef shark	**Lemon shark**	**Zebra shark**	**Grey reef shark**	**Grey carpet shark**	**Whitetip reef shark**
Habitat type	*% catch per habitat type*					
River/estuary	0	25	0	0	0	0
Shore	93	75	14	0	67	0
Inshore reef	7	0	0	100	0	100
Muddy open	0	0	86	0	33	0
Sandy open	0	0	0	0	0	0
Rocky open	0	0	0	0	0	0
	% of catch with proximity to an inshore coral reef					
Inshore reef within 2 km	98	75	25	100	66	100

Table 2.2: The percentage of the catch (calculated from the numbers of reef sharks caught) of reef sharks amongst different habitat types in the GBR lagoon, and in proximity to inshore reefs.

Model structure	**Degrees of freedom**	**AIC value**	**Δ AIC**	**AIC weight**
All reef sharks combined				
Two factor model *Habitat type + reef proximity*	7	226.17	0.00	0.36
Three factor model *Habitat type + reef proximity + mangrove proximity*	8	227.38	1.21	0.19
Three factor model *Habitat type + reef proximity + seagrass proximity*	8	228.17	2.00	0.13
Blacktip reef shark				
Two factor model *Habitat type + reef proximity*	7	123.36	0.00	0.44
Three factor model *Habitat type + reef proximity + seagrass proximity*	8	125.29	1.92	0.17
Three factor model *Habitat type + reef proximity + mangrove proximity*	8	125.36	2.00	0.16

Table 2.3: Akaike Information Criterion (AIC) model selection showing the three best models that explain the occurrence of all reef sharks, and the best three models that explain the occurrence of blacktip reef sharks. These models had the greatest support as indicated by having the highest AIC weights. The model for *in situ* habitat type + reef proximity best explained the occurrence of all reef sharks (catches of all species combined) and for the blacktip reef shark.

Predictor variables	Estimate	Standard error	Z value (Wald statistic)	Pr(>|z|)	Odds ratios
All reef sharks combined					
Intercept (Habitat type= *river/estuary*)	-0.6931	0.8660	-0.800	0.42349	0.500000[#]
Habitat type = *reef*	-1.2857	1.1386	-1.129	0.25884	0.276468
Habitat type = *open water muddy substrate*	-2.5730	0.9777	-2.632	0.00850 **	0.076309
Habitat type = *open water rocky substrate*	-17.9885	1175.6370	-0.015	0.98779	$1.540629e^{-08}$
Habitat type = *Open water sandy substrate*	-17.8345	2229.8561	-0.008	0.99362	$1.797074e^{-08}$
Habitat type = *shore*	-1.9188	0.9398	-2.042	0.04118 *	0.146788
Proximity to reef	1.2857	0.4141	3.105	0.00190 **	3.617049
Blacktip reef shark					
Intercept (Habitat type= *river/estuary*)	-20.566	7238.393	-0.003	0.99773	$1.170227e^{-09}$[#]
Habitat type = *reef*	16.155	7238.393	0.002	0.99822	$1.037966e+^{07}$
Habitat type = *open water – muddy substrate*	-2.324	7382.433	-0.000315	0.99975	0.097919
Habitat type = *open water – rocky substrate*	3.054	8896.528	-0.000343	0.99973	0.047193
Habitat type = *Open water – sandy substrate*	-2.806	12058.703	-0.000233	0.99981	0.060475
Habitat type *shore*	16.033	7238.393	0.002	0.99823	$9.188553e^{+06}$
Proximity to reef	3.312	1.041	3.183	0.00146 **	27.4426

Table 2.4: Results of the logistic regression generalised linear models for the best fitting model for all reef sharks combined, and for the blacktip reef shark.

* indicates significance at level of 0.01, ** indicates significance at level of 0.001

[#] Although R routinely provides an estimate for the intercept, this is a reference value and is not interpretable (UCLA: Academic Technology Services - Statistical Consulting Group, 2010)

3. Population structure and residency patterns of the blacktip reef shark in turbid coastal environments

3.1 Introduction

Characteristics of fish populations such as size and age structure, segregation by sex and maturity, movement, site attachment, and habitat use patterns, are important aspects in understanding the biology and ecology of fishes (Cortés, 2007, Simpfendorfer *et al.*, 2011, Wearmouth & Sims, 2008). Population characteristics can also reflect the ecosystem services habitats may provide for fish populations, and can have important implications for management and conservation (Wearmouth & Sims, 2008). These characteristics are also important considerations in managing sharks and rays (Simpfendorfer *et al.*, 2011), many of which are of increasing conservation concern (Fowler *et al.*, 2005). Sharks and rays may exhibit highly structured populations that are dominated by specific size classes or sexes, and may also have complex habitat use, behaviour and movement patterns (see Knip *et al.*, 2010, Speed *et al.*, 2010, Wearmouth & Sims, 2008 for review). Segregation by sex and size may be important reproductive strategies that maximise female fitness, reproductive success and juvenile survival (Grubbs, 2010, Heupel *et al.*, 2007, Wearmouth & Sims, 2008). For example, grey reef sharks *Carcharhinus amblyrhynchos* (Bleeker 1856) on coral atolls in the Pacific show sexual segregation that may be related to increasing reproductive rates (Economakis & Lobel, 1998), while in Alaska, female salmon sharks *Lamna ditropis* (Hubbs & Follett 1947) form seasonal feeding aggregations (Hulbert *et al.*, 2005). Australian gulper sharks (*Centrophorus* spp.) show sexual segregation by depth (Graham & Daley, 2011). Segregation by size also occurs in many sharks, some of which repeatedly use shallow nursery grounds to maximise juvenile survival (Grubbs *et al.*, 2007, Heupel *et al.*, 2007, Hueter *et al.*, 2005). These traits give rise to a range of movement patterns and size and sex structures in shark and ray populations. Examining these population characteristics can increase understanding of the spatial ecology of shark populations, as well as the ecological, physiological and/or behavioural factors that drive these patterns.

Population structure and movements studies can also demonstrate the roles habitats play in sustaining shark populations and the importance of considering population structure and movement patterns in management and conservation (Simpfendorfer *et al.*, 2011). For example, studies of smooth-hound shark (*Mustelus schmitti*) populations identified the importance of protecting shallow coastal waters. This species has highly structured populations off the coast of Argentina and uses shallow coastal habitats for key stages in the species' life history such as mating and pupping, and to enhance juvenile growth and survival (Cortes *et al.*, 2011). Similarly, studies on the movement and habitat use of the critically endangered smalltooth sawfish (*Pristis pectinata*) identified key habitats, locations and refuges that if protected, could aid sawfish recovery (Norton *et al.*, 2012, Simpfendorfer *et al.*, 2010). Knowledge of population structure and movement may also be specifically used in shark fisheries management. The spatial segregation between juvenile and adult sandbar sharks (*Carcharhinus plumbeus*) is used as a basis for managing fishing activities in the Western Australian sandbar shark fishery (McAuley *et al.*, 2007b), and fisheries management plans include “no fishing” refuges to protect aggregations of pregnant whiskery sharks (*Furgaleus macki*) (Department of Fisheries, 2012).

Reef sharks such as the blacktip reef shark, grey reef shark and the white-tip reef shark (*Triaenodon obesus*) are under increasing pressure in the Pacific and Indian Oceans (Graham *et al.*, 2010, Nadon *et al.*, 2012), including in marine protected areas such as the Great Barrier Reef World Heritage Area (GBRWHA) (Heupel *et al.*, 2009, Robbins *et al.*, 2006). The blacktip reef shark is a widely-distributed, medium sized carcharhinid (whaler shark) ranging from the Indian Ocean and Red Sea to the central Pacific (Last & Stevens, 2009). Reports on this species are usually from coral reef habitats with populations studied in remote coral dominated atolls and reefs in clear, oligotrophic waters in the Indian Ocean (Stevens, 1984) and central Pacific (Papastamatiou *et al.*, 2009a), and also in clear-water embayments associated with coastal coral reefs in Western Australia (Speed *et al.*, 2011).

However, the blacktip reef shark has also been observed in turbid eutrophic coastal environments that are dominated by non-reef habitats such as mangroves, seagrasses and coastal mudflats (Lyle, 1987), and may regularly occur in these locations (Chapter 2). Nevertheless, the characteristics (size and sex structure, residency, movement patterns) of blacktip reef shark populations in turbid coastal environments are poorly understood and may differ from populations studied in clear-water coral dominated habitats. Such differences could arise in response to the different habitat types and environmental conditions present in turbid coastal environments (Knip *et al.*, 2010) compared to clear-water coral dominated environments. Furthermore, coastal populations of reef sharks may require specific attention as coastal areas often have highest exposure to fishing pressure and to habitat loss and degradation (Brodie & Waterhouse, 2012, Knip *et al.*, 2010, Lotze *et al.*, 2006). Indeed, the blacktip reef shark is landed in coastal fisheries across its range (e.g. Marshall, 1996a, Marshall, 1996b, Teh *et al.*, 2007, see Chapter 2). This chapter examines the population characteristics – size and sex structure, site attachment and movement patterns – of the blacktip reef shark in turbid coastal environments. In doing so, the study identifies whether populations in these habitats differ from populations in clear-water coral reef habitats, and examines the implications of these population structures and habitat use patterns on the conservation and management of the species.

3.2 Materials and methods

3.2.1 Study site

Sampling for blacktip reef sharks was conducted at Magnetic Island in Cleveland Bay, Queensland, Australia. Magnetic Island lies approximately 8 km from the regional centre of Townsville and the main study site at Cockle Bay is located on the south-western side of the island (Fig. 3.1). The study site is very different from clear-water coral dominated reef habitats. This site contains a diverse range of coastal habitat types including subtidal fringing coral reefs; intertidal foreshores and flats with coral rubble, rock, sand and mud substrates; fringing mangroves; and intertidal and subtidal seagrass beds. While water depth on the intertidal rubble, sand and mud foreshores can reach 2.1 m on spring tides, these habitats are exposed at low tide. Water temperatures fluctuate between 20.7°C (winter) and 30.6°C (summer), with a mean annual temperature of 26.3°C ± 2.3 (A. Chin, unpubl. data). These coastal habitats are also subject to freshwater flood plumes and high turbidity conditions. Average annual rainfall in Townsville is 1200 mm but rainfall can reach very high levels during the summer wet season. Townsville received 1914 mm of rain between Nov 2008 and Feb 2009 (Bureau of Meteorology, 2012) resulting in plumes of turbid low salinity flood water. Cleveland Bay contains a large amount of fine sand and mud sediments and turbidity levels regularly reach 50 mg l^{-1} (Browne *et al.*, 2010), with underwater visibility typically <1 m.

3.2.2 Sampling and tagging

Field sampling began in October 2008 and ceased in March 2011. Within this period, intensive sampling was conducted every month for 17 months between October 2008 and May 2010 to record seasonal changes in population structure and biological events such as mating and parturition. Blacktip reef sharks were captured using bottom-set longlines consisting of a 500 m long, 8 mm diameter mainline anchored at each end. Gangions were 2.5 m long and constructed from a 1.5 m length of 4 mm braided cord, a 1 m length of nylon coated stainless wire leader and 14/0 Mustad tuna circle hooks. Hooks were baited with butterfly bream *Nemipterus* spp., sea mullet (*Mugil cephalus*), diamond scale mullet (*Liza vaigiensis*) and blue threadfin (*Eleutheronema tetradactylum*) with different bait types randomly mixed between hooks. These bait types were selected as they represent local potential prey species and could be reliably obtained throughout the study. Sampling occurred on the rubble and sand/mud foreshores (Fig. 3.1) throughout the rising tide, high tide and falling tide, and continued until low tide conditions made sampling impossible. At low tide, sampling was conducted in deeper waters with muddy substrate adjacent to the exposed flats (Fig. 3.1). The position of each line deployed was recorded using GPS and lines were soaked for one hour. Sampling occurred over various light levels with longlines deployed between 05:30 (dawn) and 18:00 (dusk), but sampling was not conducted at night. Fishery independent sampling using identical longline gear also occurred in adjacent areas throughout Cleveland Bay throughout the study period for other projects (see Appendix 1).

Upon capture, small sharks (<1 m total length) were placed ventral side down onto a measuring board and fork length (L_F) and stretched total length (L_{ST}) recorded to the nearest mm. Larger animals were secured alongside the boat using a nylon tail rope, and L_F and L_{ST} measured to the nearest mm using a tape measure stretched over the curve of the body (see Francis, 2006). Sharks were tagged in the first dorsal fin, with large sharks (>1 m L_{ST}) tagged with a large rototag and small sharks (<1 m L_{ST}) tagged with a small rototag (see Appendix 2). To quantify rototag loss rate, some sharks were also tagged with a plastic tipped Hallprint dart tag inserted into the base of the first dorsal fin (see Appendix 2). These more invasive tags were only applied when specimens were large enough (> 645 mm L_{ST}) and were in suitable condition (i.e. actively swimming and energetic). To encourage public tag returns all tags were printed with contact information to facilitate recapture reports, and public awareness was raised through information sessions at fishing meetings, newsletters, and promotional activities delivered under a large scale tagging program. Biological data (sex, clasper length and calcification status, presence of running sperm in males, presence of mating scars on females) were recorded to estimate the size at maturity of males and the seasonality of mating in the population. The presence and condition of umbilical scars was used to identify neonates and to estimate the seasonality of parturition. The time between birth and healing (closure) of the umbilical scar was verified using observations of umbilical scar healing rates of three neonate blacktip reef sharks born in captivity (A. Chin, unpubl. data).

3.2.3 Data analysis

The size structure of the population was described by examining the size frequency distribution of captured sharks, and sex bias examined using Chi square tests. Seasonal patterns in size and sex of the population were examined by plotting the monthly abundance of juveniles and adults between October 2008 and March 2011. Juveniles were defined as males ≤950 mm L_{ST} and as females ≤970 mm L_{ST} using size at maturity data from Lyle (1987). Seasonal occurrence of reproductive events such as mating and parturition were also identified. Trends in abundance over time were examined using catch per unit effort (CPUE) expressed as the number of sharks captured per 100 hooks hr^{-1}. Monthly CPUE was plotted over the sampling period to identify seasonal trends in blacktip reef shark catch. Variability in the raw

CPUE data prevented analysis of temporal trends (CPUE per month or season) through parametric tests such as ANOVA. Consequently, CPUE data were log transformed and analysed using linear regression including temperature as a proxy for season. Mean daily average sea temperature data were obtained from an Australian Institute of Marine Science weather station located 6 km from the study site and temperature data were ground-truthed with data collected from the study site (A. Chin, unpubl. data). CPUE per season was inferred using a classification system that assigned seasons to specific temperature ranges. Months with an average temperature $<25^{o}$C were classified as the 'winter-dry' season (May to September), while months with an average temperature $>25^{o}$C were classified as the 'summer-wet' season (October to April). This classification is consistent with long-term temperature and rainfall records that show marked declines in monthly average rainfall and mean air temperature between April and May (Bureau of Meteorology, 2012), and is also consistent with classifications used in previous studies in Cleveland Bay (e.g. Knip *et al.*, 2011b).

Records of recaptured animals were used to explore residency patterns by examining recapture frequency, time at liberty and recapture distance (measured as the shortest straight line distance travelled between capture and recapture locations). Recapture data were also used to measure growth in individuals less than the maximum size (<1,400 mm L_{ST} according to other studies) (Lyle, 1987, Speed *et al.*, 2011, Stevens, 1984, White, 2007). This 1,400 mm size limit was imposed as size changes in larger animals were more likely to reflect measurement error caused by logistical constraints in handling larger specimens than actual growth which is slower in blacktip reef sharks >1,400 mm L_{ST} (see Chapter 4). Mature males were identified by the presence of fully calcified claspers, and maturity stage was coded as binary values (0 = immature, 1 = mature) for analysis. Estimates for male length at maturity were produced using logistic regression of L_{ST} and clasper calcification status (see Appendix 3), but the lack of intermediate sized males in the sample compromised the ability of the model to provide robust estimates. Consequently the length and maturity estimates are preliminary and should be treated with caution. All statistical analyses were performed using program R (R Development Core Team, 2012).

3.3 Results

3.3.1 Catch and population structure

Over the 29 month sampling period from October 2008 to March 2011, 22 months were sampled. A total of 165 longline sets comprised of 6,712 hooks and 207 hours of sampling were completed in 37 days of sampling. Overall, 127 blacktip reef sharks were captured with 120 individuals animals tagged and released. Of the 120 tagged and released animals, 40 were tagged with both rototags and dart tags. The majority of tagged animals were classed as juveniles (n=69) according to the sizes at maturity described previously (Lyle, 1987), and adult females (n=44) with only 7 adult males captured (Fig. 3.2). A chi-square goodness of fit test showed highly significant sex bias in the adult population ($\chi^2 = 26.843$; $P = 2.21\ \mathrm{E}^{-7}$), while there was no evidence of sex bias in the juvenile population ($\chi^2 = 1.35$; $P = 0.245$).

The population had a bimodal size frequency structure (Fig. 3.2), with one size class consisting of juveniles of both sexes (range 572 to 830 mm L_{ST}; median 680 mm L_{ST}) and another size class consisting of mostly adult females (range 1,075 to 1,540 mm L_{ST}; median 1,398 mm L_{ST}). Only one individual was captured in the intermediate size range (a female of 927 mm L_{ST}) (Fig. 3.2). Males ranged in size from 613 to 1,350 mm L_{ST}, while females ranged from 572 to 1,540 mm L_{ST}. The bimodal size structure meant that captured males had either calcified or uncalcified claspers (Fig. 3.3) and no males were capture with partially calcified claspers. The smallest male with calcified claspers was 1,190 mm L_{ST} and the largest male with uncalcified claspers was 811 mm L_{ST} (Fig. 3.3). Clasper lengths for juvenile males were between 10 mm and 25 mm (median 14.4 mm), while clasper lengths for mature males ranged from 100 mm to 120 mm (median 108 mm). Logistic regression showed length at 50% maturity was 997 mm L_{ST} with 95% of males mature at 1083 mm L_{ST} (see Appendix 3), however these estimates should be considered preliminary due to the small sample size and lack of intermediate sized, maturing males to fit to the regression model.

Sampling revealed seasonal patterns in the population. Neonates (n=11) comprised 16% of the juveniles and were captured between December and March in 2009 (n=3), 2010 (n=3) and 2011 (n=5), with most neonates (n=8) encountered between February and March in all three years. Mating scars were observed in adult females in two summer-wet seasons; March and April 2009 (n=4) and December 2009 (n=2). Together these observations suggest parturition and mating during the summer-wet season (Fig. 3.4). The composition of juveniles compared to adults also varied over time. In the early summer months (November and December) of 2008-09 and 2010-11 catch composition was biased toward adult females until February and March when juveniles (including neonates) dominated the catch. However, the summer of 2009-10 showed a more even distribution of adults and juveniles (Fig. 3.4). In all three years CPUE was highest during the summer-wet period, although highly variable within-month catch rates resulted in large standard deviations (Fig. 3.5a). Catch rates were significantly higher during the warm summer-wet season and linear regression showed a significant relationship between temperature and CPUE ($P = 0.0179$; T = 2.471; residual standard error = 0.2973 on 39 degrees of freedom, multiple R^2=0.1354; $F_{(1, 39)}$= 6.107) (Fig. 3.5b). Almost all captures of adult males occurred during the summer-wet season, with 8 of 9 capture events (capture events included two recaptures) occurring between October and April.

3.3.2 Tag recaptures

During the course of the study 24 individuals (21% of the tagged and released animals) were recaptured in 33 separate recapture events with 8 individuals (33% of recaptured animals) recaptured multiple times. Sixteen animals were recaptured once, seven animals recaptured twice and one animal recaptured three times (Table 3.1). The shortest time at liberty was < 3 hours while the longest was 969 days (Table 3.1). Two of the recaptured blacktip reef sharks were juveniles caught by recreational fishers, and three adults were recaptured by the Queensland shark control program. Most animals were at liberty for at least six months (mean days at liberty ± SE = 293.8 ± 39.6) (Table I). The majority of recaptures occurred close to the original tagging sites (mean recapture distance ± SE = 0.8 km ± 1.7 km) and the most distant recapture was only 3.8 km from the tagging site (Table 3.1). Additionally, no tagged blacktip reef sharks were captured during extensive sampling at adjacent sites throughout Cleveland Bay carried out through other research projects that included 228 sampling days using identical longline gear and monofilament mesh nets deployed at sites across Cleveland Bay from 2008 to 2010 (Kinney *et al.*, 2011, Knip *et al.*, 2011b, Appendix 3 for additional details). Tagging procedures did not appear to cause stress or mortality as evidenced by the high recapture rate and the fact that one individual was recaptured within 3 hours of release indicating a rapid return to feeding behaviour. Recapture data suggest a high degree of site attachment with tagged animals repeatedly available for recapture within the sample area resulting in a high recapture rate (including 33% of recapture events being repeated recaptures) and short recapture distances. There was evidence of different levels of long-term site attachment between juveniles and adults. While the population was dominated by juveniles and adult females, only five of the 24 recaptured animals were juveniles, and no juveniles were recaptured more than once (Table 3.1). In contrast, 19 of the 24 recaptured animals were adult females, seven of which were recaptured on multiple occasions. At the time of recapture, seven animals were below the 1,400 mm L_{ST} limit previously described and these animals were used to measure growth. Differences in size between capture and recapture suggested a median growth rate of 65.3 mm yr^{-1} L_{ST} (mean 62.9 mm-yr^{-1} ± 30 mm). Recaptures included 17 individuals tagged with both rototags and plastic dart tags. Double tagging suggested that rototags had low tag loss rates. All rototags on recaptured animals were intact and in good condition. In contrast, three dart tags were broken rendering the tag numbers unreadable and a further five dart tags were missing, resulting in a tag loss rate of 47% of dart tags over a period ranging from 29 days to 503 days.

3.4 Discussion

This study of blacktip reef sharks focused on poorly known populations in turbid coastal waters and revealed distinctive population characteristics that provide new insights into the species’ spatial ecology, and demonstrate the importance of shallow coastal habitats. Catch data indicate a population dominated by juveniles and adult females with a ‘missing size class’ between the two groups, and an absence of adult males. This bimodal population size structure with strong adult female bias differs from blacktip reef shark population structures seen in Australia's Gulf of Carpentaria (Lyle, 1987), Seychelles' Aldabra Atoll (Stevens, 1984) and Indonesia (White, 2007) which generally show more even distributions of adult males and females and the presence of animals throughout the size range. While a bimodal population structure for blacktip reef sharks has been observed at Palmyra Atoll, no sex bias was evident (Papastamatiou *et al.*, 2009a). The data presented here also suggest that shallow coastal habitats may support localised groups of juveniles and adult females, and that adult females may exhibit high levels of long-term site attachment. Blacktip reef sharks appear to be highly localised to the specific study site with extensive sampling in adjacent areas throughout Cleveland Bay over the three years yielding only 10 blacktip reef sharks (Kinney *et al.*, 2011, Knip *et al.*, 2011b for sampling details). Additionally, high site attachment of adult females is indicated by the elevated CPUE and recapture rate, short recapture distances, extended times at liberty between recaptures and high incidence of multiple recaptures. High site attachment and localised distributions have also been observed in mixed size and sex blacktip reef shark populations in coral reef dominated environments (Papastamatiou *et al.*, 2009a, Speed *et al.*, 2011, Stevens, 1984).

The observed population characteristics (a highly site attached population comprised of juveniles and adult females) may reflect strategies and behaviours to enhance reproductive success and juvenile survival. The prevalence of juveniles and/or adult females in specific locations has been recorded in a range of sharks and rays and may represent behaviours that increase offspring growth and survival (Ebert & Ebert, 2005, Grubbs, 2010, Heupel & Hueter, 2002, Heupel *et al.*, 2004). Adult females may use specific habitats and locations to access favourable environmental conditions that optimise embryo development and metabolic functions (Economakis & Lobel, 1998, Hight & Lowe, 2007, Sims *et al.*, 2006). Indeed, behavioural thermoregulation to enhance blacktip reef shark reproduction has recently been reported from Western Australia (Speed *et al.*, 2012). Sex structuring can also arise from avoidance behaviour with females suggested to form sex specific groups to avoid harassment by males and subsequent injury during mating (Jacoby *et al.*, 2010, Mucientes *et al.*, 2009, Sims, 2003). Groups of specific individuals in a population can also form due to social factors and interactions that create persistent associations between specific individuals (Mourier *et al.*, 2012). However, sex segregation may also arise from differences in prey preference and sex-specific dietary requirements (Klimley, 1987, Wearmouth & Sims, 2008). Nevertheless, while prey preference and dietary or metabolic requirements could explain the observed sex bias towards adult females, previous studies of blacktip reef sharks have found similar abundances of males and females together in the same location (Lyle, 1987, Papastamatiou *et al.*, 2009a, Stevens, 1984) which suggests that both sexes have similar dietary and environmental requirements. Additionally, the majority of adult females observed here were at or near maximum size and would thus be unlikely to use this site to maximise growth. An alternative rationale to explain the observed population structure is that this location supports reproductive functions in coastal blacktip reef shark populations. Nonetheless, sex-specific dietary and environmental requirements of blacktip reef sharks have not been thoroughly investigated and cannot be discounted as factors that might drive the population structures observed in this study.

The high, localised abundance of juvenile blacktip reef sharks observed in shallow coastal foreshores may reflect the importance of these habitats for juvenile growth and survival (Papastamatiou *et al.*, 2009a, Speed *et al.*, 2011). However, several aspects of this juvenile blacktip reef shark population differ from data recorded elsewhere. This study identified a higher proportion of juveniles in the population compared to populations studied in Aldabra Atoll (Stevens, 1984), Indonesia (White, 2007), northern Australia (Lyle, 1987) and Western Australia (Speed *et al.*, 2011). Recaptured juvenile blacktip reef sharks also showed growth rates almost double those reported from Aldabra Atoll (35 mm yr^{-1}) and Palmyra Atoll (43mm yr^{-1}) (Papastamatiou *et al.*, 2009a, Stevens, 1984). Additionally, the size at birth and maximum size of blacktip reef sharks measured in this study were larger than those recorded at Aldabra and Palmyra Atolls. These differences in size and growth rate may reflect greater productivity and subsequent prey quality and/or availability in eutrophic coastal environments compared to isolated, oligotrophic coral reefs and atolls which may pose resource limitations to juvenile sharks (Duncan & Holland, 2006, Lowe, 2002, Papastamatiou *et al.*, 2009a). The high productivity of Cleveland

Bay has been reported to support juvenile sharks from several species with evidence that competition is reduced due to the presence of abundant prey and niche partitioning between shark species (Kinney *et al.*, 2011, Simpfendorfer & Milward, 1993). These factors could enhance growth rates and survival of juvenile blacktip reef sharks in turbid coastal environments.

Many sharks have also been reported to use certain habitats and locations such as shallow banks and foreshores as refuges for neonates and juveniles to avoid predation (e.g. DeAngelis *et al.*, 2008, Heupel *et al.*, 2007, Simpfendorfer *et al.*, 2010), and the study site could provide such a refuge for juvenile blacktip reef sharks. Other shark species that commonly occur in adjacent areas (see Kinney *et al.*, 2011, Knip *et al.*, 2011b) were rarely captured at the study site, which may represent reduced abundance of these other species and lower inter-specific competition and predation upon juvenile blacktip reef sharks. Additionally, the high turbidity may also contribute to increased size and growth rates compared to juvenile blacktip reef sharks studied in clear-water coral dominated environments. Turbidity is a significant factor driving the behaviour and distribution of some fishes (Cyrus & Blaber, 1992) and high turbidity can reduce predators' ability to detect prey (Radke & Gaupisch, 2005, Sweka & Hartman, 2003). The turbid conditions in Cleveland Bay could reduce predation pressure on juvenile blacktip reef sharks and allow them to feed with less disruption from predators, leading to increased growth and survival. Indeed, in some coral reef environments high numbers of blacktip reef sharks have been observed in turbid atoll lagoons (Papastamatiou pers comm). Nevertheless, the suggestion that turbidity may offer refuge to blacktip reef sharks is speculative and more data are needed on the effects of turbidity on foraging, growth and survival to predict how water clarity might affect blacktip reef shark populations.

Commercial fisheries catch data suggest the presence of other localised groups of juvenile blacktip reef sharks in shallow coastal habitats along the Queensland east coast (Chapter 2), and these shallow coastal rubble and mud flat habitats may provide important refuges for these animals. Once juveniles grow to between 850 mm and 900 mm L_{ST} (the lower margin of the 'missing size class' and also the estimated onset of male sexual maturity) animals appear to leave Cockle Bay and presumably disperse to other locations. Recapture data also suggest potential dispersal of juveniles. Only five of the 24 recaptured individuals were juveniles and only one juvenile was recaptured after a year at liberty, suggesting low long-term residency for juveniles. In contrast, adult females were recaptured more frequently, and multiple times across three years. Dispersal of juveniles from natal sites has been recorded in several sharks with suggestions that juvenile dispersal could reduce competition, increase resource access, promote genetic mixing, or occur in response to changing environmental conditions or requirements (Chapman *et al.*, 2009, Grubbs, 2010, Heupel *et al.*, 2004, Meyer *et al.*, 2009). While any of these mechanisms could explain the dispersal of juvenile blacktip reef sharks, identifying the specific factors that drive dispersal in juveniles was beyond the scope of this study.

The observation of seasonally occurring mating scars in adult females, parturition across years and seasonal peaks in CPUE suggest that some blacktip reef shark populations use shallow coastal habitats for mating and pupping. These events occur during the summer-wet season, and the timing of parturition and mating found in this study are broadly consistent with previous reports (Lyle, 1987, Porcher, 2005, Stevens, 1984, White, 2007). Six pregnant females were obtained from commercial fisheries and recaptured animals during the study, with three captured in March and three in October. Embryo lengths suggested a gestation period >8 months which is consistent with Lyle (1987) and Porcher (2005). However, more data are required to clarify gestation time for the study population.

Collectively, the data suggest that shallow coastal habitats may provide important functions for coastal blacktip reef shark populations. While the observed size structure, site attachment and reproductive behaviours are consistent with published accounts of the importance of coastal habitats for many shark populations (e.g. Knip *et al.*, 2010, Speed *et al.*, 2010), effects of sampling bias and gear selectivity need to be considered. Inferring population structure from CPUE assumes that the catchability of sharks is constant and is unaffected by ontogeny or season, which may not always be the case. Nevertheless, gear selectivity is unlikely to have caused the size structure evident as the longline gear captured animals ranging from neonates to maximum size adults. Additionally, while ontogenetic shifts in diet could cause larger juveniles to begin to reject baits, no such ontogenetic shifts have been reported for blacktip reef sharks. Diel differences in behaviour and movement could also introduce affect catch rates between males, females and juveniles and subsequent interpretations of population structure. Different sizes and sexes may favour different habitats across the diel cycle, affecting their catchability. While acoustic telemetry studies suggest that juvenile and adult blacktip reef sharks may have different diel patterns in habitat use (Speed *et al.*, 2011), peak periods of shallow habitat use of all sexes and sizes fall within the hours sampled during this study, meaning that all size classes and sexes should have been available for capture during sampling. Nevertheless, future studies using acoustic telemetry could address potential biases in catch sampling techniques by directly recording residency and movement patterns of juveniles, adult males and adult females, and could also record juvenile dispersal. Similarly, additional data on ontogenetic and seasonal shifts in diet, behavioural and metabolic studies would provide additional clarification about the factors influencing coastal blacktip reef shark populations.

Seasonal catch patterns, size and sex structure, and tag-recapture data suggest that shallow coastal habitats such as Cockle Bay may be important habitats for blacktip reef sharks, and dependence on these habitats by blacktip reef sharks and other coastal sharks may have important conservation and management implications (Simpfendorfer *et al.*, 2011, Wearmouth & Sims, 2008). The blacktip reef shark is taken in numerous coastal fisheries around the world (Heupel, 2009, Marshall, 1996a, Marshall, 1996b, Teh *et al.*, 2007), and in the GBRWHA is the most commonly taken reef shark in commercial net fisheries (Chapter 2) and third most common in the reef line fishery. The low reproductive capacity of the blacktip reef shark (Chapter 4) coupled with moderate fishing pressure makes them susceptible to overfishing in the GBRWHA (Salini *et al.*, 2007, Tobin *et al.*, 2010). Given these factors, protecting the reproductive potential of populations, i.e. groups of breeding females, could prove invaluable in promoting the long-term sustainability of populations. Management to protect adult females has been applied to other sharks such as the sandbar shark, whiskery shark and gummy shark where management includes spatial refuges to preserve the reproductive potential of exploited sharks (Department of Fisheries, 2012, McAuley *et al.*, 2007b, Prince, 2005). Approximately 37% of the GBRWHA is closed to commercial net fishing and 33% to line fishing, and these measures will provide protection for some coastal blacktip reef shark populations. Nevertheless, the strong site attachment, localised abundance and long-term residency of coastal blacktip reef sharks could make some populations vulnerable to localised depletion. Additionally, many inshore habitats are also threatened by habitat loss and degradation (Brodie & Waterhouse, 2012, GBRMPA, 2009, Lotze *et al.*, 2006) that may have negative impacts on shark populations (Jennings *et al.*, 2008, Knip *et al.*, 2010). The long-term effects of localised fishing effort, selective mortality on different population components (e.g. neonates and resident adult females compared to dispersing sub adults and adult males) and the cumulative effects of the loss or degradation of coastal habitats are unknown. Addressing these knowledge gaps will provide managers with the information to assess the efficacy of existing measures in protecting this species, and help to determine the long-term sustainability for this widely distributed shark in coastal and coral reef environments.

