Habitat ecology of the bull shark, *Carcharhinus leucas*, on urban coasts in eastern Queensland, Australia

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STATEMENT OF ORGINALITY

This work has not previously been submitted for a degree or diploma in any university.

To the best of my knowledge and belief, the thesis contains no material previously published or written by another person except where due reference is made in the thesis itself.

..............................................................

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15\textsuperscript{th} April 2010
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ABSTRACT

The habitat ecology of the euryhaline bull shark (*Carcharhinus leucas*) is poorly understood, yet vital for their conservation and management on our rapidly urbanising coastlines. This study investigated the habitat ecology of the bull shark in relation to ontogeny using a variety of approaches, including long-term catch data, acoustic telemetry, chemical indicators for trophic and habitat preferences and conventional methods for dietary analysis.

Fishery-independent data from 1,060 *C. leucas* caught at ten locations along the east coast of Queensland (17 to 28°S) by the Queensland Shark Control Program (QSCP) from 1996 to 2006 indicated size of sharks captured ranged from 0.6 to 4 m total length (TL). Onset of female maturity was determined at 1.8 to 2 m TL. Catch per unit effort (CPUE) was higher during summer for drumlines and gill nets in tropical north QLD. Significantly larger individuals were caught on both gears in the sub-tropical southeast of Queensland compared to the tropical north. Principal components-regression analysis indicated this difference could be attributed to coastal bathymetry, i.e. distance to the 100 m contour. The number of estuaries in a region also directly influenced the *C. leucas* catch. General linear models (GLMs) indicated latitudinal differences in CPUE along the eastern Queensland coast with a significant decline in sub-tropical areas.

QSCP data from 1996 to 2007 were analysed to investigate the effects of climate parameters on catch of this species in the nearshore habitat. Conditional generalised linear modelling (CGLM) showed that the numbers of *C. leucas* caught by both techniques were significantly correlated with total rainfall within eight days prior to capture. *C. leucas* catch on drumlines increased with prior rainfall > 300 mm and sea surface temperature, as these conditions may encourage feeding in nearshore areas. Pregnant *C. leucas* caught in gill nets increased with a positive Southern Oscillation Index, suggesting higher pupping during wet periods. Catch of sharks < 2 m in TL in nets increased with prior rainfall and were negatively correlated with lunar phase (i.e. lowest catches during full moon).
Eleven juvenile and sub-adult *C. leucas* were tagged with V16 acoustic tags and movements tracked for durations of 2 – 18 hours in southern Moreton Bay and the Gold Coast canals. Three *C. leucas* were also tagged with animal-borne video cameras (crittercam). Directions and rates of movement (ROM) varied (0.03 - 0.92 m s\(^{-1}\)), with an overall mean of 0.27 ± 0.25 m s\(^{-1}\). Tracking showed that one-third of shark movements were random and did not correlate with current flow direction. The movements across all animals could be explained by shark activity being restricted to key locations over deep holes, with consistent directional movements between deep holes.

Stable isotope analysis (\(\delta^{13}\)C and \(\delta^{15}\)N) of *C. leucas* tissue collected from three pairs of natural rivers (with greater mangrove cover) versus urban rivers in southeast QLD suggested that small juveniles feed and remain within a river system, sufficient to attain distinct signatures that were more enriched for \(\delta^{15}\)N, but depleted for \(\delta^{13}\)C in rivers with greater urban influence. Fifty-nine *C. leucas* were captured in quarterly long-line surveys (2006 to 2008) and 24 individuals, including neonate (n = 10), small (n = 6, 0.87 – 0.97 m TL) and large juvenile (n = 8, 1 – 1.53 m TL), were tagged with acoustic tags between February 2007 and March 2008 to determine the use of urban habitat by various ontogenetic stages in the Gold Coast canal system. Electivity analysis of long-term movements suggested a preference for the Nerang River over adjoining man-made canals during non-flood periods. Neonates resided mainly in the top tidal reaches of the river and made short excursions into adjoining canals that were frequented by small juveniles, while large juveniles ranged beyond the Gold Coast canal system. All size classes were more dispersed during flooding, with neonates and small juveniles moving further downstream. Reduced detections of *C. leucas* in upper river habitat occurred when daily rainfall was > 35 mm. Detections of neonate, small and large juveniles peaked at 17 – 22, 24 - 26 and 24 ppt, respectively, during non-flood periods across all habitats. Peak movement of *C. leucas* was evident during dusk, early morning and dawn. Increased movements also occurred at 1500 hrs during low tides for all sizes.

R-coded acoustic tagging of 12 large juvenile and sub-adult (1.3-1.8 m TL) *C. leucas* indicated they remained in estuarine habitats and were not detected in rivers or the
nearshore habitats. Sequential elemental and stable isotope analyses of five adult *C. leucas* vertebrae and laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS) from 32 individuals suggested ontogenetic habitat changes. $\delta^{15}$N values across shark vertebrae showed an ontogenetic shift in diet with increasing TL, which was confirmed by 1,042 stomach content samples from the QSCP. LA-ICPMS elemental data correlated with the ontogenetic movements of *C. leucas* from natal habitats and differences among adults were gender related. Shifts in habitat use by sub-adults were also reflected by a shift in $\delta^{13}$C relationship with size.

Combined, the above data enabled the construction of a conceptual model of the habitat ecology of *C. leucas* in relation to its life cycle on urban coasts. The model suggests *C. leucas* utilise defined areas of natural habitat (in preference to urban habitat) along the marine-estuarine continuum with three ontogenetic phases present in the life cycle. The model proposes that the nursery phase comprising neonate and small juveniles use low saline areas of rivers, the transitional phase comprising large juveniles and sub-adults use the interface between the estuarine and oceanic habitat, and the coastal phase comprising adults that occur in a range of nearshore and oceanic habitats. Movement of early ontogenetic stages from river to nearshore habitats probably occurs with growth and a shift in diet towards larger and more varied prey. Rainfall patterns create short-term alteration to ontogenetic habitat segregation, with small juveniles moving closer to nearshore areas. Adults remain predominantly in nearshore habitats, with females returning to rivers on occasion to pup.