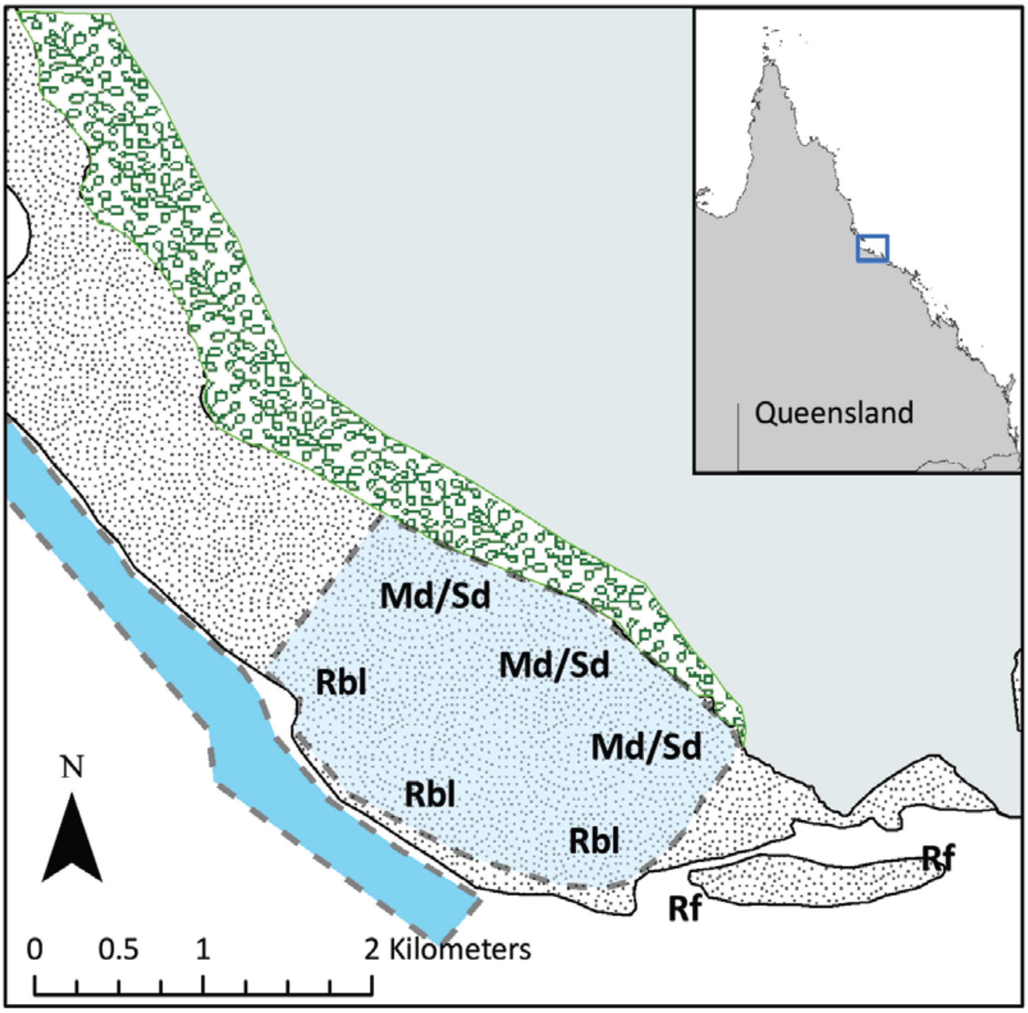


Figure 3.1: Location map showing Cockle Bay and surrounds. Rbl = intertidal foreshore with rubble substrate; Rf = coral boulders and fringing coral reef; Md/Sd = intertidal foreshore with mud and sand substrate; Sg = seagrass, green leaf motif = intertidal fringing mangrove. Sampling areas are indicated by the light blue box (high tide sampling area) and dark blue box (low tide sampling area).

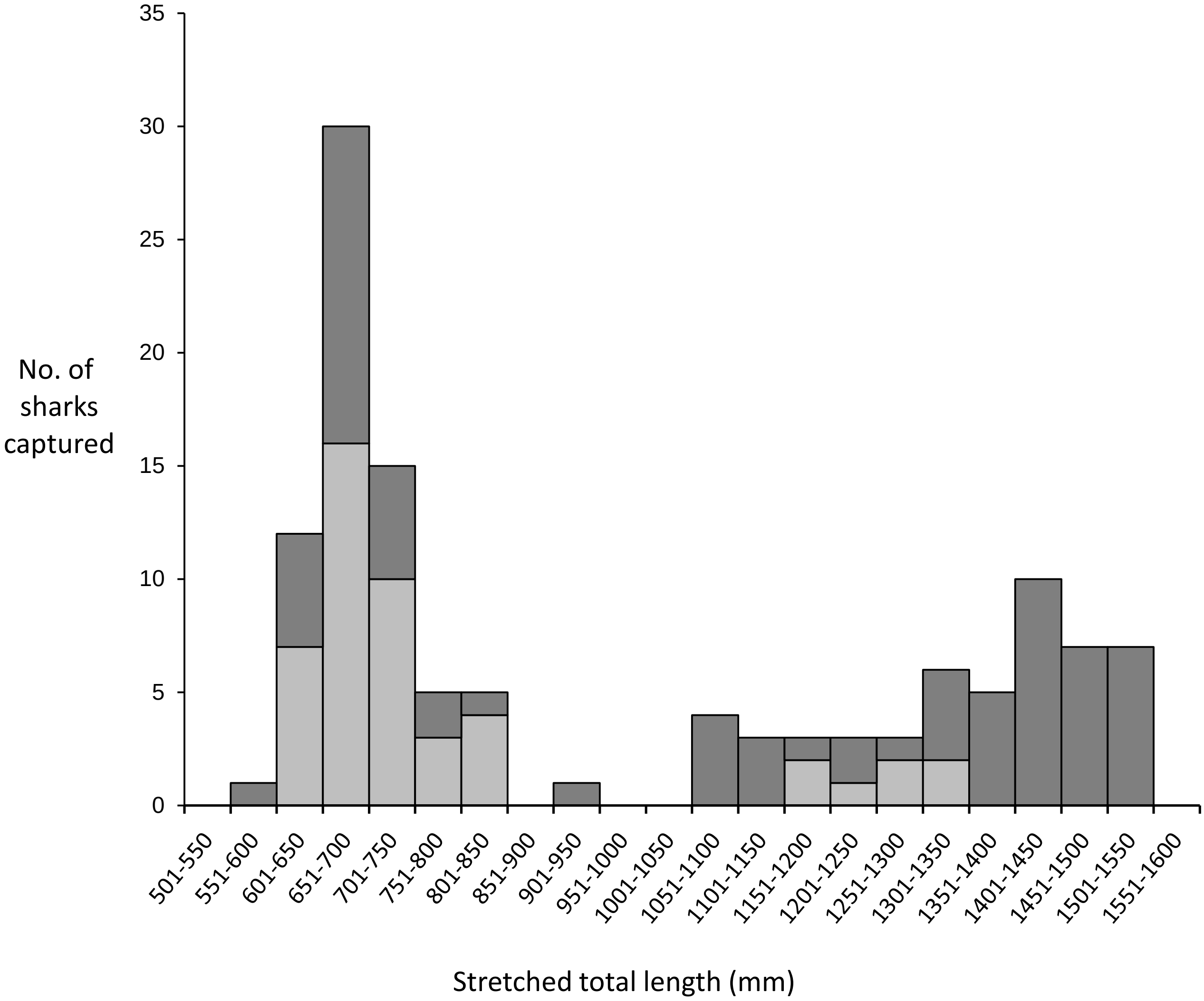


Figure 3.2: Size frequency distribution of the coastal *C. melanopterus* population sampled from October 2008 to March 2011. Dark grey bars indicate females, light grey bars indicate males. Note the paucity of animals between 850 mm to 1050 mm Stretched total length (L_{ST}).

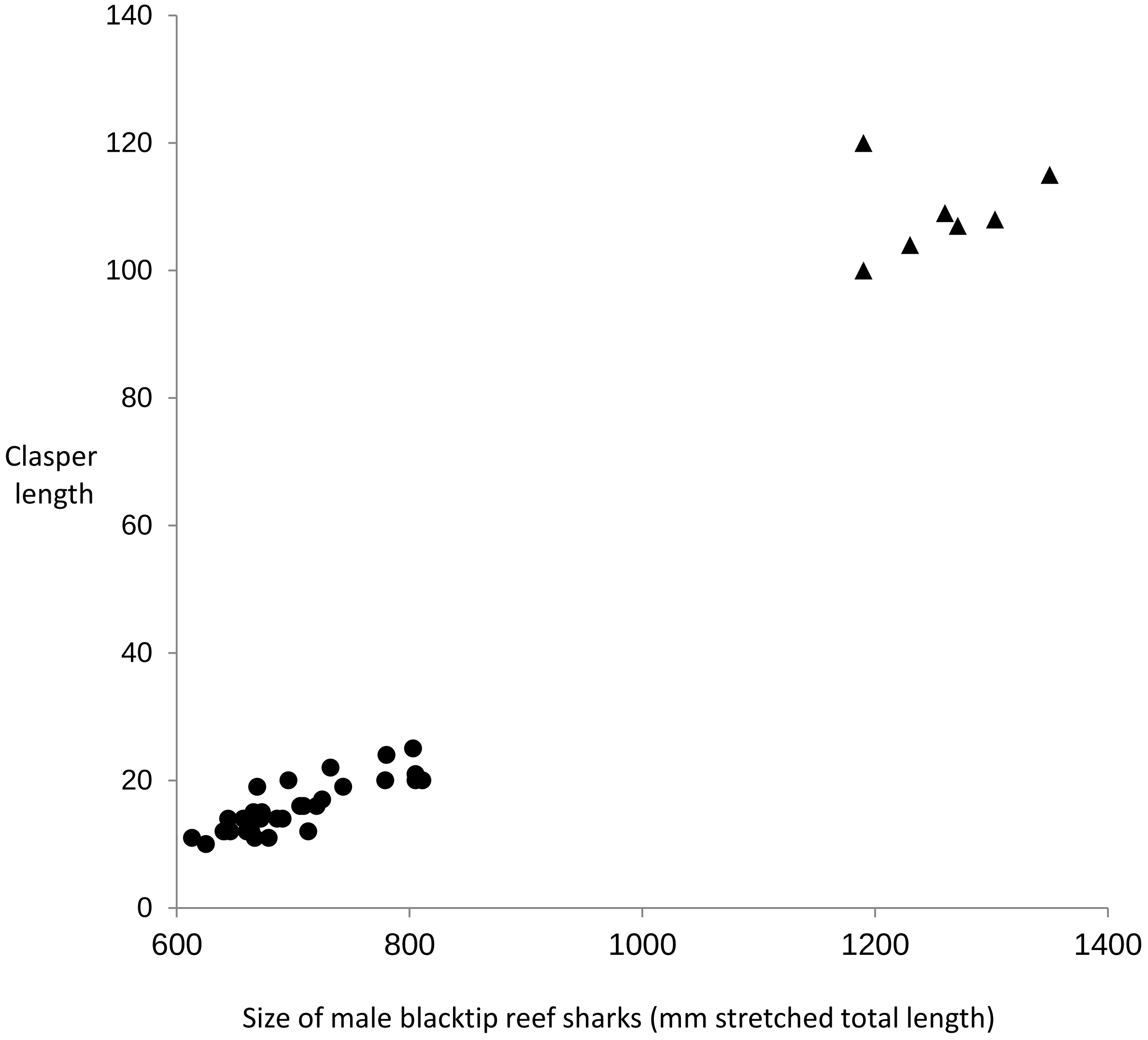


Figure 3.3: Maturity of male *C. melanopterus* expressed as clasper length and condition against size; circles denote uncalcified claspers, triangles denote calcified claspers.

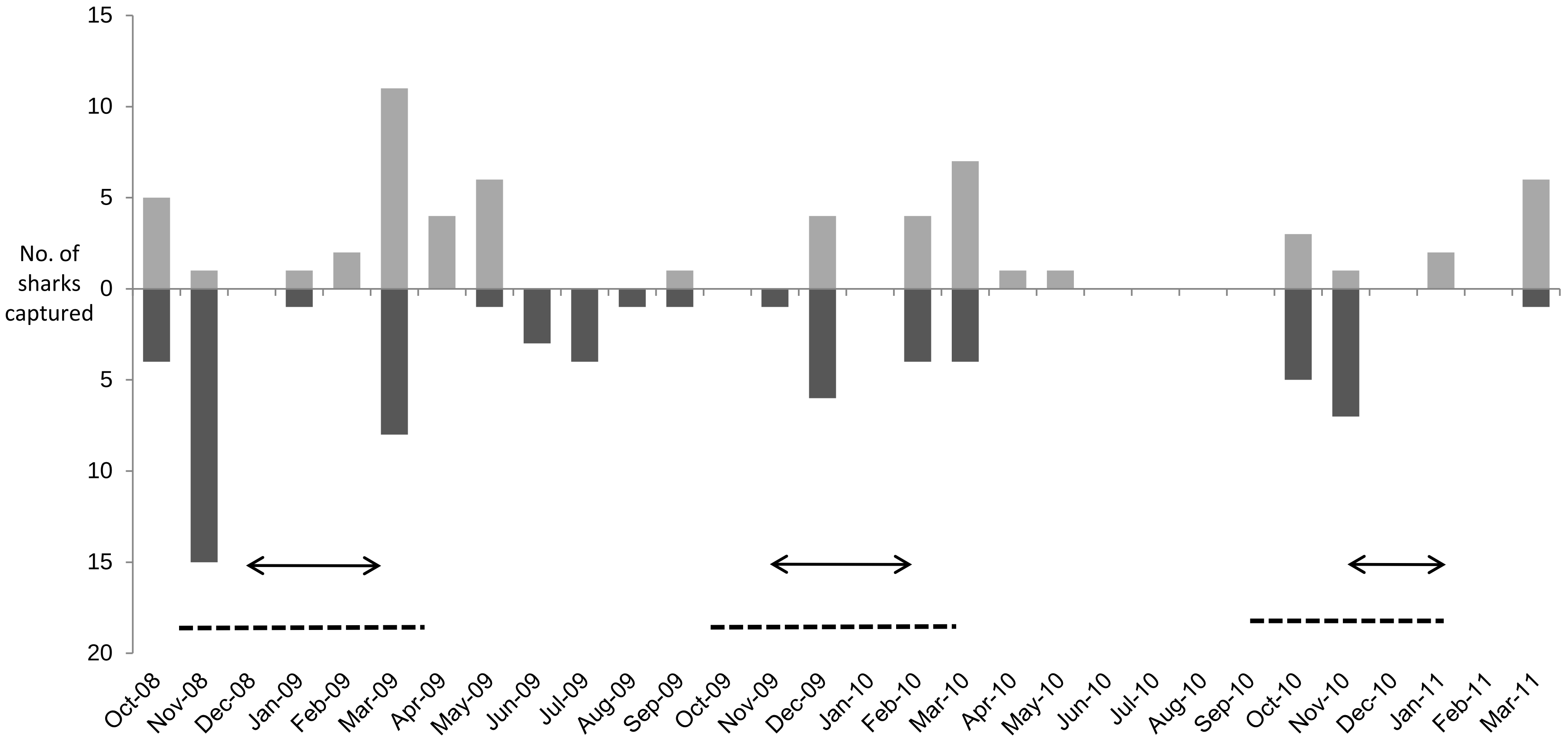


Figure 3.4: Abundance of juvenile (light grey bars) and adult (dark grey bars) *C. melanopterus* tagged at Cockle Bay per month. Dashed lines indicate the summer-wet season; arrows indicate the timing of parturition; dashed lines indicate presence of mating scars on females.

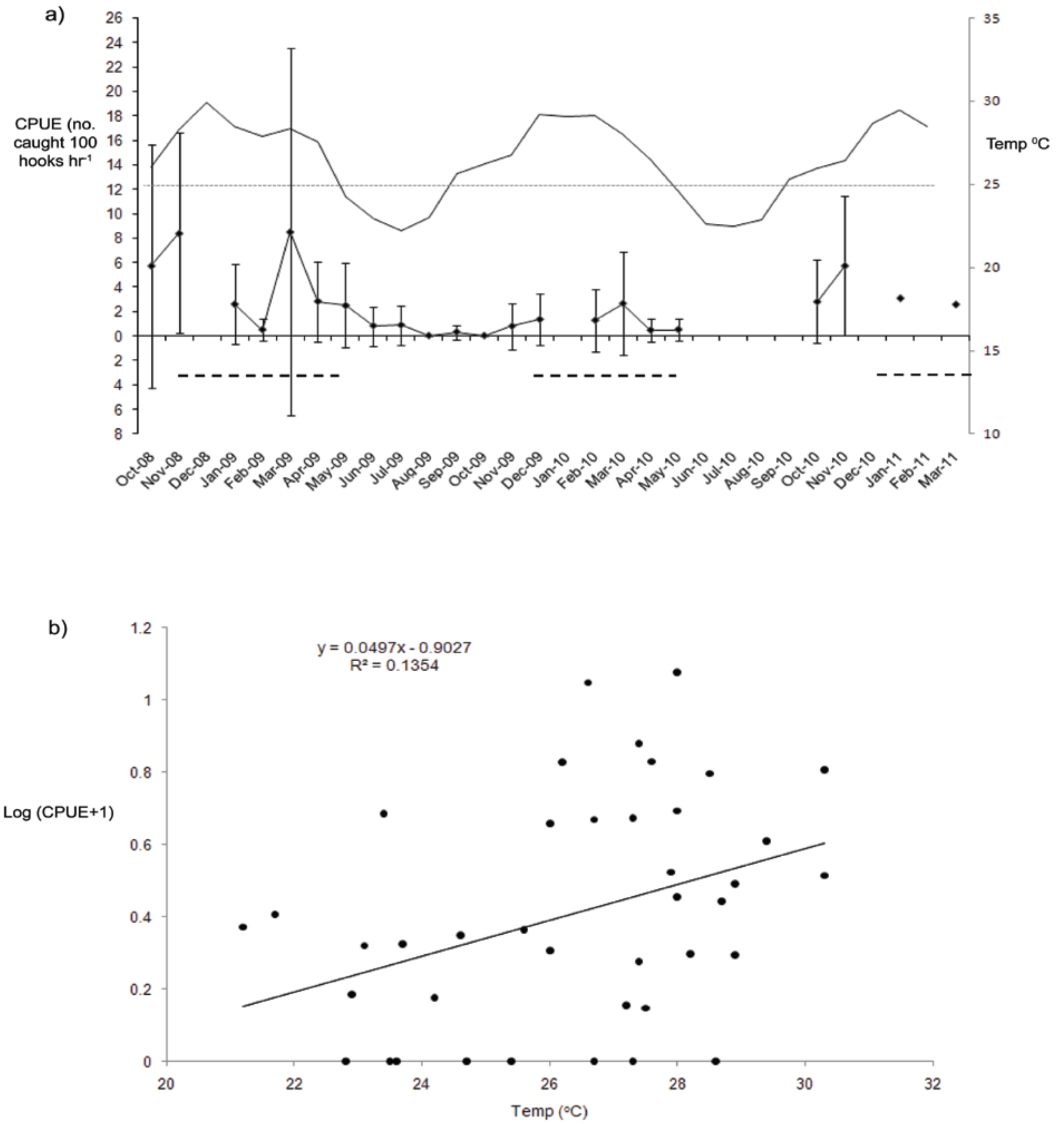


Figure 3.5: Trends in CPUE over the sampling period: (Fig. 5a) monthly average catch-per-unit-effort (no. per 100 hooks hr^{-1}) of *C. melanopterus* at Cockle Bay between October 2008 and March 2011. Months without a data point indicate sampling was not conducted; grey solid line indicates sea temperature at 1.9 m depth from a weather station in Cleveland Bay maintained by the Australian Institute of Marine Science. Horizontal dotted line indicates 25°C reflecting the change from summer-wet to the winter-dry season. (Fig. 5b) linear regression of Log CPUE with sea temperature.

Tag no.	No. recaptures	Date(s) capture	Date(s) recaptured	Days at liberty	Recapture distance	Sex	Maturity	L_{ST} at recapture (mm)	Δ L_{ST} (mm)
R0095	1	28-Oct-08	26-Oct-10	728	≤2.5 km	F	Juvenile	1031	104
R0276	1	11-May-11	24-Jan-12	258	≤2.5 km	F	Juvenile	740	34
R0081	1	08-Oct-08	27-May-09	231	≤2.5 km	M	Juvenile	731	61
R0213	1	27-May-09	17-Feb-10	266	0.6 km	M	Juvenile	752	73
R0236	1	03-Mar-10	24-Oct-10	235	≤2.5 km	M	Juvenile	NA	-
J0145	1	28-Oct-08	22-Apr-09	176	≤2.5 km	F	Adult	1449	-39
J0148	2	28-Oct-08	11-Mar-09	**134**	≤2.5 km	F	Adult	1460	-43
J0148		11-Mar-09	25-Jun-09	**106**	0.7 km	F	Adult	1510	50
		Total days at liberty		**240**			**Total Δ L_{ST} = 7**		
J0192	1	19-Nov-08	27-Jun-10	585	1.6 km	F	Adult	1328	-52
J0307	2	21-Jan-09	03-Mar-10	**406**	0.8 km	F	Adult	1500	14
J0307		03-Mar-10	29-Nov-10	**271**	0.5 km	F	Adult	1512	12
		Total days at liberty		**677**			**Total Δ L_{ST} = 26**		
J0314	1	28-May-09	21-May-10	358	2.6 km	F	Adult	1427	-3
J0325	1	24-Jun-09	18-Dec-09	177	0.3 km	F	Adult	1454	53
J0338	1	30-Mar-09	29-Nov-10	609	0.2 km	F	Adult	1458	36
J0340	2	30-Mar-09	20-Aug-09	**143**	0.1 km	F	Adult	1422	12
J0340		20-Aug-09	24-Nov-11	**826**	3.8 km	F	Adult	1425	3
		Total days at liberty		**969**			**Total Δ L_{ST} = 15**		
J0342	1	21-Apr-09	25-Mar-11	703	0.1 km	F	Adult	1298	18
J0343	1	21-Apr-09	18-Dec-09	241	0.2 km	F	Adult	1480	28
J0345	1	22-Apr-09	23-Jul-09	92	0.2 km	F	Adult	1364	54
J1110	1	02-Feb-10	03-Mar-10	29	0.1 km	F	Adult	NA	-

R0116	2	25-Nov-08	21-Apr-09	**147**	0.9 km	F	Adult	1488	8
R0116		21-Apr-09	29-Nov-09	**222**	0.2 km	F	Adult	1471	-17
		Total days at liberty		**369**			**Total Δ L_{ST} = -9**		
R0117	1	25-Nov-08	18-Dec-09	388	0.8 km	F	Adult	1400	-10
R0120	3	25-Nov-08	25-Jun-09	**212**	0.2 km	F	Adult	1150	20
R0120		25-Jun-09	19-Nov-09	**147**	0.9 km	F	Adult	1172	22
R0120		19-Nov-09	03-Mar-10	**104**	0.8 km	F	Adult	1218	46
		Total days at liberty		**463**			**Total Δ L_{ST} = 88**		
R0123	2	25-Nov-08	18-Dec-09	**388**	0.1 km	F	Adult	1420	52
R0123		18-Dec-09	02-Feb-10	**46**	0.5 km	F	Adult	NA	-
		Total days at liberty		**434**			**Total Δ L_{ST} = ?**		
R0129	2	25-Nov-08	27-May-09	**183**	2.3 km	F	Adult	1340	201
R0129		27-May-09	27-May-09	**0**	0.3 km	F	Adult	NA	-
		Total days at liberty		**183**			**Total Δ L_{ST} = ?**		
R0121	1	25-Nov-08	17-Jan-11	783	1.6 km	M	Adult	1260	70
R0200	2	25-Nov-08	02-Feb-10	**434**	0.4 km	M	Adult	1250	-10
R0200		02-Feb-10	12-Apr-10	**69**	0.9 km	M	Adult	1280	30
		Total days at liberty		**503**			**Total Δ L_{ST} = 20**		

Table 3.1: Size, sex, movement distance and days at liberty for recaptured blacktip reef sharks from Cockle Bay. A total of 33 recapture events occurred from 24 individual sharks with 16 animals recaptured once, 7 animals recaptured twice and 1 recaptured three times. Bold text indicates animals recaptured multiple times. Δ L_{ST} is the difference in animal length between capture and recapture, NA denotes where length at recapture was not available and thus total change in L_{ST} could not be calculated (indicated as L_{ST} ?).

4. Age, growth and reproductive biology of the blacktip reef shark and implications for vulnerability

4.1 Introduction

There is widespread concern over declining populations of sharks and rays around the world and especially for reef sharks which have experienced declines on reefs in the Indian Ocean (Graham *et al.*, 2010), Pacific Ocean (Nadon *et al.*, 2012), the Indo-Pacific region (White & Kyne, 2010) and in Australia's Great Barrier Reef (Heupel *et al.*, 2009, Robbins *et al.*, 2006). These declines have highlighted the need for robust data to inform the conservation and management of these shark populations, especially life history information such as age and growth data, size at age relationships, and reproductive data related to fecundity (Simpfendorfer *et al.*, 2011). Characterising the age, growth, and reproductive biology (henceforth collectively referred to as life history) of sharks and rays is crucial to understanding the population dynamics of these species and is vital for fisheries stock assessment, conservation and management (Heupel & Simpfendorfer, 2010, Simpfendorfer *et al.*, 2011, Walker, 2005b). It is also desirable to determine life history characteristics from local populations as life history parameters can differ between populations in different geographic locations (e.g. Carlson & Baremore, 2003, Cope, 2006, Lombardi-Carlson *et al.*, 2003, Yamaguchi *et al.*, 2000). Consequently using life history parameters derived from con-specifics in other locations can compromise the accuracy of population models and risk assessments.

Life history studies and population assessments are especially important for sharks and rays which are generally long lived, late maturing and slow growing fishes (Cortés, 2000), traits that have contributed to their over-exploitation and decline in various locations (e.g. Blaber *et al.*, 2009, Dulvy *et al.*, 2008, Graham *et al.*, 2001). While the number of published life history studies has increased since the 1980s (Cailliet & Goldman, 2004), the biology of many species remains poorly understood (Fowler *et al.*, 2005, Heupel & Simpfendorfer, 2010, Simpfendorfer *et al.*, 2011). This lack of data is a significant concern in ongoing efforts to manage and conserve sharks and rays in many locations around the world (FAO, 1999, Shark Advisory Group & Lack, 2004).

As described in the preceding chapters, the blacktip reef shark is a widely distributed reef shark that occurs in coral reef habitats as well as shallow coastal habitats such as intertidal foreshores and mangroves (Chapter 2) where it may use coastal habitats for reproductive purposes (Chapter 3). The blacktip reef shark is also one of the most commonly observed reef sharks by divers and snorkelers, with reef sharks making valuable contributions to reef-based tourism in locations such as French Polynesia, Palau and the Great Barrier Reef (Vianna *et al.*, 2012, Vignon *et al.*, 2010, Whatmough *et al.*, 2011). Despite its wide distribution and growing interest in the species, knowledge of the species' biology is incomplete. While data on the blacktip reef shark size, population structure and reproductive biology are available from the Indian Ocean (Stevens, 1984), northern Australia, Indonesia (Lyle, 1987, White, 2007) and the Central Pacific (Papastamatiou *et al.*, 2009a, Porcher, 2005), reproductive traits vary between location and the available reproductive data are "limited and conflicting" (Heupel, 2005). There are no published age and growth data for the blacktip reef shark.

Like other reef sharks such as the grey reef shark (*C. amblyrhynchos*), the blacktip reef shark is taken in artisanal and commercial fisheries in Africa, Asia and the Pacific (Barnett, 1996a, Teh *et al.*, 2007, White, 2007), and in coral reef habitats (Heupel *et al.*, 2009) and coastal habitats (Chapter 2) of the GBRWHA. Fishing pressure is intense in some of these regions with declines in reef sharks evident (Blaber *et al.*, 2009, Graham *et al.*, 2010, Heupel *et al.*, 2009, Nadon *et al.*, 2012, Robbins *et al.*, 2006). The IUCN lists the blacktip reef shark as "Near Threatened" globally owing to what is known of its life history and the potential for depletion in some locations (Heupel, 2005). In eastern Australia managers have expressed increasing concern over the status of sharks and rays (GBRMPA, 2009). The blacktip reef shark is one of the three most commonly taken sharks in the GBR coral reef fishery (Heupel *et al.*, 2009) and is also the most commonly taken reef shark in the GBR coastal net fishery (Chapter 2). The blacktip reef shark's use of coastal habitats exposes it to a wide range of pressures including potential cumulative impacts (Chapter 2), and the coastal zone along the Queensland coast is under increasing pressure from direct uses and pressures such as habitat degradation (Brodie & Waterhouse, 2012, GBRMPA, 2009). Information about exploited GBR sharks and rays such as the blacktip reef shark is one of the two highest priority information needs identified by reef managers (GBRMPA, 2010).

This chapter investigated the life history of the blacktip reef shark and aimed to characterise age and growth parameters and verify reproductive biology for populations on the Australian east coast. These data provide essential information to inform future risk assessments and demographic analyses that would determine the conservation risks and sustainability issues facing this species.

4.2 Materials and methods

4.2.1 Sample collection

A total of 205 blacktip reef sharks from the east coast of Queensland, Australia were captured and measured between October 2008 and February 2012. Fisheries observers onboard commercial net fishing vessels (see Chapter 2 for details) measured 63 blacktip reef sharks while fishery independent sampling captured and measured 138 blacktip reef sharks. Length measurements and samples for four additional specimens were provided by the Queensland shark control program and commercial aquarium collectors.The sampling region included tidal waters along the Queensland east coast stretching eastward of 142º09’E near Crab Island (approx. 11.0ºS Lat.) southwards to Baffle Creek (approx. $24^{o}29^{'}$S). Sharks sampled in the commercial fishery were captured using mesh-nets of between 115-165 mm mesh size and 300 m to 600 m in length. Sharks obtained through fishery independent sampling were captured using multi-hook research lines with 40 to 50 baited hooks set at 10 m intervals and using a variety of locally available bait (see Chapter 3 for details).

Captured sharks were sexed, and fork length (L_F) and stretched total length (L_{ST}) measured to the nearest mm. To maximise measurement accuracy, sharks <1 m were measured onboard the vessel with a measuring board (animal ventral side down). Sharks >1 m length were measured over the side of the vessel with a measuring tape stretched “over the body” from snout to the caudal fin fork (L_F) and tip (L_{ST}) (Francis, 2006). The relationship between L_F and L_{ST} was determined using linear regression. Observers also recorded the reproductive status of males using clasper condition and length (see reproductive analysis). The timing of mating and parturition was inferred from the presence of mating scars in females and umbilical scars in all specimens.

4.2.2 Vertebral processing and analysis

Thoracic vertebrae were taken from below the anterior margin of the first dorsal fin and most were obtained from commercial fisheries. Vertebral processing generally followed methods described in Goldman (2005), with vertebrae stored frozen until processing. Thawed vertebrae were separated into individual centra with a scalpel and between five and ten centra were retained from each sample. The neural arch, haemal arch and extraneous tissue were carefully removed with a scalpel and centra were soaked in a 5% sodium hypochlorite solution (bleach) for up to 30 mins to remove residual tissue. Vertebrae were thoroughly rinsed and then dried for 24 hours at 60^{o}C. Once dry, a single centrum was randomly selected and a 400-600 μm thick longitudinal section taken through the centre (focus) of the centrum using a double-bladed, low speed rotary saw with diamond-tipped saw blades (Beuhler, Illinois, USA). Small centra (<10 mm diameter) were set in blocks of clear polyester resin so that they could be firmly secured in the saw for sectioning. Vertebral sections were fixed to glass slides using Crystal Bond (SPI supplies, Pennsylvania, USA) adhesive for analysis and storage. Vertebral sections were examined using a dissecting microscope with transmitted light and the number of growth bands present in the corpus calcareum recorded. Following Cailliet *et al.* (2006), a growth band was defined as a band pair comprised of dark opaque band and a light translucent band. The birth mark was assigned using the angle change in the corpus calcareum (Goldman, 2005). To estimate the age of each animal two separate readers independently counted the number of band pairs on each section with counts commencing after the birth mark. The interpretability of each vertebral section was independently scored by both readers on a scale of 0 to 4 with the following definitions: 0 – unreadable; 1 – bands visible but difficult to interpret; 2 – bands visible but most bands difficult to interpret; 3 – bands visible but a minority difficult to interpret; and 4 – all bands unambiguous (McAuley *et al.*, 2006). The age estimates derived from the two readers were compared and where age estimates did not agree, both readers re-analysed the vertebrae to reach an 'agreed age estimate'.

4.2.3 Age and growth validation

As recommended by Cailliet *et al.* (2006), precision and bias between readers and across the sample range were calculated using several methods; Average Percent Error (APE) (Beamish & Fournier, 1981), contingency tables, Bowker's test for symmetry (Bowker, 1948), and the coefficient of variation (Chang, 1982). An age-bias plot was also constructed to identify potential systematic biases between readers (Cailliet *et al.*, 2006, Campana *et al.*, 1995). Precision and bias analyses were performed in the R program environment (R Development Core Team, 2012) using the *FSA* package (Ogle, 2012).

Validating the timing (when bands were deposited) and periodicity (how often bands were deposited) of band pair formation was accomplished by the recapture of chemically marked individuals. Throughout the tagging study 63 sharks were injected with calcein at a dose of 5 mg per kg body weight (McAuley *et al.*, 2006). To minimise handling stress only individuals deemed to be in good condition at the time of capture (i.e. strong and active swimming and responses) were chemically tagged. Blacktip reef sharks were also kept in captivity in a commercial aquarium in an open tank system; one shark for 8 months (260 days) and three sharks for 1.16 years (431 days). Aquarium water quality mirrored ambient conditions at the capture location as the facility was located only 8.4 km from the sampling site and the holding tank received regular water exchanges with the adjacent estuary.

4.2.4 Age and growth estimation

Following Cailliet *et al.* (2006), a selection of models were used to estimate growth parameters for the species including five of the models often used in age and growth studies in elasmobranch fishes (Cailliet *et al.*, 2006, Goldman, 2005, Thorson & Simpfendorfer, 2009). Growth models included the 3 parameter von Bertalanffy (VonB3) and 3 parameter Gompertz (GPZ3) growth models, the 2 parameter von Bertalanffy (VBG2) and 2 parameter Gompertz (GPZ2) growth models (where L_0 – length at birth was fixed at 587 mm using data from this study); and the logistic (Log) growth model. Growth models were fitted to the age-at-length data derived from vertebral analysis, and used to estimate the maximum (asymptotic) length L_∞, size at birth L_0 and the growth coefficient k. Because the values of k derived from different growth models are not comparable, the model from which a k value was derived is henceforth identified in subscripts (e.g. k_{lgst} for the value of k derived from the logistic model). The equations for growth models are included at Appendix 4.

The model with the best fit to the data was selected using the Akaike Information Criterion. Given the relatively small sample size of vertebral sections recovered during the study, a second-order information criteria (AICc) was used to assess model performance (Burnham & Anderson, 2002). AICc values were used to calculate the differences in AIC values between the models (Δ AICc) and AICc weights. The best performing models had the lowest AICc values and highest AICc weights. The relative performance of the different models compared to the best fitting models was assessed using Δ AICc (Burnham & Anderson, 2002). Growth models and AICc model selection were performed in the R program environment (R Development Core Team, 2012) using the *FSA* (Ogle, 2012), *qpcR* and *AICcmodavg* packages. The performance of growth models was also assessed by comparing the estimates of L_0 and L_∞ derived from growth models against values measured in the field during this study. Additionally, the absolute growth (ΔL_{ST}) of recaptured animals that were at liberty >1 year was plotted with the growth models to compare modelled growth rates with actual growth rates derived from field measurements.

4.2.5 Reproductive analysis

Reproductive activity and maturity status of 124 blacktip reef sharks was determined by examining external indicators such as clasper condition. Female maturity status could not be determined using external characters and was only identified for dissected specimens (see below). Males were classified as immature (small, flexible claspers that can be bent along the entire length); maturing (partially calcified claspers that were beginning to harden but could still be bent); and mature (claspers large, elongated and inflexible) as per McAuley *et al.* (2006). Mating activity was recorded by evidence of mating scars on adult females, and open umbilical scars indicated parturition within six to eight weeks. This timing was based on umbilical scar healing rates recorded in three blacktip reef sharks born and raised in commercial aquaria during the study (A. Chin, unpubl. data).

Maturity and gonad development were assessed through dissection and internal examination of a further 79 blacktip reef sharks provided by commercial fisheries observers, fishery independent sampling and other sources. Following Walker (2005b), maturity status for males was classified according to the development of the testes and seminal vesicle, while maturity status of females was classified according to the development of the ovary and uterus (Table 4.1). To determine whether mature females were actively breeding or resting, the number of yolky ova and maximum ova diameter were examined, with the presence of large, yolky ova indicating a female was in breeding condition. If present, the weight, sex and length of embryos were recorded.

Using the results of the age and growth analysis, age at maturity for males and females was calculated. The age at which 50% (Ag_{50}) and 95% (Ag_{95}) of animals were mature was determined through a logistic regression of estimated age and clasper calcification status (for males), and estimated age and ovary and uterine developmental stage (for females) using the following equation as per Walker (2005b, 2007).

$$P(Y) = P_{max} \left(1 + e^{-\ln(19)\left[\frac{l-\beta_1}{\beta_2-\beta_1}\right]}\right)^{-1}$$

where $P(Y)$ is proportion of males in the population that are mature at age, y; where $\beta 1$ and $\beta 2$ are parameters derived from the regression model which correspond to Ag_{50} and Ag_{95}, respectively; and $P_{\max}$ is the asymptote of the model and was fixed at 1 (i.e. all individuals classified as mature). A generalised linear model (GLM) with a binomial error structure and logit link function was run in the R program environment to estimate parameters $\beta 1$ and $\beta 2$.

4.3 Results

4.3.1 Sampling and collection

The sample population (n=205) was biased towards juvenile and adult females, with only 15 males >1000 mm L_{ST} captured (Fig. 4.1). There was also a paucity of animals between 950 mm and 1050 mm L_{ST} (Fig. 4.1). As a result, both sexes were pooled for age and growth analysis. Males ranged from 543 to 1390 mm L_{ST}, while females ranged from 514 to 1600 mm L_{ST}. Linear regression showed a consistent relationship between L_F and L_{ST} across the size range with the relationship between L_F and L_{ST}: $L_{ST} = L_F \times 1.17 + 41.23$ ($R^2 = 0.992$) for males and $L_{ST} = L_F \times 1.15 + 49.06$ ($R^2 = 0.996$) for females.

4.3.2 Age and growth validation

Size at age estimates were derived from vertebral analysis (n=72). The age estimates derived from both readers were similar and indicated acceptable levels of precision. Specifically, contingency tables and *p* values resulting from Bowker's test showed no significant differences in age estimates between readers ($p = 0.287$, see Appendix 5). Vertebrae were generally easily interpretable with both readers reporting a mean score of 2.94 for vertebrae readability, and the mode of readability scores was 4 (all bands unambiguous). While the values for the Average Percent Error (APE = 20.61) and Coefficient of Variation (CV = 29.14) were high compared to studies of teleost fishes, they were comparable to the ranges evident in chondrichthyan studies (Campana, 2001). Additionally, sensitivity analysis revealed that these error values resulted from the small sample size, with disagreements of 1 year in five individuals between the two readers resulting in CV values >20. There was no systematic bias apparent between the age estimates of the two readers, with the age bias plot showing that age estimates agreed within the 95% confidence interval (Appendix 5).

Eleven calcein tagged specimens were recovered for age validation. Four were captive specimens kept for 423 d (n=3) and 260 d (n=1). Similar to McAuley *et al.* (2006) captive sharks in this study showed no adverse effects from chemical marking with calcein. A further seven calcein tagged animals were recaptured from the wild, with time at liberty ranging between 176 and 939 d. Calcein marks were present and interpretable in eight of the calcein tagged animals and indicated that band pairs were deposited annually (Fig. 4.2), with the translucent band deposited during the summer and early autumn (Nov to Mar). Of the three vertebrae that were not interpretable two had no visible calcein mark. The calcein mark in the third vertebrae was deposited close to the edge of the vertebrae and the banding pattern visible after the mark was inconsistent with the time at liberty (969 days) (see Appendix 6). These vertebrae came from older individuals (8-11 years estimated age) close to the maximum sizes measured during this study. It appears that terminal band pairs may become increasingly difficult to identify in older animals resulting in underestimating maximum ages.

4.3.3 Age and growth model selection

The oldest agreed age estimate derived in this study was 15 years for an adult female of 1521 mm L_{ST}. Males had lower maximum size and age, with the 2 oldest and largest males (1390 and 1321 mm L_{ST}) estimated to be 10 years old. The logistic growth model was the best performing model with an AICc weight of 0.75, while the Gompertz 3 parameter model was the second best performing model with an AICc weight of 0.21 (Table 4.2). The growth curves for both models were similar (Fig.4.3), with models reaching growth asymptotes earlier than the 2 and 3 parameter von Bertalanffy models and the 2 parameter Gompertz model. These other models had relatively little support with high Δ AICc values and low AICc weights (Table 4.2). The logistic model produced growth parameters estimates of length at birth L_0 and asymptotic length L_∞ that were comparable to the observed median size of captured neonates (587 mm L_{ST}) and the largest animal measured (1600 mm L_{ST}). The growth coefficient k_{lgst} estimated by the logistic model was 0.25 yr^{-1}. Growth measurements obtained from 12 individuals at liberty >1 year matched the logistic and Gompertz 3 parameter models most closely (Fig. 4.3). However, the growth of animals over 1200 mm L_{ST} tended to deviate more from the models compared to smaller animals but this could indicate that measurement error increases above this length (Francis, 2006).

4.3.4 Age at maturity and reproductive characters

Reproductive information was drawn from external marks in tagged and released sharks (n=128) and from animals and samples examined in laboratory studies (n=79). Field observations suggest that parturition occurred during the Austral summer and into early autumn (i.e. November to February), with the tagging study capturing 13 neonates with open umbilical scars and 18 young of the year with partially closed umbilical scars during this period. Most (n=10) of the open umbilical scars were observed in November and December with closure occurring between January and March. Size at birth was estimated at 587 mm L_{ST} based on the median size of neonates. Mating scars were observed between December and March on six adult females (ranging between 1280 to 1480 mm L_{ST}). This timing was consistent with observations of mating scars seen in blacktip reef sharks in other locations on the Australian east coast (A. Schlaff pers comm.), and in a commercial Aquarium in Townsville (A. Chin, unpubl. data). Age at maturity differed between males and females. Males matured earlier with 50% reaching maturity at 3.19 years (~970 mm L_{ST}) and 95% reaching maturity at 4.2 years (~1050 mm L_{ST}). Females matured later, with 50% mature at 8.0 years (~1300 mm L_{ST}) and 95% mature at 8.5 years (~1335 mm L_{ST}) (Fig. 4.4).

Reproductive tracts of 12 adult females were examined and ova diameter ranged from 4 mm to 22 mm with a mean diameter of 10.7 mm. Internal examination also confirmed the timing of parturition. Five females (ranging from 1348 to 1600 mm L_{ST}) were pregnant with embryos macroscopically visible in the uterus. Near term embryos (535 to 605 mm L_{ST}) were present in November and December, consistent with the capture of neonates during the early summer, and post parturition females (uterus stage 6) were found in November and April. Mean litter size was 3.4 pups (range = 2 to 4 pups) per litter and Chi square tests showed that embryo sex ratio did not differ from unity ($\chi^2 = 1.33$, df = 1, $P = 0.248$). Pups were evenly distributed between the two uteri.

Data about reproductive periodicity were inconclusive. There was some evidence of an annual reproductive cycle with two females found with large yolky ova (diameter >20 mm) when they were sampled in October and November, suggesting an active reproductive phase in early summer. One of these females was pregnant with near term embryos, indicating reproductive readiness following parturition. The onset of mating (December) and parturition (November) suggests that gestation period could be 11 months for annually reproducing animals. However, another pregnant female sampled with similar sized embryos did not have yolky ova present, potentially indicating a summer resting phase following parturition which indicates a biannual reproductive cycle.

4.4 Discussion

This study contributes valuable data to inform the conservation and management of the blacktip reef shark by providing validated age and growth parameters for the species and regionally verified reproductive data for GBR populations. While there are no other published age and growth data available on the blacktip reef shark for comparison, the species is often considered as a congeneric species for other reef sharks such as the grey reef shark (*C. amblyrhynchos*) in discussions of reef shark ecology and conservation (e.g. Dale *et al.*, 2011, DeCrosta *et al.*, 1984, Heupel *et al.*, 2009). This study suggests that blacktip reef sharks have slow growth rates and low reproductive capacity similar to that of the grey reef shark. Comparing growth curves for the blacktip reef shark (this study) with that of the grey reef shark (DeCrosta *et al.* 1984) shows that the blacktip reef shark has slower growth over its life span (Fig. 4.5). Likewise, age at maturity of female blacktip reef sharks (8 years) is more conservative than that of female grey reef sharks (6 yrs) while litter sizes are similar (DeCrosta *et al.*, 1984). The slow growth and low fecundity of grey reef sharks appears to have contributed to fishery-derived population declines in numerous locations (Graham *et al.*, 2010, Heupel *et al.*, 2009, Robbins *et al.*, 2006). Given the similarities in life history traits between the two species, the blacktip reef shark may be correspondingly sensitive to high levels of fishing mortality. This sensitivity should be considered in managing commercial and artisanal fisheries which take reef sharks from coastal habitats and coral reefs across the tropics (Heupel *et al.*, 2009, Chapter 2, Marshall, 1996a, Teh *et al.*, 2007). The slow growth and low reproductive capacity of the blacktip reef shark may be particularly important in the GBR where the species is taken in multiple fisheries and potentially exposed to localised depletion (Chapter 2).

4.4.1 Regional patterns in life history

This study provided regionally verified reproductive information about the species for use in risk assessments in eastern Australia and the GBR. Previous risk assessments have used proxy data from con-specifics from other regions (e.g. Gribble *et al.*, 2005, Salini *et al.*, 2007). While the use of proxy life history data is sometimes necessary, life history traits can vary significantly between different locations as reported in sharks such as the bonnethead (*Sphyrna tiburo*) in the Atlantic and Gulf of Mexico (Lombardi-Carlson *et al.*, 2003) and the starspotted dogfish (*Mustelus manazo*) in Japan and Taiwan (Yamaguchi *et al.*, 2000). Regional variations in life history traits can reduce the accuracy of assessments based on proxy data, highlighting the importance of regionally collected data such as those presented here.

Blacktip reef sharks of the Australian east coast have larger size at birth, maximum size, and size at maturity compared to con-specifics from other locations. Maximum sizes recorded in this study (males to 139 cm; females to 160 cm) exceeded lengths recorded at Aldabra Atoll in the Indian Ocean (males to 130 cm; females to140 cm); Palmyra Atoll in the central Pacific (males to 102 cm; females to137 cm); and in northern Australia (125 cm for both males and females) (Lyle, 1987, Papastamatiou *et al.*, 2009a, Papastamatiou *et al.*, 2009b, Stevens, 1984). Likewise, size at birth determined from this study (587 mm) was larger than reported in previous studies. Regional size differences have been found in a range of carcharhinid species, for example bull sharks (*Carcharhinus leucas*) and blacktip sharks (*Carcharhinus limbatus*) in South Africa were found to be larger than con-specifics in the Gulf of Mexico and Atlantic (Wintner *et al.*, 2002). The size divergences observed in blacktip reef sharks from various regions could reflect differences in habitat types and resource availability. Previous studies have suggested that blacktip reef sharks in small, isolated coral atolls may have reduced size and growth due to reduced prey availability and quality as well as increased competition, while those from larger atolls or coastal habitats may be larger due to greater resource availability in those habitats and locations (Papastamatiou *et al.*, 2009a). Indeed, Bonham (1960) found free swimming blacktip reef sharks as small as 330 mm (TL) in isolated atolls in the Marshall Islands (cited in Papastamatiou *et al.*, 2009a). Resource limitation can reduce the growth and survival of sharks in atoll systems as evident in hammerhead sharks in the Hawaiian Islands (Lowe, 2002). In contrast, coastal regions such as the inshore and coastal regions of the GBR are productive systems that support a diverse range of sharks and potential prey species (Kinney *et al.*, 2011, Simpfendorfer & Milward, 1993). Increased resource availability in coastal habitats may result in larger maximum sizes and perhaps associated with increased female size, larger sizes at birth. While increased resource availability may account for increased size, the relationship between habitat type, provisioning and resulting size of reef sharks has not been explored, and the causative factors behind the relatively large size of blacktip reef sharks on Australia’s east coast remain unknown.

4.4.2 Litter size and reproductive periodicity

Blacktip reef sharks in the GBR showed seasonal reproductive patterns with parturition and mating occurring during the summer and early autumn. These patterns are consistent with other accounts of the timing of mating and parturition, and litter size also corresponds with reports from other regions (Lyle, 1987, Porcher, 2005, White, 2007). However, information about gestation time and reproductive periodicity are inconsistent. Studies from the Red Sea, Madagascar and French

Polynesia reported a biennual reproductive cycle (Johnson 1978; Fourmanoir, 1961; Melouk 1954; cited in Lyle, 1987), contradicting studies from northern Australia (Lyle, 1987), Aldabra Atoll (Stevens, 1984) and another study from French Polynesia (Porcher, 2005) which showed annual reproduction. Unfortunately, the data from this study do not clarify this discrepancy with evidence of both an annual and biennial cycle. Variation in female reproductive periodicity within a single population has been reported in other species such as whiskery sharks (*Furgaleus macki*) where smaller adult females had biennial reproductive cycles while larger females reproduced annually (Simpfendorfer & Unsworth, 1998). A similar pattern was evident in female blacktip reef sharks observed in this study, with smaller females showing evidence of biennial cycles and larger females having annual cycles. It is possible that smaller females do not have sufficient energy intake to support annual reproduction (Simpfendorfer & Unsworth, 1998), which could also suggest differential foraging success or dietary intake between small and large adult females. Nevertheless this hypothesis is untested. Additionally, very few adult females were available for reproductive analysis, and samples were also limited to the summer and autumn months, restricting the ability to monitor ova and embryo development throughout a complete annual cycle. More data on reproductive periodicity, gestation time and embryo development are needed to resolve the reproductive cycle for the species.

4.4.3 Veracity of derived life history parameters

Vertebral analysis for this species was relatively simple as band pairs were easy to distinguish with high readability scores and no evidence of systematic biases between readers. Furthermore, vertebrae were available from neonates and young-of-the-year sharks to maximum size adults, providing a broad set of length-at-age data to generate growth curves. While the number of samples available to this study was relatively small, the spread of sizes and ages across the growth curve can compensate for small sample sizes in age and growth studies of sharks (Smart *et al.*, 2012) where it may not be possible to sample large numbers for logistical or ethical reasons (Heupel & Simpfendorfer, 2010). Age validation confirmed annual deposition of band pairs and deposition of the translucent band during the austral summer and early autumn. Water temperature is highest during these months and blacktip reef sharks may grow fastest during this period, resulting in less dense (translucent) bands. Age and growth validation in this study is strengthened by the relatively high number (11) of calcein-injected vertebrae recovered, with recaptured animals spanning a range of sizes (627 to 1510 mm L_{ST}) allowing validation of band pair periodicity and timing across different growth stages. Additionally, this is one of only a few studies (Cailliet *et al.*, 2006) to include age validation from both wild and captive animals. Comparisons between wild and captive animals showed identical timing and periodicity of band pair formation, potentially due to similarity of the aquarium conditions to the capture site. Growth data from captive individuals (as measured by changes in length or weight) was not included in growth models as these metrics vary according to captive diet and feeding regimes (Janse, 2003).

This study also demonstrated that vertebral analysis may underestimate maximum age. Underestimates arise from difficulties in interpreting terminal band pairs in older animals, with two of the eleven calcein marked animals failing to assimilate a calcein band and one animal presenting a number of band pairs after the calcein mark that was inconsistent with time at liberty. Similar complications have been reported in other sharks where band deposition ceases when the animal stops growing, and can lead to age underestimation by as much as 50% (Francis *et al.*, 2007). Additionally, while the logistic model was far superior to the other growth models tested (according to AICc weight), the model appears to indicate more rapid growth than that observed in recaptured animals, with all observations of measured growth lying below the estimated growth derived from vertebral analyses. This discrepancy could represent age underestimation from the vertebral analysis. Blacktip reef sharks also appear to have the capacity to live for a decade longer than the maximum age recorded in this study with blacktip reef sharks at the Reef HQ Aquarium being at least 25 years old (S. Menzies pers comm.). Underestimating longevity would have significant effects on demographic analyses, and the potential for age underestimation should be carefully considered in age and growth studies and demographic analyses based on vertebral band counts. The limitations of the small sample sizes available for exploring reproductive traits should also be acknowledged. There were no maturing males in the sample, with a large size and age gap between the largest juvenile male and smallest adult male. These sampling issues may also explain the large difference in estimated age at maturity between males (4 yrs) and females (8 yrs).

This study provides age and growth data for the blacktip reef shark and regionally verified reproductive data. This information provides the basis for revised risk assessments for blacktip reef shark populations on the GBR and Australian east coast. While not a targeted species in the GBR, the blacktip reef shark may be exposed to localised fishing pressure and cumulative impacts (Chapter 2; Chapter 3). This exposure combined with relatively slow growth and low reproductive output could make some populations highly vulnerable to intensive pressures from fishing and habitat loss and suggests that a cautious approach to their management and conservation is warranted.

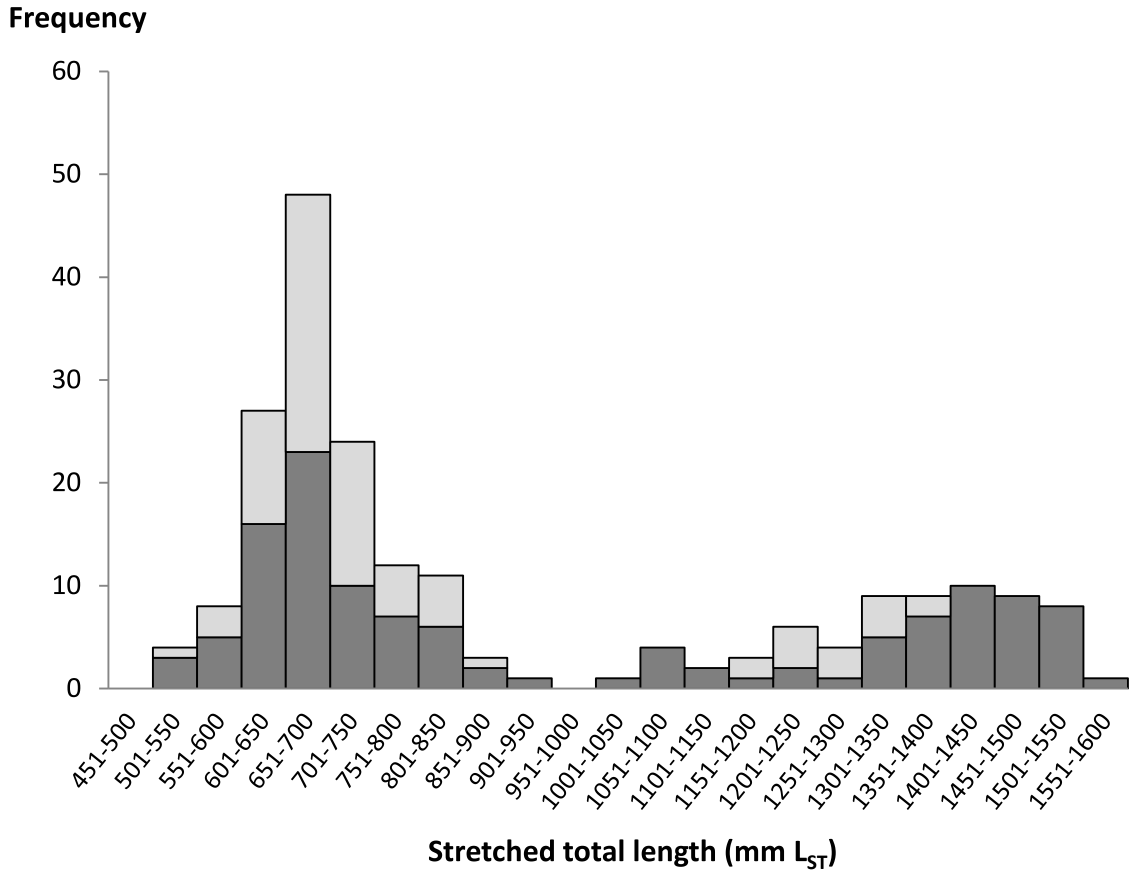


Figure 4.1: Size frequency distribution of 205 captured blacktip reef sharks showing size (mm L_{ST}) and sex (light grey for males, dark grey for females). The sample population was dominated by juveniles of both sexes and by adult females, with very few animals captured between 950 and 1050 mm L_{ST}.

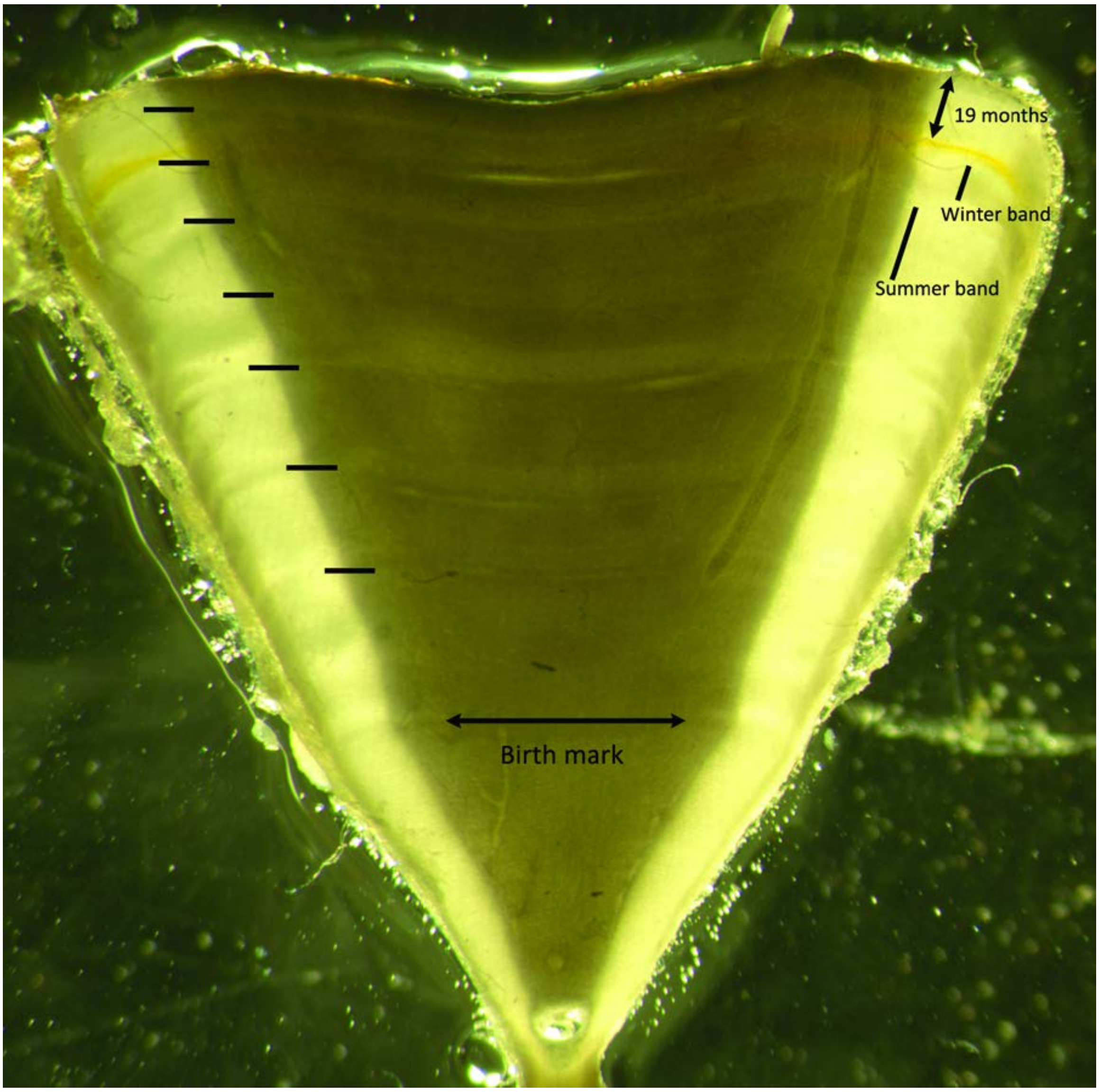


Figure 4.2: Vertebral section from 7 year old female blacktip reef shark J0192 measuring 1380 mm L_{ST}, captured and tagged on 19 Nov 2008, and recaptured after 585 days at liberty. The band pairs are readily identified and the yellow calcein band can be clearly distinguished.

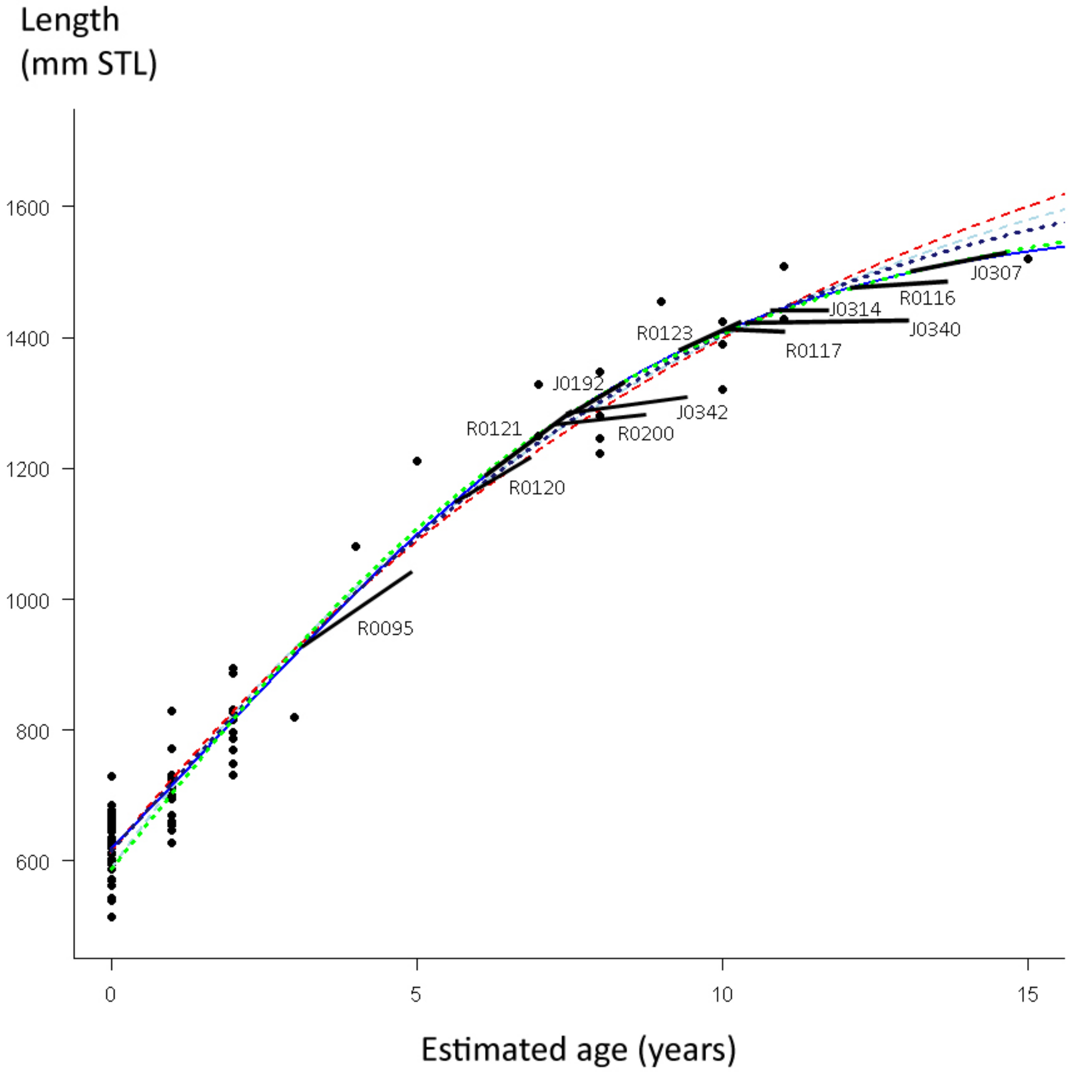


Figure 4.3: Age and growth curves for the blacktip reef shark using age estimates from vertebral counts and using five different growth models: Logistic (solid blue line); Gompertz 3 parameter (green dashed line); Gompertz 2 parameter (dark blue dashed line); von Bertalanffy 3 parameter (red dashed line); von Bertalanffy 2 parameter (light blue dashed line). Solid black lines plot growth observed in recaptured animals (identified by individual tag numbers).