Conservation efforts should recognise the multipartite life cycle of *C. leucas* with dependency on multiple, connected, habitats during the species’ stage-specific occupation of nearshore and coastal habitats. *C. leucas* are directly impacted by several anthropogenic factors: (1) rainfall, as part of future climate change, drives movement between habitats for different ontogenetic stages; (2) the limited availability of habitat to each life cycle phase makes this species particularly susceptible to overfishing and habitat alteration; (3) urban habitats are not prime habitats to *C. leucas*; the removal of significant habitat components and alteration of the hydrological regime by urbanisation have significant negative impacts on *C. leucas* populations.
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**TERMINOLOGY AND ABBREVIATION**

List of terms and abbreviations used within this thesis.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tbody>
<tr>
<td>ANODEV</td>
<td>Analysis of deviance</td>
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<tr>
<td>ANOVA</td>
<td>Analysis of variance</td>
</tr>
<tr>
<td>ASAF</td>
<td>Australian Shark Attack File</td>
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<tr>
<td>CGLM</td>
<td>Conditional general linear model</td>
</tr>
<tr>
<td>CPUE</td>
<td>Catch per unit effort</td>
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<tr>
<td>CTD</td>
<td>Conductivity, temperature and depth</td>
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<tr>
<td>DHI</td>
<td>Danish Hydraulic Institute</td>
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<td>E</td>
<td>East</td>
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<td>FL</td>
<td>Fork length</td>
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<td>GLM</td>
<td>General linear model</td>
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<td>h</td>
<td>hour</td>
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<td>km</td>
<td>kilometres</td>
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<tr>
<td>LA-ICPMS</td>
<td>Laser ablation inductively coupled mass spectrometry</td>
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<tr>
<td>LJ</td>
<td>Large juvenile</td>
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<tr>
<td>LR</td>
<td>Lower river</td>
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<tr>
<td>MPA</td>
<td>Marine Protected Area</td>
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<td>N</td>
<td>Neonate</td>
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<td>NSW</td>
<td>New South Wales</td>
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<tr>
<td>Nth</td>
<td>North</td>
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<tr>
<td>PAT</td>
<td>Pop-off archival tag</td>
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<tr>
<td>PCA</td>
<td>Principal components analysis</td>
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<td>ppt</td>
<td>parts per thousand</td>
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<td>QLD</td>
<td>Queensland</td>
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<td>QSCP</td>
<td>Queensland Shark Control Program</td>
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<td>ROM</td>
<td>Rate of Movement</td>
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<td>S</td>
<td>South</td>
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<td>SC</td>
<td>South canals</td>
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<td>SCA</td>
<td>Stomach content analysis</td>
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<td>SEQ</td>
<td>Southeast Queensland</td>
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<td>SJ</td>
<td>Small juvenile</td>
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<td>SOI</td>
<td>Southern Oscillation Index</td>
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<td>SPSS</td>
<td>Statistical Package for the Social Sciences</td>
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<td>SST</td>
<td>Sea surface temperature</td>
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<td>TL</td>
<td>Total length</td>
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<tr>
<td>U</td>
<td>Urban</td>
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<tr>
<td>UR</td>
<td>Upper river</td>
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<tr>
<td>USA</td>
<td>United States of America</td>
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<tr>
<td>VHF</td>
<td>Very high frequency</td>
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<tr>
<td>VR2</td>
<td>Vemco receiver model 2</td>
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<td>VR2W</td>
<td>Vemco receiver model 2 wireless</td>
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CHAPTER 1

HABITAT, BIOLOGY AND THREATS TO THE BULL SHARK (CARCHARHINUS LEUCAS): A GENERAL INTRODUCTION

1.1 Movement and Migration – critical to an animal’s habitat ecology

The migration and movement patterns of an animal in time and space is fundamental to the study of its habitat ecology, interpreting the influence of human activities on the species and to the design of effective conservation and resource management (Pittman & McAlpine 2001). Habitats constitute a defined set of conditions under which an animal can exploit energy sources (Leveque & Mounolou 2003), but preference may vary with ontogeny, as many marine organisms exhibit a wide range of movements that over a life cycle often covers increasing distances and time scales of several orders of magnitude. Movements and migrations are hypothesised to be driven by physical conditions, biological requirements and competitive interactions (Hobday & Boehlert 2001, Cortes 2004, Heithaus 2004, Heithaus et al 2009). These patterns are poorly understood, however, for large and elusive top-level predators such as sharks (Pittman & McAlpine 2001, Simpfendorfer & Huepel 2004, Heithaus et al. 2007).

Understanding linkages between areas or habitats used by an animal throughout their life history is also critical to their effective conservation, since efforts can be directed at sites of critical importance to a species (Hodson 1999). Therefore, the ability to trace or follow the movements of animals is essential, but has been largely limited to the use of extrinsic markers and tags that require the capture and resighting of individuals (Hodson 1999, Kohler & Turner 2001). Sharks are elusive, exist at low abundance, in many cases are wide-ranging and are capable of shedding external tags; as such mark-recapture methods have only provided minimal and coarse insight into the movement of sharks (Heithaus et al 2002, Kohler & Turner 2001). Most of the successful mark-recapture studies on sharks average a 10% recapture rate, requiring substantial tagging efforts (i.e. usually 200 to 300 sharks tagged) in order to obtain useful data (Heithaus 1999, Kohler & Turner 2001). In the last decade, however,
extensive advancements in tracking capabilities, both chemical and technological, have resulted in rapid development of insight into the long-range, long-term and fine-scale movements of sharks (Simpfendorfer & Heupel 2004). Remote sensing capabilities, such as satellite and acoustic tagging, that do not necessarily rely on recapture abilities represent a technological advantage over many mark-recapture methods. Further, intrinsic methods such as chemical analysis of animal tissues allow the identification of animal natal habitats and their movements into other geographical areas. An example is the identification of use of marine versus freshwater ecosystems and terrigenous versus oceanic sources of nutrition in an animal’s habitat ecology using stable isotope analysis (Dunton et al 1989, Hodson et al 1994, France 1995).

Advancements in the use of acoustic technology to track long-term shark movements have seen the development of a rapid body of knowledge on the use of areas of importance to neonate and juvenile sharks, referred to as nursery areas (Simpfendorfer and Milward 1993, Heupel and Heuter 2002, Garla et al. 2006, Heupel et al. 2006b, Heupel and Simpfendorfer 2008). Use of this technology for larger ontogenetic stages of sharks is, however, very much in its infancy. The ability to track an animal’s movement through time and space enables hypotheses on the drivers of habitat use to be examined. While the general concept of shark nurseries has been an accepted paradigm in shark biology and behaviour for several decades, only recently has a shark nursery been defined with long-term empirical movement data by Heupel et al. (2007) on the basis of (1) neonate and small juvenile sharks are more commonly encountered in the area than other areas; (2) sharks have a tendency to remain or return for extended periods; and (3) the area or habitat is repeatedly used across years. There is consistent conflict, however, among long-term tracking studies and between shark species studied as to these patterns of habitat use. Recent studies argue that the use of specific nursery habitats is driven by physiological needs (e.g. Heupel & Simpfendorfer 2008, Heithaus et al. 2009) or predator avoidance (e.g. Heupel & Heuter 2002) rather than requirements such as the abundance and distribution of prey. These studies assume the movement of sharks is non-random and on this basis have attempted to draw correlations between presence of prey and/or physical water parameters. These studies acknowledge the difficulty in measuring prey abundance and distribution in relation to shark movement. Many shark species, however, are considered top-level predators that have confirmed top-down effects on the
distribution and abundance of prey (Heithaus et al. 2007) in both estuarine (e.g. bull shark, *Carcharhinus leucas*, in O’Connell et al. 2007) and coastal environments (e.g. Myers et al. 2007). While the identification of important habitats or areas to sharks is essential for their conservation, investigation of long-term patterns may define areas to which a shark consistently returns as preferred ‘resting or residing areas’, but may overlook the importance of less ‘structured’ foraging events for prey. The vulnerability of sharks to fishing pressures may actually increase during foraging for prey outside resting areas. To guide effective conservation of sharks, a complementary, multi-technique, approach including both chemical tracing and short-term tracking techniques may better define movement associated with foraging events in addition to sites of residency identified through long-term movement studies.