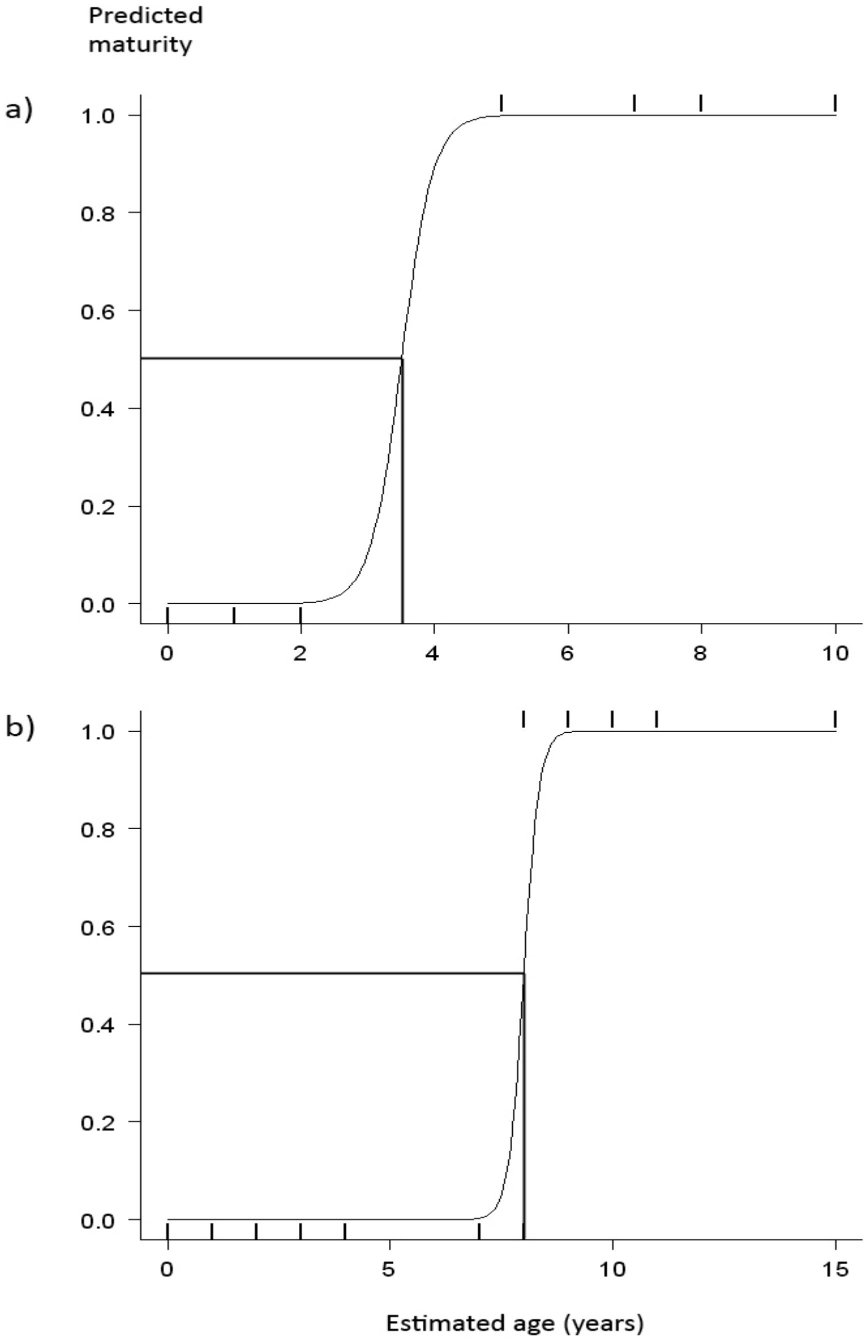


Figure 4.4: Maturity ogives from logistic Generalised Linear Models of estimated age. Curves show the proportion of males (a) and females (b) predicted to be mature at a given age. Straight lines show that 50% of males mature at 3.8 years, and 50% of females are mature at 8 years. Tick marks on the x axis show the distribution of samples used in the analysis. Note different scales on X axes.

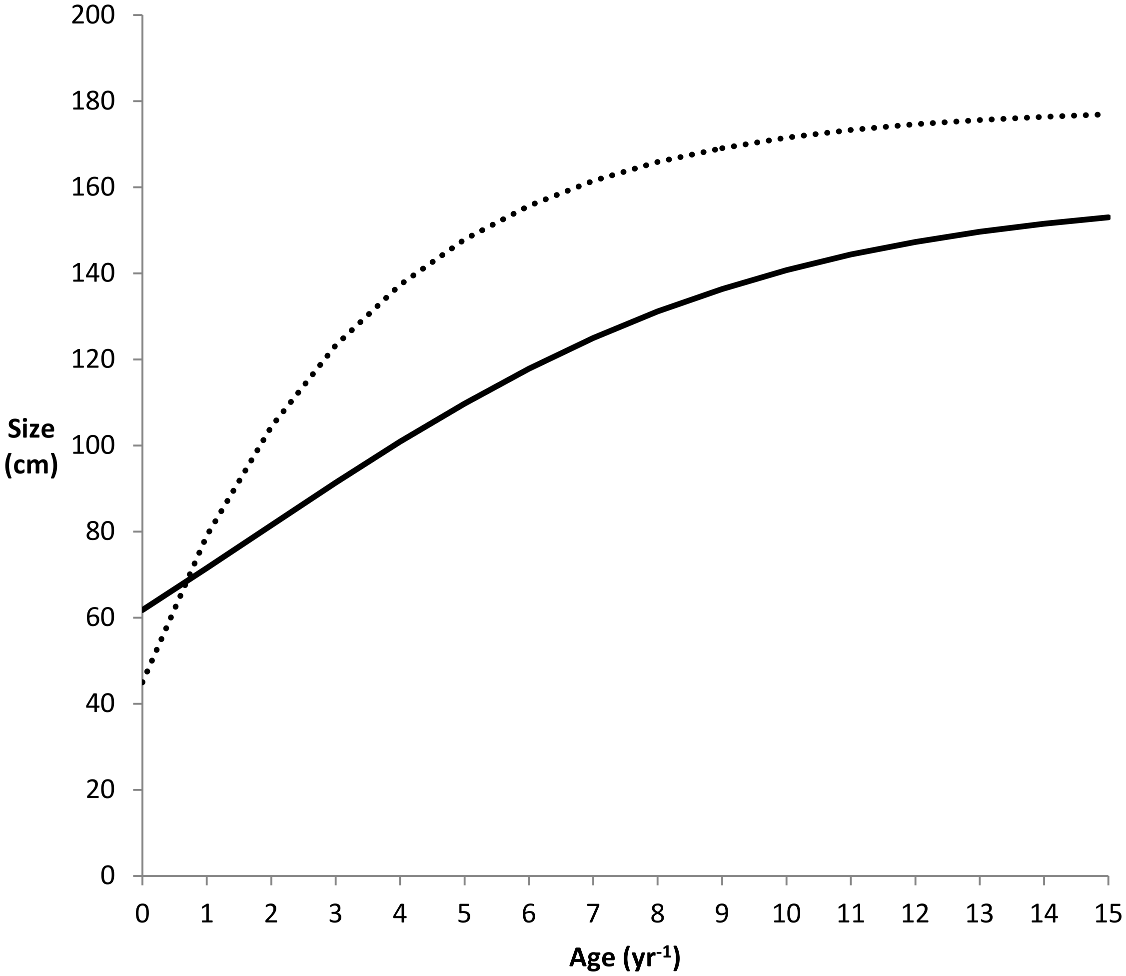


Figure 4.5: Comparison of growth curves for the grey reef shark and blacktip reef shark showing conservative growth for the latter. Growth curves for the grey reef shark (dotted line) derived from the von Bertalanffy growth model and growth parameters from DeCrosta *et al.* (1984). Growth curve for the blacktip reef shark (solid line) derived from the logistic growth model using growth parameters from this study.

Organ	Description	Stage	Maturity classification
Uterus	Uterus uniformly thin and white	1	Immature
	Uterus thin and white but partly enlarged posteriorly	2	Immature
	Uterus and ovary enlarged	3	Maturing
	Uterus enlarged, ovary enlarged with visible ova	4	Mature
	Uterus enlarged with visible embryos – pregnant	5	Mature, pregnant
	Uterus greatly enlarged, flaccid and distended, possible placental scars present on internal uterine wall	6	Mature, post parturition
Testis, seminal vesicle and claspers	Testis thin strip of tissue with epigonal tissue predominant, seminal vesicle with thin translucent walls, clasper uncalcified	1	Immature
	Testis thickened with extensive epigonal tissue, seminal vesicle with thickened opaque walls, seminal fluid may be present, claspers partially calcified	2	Maturing
	Testis enlarged and predominant, seminal vesicle with thickened opaque walls, seminal fluid may be present, claspers rigid and fully calcified	3	Mature

Table 4.1: Reproductive indices used to determine maturity based on Walker (2005).

Model	Model estimates			Model performance			
	L_0 (mm)	L_∞ (mm)	k (yr^{-1})	df	AICc	Δ AICc	AICc wt
Von Bertalanffy 3 parameter	613 (± 9.8)	1979 (± 189.3)	0.0854 (± 0.0179)	4	799.0186	7.09687	0.02168
Von Bertalanffy 2 parameter	NA	1840 (± 127.1)	0.1047 (± 0.01686)	3	803.9890	12.06726	0.00180
Gompertz 3 parameter	615 (± 9.2)	1698 (± 83.5)	0.1673 (± 0.0197)	4	794.4196	2.49788	0.21613
Gompertz 2 parameter	NA	1622 (± 61.6)	0.1956 (± 0.0180)	3	801.3430	9.42131	0.00678
Logistic	617.9 (± 8.9)	1585 (± 54.3)	0.2519 (± 0.021)	4	791.9217	0.00000	0.75359

Table 4.2: Parameter estimates and performance of age and growth models used for the blacktip reef shark. The best performing models were the Logistic and Gompertz 3 parameter models which had the lowest AICc value, the lowest Δ AICc values and the highest AICc weight. Numbers in parenthesis following estimates of L_0 and L_∞ and k are std. error.

5. Population organisation in blacktip reef sharks: residency, movement and the importance of coastal habitats for reef shark populations

5.1 Introduction

There is increasing recognition of the need to identify and protect key habitats to manage and conserve marine species. Shallow coastal and estuarine ecosystems provide important habitats for many species and there is a growing body of knowledge about the ecological significance of coastal habitats and estuaries, their social, cultural and economic value, and their utility to marine and terrestrial fauna (Barbier *et al.*, 2011, Faunce & Serafy, 2006, Nagelkerken, 2009). In particular, shallow coastal habitats such as mangroves, seagrass beds, and intertidal foreshores perform important ecosystem roles such as functioning as foraging grounds and nursery areas (Beck *et al.*, 2001, Blaber, 2007, Nagelkerken, 2009). Coastal habitats may also be intricately linked to populations and ecosystems further offshore, as illustrated by the connectivity and ontogenetic movements of fishes between coastal mangroves and coral reefs in the Caribbean (Mumby *et al.*, 2004, Nagelkerken *et al.*, 2008b), Gulf of Mexico (Jones *et al.*, 2010) and Great Barrier Reef (Russell & McDougall, 2005, Chapter 6). Inversely, degradation and loss of coastal habitats has been linked to decreased abundance and diversity of fishes (Taylor *et al.*, 2007) providing corroborating evidence of the importance of coastal ecosystems to fish communities. The importance of coastal ecosystems in conserving marine species is widely acknowledged and has been explicitly considered in seascape level planning of marine protected areas (MPAs) (Mumby, 2006) and some coastal habitats are afforded special protection (e.g. *Essential Fish Habitats* in the United States; *Fish Habitat Areas* in Queensland, Australia (Zeller, 1998)).

Coastal habitats are important to a wide range of elasmobranchs (sharks and rays) with a growing number of studies documenting the value of these systems (Knip *et* *al.*, 2010, Pierce *et al.*, 2011, e.g. Vaudo & Heithaus, 2009). Coastal areas may have high productivity which can reduce inter- and intra-specific competition and provide abundant resources to support shark populations (Kinney *et al.*, 2011, Simpfendorfer & Milward, 1993, Wiley & Simpfendorfer, 2007). Coastal habitats may also function as important nursery areas. Springer (1967) provided one of the earliest accounts of coastal shark nurseries and proposed a model of social organisation in shark populations based on patterns of size and sex segregation and movement. This model suggests that adult female sharks seasonally visit shallow coastal environments to give birth and then depart, leaving the neonates to mature in nursery grounds. Meanwhile adult males are transient visitors that seasonally enter shallow habitats to mate and depart once mating is complete (Springer, 1967). Numerous sharks in both temperate and tropical waters have since been found to conform to this model (e.g. Castro, 1993, Conrath & Musick, 2010, DeAngelis *et al.*, 2008, Ebert & Ebert, 2005, Grubbs *et al.*, 2007). Coastal nurseries can enhance growth and survival of juvenile sharks by providing abundant prey and/or reducing competition and predation (Branstetter, 1990, Heupel *et al.*, 2007, Springer, 1967). By enhancing juvenile growth and survival, coastal habitats play an important role in supporting marine ecosystems further offshore and may be crucial to continued recruitment into offshore populations and fisheries (Beck *et al.*, 2001, Jones *et al.*, 2010, Nagelkerken *et al.*, 2008b).

While coastal habitats provide important ecosystem functions for sharks and rays, use of these habitats may also increase exposure and vulnerability to environmental stressors and human impacts. Globally, coastal habitats are experiencing increasing pressure from human activities with many coastal areas affected by fishing, pollution, habitat loss and degradation (Lotze *et al.*, 2006, Mee, 2012). Shark and ray populations are in decline in many parts of the world and pressures in the coastal zone may exacerbate these declines (Fowler *et al.*, 2005, Simpfendorfer, 2000, White & Kyne, 2010). Furthermore, the effects of climate change are predicted to be greatest on sharks in the coastal zone (Chin *et al.*, 2010). The combination of pressures in the coastal zone and concerns over declining shark populations, juxtaposed against the important ecological functions coastal habitats provide, is stimulating debate about the contribution coastal habitats may make to the conservation of sharks and rays (Chapman *et al.*, 2005, Knip *et al.*, 2010, Knip *et al.*, 2012a)

The blacktip reef shark is a widely distributed species that is most often reported from clear-water coral reef habitats in the Indo-Pacific and Indian Oceans (Last & Stevens, 2009). However, it also frequents turbid coastal habitats such as mangroves, seagrasses and inter-tidal sand and mud foreshores (Chapter 2, 3), and there are indications that these habitats may be important to reproduction (Chapter 3). Blacktip reef sharks are taken in numerous coastal fisheries throughout their range including fisheries in Africa, India, Thailand, Indonesia, Malaysia and Australia (Heupel, 2005, Marshall, 1996a, Teh *et al.*, 2007, Chapter 2) and their use of shallow coastal habitats may expose them to increased pressure from fishing, habitat loss, potential impacts from climate change, as well as the cumulative effects of these individual pressures. However, the species' use of turbid coastal habitats and the importance of these habitats in sustaining their populations is poorly understood (Chapter 2). This study used tagging and long-term acoustic telemetry to characterise the residency and movement patterns of a coastal blacktip reef shark population and to examine the implications of these patterns for management and conservation.

5.2 Materials and methods

5.2.1 Study area

This study was carried out in Cleveland Bay, a coastal region of the Great Barrier Reef World Heritage Area (GBRWHA) adjacent to the city of Townsville in north Queensland, Australia (Fig. 5.1). Cleveland Bay is a shallow embayment (<10 m depth) that includes a diverse range of habitat types including sudtidal fringing coral reefs, intertidal rubble, sand and mud foreshore habitats, fringing mangroves, and intertidal and subtidal seagrass beds. The Bay is a tropical environment with water temperatures fluctuating between 20.7^{o}C (winter) and 30.6^{o}C (summer) (A. Chin, unpubl. data). Substrate types are predominantly fine mud sediments and waters are highly turbid with turbidity levels regularly reaching 50 mg l^{-1} (Browne *et al.*, 2010).

The Bay also receives terrestrial sediments via flood waters during monsoon rains. Summer monsoonal rains produce floodwater plumes that increase turbidity, introduce fine sediments, and can cause salinity to fall from a mean of 32 ppt (± 4.5) to 16.2 ppt (A. Chin, unpubl. data).

5.2.2 Field sampling and telemetry

Blacktip reef sharks were opportunistically sampled in Cleveland Bay between January 2008 and March 2011 as part of a long-term sampling and tagging program operating throughout the region (Harry *et al.*, 2011, Kinney *et al.*, 2011, Chapter 2). Targeted sampling for blacktip reef sharks was also carried out from October 2008 to May 2011 at Cockle Bay on the south western side of Magnetic Island (Fig. 5.1) where blacktip reef sharks were locally abundant (Chapter 3). Sharks were captured using 500 m long bottom-set longlines made from 8 mm diameter nylon rope and anchored with 3.6 kg Danforth anchors. Gangions were 2.5 m long and constructed from a 1.5 m length of 4 mm braided cord, a 1 m length of nylon coated stainless wire leader and 14/0 Mustad tuna circle hooks. Hooks were baited with butterfly bream *Nemipterus* spp., sea mullet *Mugil cephalus*, diamond scale mullet *Liza vaigiensis* and blue threadfin *Eleutheronema tetradactylum* with different bait types randomly mixed between hooks. Upon capture, sharks were measured, tagged with external rototags, and then inverted to induce tonic immobility (Henningsen, 1994). A selection of blacktip reef sharks including neonates, juveniles and adults of both sexes were tagged with Vemco V16 acoustic transmitters (Vemco Ltd, Canada) with a pseudo-random ping rate of 45-75 seconds for long-term acoustic monitoring. A small incision (3-4 cm) was made in the abdomen and the transmitter surgically inserted into the abdominal cavity to ensure retention of the transmitter. The incision was closed with surgical sutures in both the muscle and skin layer. Surgical procedures were performed in accordance with James Cook University animal ethics approval. Following the procedure, animals were revived and released at the site of capture.

Residency and movements of blacktip reef sharks were monitored for up to 2.3 years through passive acoustic telemetry using 69 Vemco VR2 and VR2W acoustic receivers (Vemco Ltd, Canada) deployed throughout Cleveland Bay (Fig. 5.1) and covering approximately 140 km^2 (e.g. Knip *et al.*, 2012a, Knip *et al.*, 2012b). No receivers could be placed in the middle of Cleveland Bay due to the presence of designated shipping lane leading to Townsville Port and seasonal trawling for penaeid prawns. Ten receivers were deployed in Cockle Bay on the southwest side of Magnetic Island (Fig. 5.1) to specifically monitor blacktip reef shark movements in this area. Receiver performance was examined in different parts of the array and detection range established at approximately 900 m for the majority of receivers (Knip *et al.*, 2012b). Given the shallow, structurally complex environs of Cockle Bay, receiver performance in this location was determined separately. Receiver performance testing involved determining the effective detection range of receivers as well as examining diagnostic data on receiver performance recorded by the receivers during their deployment. Range testing was conducted using moored acoustic transmitters that were activated and deployed at different locations within Cockle Bay at varying distances from receivers for up to four weeks. Analysis of detection data revealed detection ranges of between 300 m and 676 m, but detection range reached 1001 m on one occasion. Diagnostic data on receiver performance for ten receivers deployed in Cockle Bay were analysed using methods described in Simpfendorfer *et al.* (2008) and are presented at Appendix 7.

5.2.3 Data analysis

Telemetry data were analysed to determine residency (temporal patterns) and movement and activity space (spatial patterns) of juvenile and adult blacktip reef sharks. Residency patterns were indicated using a *Residency Index* (*Res*) calculated by determining how many days an individual shark was detected between the time of tagging and end of the study period. *Res* was calculated using the equation:

$$Res = \frac{Dd\ (no.\ of\ days\ detected)}{Dm\ (no.\ of\ days\ in\ monitoring\ period)}$$

Where *Dd* = number of days an individual was recorded in the receiver array; and *Dm* = number of days between the date the animal was first detected after release (usually the same day) and 28 February 2012 (the end date of the study where the transmitter batteries were deemed to be exhausted). An individual was considered to be present within the array on a given day when a minimum of two detections were recorded within a 24 hour period. *Res* values ranged from 0 to 1, with 0 indicating low residency and 1 representing high residency. Drawing upon descriptions used in ornithological studies (Craig *et al.*, 2011, Robinson *et al.*, 2004), *Res* values were used to assign individuals into one of three residency categories: vagrant, short-term resident or long-term resident. Vagrants were temporary occupants that only occurred in an area for days to weeks; short-term residents (analogous to migrants) were predictably found in an area for a period of months; and long-term residents resided in an area for periods that covered multiple seasons (years) and rarely left the area. The median monitoring period (time between release date and study end date) was 744 days. Using 744 days as a reference point, vagrants were defined as individuals with a Res of 0.00 to 0.04 (present for 1-31 days); short-term residents as individuals with a Res of 0.05 to 0.46 (present for 32-356 days); and long-term residents as individuals with a Res of 0.47 to1.00 (present > 365 days).

Movement patterns were described using a *Roaming Index* (*Rom*) which indicated the extent of an individual's movements within the receiver array. *Roaming Index* was calculated using the equation:

$$Rom = \frac{Rd\ (no.\ of\ receivers\ detected)}{Ra\ (no.\ of\ receivers\ available)}$$

Where *Rd* = number of receivers an individual was recorded on during the monitoring period; and *Ra* = the number of receivers deployed during the monitoring period. *Rom* values ranged from 0 to 1, with values close to 0 indicating low roaming (individual detected on only a few receivers) and 1 representing high roaming (individual is detected on every receiver). *Res* and *Rom* were plotted together to compare residency and movement patterns for juvenile, adult male and adult female individuals.

Activity space (home range) was derived using kernel utilisation distributions. Estimated locations of individuals were calculated at 30 minute intervals using an algorithm that provided estimated centres of activity (COA) within the receiver array (Knip *et al.*, 2011a, Simpfendorfer *et al.*, 2002a). The total activity space/home range of an individual over the entire monitoring period was derived from COA estimates using 50% (core home range) and 95% (home range extent) kernel utilisation distributions (KUDs) (Worton, 1989). KUDs were plotted using Arc GIS 9.3 to illustrate patterns in home range size and location between juvenile, adult male, adult female blacktip reef sharks. All analyses for residency, roaming and activity space/home range were performed using R program (R Development Core Team, 2012), with home range analysis using the *adehabitat package* for R.

5.3 Results

One hundred and twenty blacktip reef sharks were tagged and released between 8 October 2008 and 25 March 2011. Sampling throughout Cleveland Bay showed that blacktip reef sharks were highly localised to Cockle Bay and that the population was comprised almost exclusively of neonates, juveniles and adult females with a noticeable paucity of adult males and intermediate sized individuals between 850 to 1050 mm stretched total length (L_{ST}) (Chapter 3). Of the 120 individuals tagged and released 27 were fitted with acoustic transmitters between 16 Oct 2009 and 13 April 2010 and monitored until 28 Feb 2012. Individuals fitted with transmitters ranged from neonates to mature adults (655-1550 mm L_{ST}). Telemetry data from four individuals suggested that these animals were preyed upon (n=3) or had lost their tag (n=1) and were omitted from analyses. The remaining individuals (Table 5.1) included four adult males, ten adult females, seven juvenile males and two juvenile females that were monitored for 663 - 844 days (mean = 761 days ± SE 11.69). Recaptured sharks showed advanced healing of the surgical incision by 4 weeks and complete healing with no visible scars or marks by 26 weeks (Appendix 8).

5.3.1 Residency and roaming patterns

Plots of daily residency showed three main patterns: (1) individuals that were detected consistently throughout the monitoring period; (2) individuals that were detected consistently for an intermediate period of time (32-265 days) before detections permanently ceased; and (3) individuals that were intermittently detected for short periods (<31 days) (Fig. 5.2). Only two individuals left for an extended period (> 1 month) and returned, adult female 59599 and adult male 59591 (Fig. 5.2). Residency patterns differed between adult females, adult males and juveniles. Adult females were highly resident while adult males tended to show low residency although there was high variability between individual adult males (Fig. 5.2, Table 5.2). Juveniles had intermediate residency but also exhibited high variability in residency between individuals (Fig. 5.2, Table 5.2). Adult females had significantly higher *Res* values than juveniles, but other pair-wise comparisons of *Res* values between adult males and other animals showed no significant differences (Table 5.3). Applying *Res* values to residency classifications revealed that different sizes and sexes tended to fall into different residency categories (Fig. 5.3). Juveniles were mostly classified as short-term residents while almost all adult females were classified as long-term residents (Fig. 5.3). Adult males displayed a mix of residency patterns, with two individuals classed as vagrants, one a short-term resident and one a long-term resident (Fig. 5.3).

Roaming patterns also differed with sex and size. Adult males showed varying trends, most were low roamers but one male was detected on a large number of receivers resulting in the highest *Rom* value derived from the study (Table 5.2). Juveniles and adult females were more consistent in behaviour and tended to have low *Rom* values (Table 5.2). Nevertheless differences in *Rom* values were not statistically significant between juveniles, adult males and adult females (Table 5.3). However, it should be noted that comparisons of *Res* and *Rom* between adult males and other animals were compromised by the small number of adult males available to include in the analysis and the high variability in *Res* and *Rom* values between these individuals.

Plotting *Res* and *Rom* values together illustrated differences in residency and roaming patterns between groups with juveniles, adult males and adult females tending to fall in different sectors (Fig. 5.4). Both juveniles and adult females showed low roaming, but juveniles showed a range of residency patterns and adult females were slightly more likely to roam. Almost all males were low residents and low roamers. However, it should be noted that *Rom* values only reflect movement within the array and thus the combination of low *Res* and low *Rom* values for adult males may reflect broader movements outside detection range of the receiver array.

5.3.2 Activity space and home range

Analysis of activity space data showed two distinct patterns; juveniles (short-term residents) and adult females (long-term residents) had small home ranges and were highly resident to a specific location, while adult males (vagrants) used larger areas and were detected in different areas of the bay. Juveniles and adult females had mean 50% KUDs of 3.32 km^2 and 4.29 km^2 respectively (Table 5.2). Sizes of 95% KUDs were also similar between these two groups with means of 19.4 km^2 and 21.2 km^2 for juveniles and adult females respectively (Table 5.2). As KUD values were not normally distributed ($\chi^2 = 20.511$, $P < 0.001$), KUD size comparisons between groups were performed using Kolmogorov-Smirnov tests. Juveniles and adult females had similar 50% and 95% KUD sizes (Table 5.4) although adult females showed more variation in activity space size between individuals (Table 5.2). Adult males appeared to have larger activity spaces with mean 50% KUD of 6.19 km^2 and mean 95% KUD of 36.1 km^2. While adult male KUD sizes were not statistically different from those of juveniles or adult females (Table 5.4), the low residency and high variability between individual adult males (Table 5.2) made it difficult to estimate KUDs for these individuals. Transient, vagrant males appeared to have wider ranging movements and the *Rom* values and activity space (KUD) estimates generated for these individuals only represent their limited movements within the detection range of the Cleveland Bay receiver array. However, the only long-term resident adult male had the largest activity space recorded in the study with a 50% KUD and 95% KUD of 14.56 km^2 and 74.2 km^2, respectively (Table 5.2). Juveniles and adult females showed high affinity to the same confined area of Cockle Bay (Fig. 5.5). In contrast, the single resident adult male had two core use areas, one centered around Cockle Bay and the other around a subtidal shoal (Virago Shoal) close to the mainland (Fig. 5.5). The male’s 95% KUD encompassed the whole area of the receiver array between Magnetic Island and the mainland, and also included some of the eastern side of Cleveland Bay.

5.4 Discussion

Coastal blacktip reef sharks displayed three broad patterns of movement and habitat use: (1) limited occurrence of adult males that when present tended to show wide ranging, transient movements (short-term residents or vagrants); (2) adult females that were long-term residents with movements concentrated in a small area within a specific location; and (3) juveniles (both sexes) that were short-term residents with movements concentrated in a small area of a specific location. Importantly, both adult females and juveniles used the same habitat and location within Cockle Bay. These residency and movement patterns differ from those observed in other sharks and conspecifics in other locations, and provide a new variation of coastal habitat use by sharks. These patterns also have important implications for reef shark management and conservation.

5.4.1 Population organisation and movement patterns

The movement patterns and population organisation of blacktip reef sharks in this study contrast with patterns observed in previous studies on this species. While blacktip reef sharks in French Polynesia, Palmyra Atoll (Central Pacific), and Western Australia showed similar scales of movement and activity space to this study (Mourier & Planes, 2013, Papastamatiou *et al.*, 2009a, Papastamatiou *et al.*, 2010, Speed *et al.*, 2011), blacktip reef sharks in Cleveland Bay displayed different movement patterns from these conspecifics. In Cleveland Bay, adult females are long term residents with limited movement over multiple years and share the same space with juveniles, while juveniles are temporary residents that appear to disperse. Males are largely absent. In contrast, at Aldabra Atoll male and female adults had similar movement patterns (Stevens, 1984) whereas in this study, males were rarely encountered and displayed larger scale movements than the resident females. In French Polynesia adult females moved from their normal area of residence to other locations to give birth and this movement of adult females, not juveniles, accounted for dispersal within the population (Mourier & Planes, 2013). In Western Australia, adult female blacktip reef sharks also showed evidence of wide ranging movements with seasonal migrations into shallow coastal sand flats and fringing reefs during spring, at which time some were also pregnant (Speed *et al.*, 2011). At Palmyra

Atoll, juveniles appeared to be separated from adults and similar numbers of adult males and females were observed (Papastamatiou *et al.*, 2009a). The movement patterns from Cleveland Bay also differ from those observed in other reef sharks such as the grey reef shark (*Carcharhinus amblyrhynchos*), Caribbean reef shark (*Carcharhinus perezi*) and whitetip reef shark (*Triaenodon obesus*). Wide-ranging movement of adult females has been recorded in grey reef sharks, whitetip reef sharks and Caribbean reef sharks, and these populations also lacked the strong female sex bias evident in this study (Chapman *et al.*, 2005, Heupel *et al.*, 2010, Pikitch *et al.*, 2005, Whitney *et al.*, 2012).

Blacktip reef sharks in Cleveland Bay also show a different pattern of population organisation. The strong sex bias and lack of intermediate sized animals is not seen in blacktip reef sharks in French Polynesia (Mourier & Planes, 2013), Palmyra Atoll (Papastamatiou *et al.*, 2009a) or Aldabra Atoll (Stevens, 1984). Habitat use patterns between different size classes were also different. In French Polynesia, Western Australia and Palmyra Atoll, neonates and juveniles were separated from adults whereas in this study, adult females and juveniles co-occurred within the same small area < 5 km^2 over periods of months to years. Catch data provide additional evidence for co-occurrence of adult females and juveniles as both size classes were regularly captured on the same longline (A. Chin, unpubl. data).

The blacktip reef shark's range of population organisation and movement patterns across different habitats and locations suggest that the species is ecologically flexible and can adopt population structures and behaviours that optimise use of local conditions. Indeed, the Cleveland Bay population experiences very different environmental conditions than reef sharks on offshore coral reefs including high turbidity, complex bathymetry and habitat types, freshwater flows and extreme salinity changes (see Appendix 9 for photographs of Cockle Bay). These dynamic conditions can affect the structure of marine communities (Sheaves & Johnston, 2009), but coastal habitats also support high biodiversity and biological productivity (Blaber *et al.*, 1989, Nagelkerken *et al.*, 2008a). The blacktip reef shark's ecological flexibility may enable the species to use shallow, turbid coastal habitats to take advantage of increased resource opportunities resulting from the diversity and productivity of coastal habitats.

Interestingly, the blacktip reef sharks' intensive use of a small area of Cockle Bay does not appear to be linked to the availability of specific habitat types. There are extensive areas of mangroves and mudflats along the northwest coast of Magnetic Island, and extensive fringing reef habitat and sand, mud and rubble flats along the island's southeastern coast. However, blacktip reef sharks from Cockle Bay did not appear to use these adjacent locations and were not detected on receivers specifically deployed to detect such movements. The blacktip reef sharks' attachment to Cockle Bay was also particularly strong. Individuals elected to stay in Cockle Bay during a category five cyclone while other sharks in adjacent locations departed prior to the storm's arrival (Udyawer *et al.*, 2013). Intensive use of Cockle Bay suggests that this location may have a unique combination of environmental variables that confer advantages in provisioning and/or survival that outweigh the potential risks from intra-specific competition and predation between adult females and juveniles and potential impacts from extreme weather events. Blacktip reef sharks in other locations are also highly site-attached which has been attributed to behavioural patterns to reduce competition and/or predation (e.g. Papastamatiou *et al.*, 2009a). While competition and predation may shape the movement patterns and site attachment of blacktip reef shark in Cleveland Bay, the causative factors behind these patterns are yet to be determined.

5.4.2 Roles of coastal habitats

The blacktip reef sharks' population organisation and movement patterns, and evidence of mating and pupping over multiple years (Chapter 3) suggest that blacktip reef sharks use Cockle Bay for reproductive purposes. Segregation in sharks can be related to reproductive functions where sexual segregation reduces harassment and injury to females, while segregation by size may reduce predation on neonates and juveniles (Wearmouth & Sims, 2008). The high productivity, prey availability and diversity of coastal ecosystems may also increase provisioning and facilitate resource partitioning that reduces competition and predation pressure

(Kinney *et al.*, 2011, Kwak & Klumpp, 2004, Simpfendorfer & Milward, 1993). Indeed, the shallow intertidal flats of Cockle Bay support a diverse community of fishes and decapods (Kwak & Klumpp, 2004) that are potential prey for juvenile blacktip reef sharks, and juveniles were regularly observed actively feeding on these flats (A. Chin pers obs.). Additionally, inter-specific predation on juvenile sharks may be reduced in the shallow intertidal foreshores as larger shark species that could potentially prey upon juvenile blacktip reefs sharks were rarely encountered during three years of sampling in these habitats (A. Chin, unpubl. data), while sampling in adjacent areas captured a range of potential predators (Kinney *et al.*, 2011, Knip *et al.*, 2011a).

The intensive use and co-occurrence of adult and juvenile blacktip reef sharks may also be made possible by the specific environmental conditions present in shallow turbid coastal habitats. The high turbidity of these systems could help juveniles evade adult females as turbidity can reduce predation success in some fishes (Radke & Gaupisch, 2005, Sweka & Hartman, 2003). Prey availability and reduced predation pressure may lead to increased juvenile growth and survival. Indeed the size at birth and growth rates of juveniles in the study site were greater than reported elsewhere (Chapter 3). While the factors and processes that attract blacktip reef sharks to these habitats are unknown, it is evident that they have strong site attachment to this area and that this attachment is linked to reproductive processes.

Cockle Bay appears to support reproduction in coastal blacktip reef sharks but it should not be considered a shark nursery ground as the patterns evident in this study do not conform to the predictions and definitions of classical shark nurseries. Previous studies of shark nurseries show that adult females enter coastal nursery areas to mate and/or pup and then disperse, leaving the neonates and juveniles to grow in the nursery ground (Heupel *et al.*, 2007, Springer, 1967). The absence of adults in nursery grounds is thought to reduce competition and predation on neonates and juveniles (Simpfendorfer & Milward, 1993, Wearmouth & Sims, 2008). Additionally, the movement of adult females to and from nursery grounds provides an important vector for genetic dispersal (e.g. Mourier & Planes, 2013) as juvenile may stay close to natal grounds even after leaving a nursery (Chapman *et* *al.*, 2009). However, in this study adult females did not leave the natal area as predicted and instead were permanent residents while the juveniles dispersed over large distances (Chapter 6). Furthermore, neonates and juveniles shared the same space with adult females until they departed.

While turbid shallow habitats in the GBRWHA do not conform to definitions of nursery grounds, they may still be important habitats to blacktip reef sharks. The long-term residency of adult females and the co-occurrence of adult females, neonates and juveniles in small areas of turbid coastal habitat represent a new variation of how reef sharks use coastal habitats, and raises the importance of juvenile dispersal as a driver of genetic mixing in coastal shark populations. Coastal habitats support permanent groups of reproductively active adult females that may be the key population component driving population dynamics in these long-lived fishes (Prince, 2005). Groups of resident adult females may be visited by transient males during the summer mating season (Chapter 3) and after pupping, shallow coastal habitats may enhance the growth and survival of neonates and juveniles until they depart from their natal grounds. Meanwhile, coastal habitats provide the necessary resources and security for adult females to regain fitness for successive breeding events.

5.4.3 Implications for management and conservation

The residency and movement patterns described in this study have several implications for reef shark conservation and management. The vulnerability of a species can be considered as the outcome of interactions between three separate components: (1) exposure to risks; (2) sensitivity to exposure; and (3) the species' adaptive capacity to compensate for impacts (Chin *et al.*, 2010). Data on movement and behaviour patterns can describe a species' exposure to risk (overlap between risks and species distribution), sensitivity (expressed through movement patterns of key components of the population); as well as its adaptive capacity (expressed as ecological flexibility and distribution). For coastal blacktip reef shark populations, intensive use of small areas of turbid coastal habitat has implications for their vulnerability.

Coastal blacktip reef shark populations appear to have high exposure to anthropogenic pressures from coastal fisheries, pollution, and habitat loss and degradation. Since the blacktip reef shark uses both coastal and coral reef environments in the GBRWHA, it is also exposed to the cumulative pressures from fishing, habitat loss and climate change impacts occurring in both coastal and coral reef environments (Chin *et al.*, 2010). The blacktip reef shark may also be highly *sensitive* to this exposure. The species' biology suggests that is has relatively slow growth compared to other fishes and low reproductive output, and that preservation of adult females may be especially important to sustaining viable populations (Chapter 4). As such, the intensive use of coastal habitats that are highly exposed to pressures by breeding females increases the species' sensitivity, especially as these areas are used for important life history events – mating, pupping and juvenile growth. For example, intensive fishing pressure within a 5 km^2 area of Cockle Bay could cause localised depletion of breeding females, removing a source of blacktip reef shark recruits to other areas along the coast and offshore coral reefs. However, the blacktip reef sharks' exposure and sensitivity may be moderated by the species' adaptive capacity. The occurrence of the species in both coral reef and coastal environments suggests an inherent ecological flexibility so that losses in one area could be offset by movement to new locations as well as recruitment from other locations through juvenile dispersal – as long as those areas continue to perform their ecological roles and to supplement recruitment. Additionally, management such as marine park zoning may help to reduce exposure and enhance adaptive capacity. Exposure to fishing and pollution is reduced in some coastal areas in the GBRWHA through marine park zoning and habitat protection (GBRMPA, 2009). For example, the activity spaces of blacktip reef sharks in Cockle Bay lie within a Conservation Park zone that excludes commercial net fishing and Marine Park and water quality regulations place some controls on pollution in Cleveland Bay (Appendix 10). These protections may help to sustain healthy habitats and populations of breeding females that supply recruits to other locations.

The population organisation and movement patterns of blacktip reef sharks in Cleveland Bay provide a new variation of how sharks use coastal habitat and illustrate how habitat use can affect conservation and management. However, the data limitations need to be acknowledged. This study occurred in one area of the GBRWHA and while there is some evidence that localised populations of blacktip reef sharks exist in other locations in the GBRWHA (Chapter 2), the residency and movements of blacktip reef sharks have yet to be examined in other turbid coastal regions. Furthermore, the contributions of coastal habitats to the wider GBRWHA population will depend on the extent to which these habitats improve survival and recruitment of juveniles into the adult population compared to other locations and habitat types. The extent to which turbid coastal habitats increase survival and recruitment of juvenile blacktip reef sharks compared to other habitat types (e.g. offshore coral reefs) is not known, and comparative studies with blacktip reef sharks in coral reefs on the GBRWHA have not been carried out. Lastly, the movement and habitat use data have only been qualitatively applied to a vulnerability framework and a more rigorous assessment (e.g. Chin *et al.* 2010) is required to fully describe the cumulative risk faced by blacktip reef sharks in coastal regions. Further studies of reef shark movements in turbid coastal habitats may resolve some of these uncertainties, providing a clearer understanding of the role turbid coastal habitats play in reef shark population dynamics and improving the rigour of risk assessments for these species.

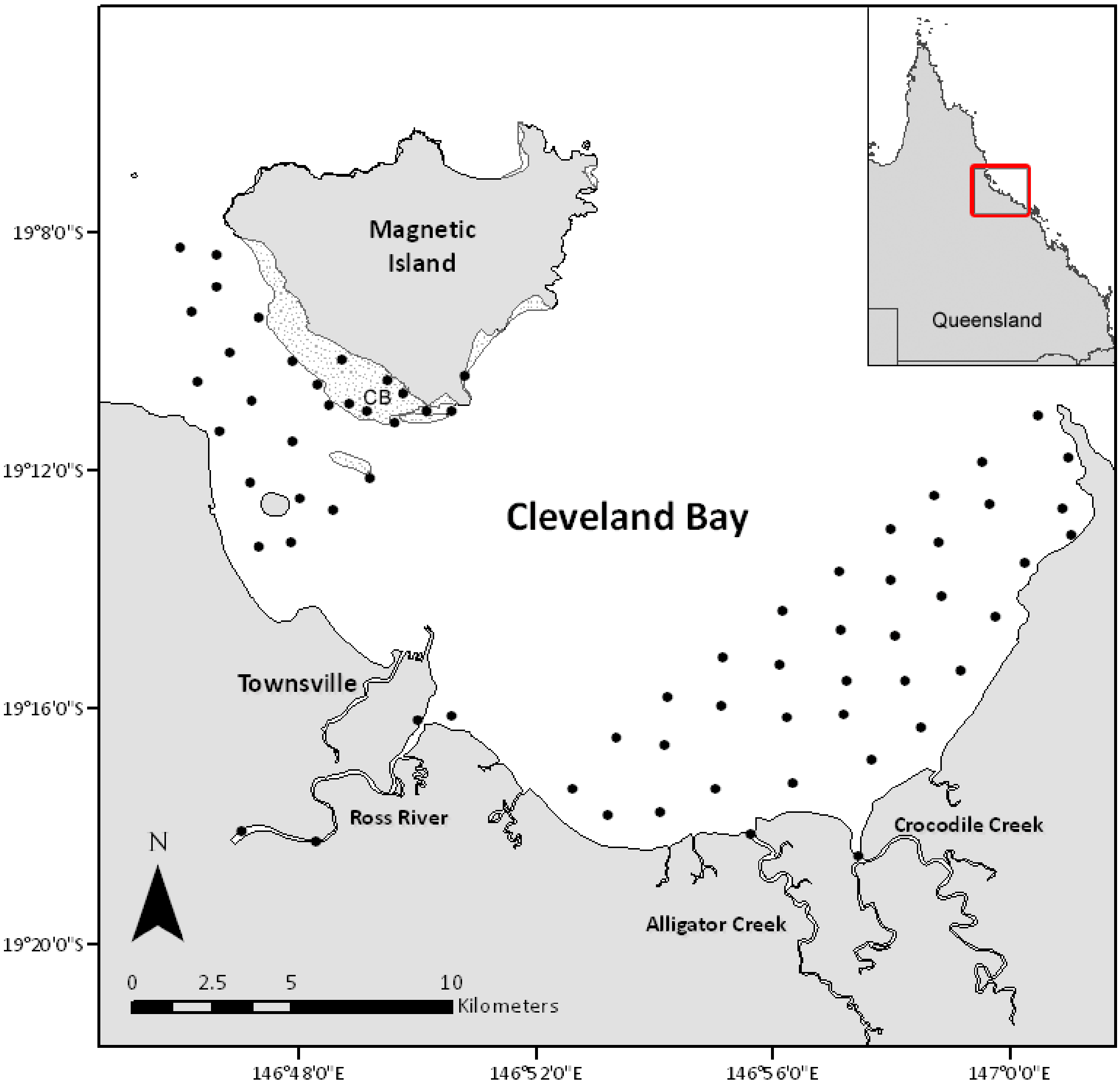


Figure 5.1: Locality map of the study site showing Cleveland Bay, Magnetic Island and Cockle Bay (CB), inset map shows location of Cleveland Bay on the Queensland coast. Light grey stippling shows intertidal habitats (mud and sand foreshores, rubble banks and seagrass beds) around Magnetic Island and Cockle Bay. Black circles denote location of Vemco acoustic receivers deployed in a grid pattern array that covered approximately 140 km^2.

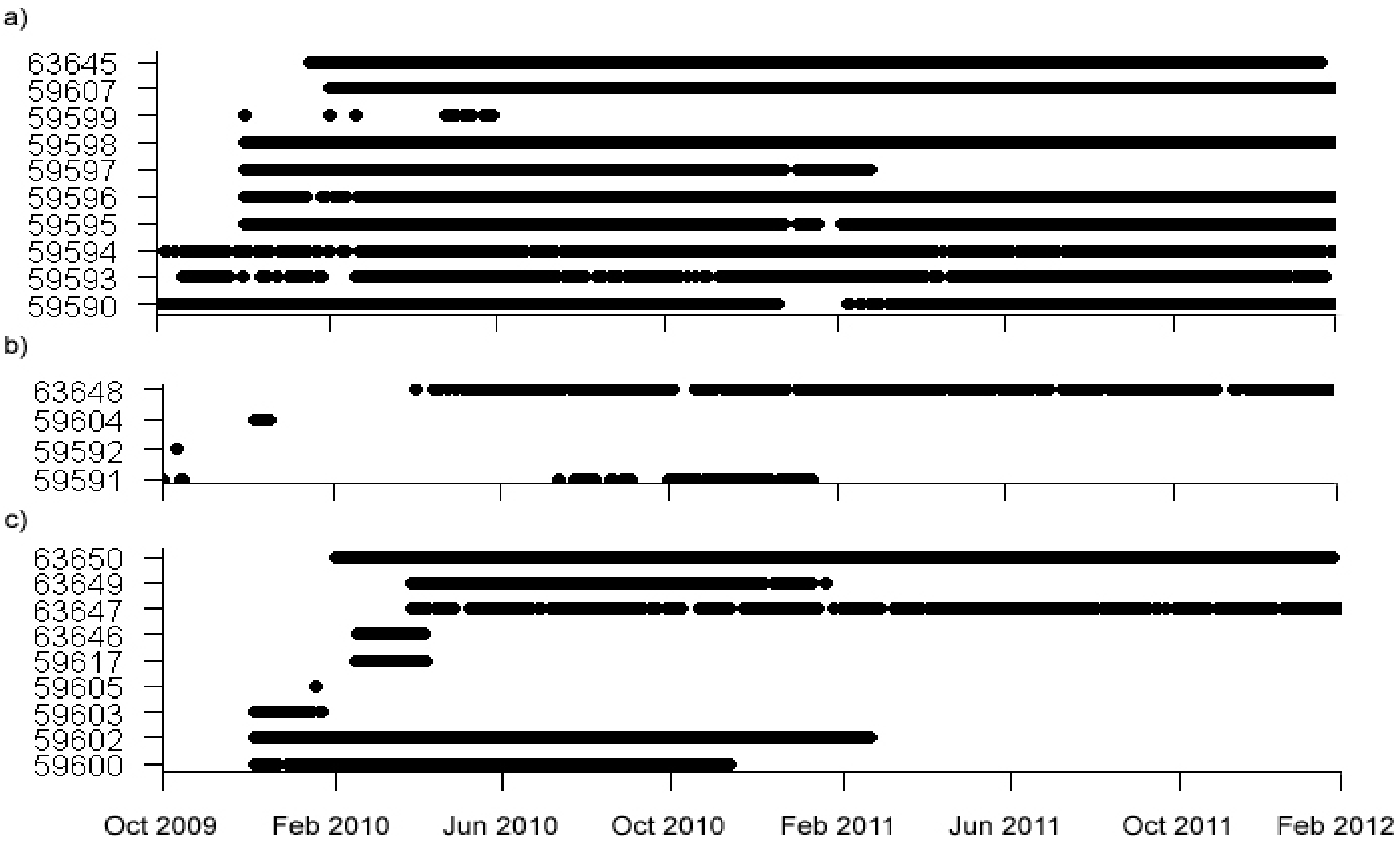


Figure 5.2: Residence plot from acoustic telemetry data for (a) 10 adult female, (b) four adult male and (c) nine juvenile blacktip reef sharks.

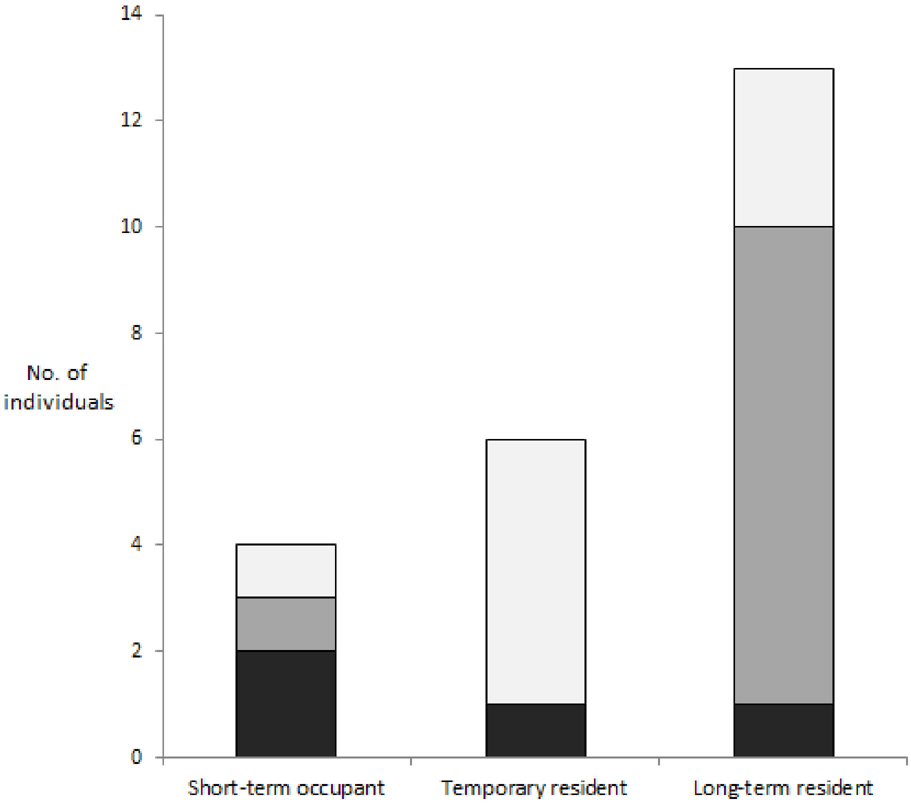


Figure 5.3: Residency classification of juvenile (light grey), adult female (dark grey) and adult male (black) blacktip reef sharks monitored for periods ranging from 663 to 844 days.

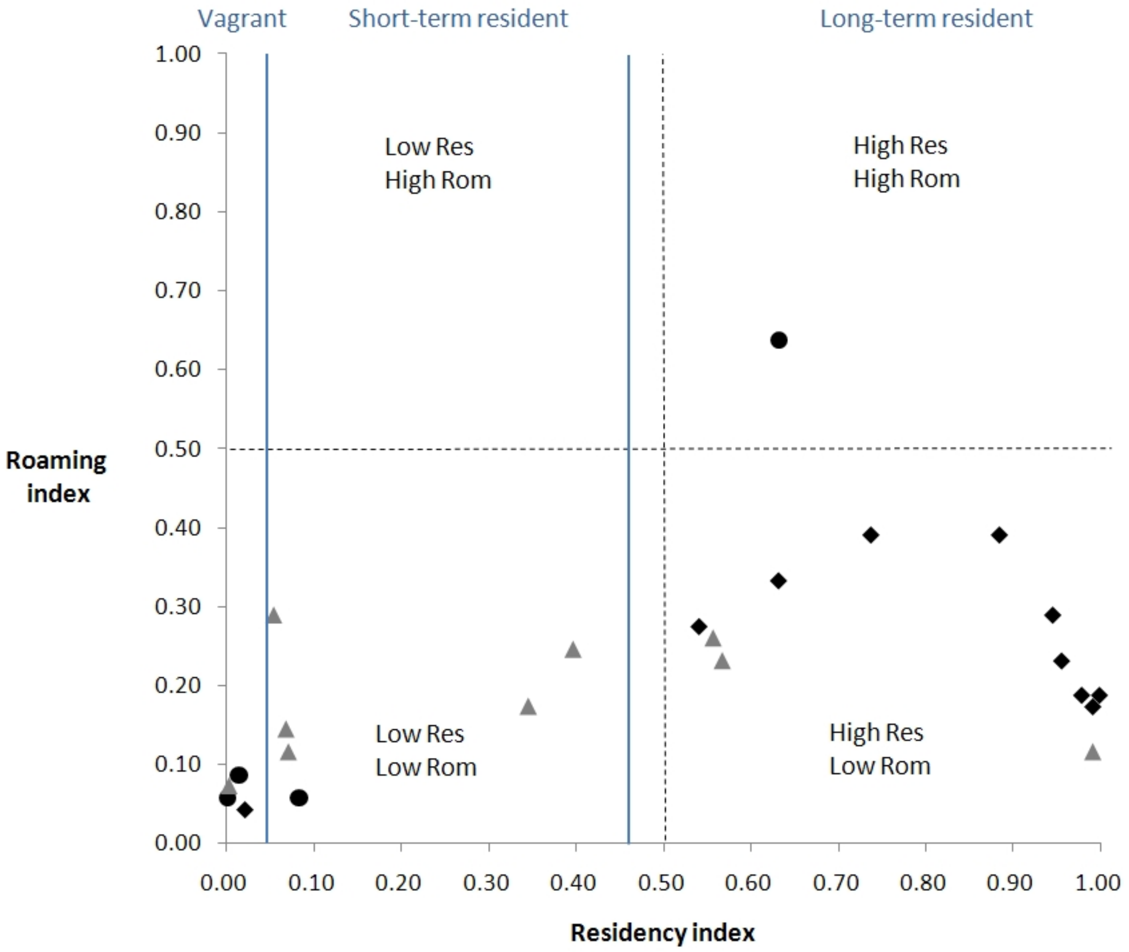


Figure 5.4: Residency and roaming plot showing the relationship between residency status and movement patterns for juveniles (grey triangles), adult males (black circles) and adult females (black diamonds). Blue lines delineate *Res* categories.

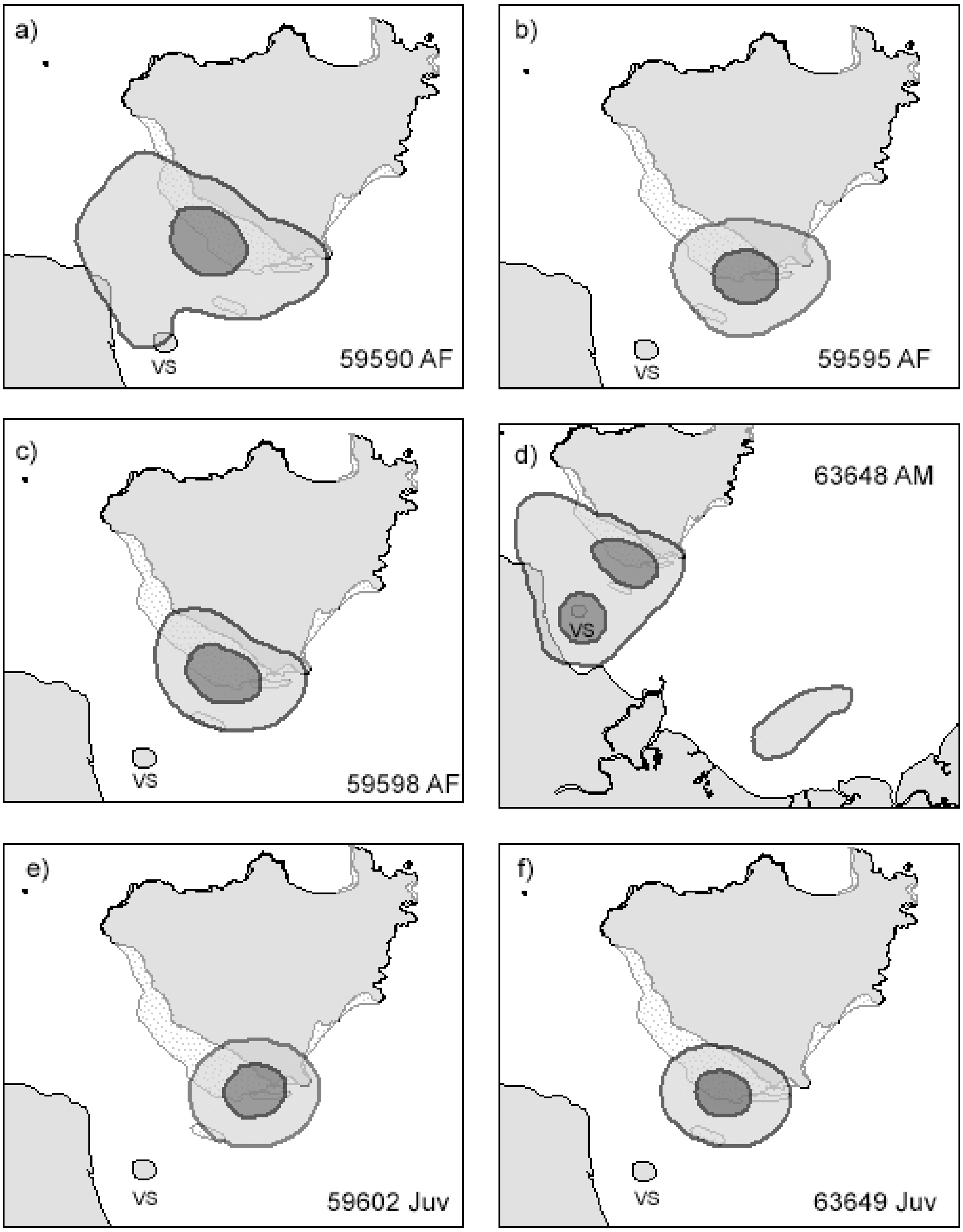


Figure 5.5: Kernel utilisation distributions (KUD) of three adult female AF (a-c), one adult male AM (d) and two juvenile Juv (e-f) blacktip reef sharks, as representatives for these groups. Dark grey denotes core use areas (50% KUD) while light grey shows home range extent (95% KUD). VS indicates Virago Shoal.

	Biological details			Residency				Activity space and home range		
Tag ID	Maturity	Sex	Size (mm L_{ST})	Date first detection	Monitoring period (days)	No. of days detected	Residency index	Roaming index	50% KUD (km^2)	95% KUD (km^2)
59590	Adult	F	1550	17/10/2009	844	747	0.88	0.39	5.04	38.11
59593	Adult	F	1420	4/11/2009	826	522	0.63	0.33	9.19	37.1
59594	Adult	F	1360	22/10/2009	839	619	0.74	0.39	4.17	28.63
59595	Adult	F	1454	18/12/2009	782	740	0.95	0.29	3.58	17.28
59596	Adult	F	1480	18/12/2009	782	748	0.96	0.23	3.56	16.8
59597	Adult	F	1420	18/12/2009	782	423	0.54	0.28	3.54	15.41
59598	Adult	F	1075	18/12/2009	782	776	0.99	0.17	4.07	17.84
59599	Adult	F	1400	18/12/2009	782	16	0.02	0.04	2.54	11.21
59607	Adult	F	1232	16/02/2010	722	722	1.00	0.19	4.04	15.4
63645	Adult	F	1400	2/02/2010	736	721	0.98	0.19	3.12	13.74
59591	Adult	M	1358	29/10/2009	832	69	0.08	0.06	2.56	12.94
59592	Adult	M	1210	26/10/2009	835	1	0.00	0.06	4.49	38.1
59604	Adult	M	1271	21/12/2009	779	11	0.01	0.09	3.16	19.34
63648	Adult	M	1340	16/04/2010	420	663	0.63	0.64	14.56	74.01
59602	Juvenile	F	730	21/12/2009	779	442	0.57	0.23	3.28	14.12
63646	Juvenile	F	735	4/03/2010	706	48	0.07	0.14	3.98	22.69
59600	Juvenile	M	709	21/12/2009	779	309	0.40	0.25	2.46	10.94
59603	Juvenile	M	780	21/12/2009	779	42	0.05	0.29	3.28	28.28
59605	Juvenile	M	665	2/02/2010	736	2	0.00	0.07	3.27	30.1
59617	Juvenile	M	721	3/03/2010	707	50	0.07	0.12	3.29	14.35
63647	Juvenile	M	889	13/04/2010	666	371	0.56	0.26	4.54	26.42
63649	Juvenile	M	811	13/04/2010	666	230	0.34	0.17	2.96	13.47
63650	Juvenile	M	752	17/02/2010	721	715	0.99	0.12	2.83	14.2

Table 5.1: Biological, residency and movement characteristics of 23 blacktip reef sharks fitted with Vemco V16 transmitters released from 16 October 2009 to 16 April 2010.

		Residency Index			**Roaming Index**			**50% KUD (km^2)**			**95% KUD (km^2)**		
	n	Min	Max	Mean ± SE	Min	Max	Mean ± SE	Min	Max	Mean ± SE	Min	Max	Mean ± SE
Adult females	10	0.02	1.00	0.77 ± 0.10	0.04	0.39	0.25 ± 0.03	2.54	9.19	4.29 ± 0.58	11.21	38.11	21.2 ± 3.10
Adult males	4	0.00	0.63	0.18 ± 0.15	0.06	0.64	0.21 ± 0.14	2.56	14.56	6.19 ± 2.82	12.94	74.01	36.1 ± 13.72
Juveniles	9	0.00	0.99	0.34 ± 0.11	0.07	0.29	0.18 ± 0.03	2.46	4.54	3.32 ± 0.21	10.94	28.28	19.4 ± 2.47

Table 5.2: Summary table showing main trends in residency and activity space between juvenile, adult male and adult female blacktip reef sharks.

	df	Residency Index		Roaming Index	
		D score	P value	D score	P value
Juveniles * adult males	12	0.3889	0.7964	0.3689	0.2083
Juveniles * adult females	18	0.6889	0.0223*	0.3889	0.4708
Adult males * adult females	13	0.7000	0.1216	0.6500	0.1787

Table 5.3: Kolmogorov-Smirnov test statistics for differences in *Res* and *Rom* values between juvenile, adult male and adult female blacktip reef sharks. * denotes statistically significant difference at (α = 0.05).

		50% KUD		**95% KUD**	
	df	D score	P value	D score	P value
Juveniles * adult males	12	0.3000	0.9191	0.5000	0.4042
Juveniles * adult females	18	0.5778	0.0846	0.3560	0.4922
Adult males * adult females	13	0.3000	0.9191	0.4500	0.4995

Table 5.4: Kolmogorov-Smirnov test statistics for differences in activity spaces (50% and 95% KUD) between juvenile, adult male and adult female blacktip reef sharks. * denotes statistically significant difference at ($\alpha = 0.05$).

6. Ontogenetic movements of juvenile blacktip reef sharks: dispersal and connectivity between habitats and populations

6.1 Introduction

The movement and dispersal of fishes between coastal habitats and other habitats such as coral reefs is a topical issue in marine and fisheries science (Blaber, 2007, Nagelkerken *et al.*, 2008a), especially considering the importance of coastal habitats to sustaining fish populations (Beck *et al.*, 2001, Pittman & McAlpine, 2003) and growing concerns over habitat loss and degradation in the coastal zone (Halpern *et al.*, 2008, Lotze *et al.*, 2006). Declining shark populations (Graham *et al.*, 2010, Nadon *et al.*, 2012) are driving an increased interest in the roles and significance of coastal ecosystems in conserving these species (Knip *et al.*, 2010, Simpfendorfer *et al.*, 2011). Many sharks and rays use coastal habitats as foraging grounds, movement corridors and as nurseries (Knip *et al.*, 2010). Sharks also show complex movement and habitat use patterns in these coastal habitats, with a range of population structures, home range patterns, migrations and movement patterns driven by ecological and behavioural factors (Grubbs, 2010, Knip *et al.*, 2010, Speed *et al.*, 2010, Chapter 5).

Sharks may also exhibit ontogenetic changes in movement and habitat use where individuals at specific life stages alter their movement and behavioural patterns to maximize resource availability and minimize risks from competition and predation (Grubbs, 2010, Pittman & McAlpine, 2003, Secor, 1999). For example, juvenile lemon sharks (*N. brevirostris*) use shallow mangrove fringed habitats and seagrass flats while larger adults use deeper offshore habitats (Wetherbee *et al.*, 2007). Similar ontogenetic shifts have been observed in bluntnose sixgill (*Hexanchus griseus*), sandbar (*Carcharhinus plumbeus*) and pigeye (*Carcharhinus amboinensis*) sharks (Andrews *et al.*, 2010, Grubbs, 2010, Knip *et al.*, 2011a). In some cases, predation (including cannibalism) is the main factor driving separation of juveniles and adults (Guttridge *et al.*, 2012, Heupel & Hueter, 2002). However, once individuals reach a larger size, reduced vulnerability to predation, increased competition and greater resource requirements may prompt individuals to leave natal grounds and disperse to new locations (Grubbs, 2010, Secor, 1999). Dispersal is a crucial phase in many marine fishes that may affect density, stock structure, genetic diversity and connectivity of adult populations (Frank, 1992, Keeney *et al.*, 2003, Mora & Sale, 2002).

The blacktip reef shark occurs in a range of shallow habitat types ranging from clear water coral reef habitats and reef associated fringing reef lagoons (Papastamatiou *et al.*, 2009b, Speed *et al.*, 2011), to turbid coastal habitats such as mangroves, seagrass beds and muddy foreshores (Chapter 2, 3,5). Habitat use studies on isolated coral atolls have shown segregation between adults and juveniles (Papastamatiou *et al.*, 2009b) and high levels of residency and site attachment with little evidence of large scale movement in juveniles (Papastamatiou *et al.*, 2009b, Speed *et al.*, 2011, Stevens, 1984). However, the movement and habitat use patterns of blacktip reef sharks in turbid coastal habitats and potential ontogenetic changes in these patterns have not been investigated. This study aimed to identify the movement and habitat use patterns of juvenile blacktip reef sharks in turbid inshore and coastal habitats. Long-term acoustic telemetry was used to track the residency and movement patterns of juvenile blacktip reef sharks for up to 2.3 years, and explore evidence of ontogenetic shifts in habitat use and dispersal.

6.2 Materials and methods

Residency and habitat use patterns of blacktip reef sharks were monitored in Cleveland Bay, north Queensland, Australia (Fig. 6.1), a shallow (<10 m depth) embayment that contains a diverse range of habitats including estuaries, intertidal sand and mud foreshores, intertidal and subtidal seagrass meadows, fringing mangroves, fringing coral reefs and open waters. The main study site was Cockle Bay on the SW side of Magnetic Island which included fringing coral reefs, rubble, sand and mud foreshores, mangroves and seagrass meadows. Sharks were captured using 500 m long bottom-set longlines set with 2.5 m long gangions terminating with 14/0 Mustad tuna circle hooks. Hooks were baited with a range of commercially available teleost fishes. Captured sharks were processed immediately at their capture site and fork length (L_F) and stretched total length (L_{ST}) measured using measuring boards (specimens < 1 m total length) or a measuring tape stretched over the body from snout to tail. Sharks were tagged with Rototags on the first dorsal fin and surgically implanted Vemco V16 acoustic transmitters (Vemco, Canada) for long-term acoustic monitoring using standard techniques (Knip *et al.*, 2012b).

Sharks were monitored using an array of 69 Vemco VR2 and VR2W acoustic receivers (Vemco, Canada) deployed in the western and eastern sides of Cleveland Bay and covering a combined area of approximately 140 km^2 (Fig. 6.1). Receiver detection range was estimated at approximately 900 m (Knip *et al.*, 2012b) and between 300 and 670 m near Cockle Bay (Chapter 5). Concurrent to this study, other unrelated acoustic telemetry projects had deployed an array of 48 receivers on 17 mid-shelf coral reefs between 60 and 90 km north-east (offshore) from Cleveland Bay, and an array of 30 receivers around Orpheus and Pelorus Islands between 60 and 80 km north-west from Magnetic Island.