1.2 Connectivity of habitats in the marine-estuarine continuum

Studies on habitat of sharks have rarely considered the potential significance of short and long-term connectivity of important habitats. Coastal fauna are associated with various nearshore habitats not only because of the physical habitat fabric that may offer protection or favourable conditions for their physiology, but also sources of energy and nutrient for growth and development. Estuarine and bay habitats have been considered as important habitats for different life cycle stages of sharks (Simpfendorfer & Milward 1993) and these areas often are of high productivity that support potential prey species. The outwelling hypothesis states that habitats along the marine-estuarine continuum are connected through export of trophically important material from estuarine wetlands such as saltmarsh and mangrove forests, the high productivity of which is used by the macrobenthos, decomposed in situ, and exported to support nearshore ecosystems (Odum 1984, Lee 1995, Winter et al. 1996). This ‘trophic relay’ (Knieb 2000) is only possible where significant habitat connectivity is present along the marine-estuarine continuum. Studies have shown significant positive correlations between the amount of mangroves on the coast and nearshore fisheries catch (e.g. Staples & Vance 1985, Primavera 1998). Meynecke et al. (2008), for example, highlighted the influence of interconnectedness of habitats to nearshore fisheries production, suggesting that coastal areas with more connected and varied estuarine habitats yield higher fish catch on the east coast of Queensland, Australia. These links between nearshore fisheries yields and adjacent mangrove have been mostly postulated to occur via benthic food chain (Robertson et al. 1992) and more
recently via links to the pelagic food chain (Werry & Lee 2005). However, the role of top-level predators in energy transfer along the marine-estuarine continuum has not been considered. Further, no studies have considered the influence of interconnectedness of nursery areas with adjoining or adjacent adult habitats on both long-term movement and the ontogenetic migrations of individuals.

1.3 *C. leucas* as a coastal wildlife species

The bull shark, *Carcharhinus leucas*, (Valenciennes 1839) is one of the few elasmobranchs that is truly euryhaline and capable of freely migrating between freshwater and saltwater environments in the marine-estuarine continuum (Jensen 1976, Montoya & Thorson 1982). Euryhaline elasmobranchs are most common in coastal marine habitats, frequently penetrating far up rivers beyond the influence of tidal action and may breed in freshwater (Martin 2005). *C. leucas* is found circum-globally in tropical and sub-tropical waters as well as in numerous river systems and some freshwater lakes (Compagno 1984, Last & Stevens 1994). It has been found 4200 km upstream in the Amazon River (Peru), 2800 km up the Mississippi River in Illinois, 1120 km up the Zambezi River in South Africa (Myers 1952, Bass et al. 1973, Thomerson et al. 1977), and has been recorded navigating rapids as it moves between nearshore coastal habitat and Lake Nicaragua in Central America (Thorson 1971). In the western Atlantic, they are believed to migrate north along the coast of the US during summer, swimming as far as Massachusetts, before returning to tropical environments when coastal waters in the higher latitudes cool. They are common in the northern Gulf of Mexico (Springer 1938, Castillo et al. 1998) and have occupied suggested nursery areas in coastal and inland waters of Southern Florida and Southeastern Louisiana (Simpfendorfer et al. 2005, O’Connell et al. 2007). Recent sightings in Tonga (Brunnshweiler & Compagno 2007) and the Breede estuary in South Africa (McCord & Lamberth 2009) have extended the known range of this species. *C. leucas* is one of the few large shark species that occur in the full range of habitats along the marine-estuarine continuum throughout its life cycle. As such, *C. leucas* represents an ideal model species to test hypotheses on both physical and biological drivers of habitat use and the interconnectedness of important habitats used by the species in its ecology and life cycle.
Within Australia, *C. leucas* is reported from most tropical and sub-tropical estuaries and waterways and is one of five euryhaline elasmobranchs reported to utilise freshwater environments for extended periods (Last & Stevens 1994). The other euryhaline species include the Bizant River or speartooth shark, *Glyphis glyphis*, (Muller and Henle 1839), the northern river shark, *Glyphis garricki* (White and Last 2008), the freshwater sawfish, *Pristis microdon*, (Latham 1794) and the giant freshwater whipray, *Himantura chaophraya* (Monkolprasit and Roberts 1990). *C. leucas* has been recorded far upstream into the freshwater reaches of southern Queensland waters (Pillans et al. 2005). In the Brisbane River, juveniles (0.55-1.69 m total length (TL)) are abundant in the freshwater sections (Pillans & Franklin 2004). *C. leucas* has also been recorded in artificial man-made canal systems on the Gold Coast (Zeller 1999).

The euryhaline capacity of *C. leucas* is attributed to its ability to control the principal plasma osmolytes of Na⁺, Cl⁻ and urea, in its body fluid in order to overcome the challenges of hyper-osmoregulation (Pillans et al. 2006). This physiological capability of *C. leucas* has been well studied (Thorson 1971, Thorson et al. 1973, Pillans & Franklin 2004, Pillans et al. 2005). Through the action of gills, rectal gland, kidney and gut, a combination of active uptake, excretion and filtration of water and plasma osmolytes enables *C. leucas* to tolerate rapid and significant changes in salinity (Pillans et al. 2005). In freshwater, *C. leucas* is significantly hyperosmotic to the surrounding medium. Small juvenile *C. leucas* experience a greater osmoregulatory challenge between 75 and 100 % seawater than large *C. leucas* (> 2 m TL), which frequently occur in marine habitats (Pillans et al. 2006). The ability of *C. leucas* to use a range of salinities makes it one of the most likely species to regularly use natural and urban coastal habitats. However, while its osmoregulatory physiology has been the focus of many past studies (Thorson 1971, Thorson et al. 1973, Pillans & Franklin 2004, Pillans et al. 2005, Pillans et al. 2006), the general biology and habitat ecology of this species is poorly understood (Martin 2005).
1.3.1 Inter-relation of life history characteristics and habitat ecology of *C. leucas*