Residency patterns of juvenile blacktip reef sharks were monitored in Cleveland Bay between 18 October 2009 (date first tagged animal was released) and 28 February 2012. Maturity status of individuals was assigned using L_{ST}, where individuals were considered to be juveniles if L_{ST} <1000 mm or adults if L_{ST} >1000mm. (Lyle, 1987, Chapter 4). The number of individuals present each month was plotted in an accumulation-decay plot to show residency patterns of juveniles over time. Residency was also expressed as a Residency Index (*Res*), where *Res* = no. of days present (>2 detections within 24 hrs) / the number of days in the monitoring period (no. of days between date of first detection and the end of the study). A residency index of 1.00 indicated complete residency.

Emigration from the study area was identified from sudden changes in established residency and movement patterns, such as a pattern of regular daily detections that abruptly and permanently ceased with the last detections recorded on receivers at the edge of the receiver array. For juveniles that showed evidence of emigration from Cleveland Bay, the estimated length at emigration was calculated using a predicted growth rate of 65.3 mm yr^{-1} L_{ST} from Chapter 3. Movement rates and distances were calculated for animals that were recaptured (detected in other locations). Movement distance was the distance between the emigration point (the position of the receiver where an animal was last detected) and the entry point (the location of the receiver where the animal was next detected). Movement rate was calculated using the time elapsed between these detections and the movement distance.

6.3 Results

Residency and movement data were analysed for nine juvenile blacktip reef sharks (seven males, two females). Juveniles ranged from 665 to 889 mm L_{ST} (Table 1) representing neonates to juveniles nearing maturity. The number of juveniles detected within the array steadily declined between April 2010 and February 2012 (Fig. 6.2), falling from a maximum of seven (April 2010) to two (February 2012) representing a 71% decline in resident juveniles. This decline in resident juveniles was reflected in *Res* values which showed that most juveniles were present for less than half of the monitoring period (Table 6.1), with mean *Res* ± SE = 0.34 ± 0.11. Daily residency patterns revealed that when juveniles were present they were detected almost daily until detections permanently ceased (Table 6.1), suggesting high residency until permanent departure occurred. The estimated length of juveniles at emigration was between 670 and 863 mm L_{ST} (mean: 768 ± 23 mm L_{ST}) when detections ceased (Table 6.1). Individuals that left the array were last detected on receivers at the edges of the array, including receivers outside their normal home range (A. Chin, unpubl. data) (Figure 6.1).

Two of the seven juveniles that left Cleveland Bay were detected on other receiver arrays. Juvenile male 63649 was detected at Magnetic Island until 3 February 2011 and was next detected at Rib Reef on 6 February 2011 (Fig. 6.3). This represented an offshore movement of 81 km in 70 hrs, with an approximate straight line swimming speed of 1.2 km hr^{-1}. This individual was detected at Rib Reef until 30 November 2011, before moving among a series of mid-shelf reefs including Kelso Reef (2 December 2011 to 20 January 2012), Bramble Reef (9 February 2012 to 29

February 2012) and Helix Reef (3 March 2012) (Fig. 6.3). Juvenile 63649 resided at Helix Reef until August 2012 when detections ceased. The cessation of detections coincided with the time at which the transmitter battery would expire and thus probably represents battery termination. The second individual detected outside Cleveland Bay was juvenile female 59602 which was detected at Magnetic Island until 8 March 2011 and next detected on 11 March 2011 at Orpheus Island, representing a longshore movement of 68 km in 74 hrs with an average straight line swimming speed of 0.91 km hr^{-1} (Fig. 6.3). Juvenile 59602 was detected on receivers around Orpheus Island for three days, showing a steady northward movement until detections ceased at the northern edge of the receiver array.

Two other juveniles also exhibited large-scale movement patterns. Juvenile males 59600 and 59603 made abrupt and rapid excursions out of their established home ranges and swam over 11 km to be detected on receivers on the eastern side of Cleveland Bay < 24 hours later. Upon entering the eastern part of the bay, juvenile 59600 moved along the western side of Cape Cleveland for two days until exiting the array at the tip of Cape Cleveland (Fig. 6.3). Juvenile 59603 resided in the eastern side for one day before moving back to the western side for one day, and then exiting the array at the south-eastern edge of Magnetic Island (Fig. 6. 3). These individuals were not detected elsewhere and their fate after leaving the array is unknown.

6.4 Discussion

This study provides new insights into habitat use and connectivity patterns in reef shark populations, with evidence of juvenile dispersal over long distances among coastal habitats and to mid-shelf and offshore coral reefs. These findings differ from previous accounts of reef shark movements. While large scale movement and dispersal of reef sharks have previously been observed in grey reef sharks and Caribbean reef sharks (*Carcharhinus perezi*) (Chapman *et al.*, 2005, Heupel *et al.*, 2010), these movements were generally made by large adults and the movements recorded were over shorter distances (<30 km). Indeed, juvenile grey reef sharks and Caribbean reef sharks appear to be highly site attached and to have limited movements (Garla *et al.*, 2006, Heupel *et al.*, 2010). Meanwhile, other studies reported limited movement of both juvenile and adult blacktip reef sharks (Field *et al.*, 2011, Papastamatiou *et al.*, 2009b, Stevens, 1984). Genetic studies also suggest limited dispersal and exchange between some reef shark populations with high incidence of inbreeding evident in blacktip reef sharks in French Polynesia (Mourier & Planes, 2013). Meanwhile along the Queensland coast, the dispersal of juvenile blacktip reef sharks as illustrated by this study may increase genetic connectivity between populations and reduce inbreeding, although this needs to be verified through genetic analyses.

The movement and dispersal patterns observed in this study may arise from differences in environmental drivers and behavioural strategies between coastal dwelling and offshore dwelling reef shark populations. Shallow coastal regions have higher habitat diversity and greater connectivity than offshore coral reef environments and reef habitats may also be isolated by deep water. Diverse coastal ecosystems such as Cleveland Bay have high productivity and many sharks and rays use such coastal habitats as nurseries (Beck *et al.*, 2001, Kinney *et al.*, 2011, Simpfendorfer & Milward, 1993). Where these habitats are accessible, blacktip reef sharks may capitalize on the productivity of these systems by using them as pupping grounds and as locations that enhance reproduction and juvenile growth and survival. Additionally, the shallow depth of the Great Barrier Reef continental shelf (<50m depth) means that maturing juveniles are able to disperse to new locations along the coast and to coral reefs offshore. In contrast, juvenile reef sharks on isolated reefs may not be able to traverse the deeper waters surrounding these habitats which limits juvenile dispersal and restricts long-distance movements to adults (e.g. Chapman *et al.*, 2005, Heupel *et al.*, 2010, Mourier & Planes, 2013). Additionally, the lower habitat diversity in offshore coral reef and atoll environments may reduce the availability of distinct types of juvenile habitats. This is consistent with observations in coral atoll environments where juvenile habitats are delineated by depth instead of habitat type (Papastamatiou *et al.*, 2009b), or may not be found at all (Stevens, 1984).

Inferring movements from acoustic telemetry data involves several assumptions that must be considered. As movement and behaviour is not directly observed, an abrupt end in detections could result from an animal moving out of detection range (emigration) but could also represent tag failure or mortality (Heupel & Simpfendorfer, 2002). Nevertheless, the movement and dispersal patterns presented here are reinforced by detections of individuals on other receiver arrays. Detection patterns also indicate emigration as last detections were recorded on receivers at the edges of the array which suggests movement out of detection range. In addition, long-term sampling in Cleveland Bay showed a lack of individuals between 850 and 1050 mm L_{ST}, suggesting that animals in this size range are not present at the site (see Chapter 3). The estimated size of juveniles at the time detections ceased indicates they were nearing maturity, a trigger that may prompt juveniles to disperse from natal grounds (Secor, 1999). Indeed these patterns have been recorded in crocodiles (Tucker *et al.*, 1997), sixgill sharks (Andrews *et al.*, 2010), and teleost fishes (Beck *et al.*, 2001, Nagelkerken *et al.*, 2008a). Lastly, conventional tag-recapture data provide direct evidence that similar sized juvenile blacktip reef sharks make long-distance movements along the Queensland coast. A juvenile blacktip reef shark was tagged in Trammel Bay (20.34^0 S; 148.82^0 E) on 21 February 2011 and recaptured on 11 March 2011 at Airlie Beach (20.26^0 S; 148.68^0 E), a minimum distance of 21 km. The shark was released and recaptured again on 30 August 2011 at Repulse Bay (20.51^0 S; 148.82^0 E), a minimum distance of 62 km from Airlie Beach (A. Tobin, unpubl. data).

Movement and dispersal patterns, both alongshore and from inshore to offshore, may represent exploratory behaviours to identify suitable habitats and resources and reduce competition in natal grounds (Grubbs, 2010). The large scale dispersal of juveniles may also maintain genetic diversity and fitness of blacktip reef shark populations at a regional scale. Alongshore and offshore movements may also increase population resilience as recovery following localized impacts or depletions may be supplemented by recruits from other areas. However, these movements also highlight the importance of maintaining the health and integrity of coastal ecosystems as they may support marine communities and populations at a regional scale, including those in offshore habitats such as coral reefs. Coastal habitats are under increasing pressure around the world (Halpern *et al.*, 2008, Lotze *et al.*, 2006) and the dependence on these habitats could expose the blacktip reef shark to additional pressures from habitat loss and degradation. Longer-term tagging and telemetry of reef sharks in both coastal and offshore habitats coupled with genetic studies would provide a more complete account of reef shark dispersal and movement at a regional level, and of the ramifications of these movements for reef shark conservation.

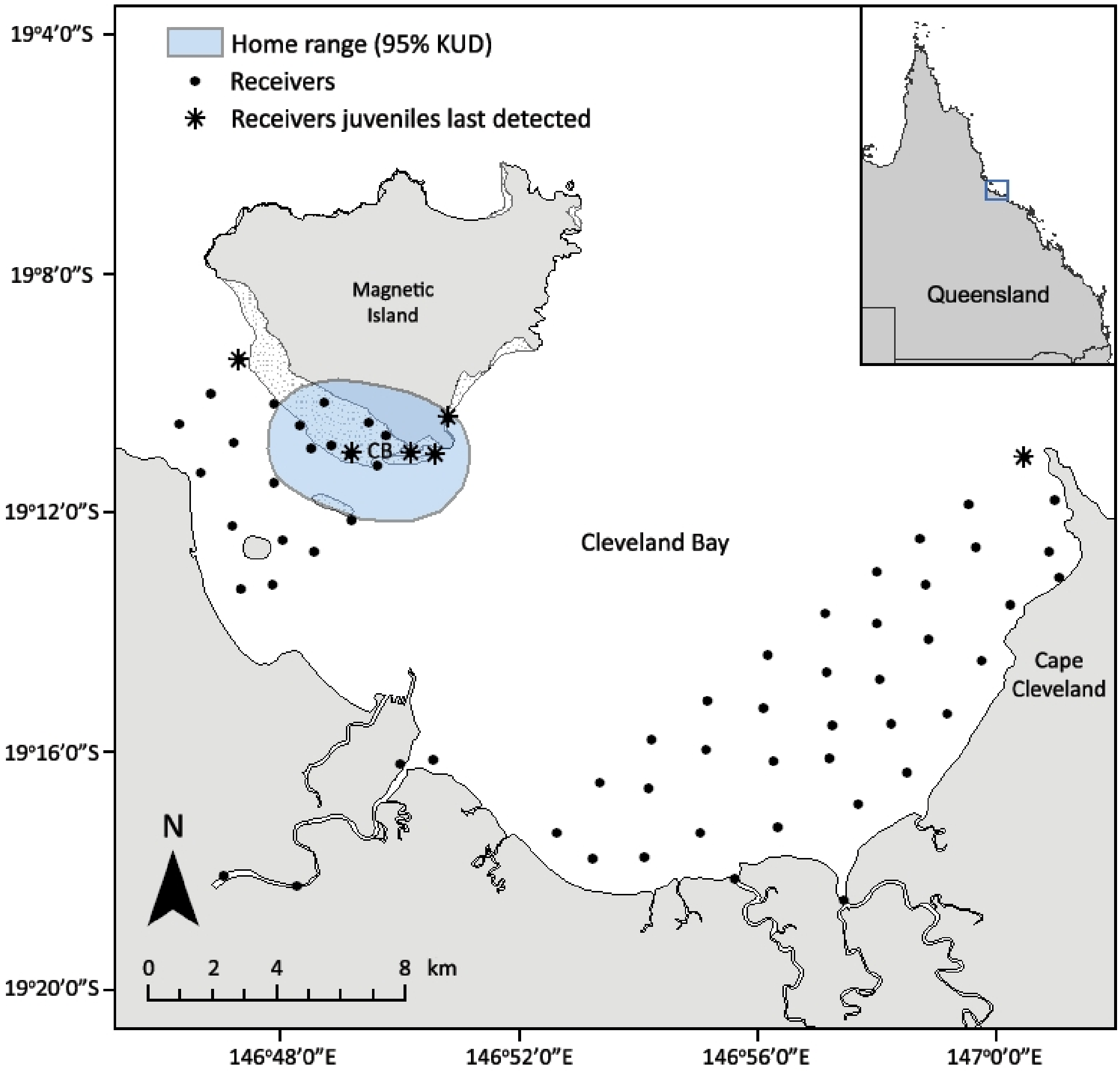


Figure 6.1: Locality map of Cleveland Bay showing nominal home range of juveniles and receivers where juveniles were last detected before departing the area.

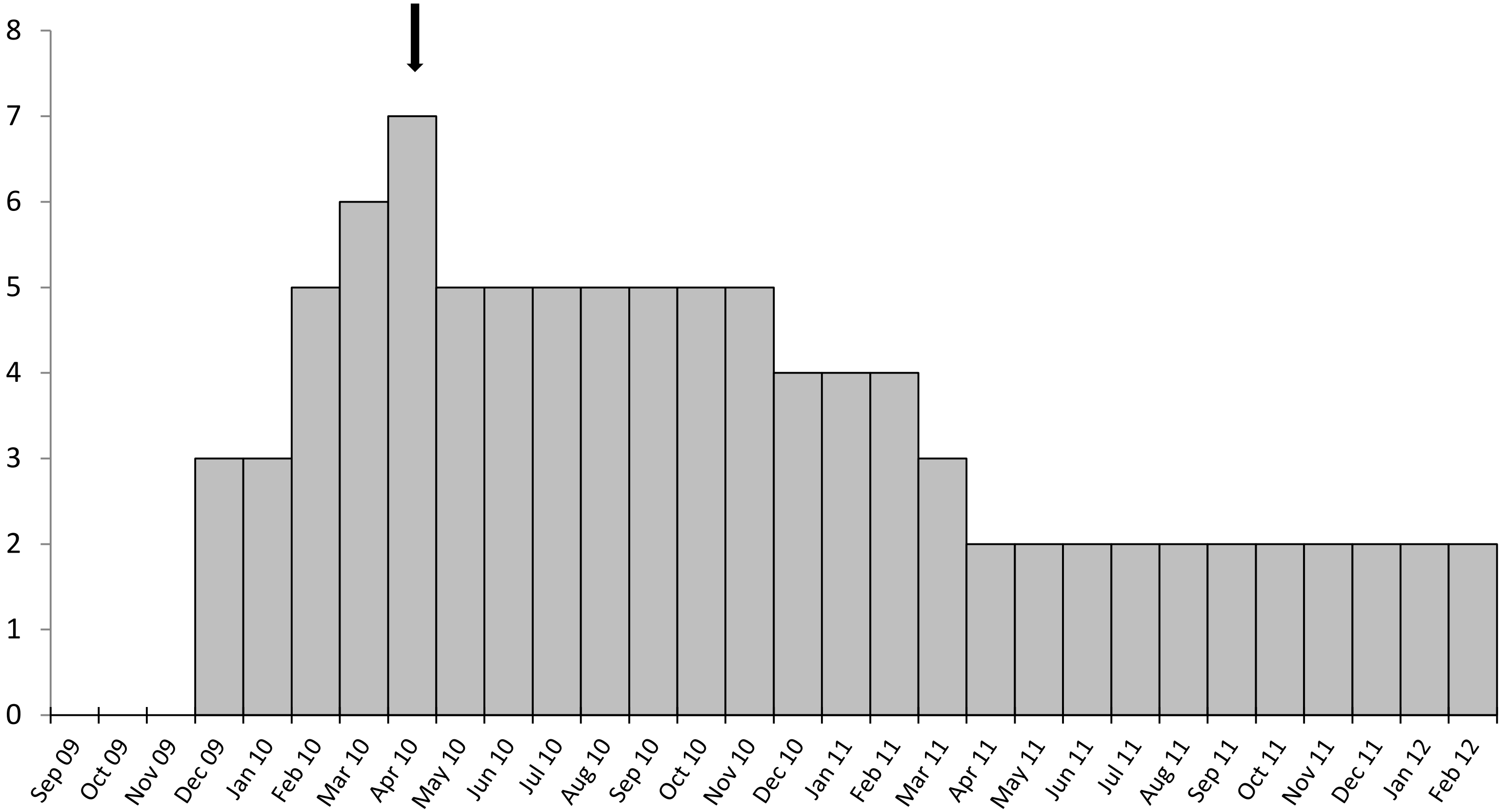


Figure 6.2: Accumulation and decay plot showing the increase and decline of the number of juveniles being detected within the Cleveland Bay receiver array. Black arrow indicates the time at which all transmitters had been deployed with no further transmitter tagged blacktip reef sharks released after this date.

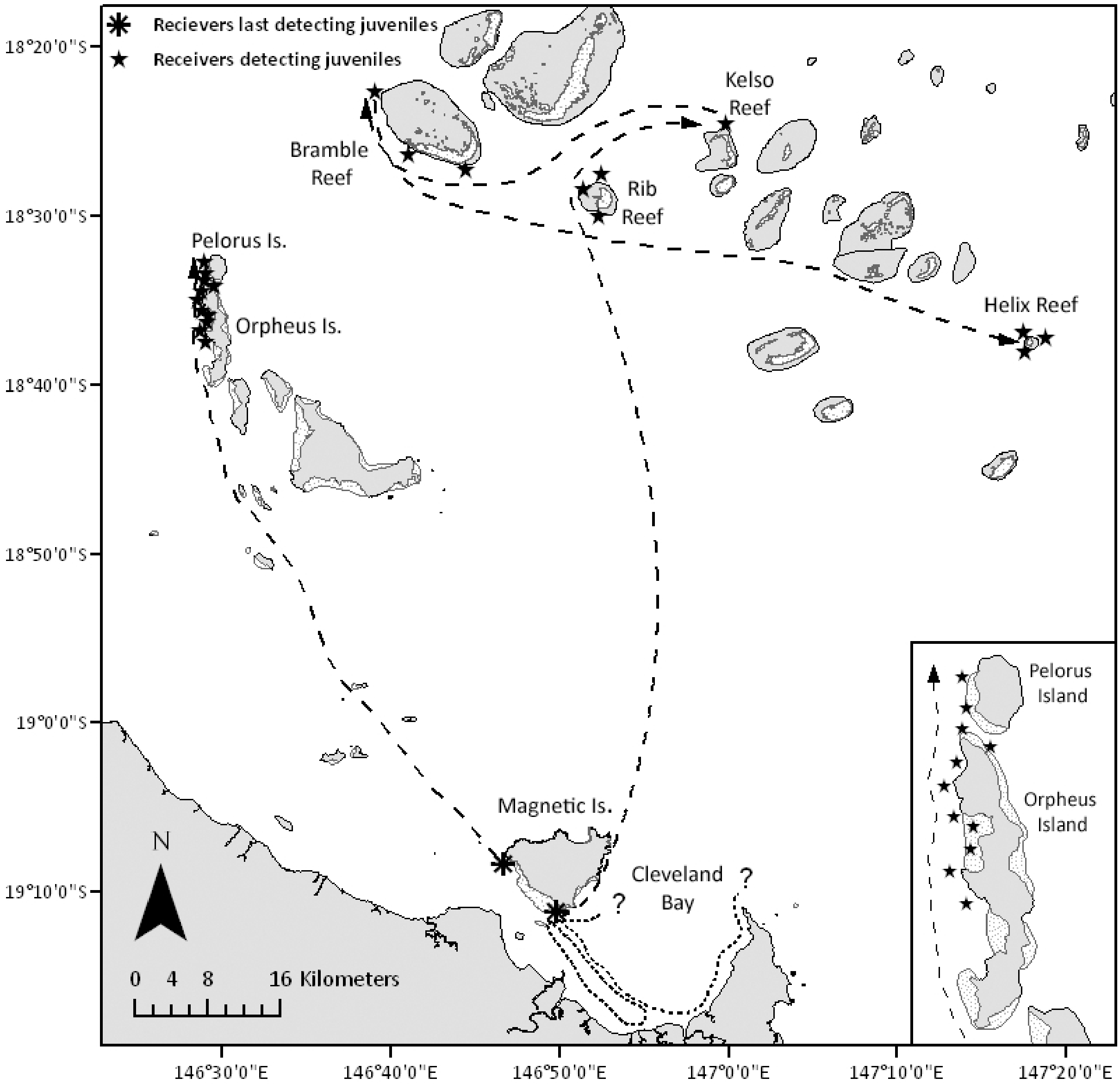


Figure 6.3: Map showing dispersal of juvenile blacktip reef sharks from Cleveland Bay offshore to coral reefs and alongshore to continental islands.

	Biological details			Residency pattern				Dispersal and movement		
Tag ID	Maturity	Sex	Size (mm L_{ST})	Date first detection in Cleveland Bay	Monitoring period	No. of days detected	Residency index (over monitoring period)	Date detections ceased in Cleveland Bay	No. days between first and last detection	Estimated length (mm L_{ST})* at emigration
59602[#]	Juvenile	F	730	21/12/2009	779	442	0.57	8/03/2011	442	809
63646	Juvenile	F	735	4/03/2010	706	48	0.07	21/04/2010	48	743
59600	Juvenile	M	709	21/12/2009	779	309	0.40	26/11/2010	340	777
59603	Juvenile	M	780	21/12/2009	779	42	0.05	6/02/2010	47	788
59605	Juvenile	M	665	2/02/2010	736	2	0.00	2/03/2010	28	670
59617	Juvenile	M	721	3/03/2010	707	50	0.07	23/04/2010	51	730
63647	Juvenile	M	889	13/04/2010	666	371	0.56	-	-	-
63649[#]	Juvenile	M	811	13/04/2010	666	230	0.34	3/02/2011	296	863
63650	Juvenile	M	752	17/02/2010	721	715	0.99	-	-	-

Table 6.1: Biological, residency and movement characteristics of nine juvenile *C. melanopterus* monitored Cleveland Bay. A mix of residency and dispersal patterns was evident. * estimated length derived from growth measurements of recapture individuals. [#] indicates individuals that were detected in receiver arrays in other locations.

7. General conclusion

The world's coastal oceans and seas face a multitude of pressures and impacts that affect coastal species, as well as the social, cultural and economic values tied to these species and habitats (Barbier *et al.*, 2011, Halpern *et al.*, 2008, Martinez *et al.*, 2007, Mee, 2012). Indeed, coastal fisheries support the lives and livelihoods of tens of millions of people and are essential for food security in many regions (Bell *et al.*, 2011, Jackson *et al.*, 2001). The importance of coastal ecosystems and increasing pressures have made them priorities for natural resource and conservation management (GBRMPA, 2013, Martinez *et al.*, 2007, Wilkinson & Brodie, 2011).

Coastal ecosystems support a diverse range of shark and rays species such as the blacktip reef shark, and these species have important ecological, social, cultural and economic values (Knip *et al.*, 2010, Simpfendorfer *et al.*, 2011, Vaudo & Heithaus, 2009, White & Sommerville, 2010). While management of the coastal zone is a recognised priority, the complexity of coastal ecosystems makes it difficult to balance human uses of resources such as coastal sharks with the long-term sustainability and conservation of these resources. Complexities in coastal management arise from many factors. Coastal ecosystems are affected by multiple drivers and pressures that have complex interactions and 'end-point' responses so that the abundance and distribution of coastal sharks may represent the combined effects of many separate factors operating over long periods (Brodie & Waterhouse, 2012, De'ath & Fabricius, 2010, Fabricius, 2005, Sheaves & Johnston, 2009). Complexity and uncertainty are further compounded by the diverse array of coastal habitat types that may each have distinct ecosystem characteristics, processes and biodiversity (Blaber, 2007, Sheaves & Johnston, 2009), and by spatial and temporal factors that can affect both coastal habitats and the species within these habitats (De'ath & Fabricius, 2010, Kimirei *et al.*, 2013, Staunton-Smith *et al.*, 2004, Yates *et al.*, 2012). For example, environmental factors and habitat-related variables result in a wide range of complex behaviours and habitat use patterns in coastal sharks (e.g. Ebert & Ebert, 2005, Heupel & Simpfendorfer, 2008, Hight & Lowe, 2007, Knip *et al.*, 2010, Speed *et al.*, 2010, Udyawer *et al.*, 2013). However, the biology and ecology of many coastal sharks remain poorly understood (Simpfendorfer *et al.*, 2011) which increases uncertainty. The complexity and uncertainty associated with coastal ecosystems complicate efforts to assess risks to coastal sharks, to identify critical ecosystem linkages and processes, prioritise management responses, and to predict and monitor the effects of management interventions (GBRMPA, 2009, GBRMPA, 2013).

7.1 Contributions to the biology and ecology of coastal sharks

Research on the biology and ecology of coastal sharks can provide new insights into the relationships between coastal species and their habitats (Simpfendorfer *et al.*, 2011) and can provide important data to inform management of coastal biodiversity (GBRMPA, 2013). The present study contributes new information about the biology and ecology of coastal sharks and provides valuable information for managing these species. Specifically:

- Chapter two demonstrated that several species that are widely regarded as reef sharks frequently occur in turbid coastal environments. While coral reefs are important habitats, these species also occur in shallow seagrass meadows and sandy and muddy foreshores. The presence of mangroves may also be an important feature influencing the distribution of some reef shark species.
- Chapter three revealed that a coastal blacktip reef shark population was highly localised, and had a population structure dominated by juveniles and adult females where maturing animals and adult males were conspicuously absent. This population structure suggests use of coastal ecosystem for reproduction and differs from that observed in conspecifics in coral reef environments in Western Australia, the Indian Ocean and the Central Pacific.
- Chapter four provided robust and validated age and growth estimates for the blacktip reef shark, and verified the reproductive biology of a local population. The data show that similar to the grey reef shark, the blacktip reef shark is relatively slow growing with low reproductive output. These are important data

for fisheries management, but the study also demonstrated the potential for underestimating maximum ages when using vertebrae for size-at-age estimates.

- Chapter five quantified the residency and movement patterns of a coastal blacktip reef shark population, finding that adult females were permanent residents; juveniles were temporary residents and adult males were vagrants. In contrast to classical models of coastal shark habitat use, adult females were resident and used the same small area of habitat as juveniles until the juveniles began to mature and disperse.
- Chapter six described the dispersal of juvenile sharks from their natal grounds over long distances alongshore and offshore, including movements from coastal habitats to offshore coral reefs and ecological connectivity between these systems.

These data provide new insights into the blacktip reef sharks' biology and spatial ecology and the ecological significance of coastal environments. While coral reefs are undoubtedly important habitats for the blacktip reef (e.g. Heupel *et al.*, 2009, Mourier & Planes, 2013, Papastamatiou *et al.*, 2010, Speed *et al.*, 2011), long-term tagging and telemetry data on the species (this study) show long-term patterns of residency and movement within shallow intertidal habitats in turbid coastal waters. The species' global distribution and diversity of habitat use (Last & Stevens, 2009, Papastamatiou *et al.*, 2009a, Speed *et al.*, 2011, this study; Stevens, 1984) suggest the blacktip reef shark has an intrinsic (or fundamental) flexibility (Devictor *et al.*, 2010) and a wide niche breadth (Price, 1971). This flexibility may represent an adaptive advantage where generalists are better able to accommodate environmental changes and pressures (Clavel *et al.*, 2011, Davies *et al.*, 2004, Julliard *et al.*, 2004, Munday, 2004). Consequently, the blacktip reef shark may be more resilient to impacts such as climate change (Chin *et al.*, 2010) and there is evidence to suggest that the species may be more resistant than other coastal sharks to extreme environmental disturbances (Udyawer *et al.*, 2013).

The population structure, residency and movement patterns evident in this study also suggest that some coastal blacktip reef shark populations may be structured to enhance reproduction. While there are many known examples of sharks using coastal habitats as nurseries (e.g. Castro, 1993, Conrath & Musick, 2010, DeAngelis *et al.*, 2008, Heupel *et al.*, 2007), this study found two important and unique differences with previous examples: (1) breeding adult females did not leave the pupping ground and (2) adult females and juveniles shared the same small area of space until the juveniles begin to mature, at which time the juveniles dispersed from their natal grounds. These two results contrast with the patterns that define classical shark nurseries (Heupel *et al.*, 2007, Springer, 1967), and also differ with the habitat use and movement patterns seen in adult females, neonates and juvenile blacktip reef sharks studied in coral reef environments (Mourier & Planes, 2013, Papastamatiou *et al.*, 2010, Speed *et al.*, 2011). Consequently shallow coastal habitats cannot be considered as nursery grounds under established definitions but may instead represent a different mode of social organisation to facilitate reproduction. This unique pattern may have resulted from the species' intrinsic flexibility that has enabled it to capitalise on opportunities present in turbid coastal environments, such as access to a range of interconnected habitat types, increased productivity and resource availability, and dynamic environmental conditions (Kimirei *et al.*, 2013, Knip *et al.*, 2010, Simpfendorfer & Milward, 1993, Yates *et al.*, 2012). The shallow, complex and dynamic nature of coastal habitats may also disadvantage other sharks that could be predators or competitors (Blaber & Blaber, 1980, Cyrus & Blaber, 1992, Sweka & Hartman, 2003), thus providing an additional advantage to the blacktip reef shark in these environments. Competitive advantages may also enhance growth and survival and hence, may explain the relatively large size of the adult individuals and neonates observed in this population compared to conspecifics in clear water coral reef habitats further offshore. The increased length and presumably, an associated increase in mass of neonates and juveniles could also reduce intraspecific predation and competition thereby making it possible for adult female and juvenile blacktip reef sharks to co-exist within a small area.

The movement and habitat use patterns described for coastal blacktip reef sharks also contribute to the scientific understanding of the function and role of coastal habitats. It is increasingly clear that shallow, turbid environments provide important habitat for many coastal sharks (Knip *et al.*, 2010, Speed *et al.*, 2010). This study confirms that the blacktip reef shark uses shallow, turbid habitats to facilitate reproduction including mating, pupping and early growth of neonates and juveniles. Tagging and telemetry data also demonstrated interconnectivity between different coastal locations alongshore, as well as between coastal habitats and offshore coral reefs. Thus shallow turbid coastal habitats appear to support key life history stages for blacktip reef sharks, and through dispersal, may play an important role in sustaining populations further offshore. Long-distance movements in juveniles differ from patterns evident in conspecifics in other regions (Mourier & Planes, 2013) and could represent an important mechanism for recruitment and for maintaining genetic diversity at a regional scale. The present study also contributes to the ongoing debate regarding the role of coastal habitats in sustaining marine fishes and maintaining connectivity between coastal habitats and offshore coral reefs (Blaber, 2007, Faunce & Serafy, 2006, Nagelkerken *et al.*, 2008a, Sheaves *et al.*, 2006). While there are several recorded examples in the Atlantic and Caribbean where mangroves and seagrass meadows function as nurseries and provide recruits to offshore reefs (Jones *et al.*, 2010, Luo *et al.*, 2009, Mumby *et al.*, 2004, Nagelkerken *et al.*, 2008b), there are few such examples from the Pacific (Kimirei *et al.*, 2013). This study provides direct evidence of these movements in a Pacific ecosystem and is one of only a few to demonstrate these movements in sharks, adding to evidence that coastal mangroves and seagrasses play important roles in sustaining marine fishes and can support marine ecosystems further offshore.

7.2 Implications for management: applying data into risk assessment frameworks

It is evident that the blacktip reef shark uses a wide range of habitat types and shows complex patterns of behaviour, movement and habitat use. It is also evident that coastal habitats are in themselves dynamic and complex. A key challenge facing natural resource managers is how to integrate the wide range of available information to provide clear guidance about the risks facing the species and the management responses necessary to ensure the species' long-term survival. In recent years, new multidisciplinary and integrative modeling approaches and risk assessment frameworks have been developed that can bring together a wide range of information types while accommodating the complexity and uncertainty of marine ecosystems. This study employed a modified risk assessment framework to integrate the data presented in the preceding chapters to present the conservation and management implications of this new information.