*C. leucas* belongs to the family Carcharhinidae and is characterised by a short-snout, heavy body and serrated teeth (Last & Stevens 1994). It is fundamentally a ‘*K*-strategist’ and as such, is long-lived, mature slowly and has low reproductive outputs. Maturity is estimated to be at 6 to 8 years of age and for females this equates to a length of 1.8 m TL to 2 m TL (Jensen 1976, Branstetter & Stiles 1987). Data from the Lake Nicaragua–San Juan River *C. leucas* population suggest that females usually give birth near river mouths and rarely in freshwater environments (Jensen 1976); however, this is assumed primarily based on the captures of pregnant females by fisherman at the river mouths and could be a reflection of fishing effort rather than actual location of pupping grounds. In sub-tropical Queensland, mating takes place in the nearshore environment during February while pupping usually takes place in summer (December to January) (Zeller 1999). Litters typically consist of 1 to 13 pups, born at a minimum 0.45 m TL, after a gestation period of 10 to 11 months (Bass et al. 1973, Camhi et al. 1998). *C. leucas* neonates and juveniles are thought to utilise shallow estuarine/freshwater environments as nursery grounds whereas adults generally inhabit deeper nearshore marine habitats (Simpfendorfer et al. 2005, Brunnshweiler & Earle 2006). Habitats of intermediate life cycle stages are poorly understood and ontogenetic differences in habitat utilisation and occurrence require further investigation.

1.3.2 Diet and ecosystem role of *C. leucas*

*C. leucas* is a generalist feeder, although mullet, *Mugil* spp., is believed to be a significant part of the diet in juveniles and sub-adults (Bass et al. 1973). In Lake Nicaragua, Tuma (1976) recorded teleosts, black land crabs, sawfish (Pristidae), tyrant flycatchers and sloths (Bradypodidae) in addition to leaves, sticks, orange peelings, pebbles, corn kernels and even a glass bottle in the stomachs of *C. leucas*. In South Africa, crabs (*Erythrodactyla* spp.), other elasmobranchs including the white shark (*Carcharodon carcharias*), seabirds (*Puffinus tenuirostris*), green turtle (*Chelonia mydas*), and juvenile bottlenose dolphins (*Tursiops truncatus*) were found in the stomachs of nearshore adult *C. leucas* (Cliff & Dudley 1991). In Australia, Zeller (1999) recorded mud crabs (*Scylla* spp.), mullet (*Mugil* spp.), and trevally (*Caranx* spp.) in the stomachs of *C. leucas* captured in artificial man-made canals.
*C. leucas* is considered a top-level consumer and probably increases its significance as a predator as the ability to consume larger and more varied prey increases with size (Cortes 1999, O’Connell et al. 2007). The mean size of prey consumed for other large shark species, for example the white shark (*Carcharidodon carcharias*), has been shown to increase with increasing body length (Estrada et al. 2003, Estrada et al. 2006). Lowe et al. (1996) suggests that factors such as increased jaw size or experience with prey may also influence an individual shark’s ontogenetic shift in diet. Juvenile *C. leucas* may be more restricted in the size range of their prey, particularly before the onset of observed ontogenetic dietary shifts. These factors probably limit them to shallow estuaries where more specific diets regulate the coastal habitats that different size classes of *C. leucas* utilise. Neonate (0.55 - 0.6 m TL) and juvenile bull sharks (0.60 - 1.1 m TL) use estuaries as nursery feeding grounds where mullet (*Mugil* spp.), a major component of the diet for *C. leucas* of this size range, are in high abundance (Cardona 2000). *C. leucas* also seem to exhibit ontogenetic changes in diet and prey size (Cliff & Dudley 1991). These shifts commonly accompany changes in foraging tactics and habitats for sharks (Cortes 2004). This change in habitat is probably a strategy to increase net energy intake with increase in size or age. Whether ontogenetic diet shifts accompany transition from estuarine nursery habitat to nearshore areas as adults remains to be established for this species.

Understanding the shift in diet with increasing TL has significant implications for interpreting the ontogenetic value of coastal habitats, such as the nearshore environment, natural estuarine and urban waterways, to *C. leucas*. Traditionally, stomach contents analysis (SCA) has been used to establish habitat use based on diet, although this method has many limitations. Sharks commonly regurgitate prey items, with up to 40 to 50 % of stomachs being empty on capture (Heithaus 2001, Joyce et al. 2002), and exhibit differential rates of prey digestion. Distinguishing between ingested and assimilated prey may bias SCA estimates and the large number of individuals required for destructive quantitative analysis is a further challenge (Cortes 1997). Chemical tracer techniques such as fatty acid and stable isotope analyses, however, can provide an indication of assimilated rather than ingested prey types and these can be used to link consumers to trophic dependence on specific habitats, identify trophic levels and interactions and movements of predators between isotopically distinct food webs (Hodson 1999, Pinnegar & Polunin 1999, Estrada et al.
2003, Estrada et al. 2005, Waltham & Connolly 2006). These chemical techniques have rarely been used in conjunction with acoustic or satellite telemetry for sharks, but represent a potentially powerful combination of methods.

The cascading effects of removing top-level predators have been demonstrated in closed lake systems where community structure and ecosystem processes are significantly altered (Schindler et al. 1997). Predators that exert large effects on fish assemblages disproportionate to their own abundance play a ‘keystone’ role in ecosystems (Myers et al. 2007, Heithaus et al. 2008). Euryhaline sharks, such as *C. leucas*, are likely to have a more direct effect on estuarine prey populations due to the likelihood of these prey being concentrated in the more limited volume of riverine and estuarine habitats compared to open nearshore environments (Martin 2005).

1.4 Drivers of ontogenetic shifts of habitat use

Physical or abiotic factors such as salinity, temperature, turbidity, depth, substrate type and tidal movements, and biological activities such as feeding, migration and reproduction can determine the movements of fish and their distributions within complex ecosystems, such as estuaries (Morin et al. 1992, Heithaus 2001). If a predator is pursuing a strategy to maximise net energy gains, it will select the habitat with the highest energetic return rate (Heithaus et al. 2002, Heithaus 2004). Basking sharks, for example, appear to prefer patches of warm-water oceanic fronts that concentrate plankton; a choice shown to be based on their potential energy intake rate (Sims & Quayle 1998). Studies suggest that habitat use by elasmobranchs is influenced by the distribution of their prey, the density of other predators in a habitat (i.e. frequency-dependent energy intake), potential net energy intake (i.e. food availability) and reproductive needs (Simpfendorfer & Milward 1993, Cortes 2002, Simpfendorfer et al. 2005).

Changes in habitat use by sharks can result from changes in vulnerability to inter- and intra-predation risk (Werner & Hall 1988, Bouskila et al. 1998). Adult bull sharks (> 1.8 m TL) are known to consume elasmobranchs, including conspecifics (Vorenberg 1962, Cliff & Dudley 1991). Juvenile *C. leucas* inhabiting nursery areas (sheltered estuarine areas) are likely to delay switching habitats if predation risk increases significantly in marine environments, where adult *C. leucas* occur (Simpfendorfer &
Milward 1993, Bouskila et al. 1998, Pillans & Franklin 2004, Brunnschweiler & Van Buskirk 2006). While several studies suggest 0+ and 1+ yr *C. leucas* remain within distinct salinity ranges and concentrate in small areas in estuaries (Heupel & Simpfendorfer 2008, Heithaus et al. 2009, Ortega et al. 2009), understanding how *C. leucas* of different ontogenetic stages use coastal habitats is essential to providing an insight into the ecology of this top-level predator in order to assist the conservation and management of this species.

1.5 Measuring movement of sharks in the marine-estuarine continuum

The movement of mobile animals both within and between habitats are affected by a variety of abiotic and biotic factors (Heupel & Hueter 2002, Simpfendorfer & Heupel 2004). When compared to the terrestrial environment, however, our understanding of the movements and behaviour of animals in the marine environment is very limited, largely due to the difficulty in observing movement in the latter habitat (Klimley et al. 2001). *C. leucas* is particularly hard to observe and track as they commonly occur in waters of high turbidity (Martin 2005).

Remote sensing techniques available for studying shark movements include: (1) acoustic (Garla et al. 2006), (2) radio (Klimley et al. 2001) and (3) satellite telemetry (Bruce et al. 2006). Telemetry further includes (i) electronic acoustic tags that allow short- (hrs), medium- (days to months) and long-term (months to years) tracking through mobile and submerged acoustic monitors (Clements et al. 2005, Finstad et al. 2005); (ii) archival tags that store information on an animal’s behaviour and provide a track of its movement (Stokesbury et al. 2005); (iii) satellite tags that provide real-time movements over large distances and, (iv) triangular arrays of radio-acoustic positioning (RAP) (Klimley et al. 2001), and the virtual-radio-acoustic-positioning VRAP (Vemco Ltd, Shad Bay, Canada) buoys that provide precise fine-scale three-dimensional position data for an individual to an accuracy of 1-2 m (Klimley et al. 1998, O'Dor et al. 1998).

Movements of sharks can occur at different spatial scales. Large-scale movements (> 100 km) such as seasonal migrations, for example, are best tracked using satellite tags. These large-scale movements may be driven by temperature (change of season) as well as reproductive and foraging needs. Whale shark, *Rhincodon typus*, at
Ningaloo Reef in Western Australia, for example, occurs in large numbers during seasonal coral spawning events (Gunn et al. 1999, Wilson et al. 2001) and tiger shark, *Galeocerdo cuvier*, on the same coast, congregates at offshore islands when food abundance peaks (Simpfendorfer et al. 2001). Further, Brunnshweiler and Van Buskirk (2006) used archival satellite tags to determine the nearshore and long-range movement of adult *C. leucas* in Walkers Cay in the Bahamas. Short and long-term tracking of smaller scale movements (to tens of km) are important for understanding localised habitat preferences and site fidelity and this information is most powerful when related to physical parameters (Hopkins & Cech 2003). These authors found that salinity, temperature and dissolved oxygen significantly affected the distribution and abundance of the bat ray (*Myliobatis californica*), leopard shark (*Triakis semifasciata*), and brown smoothhound shark (*Mustelis henlei*) in Tomales Bay, California. Understanding the small-scale ontogenetic movements of *C. leucas* in relation to physical parameters is important for the conservation of this species, determining the influence of anthropogenic habitat modification and management of shark-human interactions. Understanding these movement patterns in the light of physical drivers such as salinity is particularly pertinent, given the euryhaline capabilities of *C. leucas*.

1.6 The ecological function and value of estuaries

The life history of *C. leucas* is strongly dependent on estuarine habitats. Estuaries are biologically diverse and productive ecosystems that provide essential habitats for many flora and fauna including prawns, fish, sharks, turtles and cetaceans (Ishikawa et al. 2003). Characterised by shallow water and intertidal areas, including mangrove forests, saltmarsh, seagrass, intertidal mudflats and shallow sub-tidal habitats, they are transitional habitats between land and water and freshwater and marine environments (Hogarth 1999, Lee et al. 2006). Estuaries help to mediate water quality and influence hydrological and sedimentation processes (Faulkner 2004). As productive and spatially complex habitats, estuaries produce a large variety of food to consumers and protective habitat for associated organisms. Estuaries are therefore important to the life cycle of many commercially important species, including prawns, crabs, fish and sharks through their role as nursery habitats (Martosubroto & Naamin 1977, Staples et al. 1985, Blaber et al. 1995, Loneragan et al. 1997). Along the eastern coast of Australia, the majority of the fish taken in commercial and recreational fisheries
comprises species that depend upon estuaries for part or all of their life cycle (Pollard 1976). Estuaries are a key component of the life cycle of *C. leucas*, particularly during their nursery phase. The value of these habitats when highly modified (for example, through urbanisation) to the species, however, remains unknown.

1.7 Threats to *C. leucas*:

1.7.1 Habitat modification/urbanisation

Estuaries are particularly vulnerable to human effects such as habitat alteration and changes in freshwater input, which can have far-reaching ecological consequences leading to functional and biodiversity decline (Kennish 2002). Given the importance of estuarine areas to *C. leucas*, habitat modification may have significant ramifications on this species. Rapid urbanisation of coastal areas is a global phenomenon (Ehrenfeld 2000), as the vast majority of human population is concentrated close to rivers, estuaries and coastal areas (Moyle & Leidy 1992). Despite the recognised value of natural estuaries, resource management strategies to safeguard these habitats are often at odds with increasing urban development pressures (Stumpf & Haines 1998, Martin 2005). Pressures to develop and physically modify estuaries are accelerating, with many areas utilised for consumptive uses such as waste dumping, land reclamation, aquaculture ponds and dredging for navigational channels, marinas and residential canal systems (Morton 1992, Ehrenfeld 2000). In the United States, for example, it is estimated that up to half of the 5.8 million km of rivers and streams are significantly polluted and 360,000 km channelized to control flooding (Carr 1993, Martin 2005), with direct effects on estuaries and other coastal habitats.