Risk assessment frameworks can integrate different types of data to help fisheries managers assess risks, set priorities and identify the most suitable management options, and can also function with incomplete data (Fletcher, 2005, Hobday *et al.*, 2007, Stobutzki *et al.*, 2002, Walker *et al.*, 2008). One assessment approach often employed in fisheries is the semi-quantitative risk assessment framework (Hobday *et al.*, 2007, Stobutzki *et al.*, 2001, Walker, 2005a) which provides a simple and transparent means to integrate different types of information to illustrate what the different data mean for the conservation and management of the species (Fletcher, 2005, Hobday *et al.*, 2007, Richardson *et al.*, 2010). The generalised risk assessment illustrated in Fig 1.1 (adapted from Polsky *et al.* 2007) uses three distinct *components of vulnerability*: (1) exposure, (2) sensitivity and (3) adaptive capacity; and is referred to as an *Exposure-Sensitivity-Adaptive capacity* (ESA) framework (Richardson *et al.*, 2010). The three components of the ESA approach are used in a wide range of assessments (Adger, 2006, e.g. Turner *et al.*, 2003, Wachenfeld *et al.*, 2007) and the method described in Chin *et al.* (2010) is used here to explore the management implications arising from this study. Specifically, an ESA framework was applied to *assess the vulnerability of the blacktip reef shark across the Great Barrier Reef World Heritage Area (GBRWHA) to extant and predicted pressures over the next 100 years*.

To apply the framework, information about the blacktip reef shark was assigned to the three vulnerability components as follows:

- **Exposure**: this component describes the extent to which the species is exposed to stimuli and pressures. In this assessment, pressures include anthropogenic effects from fishing and habitat loss and degradation which are the main issues facing coastal sharks (Knip *et al.*, 2010, Stevens *et al.*, 2005), as well as the potential effects of climate change (Chin *et al.*, 2010).

- **Sensitivity**: this component describes the degree to which the species is affected by or responsive to the stimuli or pressures, i.e., its sensitivity to the natural and anthropogenic pressures it encounters. As per Chin *et al.* (2010), a species' sensitivity is considered to be an intrinsic trait that is determined by the species' biological, ecological and physiological attributes. Sensitivity does not consider behavioural responses to changes and stimuli. For this discussion *attributes* of sensitivity include:
    - Rarity (rare species are more sensitive to impacts)
    - Demographic liability (fecundity and life history traits: sharks that have relatively slow growth and low reproductive output are more sensitive to impacts)
    - Habitat specificity (the extent to which the species depends on specific habitats for key life history stages)
- **Adaptive capacity/Rigidity**: this component considers the capacity for individuals to respond to and compensate for stimuli and pressures and their effects. As per Chin *et al.* (2010), the inverse term for adaptive capacity – *Rigidity* – is used. The Rigidity of a species is defined by the following *attributes*:
    - Trophic specificity (the ability to switch between prey)
    - Mobility (ability to move between geographic locations)
    - Physiological intolerances (ability to persist and compete in a range of physio-chemical envelopes)
    - Latitudinal restriction (a general proxy for rigidity)

Each attribute was qualitatively ranked as *Low*, *Moderate* or *High* using the available information. The attribute rankings were then combined to provide an overall ranking of Low, Moderate or High for each of the vulnerability components: Exposure, Sensitivity and Rigidity. These components were then combined to derive overall vulnerability (Fig 7.1). The vulnerability assessment method used by Chin *et al.* (2010) is described in more detail in Appendix 11.

7.2.1 Exposure

The present study extends the blacktip reef sharks' nominal portfolio of habitats from coral reefs to also include long-term use of shallow turbid coastal habitats for reproductive purposes, and reveals that coastal and offshore populations may be linked through dispersal. Shallow coastal habitats are among the most affected habitats in the GBRWHA from a range of pressures including declining water quality, sedimentation, recreational and commercial use and coastal development, and climate change (Brodie & Waterhouse, 2012, De'ath & Fabricius, 2010, GBRMPA, 2013, Sheaves *et al.*, 2007). Furthermore, coral reefs are also highly vulnerable to climate change impacts (Hoegh-Guldberg *et al.*, 2007a, Hughes *et al.*, 2003). The blacktip reef shark is also susceptible to fishing (Harry *et al.*, 2011, Tobin *et al.*, 2010) and is also taken in both coastal net fisheries and offshore line fisheries, raising the prospect of cumulative fishing impacts. Given the extant and predicted impacts acting on the coastal zone and on coral reefs, the species' occurrence and use of these areas and exposure to fishing activities, the blacktip reef shark is qualitatively assessed here as having *high exposure* to pressures and impacts in the GBRWHA.

7.2.2 Sensitivity

The information in this study on the occurrence and distribution, behaviour and habitat use and reproductive biology and life history of the blacktip reef shark are relevant to understanding the species' sensitivity to impacts.

Rarity: The blacktip reef shark does not appear to be a rare species. It is recorded as being frequently encountered in reef habitats (Last & Stevens, 2009) and often occurred in commercial fisheries catches and fishery independent surveys in a range of habitat types (chapter two; Heupel *et al.*, 2009). Tagging data also suggest that hundreds of individuals may be present within discrete areas, and that several such locations may occur along the GBR coast. These data suggest that the species is widely encountered in the GBRWHA and is thus qualitatively assessed as having *low rarity*.

Demographic liability: Validated age and growth data, growth models and reproductive data suggest that the blacktip reef shark is a relatively slow growing and long lived species compared to other fishes, and also has a limited reproductive output. Life history parameters appear similar to those of the grey reef shark which has experienced fisheries induced declines in many areas throughout its range (e.g. Graham *et al.*, 2010, Heupel *et al.*, 2009, Nadon *et al.*, 2012, Robbins *et al.*, 2006). These life history traits and evidence of the effects of exploitation on congenera suggest the blacktip reef shark is sensitive to pressures and is qualitatively assessed here as having *high demographic liability*.

Habitat specificity: The blacktip reef shark uses a range of habitat types suggesting that the species is a generalist in its habitat requirements, and that it possesses an inherent ecological flexibility that allows it to exploit a wide niche breadth (Devictor *et al.*, 2010, Price, 1971). Generalist traits reduce the species' dependence on specific habitat types and thus reduce its sensitivity to impacts (Clavel *et al.*, 2011, Munday, 2004, Yates *et al.*, 2012). However, the present study also revealed that while blacktip reef sharks use a range of coastal habitat types, their activity space is discrete with core activity spaces of only several km^2. Catch surveys, tagging studies and telemetry data suggest that individuals do not make regular use of adjacent areas even though these locations had a similar range of habitat types. The observed population structure and biology also indicate that specific locations are used to facilitate reproduction. The use of discrete locations for key life history stages increases the species' apparent dependence on certain locations of coastal habitat and thus, the blacktip reef sharks' ecological flexibility may be tempered by the availability and spatial arrangement of suitable habitats in the seascape, factors which have been found to affect the spatial ecology of other marine fishes (Nagelkerken *et al.*, 2008b). The movement and habitat use patterns described suggest that the blacktip reef shark is ecologically flexible but may be dependent on specific locations, and the species is qualitatively assessed here as having *moderate habitat specificity*.

7.2.3 Rigidity

This study contributes new knowledge to existing literature that together describe aspects of the blacktip reef sharks' rigidity.

Trophic specificity: The blacktip reef shark feeds on a variety of teleosts and cephalopods, but also on terrestrial snakes, seabirds and even rats (Lyle & Timms, 1987, Papastamatiou *et al.*, 2009a, Stevens, 1984) and seasonal prey such as turtle hatchlings (A. Chin pers obs). Studies from coral atolls suggest the species' trophic ecology may vary between adjacent groups within the same atoll (Papastamatiou *et al.*, 2010). These findings show the blacktip reef shark can exploit a wide range of prey items, and its widespread distribution and occurrence in a range of habitat types provide circumstantial evidence of a wide trophic niche. Consequently, the blacktip reef shark is qualitatively assessed as having *low trophic specificity*.

Immobility: Tagging and telemetry data from this study demonstrate that adult males and dispersing juveniles are relatively mobile with recorded movements of over 80 km. Conversely in French Polynesia, adult females appear to traverse deep waters between islands (Mourier & Planes, 2013). These findings suggest that individuals have an intrinsic ability to move over considerable distances and thus immobility is qualitatively assessed here as *low*.

Physio-chemical intolerance: The blacktip reef sharks' physio-chemical tolerances have not been explicitly studied, but its ecological flexibility may be inferred from its habitat use and distribution. The blacktip reef shark occurs in a wide range of turbid coastal habitats and clear-water coral reef environments ranging across the Pacific and Indian Oceans (Mourier & Planes, 2013, Papastamatiou *et al.*, 2010, Speed *et al.*, 2011, this study, Stevens, 1984). The species is also reported to have invaded the Mediterranean from the Red Sea via the Suez Canal (Last & Stevens, 2009). These habitat associations and distributions represent a large range in environmental conditions including coastal areas that experience dynamic environmental conditions. Additionally blacktip reef sharks appear to resist severe environmental conditions such as intense storm events that cause other sharks to relocate (Udyawer *et al.*, 2013). Consequently, the blacktip reef shark is qualitatively assessed here as having *low physio-chemical intolerance*.

Latitudinal restriction: published accounts of blacktip reef shark distribution show the species occurs from 40° north latitude to 28° south latitude (Last & Stevens, 2009), indicating tolerance of a wide range of environmental conditions. The species is qualitatively ranked as having *low latitudinal restriction*.

7.3 Vulnerability of the blacktip reef shark in the GBRWHA

Following Chin *et al.* (2010), ranks for the attributes and vulnerability components were integrated to derive an overall vulnerability ranking. Applying the ranking procedures (detailed at Appendix 11) resulting in the blacktip reef shark having *low vulnerability* to extant and predicted pressures occurring in the GBRWHA over the next 100 years (Table 7.1). While the species has high exposure to impacts and its life history traits make it more sensitive to impacts, these moderate to high rankings for exposure and sensitivity are offset by the species' abundance and low rigidity (i.e. high adaptive capacity). This assessment places the species at lower risk than suggested by previous fisheries risk assessments that rank the species at moderate to high risk (Salini *et al.*, 2007, Tobin *et al.*, 2010). This apparent contradiction is due to issues of scope and scale. The ESA considers the likelihood of extirpation of the species across the entire GBRWHA over a 100 year time frame whereas the fisheries risk assessment considers immediate fishery specific risks in fished locations. The fisheries risk assessments also rely exclusively on life history and fishery data, and risk is calculated according to quantified indices of *productivity* and *susceptibility*. Meanwhile the ESA framework incorporates a wider range of information including the species' ability to compensate for high exposure and sensitivity through adaptive capacity, i.e. individuals are able to move to avoid impacts or to replenish depleted populations, and common and widespread species are able to maintain sufficient recruitment to balance mortality. Importantly, this approach allows for the effects of spatial management to be considered which in the GBRWHA includes 33% of the area enforced as no fishing zones (GBRMPA, 2009).

In this scenario the species' survival at a GBRWHA wide scale appears to be highly likely.

While the ESA and fisheries risk assessment approaches generate differing outcomes, both assessments are complimentary and accurate, albeit at different scales. The life history information gleaned from this study were used to update risk assessments for coastal sharks (Tobin *et al.*, 2010) and thus increased the confidence of the blacktip reef shark fisheries risk assessments. Given the highly localised abundance of the species in specific locations, use of specific habitats for reproductive purposes, potential susceptibility to fishing gears (Harry *et al.*, 2011, Tobin *et al.*, 2010) and demographic liability, the species is very vulnerable to *localised* depletion where fishing pressure and/or habitat degradation are high. Therefore, while the ESA suggests that species is unlikely to become extinct across the GBRWHA, blacktip reef sharks are likely to be vulnerable to localised depletion (as suggested by the fisheries risk assessment). Should localised pressures from fishing and habitat loss and degradation expand unchecked across the entire GBRWHA, over time the blacktip reef sharks' rarity would increase (increasing sensitivity) and the compensatory effects of mobility would be diminished as refuges became unavailable or unable to supply recruits to exploited areas. The increased sensitivity and rigidity resulting from an unchecked region-wide increase in fishing intensity would raise the blacktip reef sharks vulnerability to moderate or high under the ESA assessment.

Comparing the ESA framework with the fisheries risk assessment illustrates the importance of carefully defining the assessment context and using the appropriate risk assessment approach. The ESA approach is more holistic than the fisheries assessment as it considers greater spatial and temporal scales and a wider range of variables and as a result, is better suited to assessing risk at ecosystem scales. However, the ESA is not as precise as the fisheries assessments which carefully quantify individual attributes of productivity and susceptibility. Thus while the fisheries assessment's precision make it well-suited to fisheries management applications, the ESA approach and other more holistic approaches such as the IUCN Red List criteria (IUCN, 2008a), are better suited to assessing the overall risk of a species extinction from multiple pressures and cumulative impacts. This example also highlights that assessments that are based entirely on one data type such as demographic data (which is only one attribute of sensitivity) or spatial distribution (exposure) may be ill-suited to predict the extinction risk of a species as they do not consider the range of other factors operating at ecosystem scales.

7.4 Considerations for future research and management

The ESA framework highlights the key attributes and components that contribute to species vulnerability and resilience. For the blacktip reef shark, the key issue appears to be localised depletion. The species' high exposure and moderate sensitivity place it at risk to localised pressures, but at a whole-of-ecosystem scale these pressures are mitigated by its abundance, flexibility and mobility. The implications of this new information for natural resource and fisheries managers depend on the management objectives. If the management goal is to secure the continued existence of the species within the GBRWHA ecosystem, the current spatial zoning arrangements that remove fishing pressure from 33% of the GBRWHA are likely sufficient to achieve this objective. However, this conclusion is dependent upon there being sufficient habitats available to provide the ecosystem functions and processes blacktip reef sharks require into the future. Unfortunately, the quality and availability of these habitats is not assured given the documented declines in habitats and the predicted effects of climate change (Brodie & Waterhouse, 2012, De'ath *et al.*, 2013, Johnson & Marshall, 2007) and thus, management attention is needed to address the issues affecting habitat quality and availability. Alternatively if the management objective is to maintain harvest rates in fished blacktip reef shark populations or to ensure that populations are maintained at localised scales of tens to hundreds of km^2, further action may be required to compensate for the species' high exposure to multiple pressures and its sensitivity to localised impacts.

Considering these factors several management responses could be considered. To secure the species' continued existence within the GBRWHA, efforts should be focused on maintaining the availability and quality of sufficient habitats across the species' range to maintain its abundance and to preserve the ecological processes that support the regional population. This will require measures to address impacts from habitat loss and climate change, and specifically address issues such as water quality, coastal development and climate change impacts. To maintain local populations and harvest rates, managers may need to consider measures to ensure protection of breeding adults that are essential to maintaining sufficient recruitment to sustain mortality rates (Kinney & Simpfendorfer, 2009, McAuley *et al.*, 2007c, Prince, 2005), and the preservation of locations that support key life history stages such as mating, parturition and early growth. In the case of the blacktip reef shark in the GBRWHA, this would mean identifying and preserving shallow turbid coastal habitats that support localised groups of adult females, but may also require measures to protect reef dwelling populations further offshore. Management could also consider additional fisheries controls such as introducing a minimum size limit for female blacktip reef sharks fisheries of 1.3 m L_{ST} to ensure that females have the opportunity to reproduce before being removed from the population, or temporal restrictions such as no-take of females between November and February to protect pregnant females and minimise impacts on annual mating and pupping events. However the need for additional fishery controls would need to be carefully assessed against existing fisheries regulations such as seasonal and spatial closures (Queensland Primary Industries and Fisheries, 2009) and the efficacy of existing management arrangements for coastal habitats (GBRMPA, 2013).

The ESA framework makes several assumptions that highlight uncertainties and knowledge gaps in the biology and ecology of the species being assessed. While the present study indicates that shallow, turbid coastal habitats play an important role in blacktip reef shark reproduction, the study needs to be replicated to verify whether other coastal locations function in a similar manner. Commercial fishery data indicate several locations that may support similar groups of breeding adult females and juveniles with potentially similar dispersal patterns, but these locations need to be examined through further sampling and tagging and telemetry studies. Furthermore the importance of shallow coastal habitats in sustaining the GBRWHA-wide population may depend on the quality, availability, connectivity and spatial arrangement of these habitats, and the extent to which each habitat and location contributes to overall recruitment (Nagelkerken *et al.*, 2008b, Sheaves *et al.*, 2006, Yates *et al.*, 2012). Likewise, offshore coral cay habitats in the GBRWHA may also support blacktip reef shark reproduction as neonate and juvenile blacktip reef sharks are also found on coral cays such as Heron Island. As a result, the relative importance of coastal and coral reef habitats in sustaining the GBRWHA population may vary according to the spatial arrangement, quality and availability of coastal and offshore reef habitats. Genetic analysis could help to resolve connectivity patterns and philopatry between locations and habitats (Mourier & Planes, 2013), and thus improve understanding of the influence of shallow coastal habitats on coastal sharks and of the relative importance of coastal habitats and coral cays to the regional blacktip reef shark population. Another assumption identified by the ESA involves sensitivity resulting from the species life history. While the existing data suggest relatively slow growth and low reproduction, growth and reproduction may vary as population density changes in response to pressure (Cortés, 2004). The effects of density dependence on the blacktip reef shark's life history should be examined through quantitative demographic analysis which will provide a more accurate assessment of the species sensitivity.

Lastly, the present study revealed many differences in population structure, animal size, growth rate and movement patterns between coastal blacktip reef sharks in the GBRWHA and conspecifics in offshore coral reef environments elsewhere. These variations have been attributed to environmental and ecological differences between shallow, turbid coastal habitats and clear water coral reef environments offshore. However, there are no comparative studies on conspecific blacktip reef shark populations to specifically examine the effects of variables such as depth, productivity (and prey availability), substrate complexity, habitat availability and turbidity on the species' growth and behaviour. For example, the presence of mangroves may increase the survival of juvenile lemon sharks (Guttridge *et al.*, 2012) and comparative studies could examine whether mangroves increase foraging success, growth and survival of juvenile blacktip reef compared to conspecifics elsewhere. If differences exist, these studies could also help to identify the mechanisms (e.g. provisioning, reduced competition and predation) that drive these differences and threshold values and relationships between environmental variables and behavioural and physiological responses. Addressing these knowledge gaps will further our understanding of the spatial ecology of the blacktip reef shark in coastal habitats, and also further our understanding of the contribution coastal habitats make to marine ecosystems, the mechanisms by which these habitats sustain coastal biodiversity, and ultimately, the responses required by society to maintain these habitats, processes and their biodiversity.

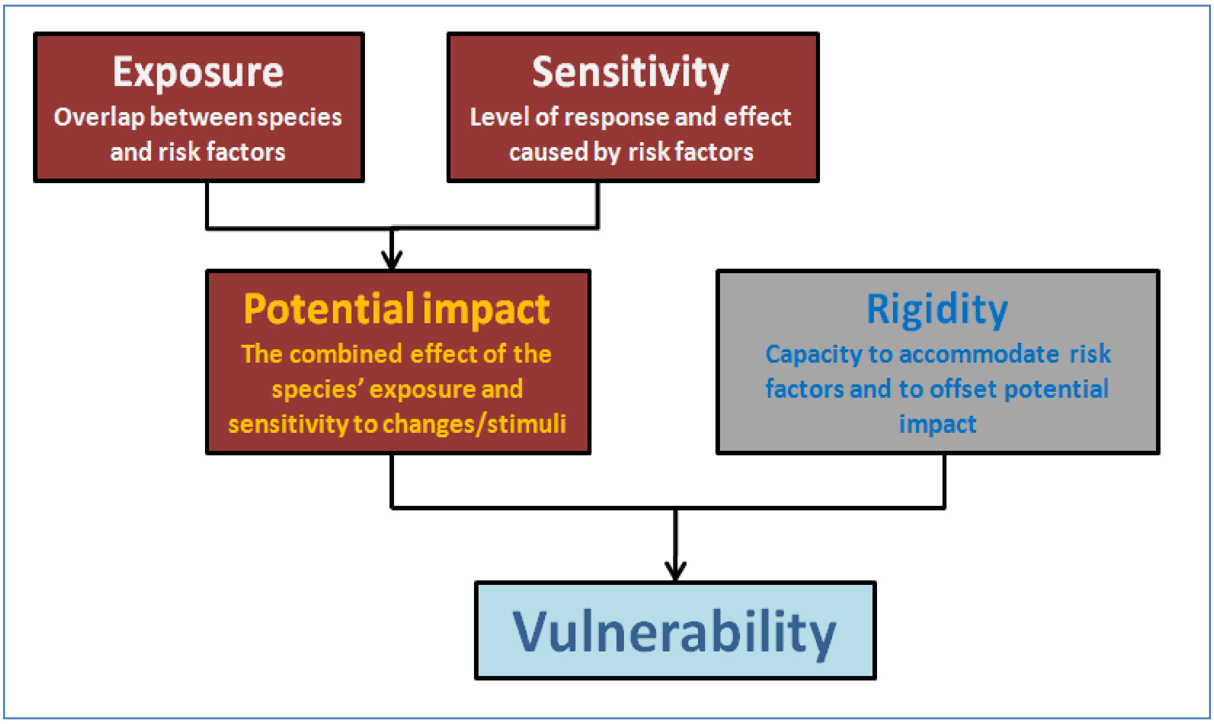


Figure 7.1: the three vulnerability components and their application in assessing species' vulnerability in the ESA framework.

Exposure	Sensitivity			Rigidity			
	Rarity	Demographic liability	Habitat specificity	Trophic specificity	Immobility	Physio-chemical intolerance	Latitudinal restriction
H	L	H	M	L	L	L	L
H	M			L			
Overall vulnerability ranking				H x M x L = Low[#]			

Table 7.1: Attribute and component rankings for an ESA framework assessment for the blacktip reef shark in the GBRWHA.

[#] See Appendix 11for details regarding the ESA method

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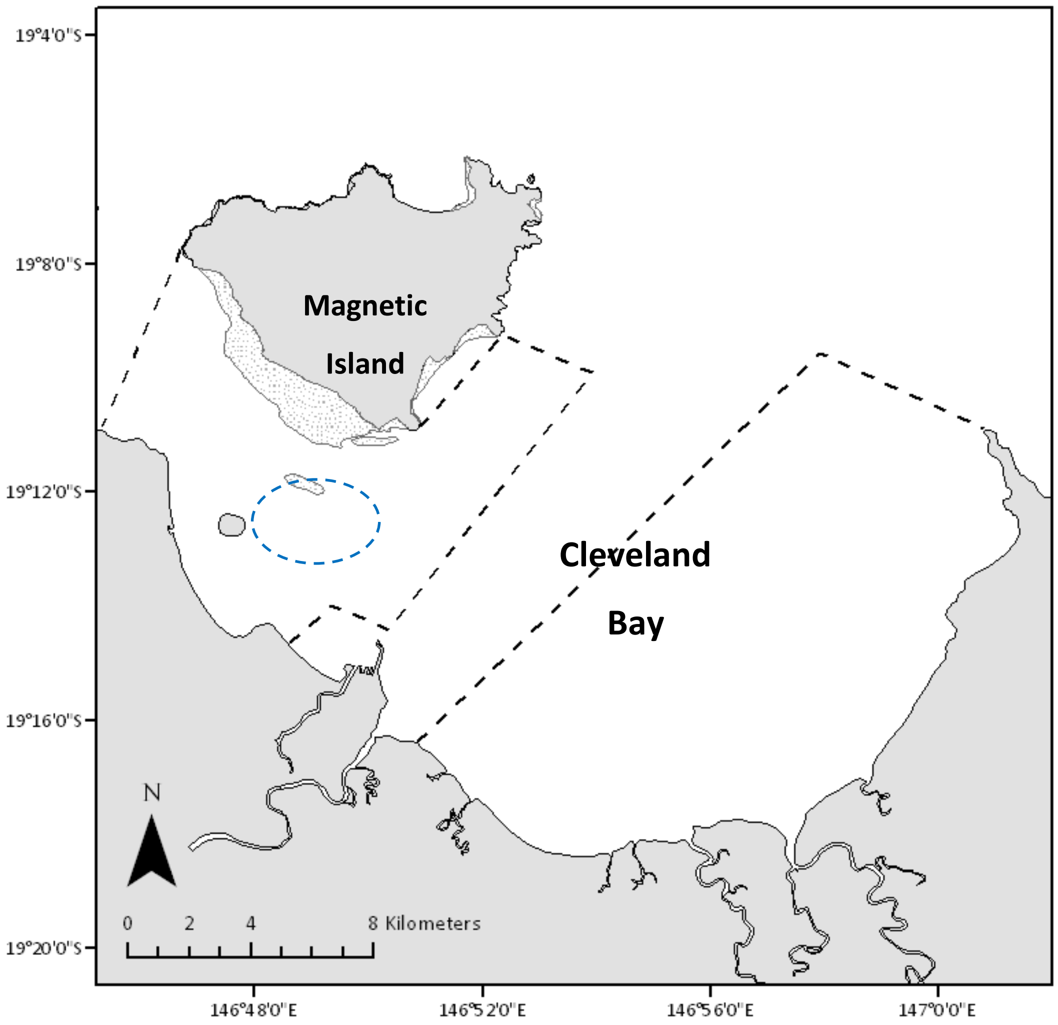
Appendices

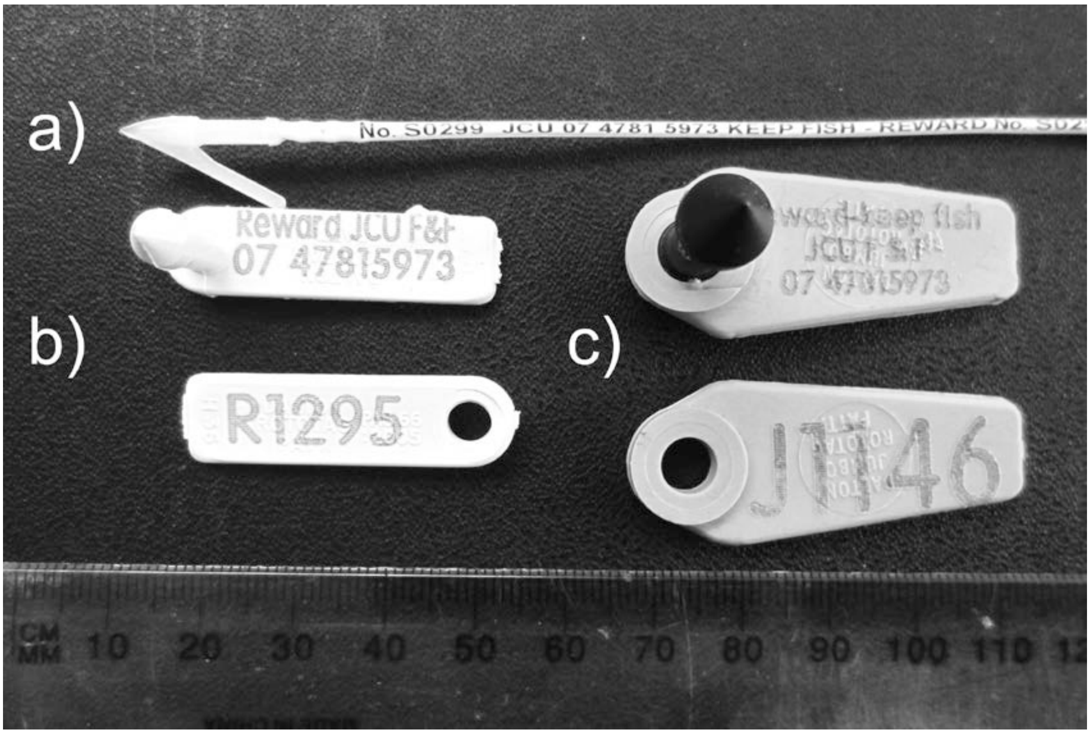
Appendix 1: location of fishery independent sampling areas in Cleveland Bay

Map of Cleveland Bay and Magnetic Island showing locations sampling areas (the area bounded by the coast and the dashed lines) adjacent to Cockle Bay (shown by the blue dashed line). Sampling in this area was carried out throughout 2008, 2009, 2010 and 2011 using longline gear and monofilament mesh nets to capture sharks for other research projects. These projects accumulated 228 days of sampling but only captured 10 blacktip reef sharks outside of the Cockle Bay study site.

Note: the area in the middle of Cleveland Bay lying in between the two fishing area is a commercial shipping channel and sampling could not be carried out in this area.



Appendix 2: Rototags and dart tags used for tag-recapture studies of blacktip reef sharks around Magnetic Island and Cleveland Bay



Captured blacktip reef sharks were tagged with plastic tipped Hallprint Dart tags (a) and small or large rototags (b), (c). Rototags were applied in the thickest portion of the first dorsal fin, while dart tags were inserted into the cartilaginous fin rays at the base of the dorsal fin.

Appendix 3: Information and models used to estimate male size at maturity

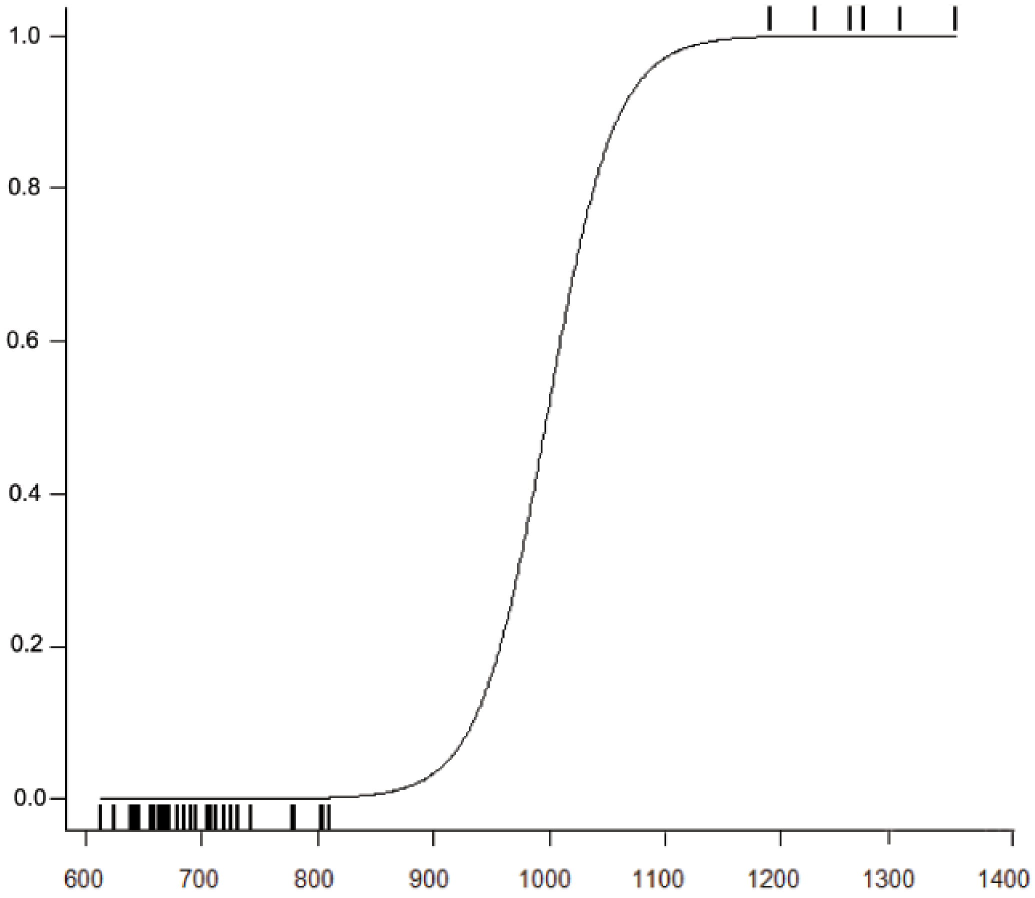
Calculations used to derive preliminary estimates of male length at maturity and resulting estimates. There were very few adult males captured and there no maturing males available for analysis. As such, the estimates of male size at maturity should be considered as preliminary data only and treated with caution.

The length (L_{ST}) at which 50% (l_{50}) and 95% (l_{95}) of males were mature was determined through a logistic regression of L_{ST} and clasper calcification status (as per Walker, 2005b, Walker, 2007).

$$P(l) = P_{max} \left(1 + e^{-\ln(19)\left[\frac{l-\beta_1}{\beta_2-\beta_1}\right]}\right)^{-1}$$

where $P(l)$ is proportion of males in the population that are mature at L_{ST}, l; where $\beta 1$ and $\beta 2$ are parameters derived from the regression model which correspond to l_{50} and l_{95},respectively; and P_{max} is the asymptote of the model and was fixed at 1. A generalised linear model (GLM) with a binomial error structure and logit link function was used to estimate parameters $\beta 1$ and $\beta 2$. The morphometric relationship between L_F and L_{ST} was calculated through linear regression.

The figure on the next page shows a rug plot and logistic regression of clasper calcification at size, straight lines indicate the length where 50% of males have calcified claspers. Rug marks on the X axis indicate data points and show the distribution of the data used in the model.


1.0
0.8
0.6
0.4
0.2
0.0
600
700
800
900
1000
1100
1200
1300
1400

Appendix 4: growth functions used in age and growth studies of chondrichthyan fishes

Model	Description	Equation
Three parameter Von Bertalanffy (VB3)	A linear function where growth rate decreases as length (age) increases	$L(t) = L_\infty - (L_\infty - L_0)exp^{-kt}$
Two parameter Von Bertalanffy (VB2)	A linear function where growth rate decreases as length (age) increases, length at birth fixed at a known value (*x*)	$L(t) = L_\infty - (L_\infty - x)exp^{-kt}$
Three parameter Gompertz (GPZ3)	Growth rate decreases exponentially with increasing length (age)	$L(t) = L_\infty\ (exp[-L_0 exp^{-kt}])$
Two parameter Gompertz (GPZ2)	Growth rate decreases exponentially with increasing length (age), length at birth (*x*) fixed at a known value	$L(t) = x\ exp\ (log_e\{L_\infty/x\}\{1 - exp^{-kt}\})$
Logistic (Log)	Growth rate has a sigmoidal relationship to length (age) where growth rate gradually increases, peaks and then decreases with increasing length (age)	$L(t) = \frac{L_\infty L_0 exp(kt)}{L_\infty + L_0(exp\{kt\} - 1)}$

L_∞ = maximum/asymptotic length (mm L_{ST}); L_0 = length at birth (mm L_{ST}), k = relative growth rate (years^{-1})

Equations sourced from Caillet *et al.* (2006) and from Thorson and Simpfendorfer (2009).