Mangroves play important roles in estuarine ecology, yet they are being rapidly cleared for aquaculture and development of shoreline real estate (Hogarth 1999, Martin 2005). The effects of natural habitat modifications on selected biota and the physical environment have been relatively well studied (Baca et al. 1988, Morton 1989, 1992, Maxted et al. 1997, Lee et al. 2006). However, there is little information on their impact on less well known megafauna, such as sharks. Urbanisation replaces natural wetlands with impervious surface, resulting in concentrated rain runoff with increased loads of sediment, nutrients and pollutants. Fish are responsive to these
changes in environmental conditions and, as high-level consumers, exert a major secondary impact on the distribution and abundance of other organisms in waters they inhabit (Moyle & Leidy 1992) leading to long-term alterations in fish community structure.

In Australia, which is primarily a coastal society, >80% of the population live within 50 km of the coastline (SABS 2002). Rapid population growth has occurred in many sub-tropical coastal regions within Australia, with sub-tropical Queensland a prime example. Lee et al. (2006) noted that the city of the Gold Coast, a prominent sub-tropical Queensland city, increased by around 240,500 people between 1986 and 2003. This rapid urban growth has had direct impacts on coastal habitats in sub-tropical Queensland. Developers for example, have extended the limited areas of natural waterfront land by the creation of tidally flushed canals for boating marinas or residential developments (Morton 1992) (Figure 1). Lee et al. (2006) noted that canal developments increased to ~5% of the area of natural mangroves and saltmarsh-claypan in the region during the same period. Typically these urban canal developments excavate or reclaim natural habitat and use cut-and-fill construction techniques, providing fill material to elevate part of the land and reduce its susceptibility to flooding. While still tidal, these artificial canals provide habitats for selected estuarine fauna and support different fish assemblages to natural estuarine habitats (Morton 1989, 1992, Waltham & Connolly 2006). The extent of this impact, however, requires further investigation.

![a) b)](image)

Figure 1. Comparison of a natural estuary (a) in sub-tropical Queensland and the highly modified Nerang River with its associated man-made canals (b). Both habitats have recorded use by *C. leucas*. 
1.7.2 Alteration in rainfall and flood events

Elasmobranchs and their prey that have life cycles closely tied to river and estuarine environments are likely to be directly influenced by large-scale shifts in rainfall and flood events (Staunton-Smith et al. 2004, Robins et al. 2005, Meynecke et al. 2006, Heupel & Simpfendorfer 2008). As mentioned earlier, the abundance of impervious surfaces is expected to influence the hydrograph of urban estuaries. Rainfall has shown to be closely tied to nearshore fisheries production (Meynecke et al. 2006). For example, movement of euryhaline barramundi (Lates calcarifer) has been demonstrated to be strongly linked to rainfall and freshwater flow (Staunton-Smith et al. 2004). Young of the year (YOY) C. leucas have been shown to be influenced by artificial “flood” events from the release of freshwater from a dam at the head of the Caloosahatchee River of southwest Florida, moving further downstream to remain within optimal salinity (7-20 ppt) (Heupel & Simpfendorfer 2008), although Heithaus et al. (2009) found no such trend in C. leucas catches in the Everglades. Extreme rainfall events can lead to spikes in turbidity and rapid infilling of channels with coarse sediment in urbanised estuaries, particularly in systems with the absence of mangrove riparian vegetation, which can help stabilise river banks and retain sediment (Brooke 2002). These alterations can affect the occurrence of C. leucas in riverine habitats (Heithaus et al. 2009). The paradigm of a “drought on land is a drought in the sea” may mean long-term changes (years) in frequency and volume of rainfall could have direct ramifications for the abundance and diversity of prey for C. leucas that rely on estuarine habitats in their life cycle.

1.7.3 Overfishing

The consequences to marine ecosystems have recently become apparent with the profound global declines in large pelagic fish populations, including sharks, tuna and billfish (Jackson et al. 2001, Baum et al. 2003, Myers & Worm 2003). Despite their ecological significance, however, populations of many species of sharks are declining on a global scale, mainly due to illegal and unsustainable fishing practices (Stevens et al. 2000, Schindler et al. 2002, Field et al. 2009a). Several studies have shown that the removal of these large fish from tropical and temperate communities creates substantial and sustained changes that can affect the abundance and diversity of their prey populations and other fishes across many trophic levels (Botsford et al. 1997,
Pace et al. 1999, Stevens et al. 2000, Cox et al. 2002, Essington et al. 2002, Kitchell et al. 2002). Approximately one million *C. leucas*, equating to 30 000 t, are killed for the shark fin trade worldwide per year (Clarke et al. 2006). These declines are hypothesised to lead to wide-ranging ecological consequences such as reduce biodiversity and ecosystem health and can have dramatic ecological ramifications, altering the functioning and community structure of coastal habitats (Baum et al. 2003, O’Connell et al. 2006, Myers at al. 2007). One documented example is that of shifts in coral-dominated habitats to algae, which have been attributed to the absence of sharks from coral reef systems (Bascompte et al. 2005). In the next 25 years, overfishing is expected to become an even more significant factor mediating global-scale change to estuaries, with the potential for extinction of some elasmobranchs (Kennish 2002, Field et al. 2009b).

*C. leucas* are top predators and their long-term presence in a natural or urban habitat could therefore be an indicator of the quality of that ecosystem, i.e. the physical hydrographic conditions and available prey are at levels suitable to sustaining a local population of *C. leucas*. Association with coastal and estuarine habitats can vary with shark size and maturity, with some more sedentary and others far ranging or migratory in their behaviour. The range of movement of *C. leucas* can therefore determine the species’ potential interaction with fishing activities and their vulnerability to these pressures (Stevens et al. 2000). However, to fully interpret their vulnerability a comprehensive understanding on ontogenetic habitat use and migratory movements is necessary. Declines in *C. leucas* populations have already been noted in Louisiana, USA (O’Connell et al. 2007) and decline in size has also been reported in South Africa (Cliff & Dudley 1991). Understanding the movement and habitat use (and thus habitat connectivity) of *C. leucas* is therefore essential for both management and conservation of estuarine *C. leucas* populations and the coastal ecosystems they are part of.

**1.8 C. leucas -human interactions**

*C. leucas* is a much-feared predator in coastal areas. However, coastal areas including lakesides, riverside and streamside, have been favoured habitats of humans as they afford ready access to water, food, building materials, transport and recreation (Renfrew & Bahn 1996). As discussed, humans frequently exert rapid, large-scale
influence on their immediate environment in these areas, such as the modification of waterways (e.g. urbanised canal systems) (Ehrenfeld 2000) and as such often have a false sense of security when engaging in recreational activities in these waterways. With the recent ‘seachange’ phenomenon and the increased growth of urban populations in coastal areas, however, human interactions with co-users of coastal habitats, such as *C. leucas*, are likely to increase. In Australia, numerous adverse shark-human interactions have been recorded, with 746 recorded shark attacks from 1791 to March 2010 (Table 1). In Queensland, 244 attacks have been documented, with 73 of these fatal (Table 1) and *C. leucas* have been implicated in many of these attacks (Bass *et al.* 1973, ASAF 2010). The osmoregulatory ability of *C. leucas* (Evans *et al.* 2004) enables this species to use a wider variety of coastal habitats than can most other sharks, making it one of the most likely shark species to regularly occur in urban systems and to be involved in shark-human interactions. *C. leucas* is thus threatened by a collision between the effects of increasing human population, its own inherent biological adaptability to estuarine ecosystems and its apparent ability to use urban environments (Compagno & Cook 1995, Martin 2005).

<table>
<thead>
<tr>
<th>State</th>
<th>Total Attacks</th>
<th>Av. Annual Attacks</th>
<th>Fatal Attacks</th>
<th>Av. Annual Fatal Attacks</th>
<th>Last Fatal Attack</th>
</tr>
</thead>
<tbody>
<tr>
<td>NSW</td>
<td>272</td>
<td>0.96</td>
<td>69</td>
<td>0.32</td>
<td>2008 Ballina, Lighthouse Beach</td>
</tr>
<tr>
<td>QLD</td>
<td>244</td>
<td>1</td>
<td>73</td>
<td>0.32</td>
<td>2006 North Stradbroke Island</td>
</tr>
<tr>
<td>WA</td>
<td>97</td>
<td>0.29</td>
<td>15</td>
<td>0.07</td>
<td>2008 Port Kennedy Beach</td>
</tr>
<tr>
<td>SA</td>
<td>52</td>
<td>0.2</td>
<td>18</td>
<td>0.07</td>
<td>2005 Glenelg Beach</td>
</tr>
<tr>
<td>VIC</td>
<td>49</td>
<td>0.17</td>
<td>9</td>
<td>0.03</td>
<td>1977 Mornington Peninsula</td>
</tr>
<tr>
<td>TAS</td>
<td>21</td>
<td>0.08</td>
<td>5</td>
<td>0.01</td>
<td>1993 Tenth Is, Georgetown</td>
</tr>
<tr>
<td>NT</td>
<td>11</td>
<td>0.04</td>
<td>2</td>
<td>0.01</td>
<td>1938 Bathurst Island</td>
</tr>
<tr>
<td>Total</td>
<td>746</td>
<td></td>
<td>191</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>


1.9 The Queensland Shark Control Program
In Queensland, Australia, a management initiative, called the Queensland Shark Safety Program (QSCP), was implemented in response to public concern over the threat of large and dangerous sharks to beachgoers (Gribble *et al.* 1998). A shark meshing and drum line program was implemented in nearshore coastal areas along the east coast of Queensland with the aim of reducing contact between beachgoers and
local shark populations. This program began in 1962 (Gribble et al. 1998), with a similar program in NSW (Reid & Krogh 1992) and South Africa (Dudley 1997). Prior to the start of the QSSP, 64% of 42 reported shark incidents in Queensland were fatal, whereas subsequent to 1962 only one fatality has occurred (ASAF 2010, Sumpton pers. comm.). This program has been effective in managing threats from dangerous sharks to coastal human populations. Current understanding of the biology of *C. leucas* and the likely localisation of populations do raise concerns over the long-term sustainability of *C. leucas* populations in areas where their numbers are managed. Cliff and Dudley (1991) noticed a decline in the average length of *C. leucas* caught in the South Africa program over 30 years, implying that the larger individuals had been removed from the local population. The long-term effects of shark control programs on the sustainability of local *C. leucas* populations in Queensland are, however, unknown. Monitoring of the abundance of juveniles in estuarine and urban nursery areas will aid in assessing parental shark stocks, based on the direct relationship between stock and recruitment for sharks (Holden 1977).

1.10 Gold Coast canal system

Although the QSCP has reduced fatal shark-human interactions in nearshore coastal waters, a string of *C. leucas* -human interaction incidents has occurred in other coastal (estuarine and canal) habitats within Queensland. Over the last decade, public concern has grown about the existence of large and dangerous sharks in urban coastal canal systems, such as those on the Gold Coast. In 2003, two human fatalities occurred in the Gold Coast canals in addition to several attacks back to 1989 (Australian Shark Attack File 2009) (Figure 2). Zeller (1999), in his study of *C. leucas* in the Gold Coast canal system, compared the size distribution of *C. leucas* in the Gold Coast canals to that of the QSCP nearshore catch in the same area. He noted that small *C. leucas* (0.85 to 2 m TL) were caught in the canals, whereas larger individuals (1.55 to 3.4 m TL) were caught in the QSCP. He hypothesised that neonate, juvenile and sub-adult *C. leucas* use the canals as a nursery and migrate offshore when mature, moving in a southerly direction. The Gold Coast canal system, with ~ 200 km of artificial waterways connected to an open estuary (Morton 1989), provides an ideal location for investigating the use of urban habitats by *C. leucas*. *C. leucas* can act as a model species in studying the balance between conservation and management needs of major urban wildlife species. Despite these concerns, very little information is available on
how to manage these sharks in urban waterways and the potential value of such systems to the life cycle of this species (Compagno & Cook 1995, Martin 2005).

Figure 2. The Nerang River and adjoining man-made canals on the Gold Coast, Queensland, Australia. Locations of *C. leucas* attacks from 1989 to 2003 are highlighted by the black circles.
1.11 Research questions and framework

The main purpose of this study is to improve our understanding of the habitat ecology and biology of *C. leucas* in Queensland waters, with a particular focus on habitat use and connectivity on urban coasts. The lack of information on the ecology of *C. leucas*, particularly its habitat requirements, movement patterns within and between urban and other habitats, population dynamics and trophodynamics in different habitats, is a significant obstacle to its conservation and management, particularly as this species utilises coastal habitats in its life cycle. Further, understanding the importance of coastal habitats to *C. leucas*, and its movements in these different habitats, is essential to understanding the impact and value of urban habitats to this species. The dangerous nature of the *C. leucas* also makes this information critical in managing shark-human interactions.