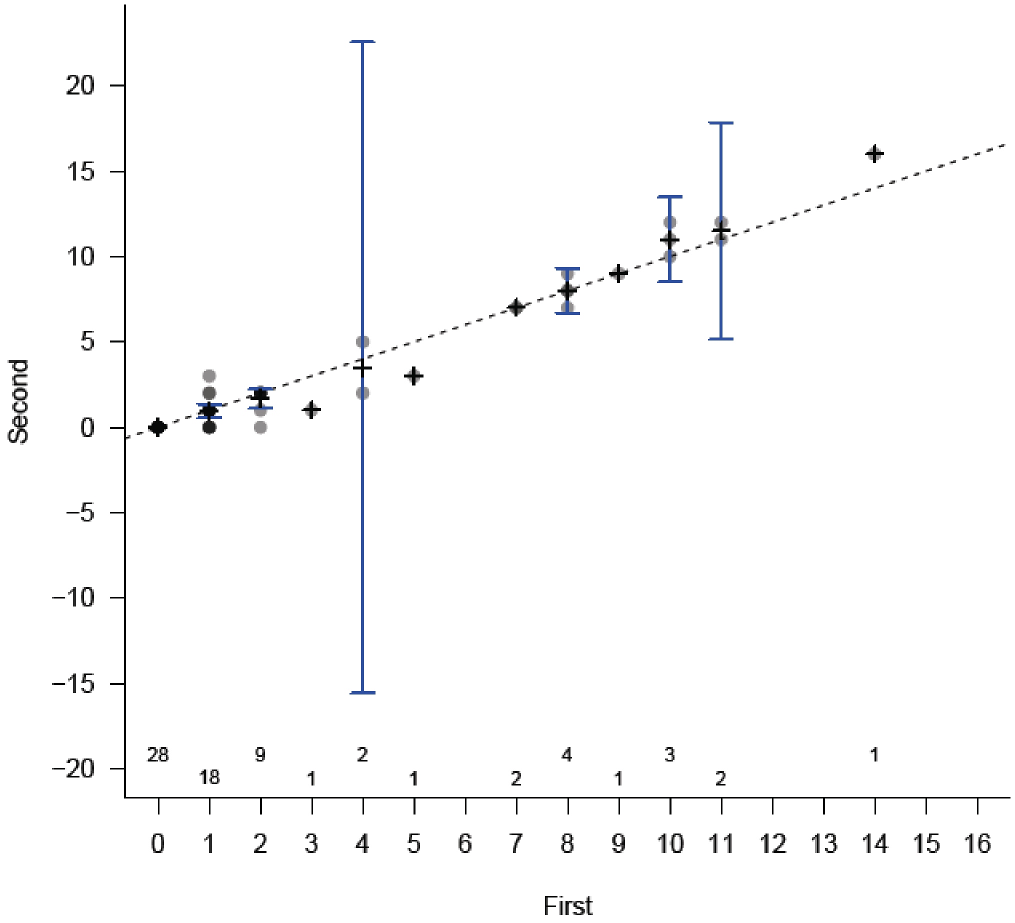
Appendix 5: reader precision and bias for age estimation

Precision summary statistics

n	Percent agreement	Average Percent Error	Coefficient of variation
72	72.22	20.61	29.14

Bowker's (Hoenig's) test of Symmetry

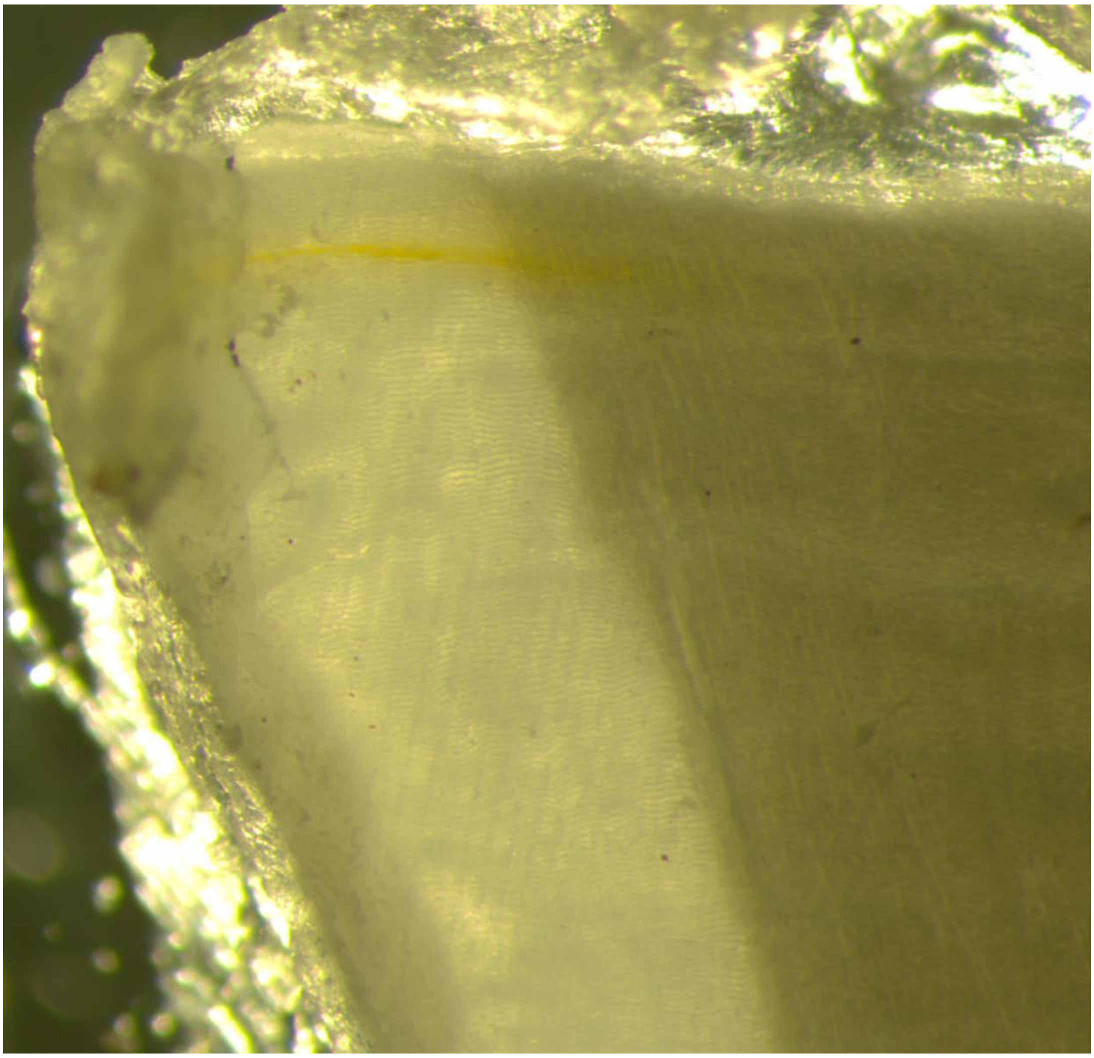
df	Chi square	p
13	15.33333	0.28700



Intra-reader age bias plot showing age estimates determined by both two independent readers (first and second reader). Dots represent age estimates derived by both readers with darker shading indicating increasing overlap of estimates. Error bars represent the 95% confidence interval around the 1:1 agreement line (dotted grey line). Numbers above the *x* axis show the number of samples of each age.

Appendix 6: example of vertebrae showing lack of readable terminal bands which lead to age underestimation

Photograph of calcein marked vertebrae from blacktip reef shark J0340, an adult female measuring 1398 mm L_{ST} at first capture and 1422 mm L_{ST} when recaptured after 969 days at liberty. The calcein band was deposited close to the edge of the centrum and visible band pairs are difficult to distinguish after the calcein mark, even though the animal was at liberty for over three years.



Appendix 7: performance metrics for Vemco VR2W receivers deployed in Cockle Bay

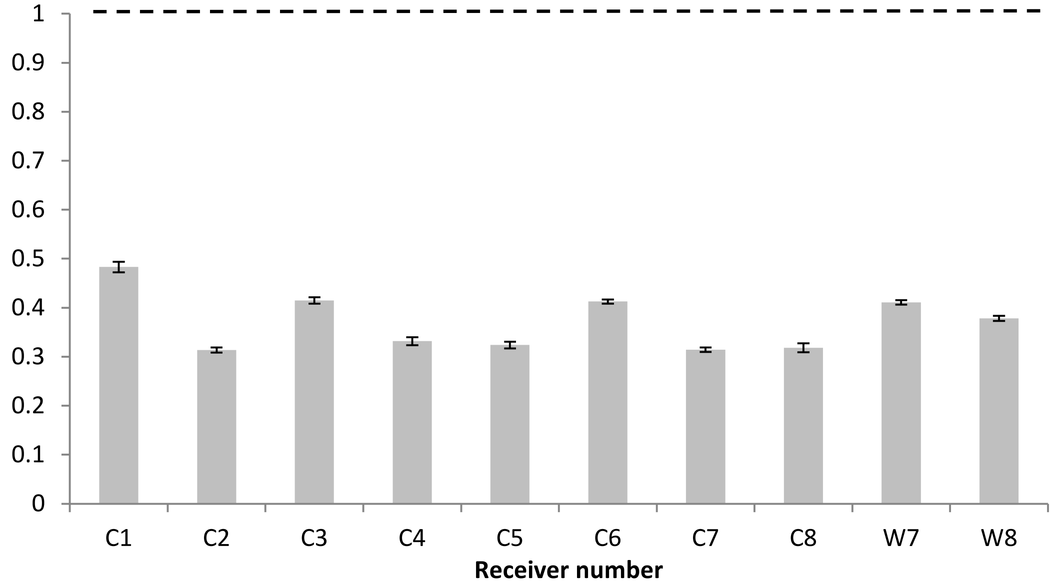
Vemco VR2W receiver performance data from ten receivers deployed in Cockle Bay (Fig. S1). These performance metrics are derived according to Simpfendorfer *et al.* (2008) and include code detection efficiency (CDE), rejection coefficient (RCF) and noise quotient (NQ). These metrics are calculated using data collected by the receivers during their deployment on the quantity and nature of acoustic signals received. CDE, RCF and NQ are calculated according to the following functions (Simpfendorfer *et al.*, 2008).

Metric	Equation	Comments
Code detection efficiency (CDE)	$CDE = D/S$	Ranges from 0-1 with 1 indicating 100% efficiency (very good performance – every synch resulting in a valid detection)
Rejection coefficient (RCF)	$RCF = C/S$	Ranges from 0-1 with 1 indicating 100% rejection (very poor performance – every synch discarded due to an invalid check sum)
Noise Quotient	$NQ = P - (S \cdot cl)$	Can be positive or negative. Positive values reflect environmental noise. Negative values indicate tag collision

D = number of valid detections; S = number of synchs (an estimate of how many codes were transmitted); C = number of codes rejected by the receiver due to an invalid checksum; P = number of pulses detected; and cl = the number of pulses used to make a valid code (7 in the case of the transmitters used in the present study)

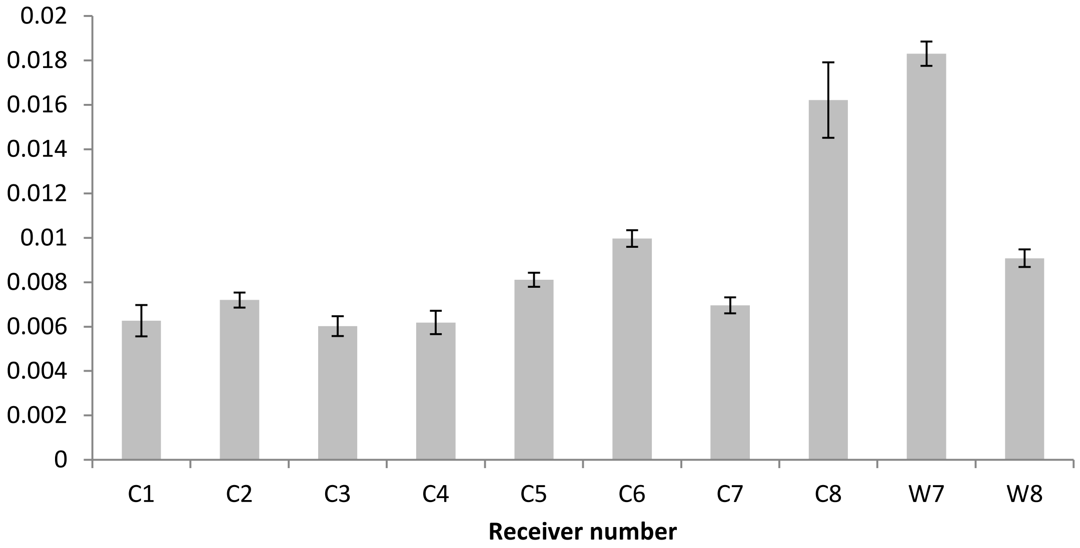
Map showing the location of the ten receivers deployed in shallow complex habitats in Cockle Bay that were analysed for performance (C1 - C8; W7 and W8).

Performance metrics for the ten receivers were extracted for the period 01 September 2009 and 05 May 2011 and are presented below.



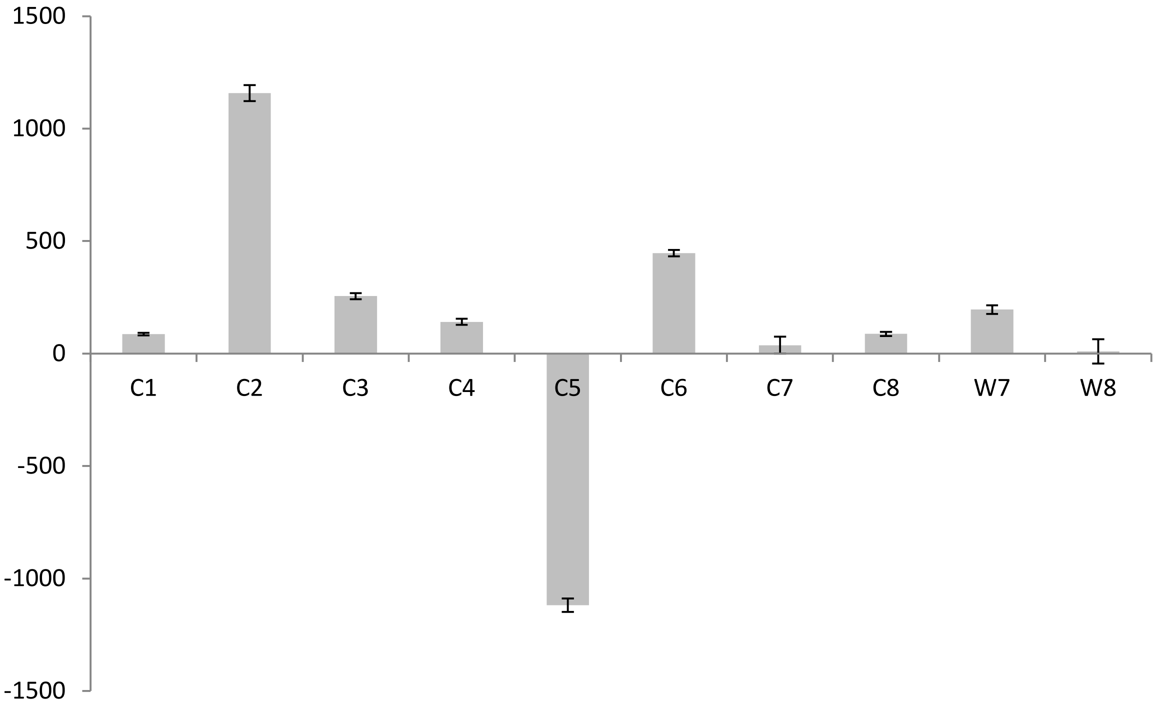
Code detection efficiency for ten receivers in Cockle Bay. Dashed line indicates a CDE value of 1 (i.e. every synch resulting in a valid detection indicating excellent receiver performance). Error bars are SE.

The code detection efficiency (CDE) data suggest that under half of the codes transmitted (synchs) were detected, with a range from 0.31 to 0.48 detections per synch, with a mean CDE of 0.37 across all ten receivers. This performance is slightly poorer than that reported previously: mean CDE 0.41 detections per synch (Simpfendorfer *et al.*, 2008); and 0.52 detections per synch (Welsh *et al.*, 2012) and may reflect the very shallow and turbid nature of the study site which may have interfered with signal transmission (Simpfendorfer *et al.*, 2008, Welsh *et al.*, 2012).



Rejection coefficient data for ten receivers in Cockle Bay. Note that Y axis only extends to 0.02 and this, RQF is still very low. Error bars are SE.

The rejection coefficient (RQF) was very low (Fig. S3) indicating that very few synchs were rejected due to invalid check sums (the pulses at the end of the synch). RQF ranged from 0.006 to 0.018 rejections per synch, with a mean RQF of 0.009 (i.e. <1% of synchs were rejected) across all ten receivers. As synchs are only rejected when a receiver detects all seven pulses and then logs an incorrect check sum, this low RQF suggests that most of the tag detection inefficiency was caused by receivers rejecting incomplete code sequences (i.e. fewer than seven pulses received) (Simpfendorfer *et al.*, 2008). This RQF is comparable to other studies: 0.041 (Simpfendorfer *et al.*, 2008); and 0.022 (Welsh *et al.*, 2012).



Noise quotient data for ten receivers in Cockle Bay. Positive values indicate levels of environmental noise (more pulses received that would have been generated by tags), while negative values indicate high levels of tag collision. Error bars are SE.

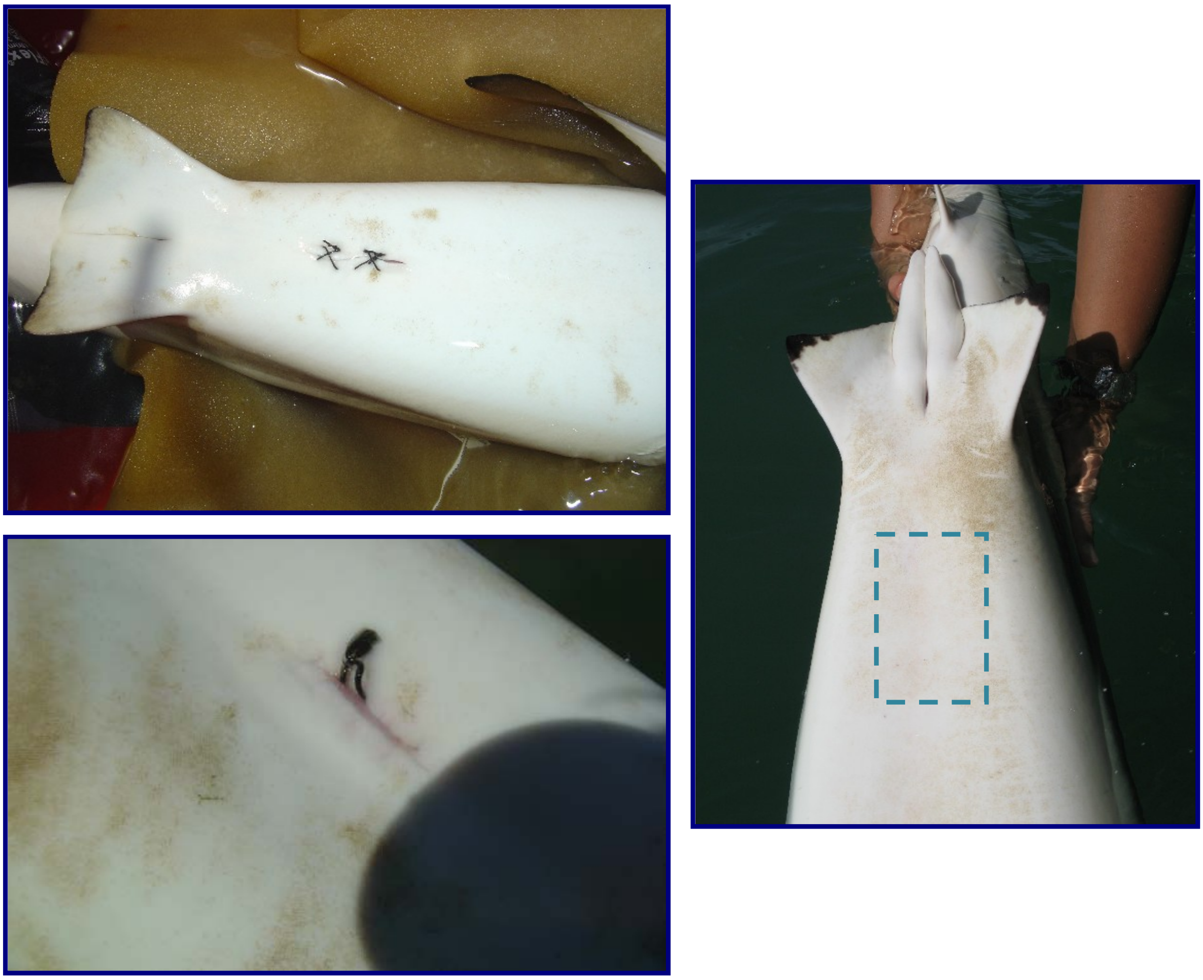
Noise quotient (NQ) ranged from -1118 to 1157, with a mean NQ across all ten receivers of 129 (Fig. S4). This variability in noise quotient was also reported in Simpfendorfer *et al.* (2008), and represents a high level of environmental noise that could interfere with tag detection. The only receiver with a negative value (indicating tag collision) was located within the confined spaces of an artificial dredge channel with steep sides that may have resulted high levels of signal reflection and rebound, resulting in high tag collisions.

Overall, receiver performance appeared to be comparable to that recorded in estuarine environments (Simpfendorfer *et al.*, 2008) although receiver range was greater than that reported in complex coral reef environments (Welsh *et al.*, 2012). Furthermore, the effects of lost detections, relatively high ambient noise and reduced detection range are moderated by the analysis used in this study, and the large number of detections recorded. The focus on long-term residency (was an animal present during a 24 hour period), roaming (was an animal detected on a receiver) and the use of 30 min time steps meant that the analysis was not compromised by incomplete code detections as only two valid codes needed to be detected in a 24 hour period (for residence and roaming index), or within a 30 min period (for centre of activity calculations to derive kernel utilisation distributions). Additionally, the spatial scale of the study, inaccuracies in position estimates caused by low detection ranges and tag inefficiency would not alter the descriptions of habitats used or the comparisons of habitat use patterns between sizes and sexes (Simpfendorfer *et al.*, 2008).

Nevertheless, we acknowledge that tag inefficiency and reduced range would compromise analyses of fine scale movements and habitat use, and we would recommend the use of alternative methods such as active tracking or potentially, the Vemco VRAP system if behaviour and movement needs to be analysed at a finer spatial scale.

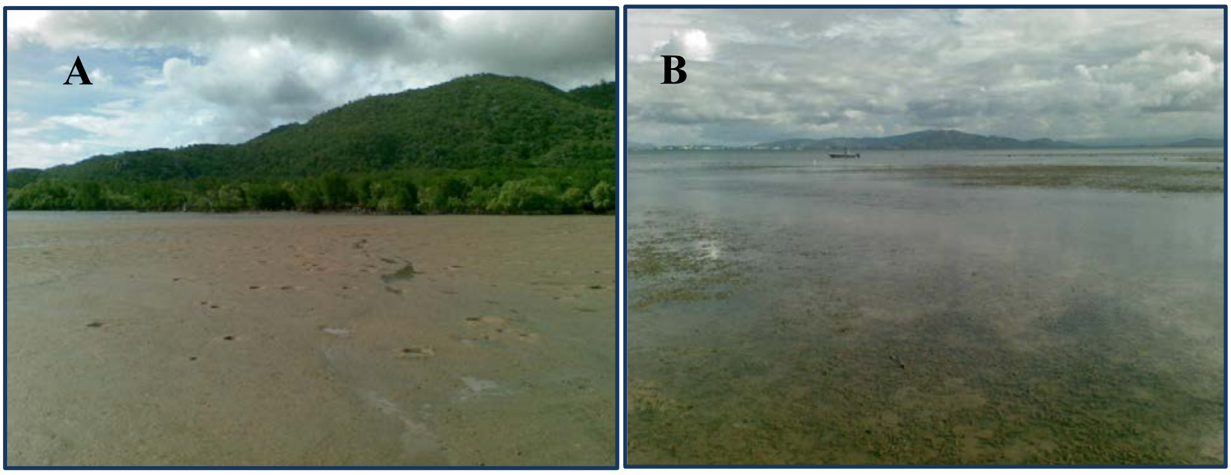
Appendix 8: rapid recovery of blacktip reef sharks following insertion of acoustic transmitters

Sequence of photographs demonstrating rapid recovery of blacktip reef sharks following internal insertion of Vemco V16 transmitters. Photos show an animal immediately following surgery; close up photograph of recovery on an individual recaptured after 4 weeks; and an individual recaptured after 26 weeks showing complete recovery (no visible scar within the dashed box where the incision was originally made).



Appendix 9: Indicative photographs of the study site illustrating habitat types and environmental conditions

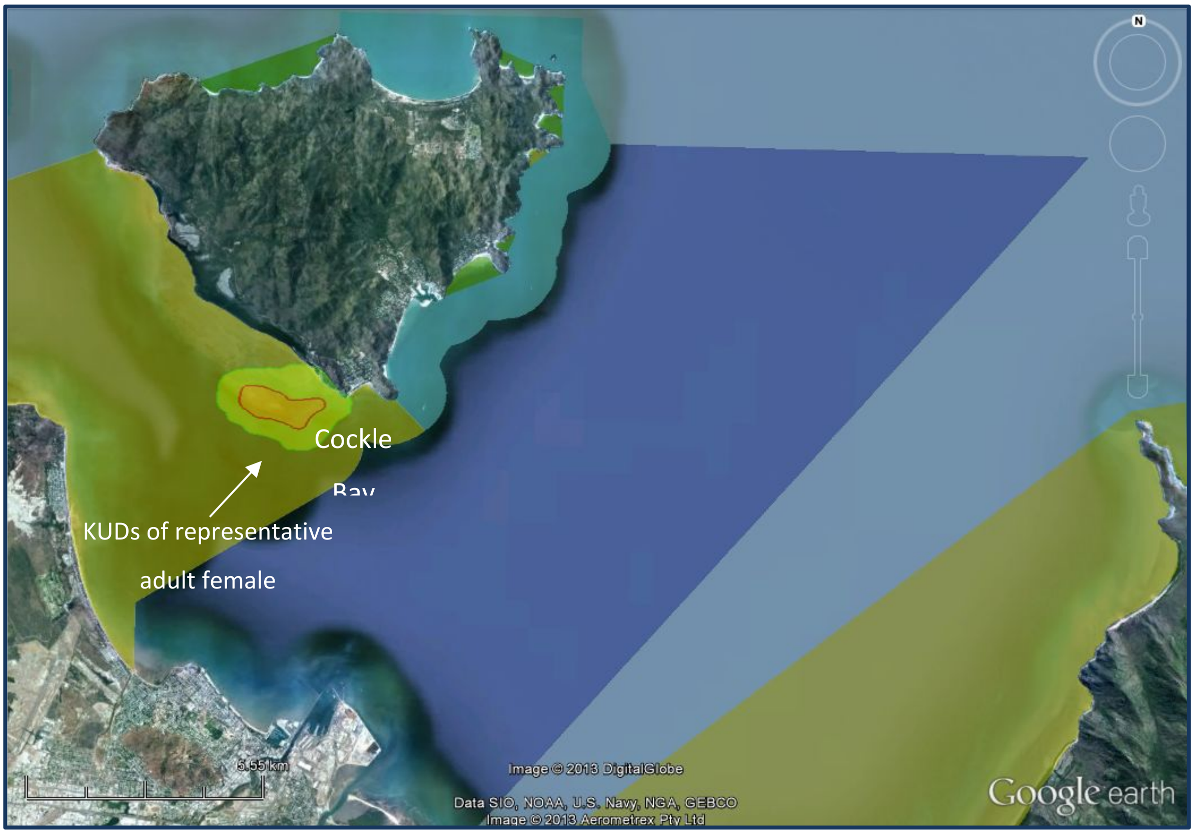
View of intertidal rubble flats and mud flats at low tide with Magnetic Island in the background. Photograph taken south from receiver W8, looking northeast towards Cockle Bay.



View of intertidal mud flats and fringing mangrove (A) and intertidal seagrasses (B) at low tide. Photograph A taken eastwards of receiver C4; photograph B taken northeast from receiver C5.

Appendix 10: interaction between Marine Park zoning and activity spaces of blacktip reef sharks in Cleveland Bay

The GBRWHA is divided into a series of marine park zones that prescribe the types of activities that may occur, and in some cases also manage activities such as developments and discharge of effluent. The intertidal habitats and waters adjacent to Cockle Bay are included in a Conservation Park zone that prohibits net fishing, the fishing activity that accounts for the majority of sharks taken in the GBRWHA (see Chapter 3). This Conservation Park zone thus protects adult female blacktip reef sharks - the most important component of the population in maintaining population levels – and thus helps to secure continued production of offspring and juveniles.



Map of Cleveland Bay showing how Conservation Park zones (yellow shading) cover the activity space of adult female blacktip reef sharks in Cockle Bay (50% and 95% KUD of a representative adult female blacktip reef shark shown as red and green shading).

Appendix 11: ranking methods used in the ESA vulnerability assessment for blacktip reef sharks

The risk assessment framework is modeled on Productivity-Susceptibility Analyses developed and implemented for data poor species in Australian fisheries (Griffiths *et al.*, 2006, Hobday *et al.*, 2007, Hobday *et al.*, 2004, Milton, 2001, Stobutzki *et al.*, 2001, Stobutzki *et al.*, 2002, Zhou & Griffiths, 2008, Zhou *et al.*, 2009). It is an "intermediate level assessment" that is more advanced and comprehensive than simple risk-consequence assessment, but is not as detailed as species specific stock assessment or population models (Hobday *et al.* 2007). Once variables and components of risk are identified and qualitatively ranked as Low, Moderate or High, these rankings are combined to produce a final ranking of risk for each species (see Table 1 of the paper). The component integration matrix used to combine these rankings is based mathematical relationships illustrated below. Qualitative rankings (low, moderate, high) are coded into categorical data based on proportionality. The categories range from 0.00 to 1.00 where 0.00 means no effect (no exposure, sensitivity, rigidity) and 1.00 means absolute effect (absolute exposure, sensitivity, rigidity). Consider exposure of a population to pressure. If the entire population occurs in habitats that are predicted to experience significant effects of a climate change factor, the proportion of the population that has high exposure is equal to 1.00. If only a small proportion of the population occurs in the affected habitats, exposure is low, or <0.33. Accordingly, in this assessment rankings are categorised as 0.00 to 0.33 (low), 0.34 to 0.66 (moderate) and 0.67 to 1.00 (high).

The component integration matrix multiplies the rankings of exposure, sensitivity and rigidity to calculate an overall vulnerability for that species that is expressed as a proportion ranging from 0.00 to 1.00, where 0.00 to 0.33 equals low vulnerability, 0.34 to 0.66 equates to moderate vulnerability, and 0.67 to 1.00 equates to high vulnerability.

Component integration matrix

	Sensitivity x rigidity					
Exposure	**L*L**	**L*M**	**L*H**	**M*M**	**M*H**	**H*H**
H	0.11 (L)	0.22 (L)	0.33 (L)	0.44 (M)	0.66 (M)	1.00 (H)
M	0.07 (L)	0.14 (L)	0.22 (L)	$0.29^{\#}$ (M)	0.44 (M)	0.66 (M)
L	0.03 (L)	0.07 (L)	0.11 (L)	0.14 (L)	0.22 (L)	0.33 (L)

(L = low, M = moderate, H = high)

[#] A mathematical idiosyncrasy of this approach is that when all the vulnerability components are moderate, the calculated vulnerability is low (0.66*0.66*0.66 = 0.29 = low). In this case vulnerability is set as moderate.

Most permutations produce scores of less than 0.33 and while this may appear overly conservative, the multiplicative approach is appropriate in that it based on likelihood and probability and is specific to the spatial and temporal context in which it is applied. For example, if a given species in the Great Barrier Reef is unlikely to encounter a particular climate change factor (low exposure), the species cannot be highly vulnerable to that factor in the GBR, regardless of its sensitivity and rigidity as it never encounters the climate change factor and thus, never experiences its direct or indirect effects. Similarly, if another species is a highly sensitive species that also had high exposure to a climate change factor, it may not be especially vulnerable *if* it has the ability to rapidly adapt to the change and continue to be successful (low rigidity). However, we reiterate that the vulnerability assessments derived here are specific to the context, that is, sharks and rays in the Great Barrier Reef over the next 100 years. Exposure, sensitivity and rigidity, and thus the overall vulnerability, will depend on the spatial and temporal context. The framework also entails several assumptions (see Discussion in the paper).