Determining the interaction of *C. leucas* with complex ecological and habitat patterns, processes and alterations is particularly useful in conservation and resource management and to balancing the need for safety of humans using dangerous wildlife habitats (Zeller 1999). Knowledge of the directions of movement, pathways and distances moved, together with technologies and chemical techniques to measure spatial habitat use enables a range of shark-environment hypotheses to be determined for highly mobile species such as *C. leucas* (Pittman & McAlpine 2001). The global overexploitation of sharks is an ongoing phenomenon and many management strategies are constrained by a lack of fundamental data on the way sharks, such as *C. leucas*, use their environment throughout the life cycle (Baum et al. 2003, Clarke et al. 2006). Pittman and McAlpine (2001) suggest life cycle trajectories in relation to environmental data and understanding the relationship between animal movement patterns and management strategies such as marine protected area design and placement are essential to the decision making process of ecologically meaningful resource management strategies. This study will construct a conceptual model of anthropogenic and climatic influence on the life cycle of *C. leucas* in relation to its habitat ecology for the conservation and management of dangerous wildlife species to guide these decision processes in the context of eastern Queensland, Australia. Specifically, this study will address the following hypotheses:
1. Fishery-independent patterns in historical catch for juvenile and adult *C. leucas* along the east coast of Queensland are linked to coastal and shelf habitat characteristics (Chapter 2);

2. Rainfall is a key driver for the fishery independent patterns in historical catch of juvenile and adult *C. leucas* in inshore habitats along the east coast of Queensland (Chapter 3);

3. Short-term movements of *C. leucas* are directly influenced by the tidal indunation, strength of current flow and associated bathymetry in river and estuarine habitats (Chapter 4);

4. The value of urban habitat to *C. leucas*, connectivity with natural and urban habitats and response to physical parameters is determined by ontogeny in the lifecycle of *C. leucas* (Chapter 5);

5. Sub-adult *C. leucas* use transitional habitats between river and nearshore habitats in preference to river habitat. Chemical tracing techniques such as laser ablation inductively-coupled mass spectrometry (LA-ICPMS) and isotope analysis across long-term skeletal records (vertebrae) can provide a history of habitat transition and ontogenetic diet shift and these patterns are associated with the size of *C. leucas* (Chapter 6).

The results of these study components will help define a conceptual model of anthropogenic and climatic influence on the life cycle of *C. leucas* in relation to its habitat ecology, for the conservation and management of dangerous wildlife species (Chapter 7).
CHAPTER 2

LINKAGES BETWEEN NEARSHORE BULL SHARK CATCH AND HABITAT CHARACTERISTICS IN EASTERN QUEENSLAND

2.1 Introduction
Sharks are among the most threatened marine species worldwide and numbers have suffered significant recent decline (del Monte-Luna et al. 2007). Historically a major impediment to conservation and management of large and potentially dangerous sharks is a lack of information about their basic biology (Brunnshweiler & Van Buskirk 2006, Weng et al. 2007a), which is, in part, due to their elusive nature and naturally low abundances (Stevens et al. 2000). The protection of essential habitats and the design of marine protected areas (MPAs) for the conservation of coastal sharks are becoming increasingly important in marine and fisheries management (Dulvy et al. 2006, Heupel et al. 2006a, Heupel et al. 2009, Robbins et al. 2006). While key insights into the biology of large coastal sharks have been obtained in the last decade (e.g. Weng et al. 2007b), data for many species are still lacking.

The bull shark, *Carcharhinus leucas* (Valenciennes), is one of the few elasmobranchs that is euryhaline in its distribution and biology (Thorson 1971, Montoya and Thorson 1982). It is found circum-globally within coastal tropical and subtropical riverine, estuarine and marine environments (Compagno 1984), having been recorded over 1,000 km up the Amazon, Zambezi, and Mississippi Rivers (Myers 1952, Bass et al. 1973, Thomerson et al. 1977). In Australia, it occurs from the southern New South Wales (NSW) coast (34° S) and north across to Western Australia (30° S) (Last and Stevens 1994) and is commonly caught in gill nets and baited drumlines in the Queensland Shark Control Program (QSCP) and occasionally in summer months in the NSW shark meshing program (Reid & Krogh 1992). The intensive use of coastal habitats by *C. leucas* makes it one of the most likely species to be involved in adverse shark-human interactions (Dudley 1997) and as such it is considered to be the most dangerous shark species to humans (Last & Stevens 1994). In Australian waters, the
Queensland Shark Control Program (QSCP) was implemented as a management initiative designed to minimise adverse shark-human interactions by reducing the abundance of potentially dangerous, large sharks in the vicinity of popular bathing beaches in the State. Gill nets and drumlines have been deployed since 1963 as part of the QSCP and the long-term historical catch records provide a valuable insight into the biology and population ecology of coastal sharks.

The use of coastal habitats by *C. leucas*, while posing a threat to humans (Dudley 1997), can also make them particularly susceptible to human influence (Martin 2005). Understanding the long-term spatial and temporal trends in catch and the biology of this species is essential for determining conservation initiatives. Long-term catch data from commercial log books and observer data, for example, suggest that no-take fishing zones within the Great Barrier Reef Marine Park (Australia) are effective at protecting a portion of reef shark populations from exploitation despite an overall population decline due to fishing (Heupel et al. 2009). Historical catch records may also provide an effective conservation tool by enabling linkages between the species’ ecology with local habitat characteristics to be determined. Worldwide, several permanent shark control programs have been implemented to reduce local populations of dangerous shark species. The KwaZulu-Natal Shark Board (KZN) in South Africa is probably the most recognized program and long-term catch data have provided important insight into the biology of coastal sharks, particularly *C. leucas* (Cliff & Dudley 1991, Dudley 1997, Dudley & Simpfendorfer 2006). However, few data exist to provide insight into catch trends and biology across the latitudinal tropical/sub-tropical range of the species. The QSCP extends well into the tropical and sub-tropical distribution of this species and provides latitudinal data of some power.

Elasmobranchs are long-lived and produce few offspring. These life-history traits make them particularly vulnerable to overfishing (Stevens et al. 2000). Although infrequently a target species, *C. leucas* are taken commercially and recreationally as part of the large coastal shark fishery complex in the Gulf of Mexico and the northwest Atlantic Ocean (Castillo-Geniz et al. 1998) and increasingly in the world shark fin trade (Clarke et al. 2006). Growing to recorded sizes of 3.4 m in Australia (Last & Stevens, 1994) and recently recorded at 4 m in South Africa (McCord & Lamberth 2009), adult *C. leucas* are often sighted in the nearshore environment.
(Brunnshweiler & Van Buskirk 2006). In South Africa, research by the KZN Sharks Board meshing program has shown that the mean size of bull sharks captured in the nets has declined over a 30-year period. Their research also suggested that adult *C. leucas* were largely site-attached (based on recapture of six tagged sharks) and subjected to local fishing pressure (Cliff & Dudley 1991). Recent work by Brunnsweiler and Van Buskirk (2006), however, has found females may travel hundreds of kilometres to estuarine nursery grounds to pup, suggesting one large population with many sub-populations or one large population with regular large-scale movements.

Many studies have determined the value of estuarine (Blaber et al. 1995, Gillanders et al. 2003, Meynecke et al. 2008), coral reef (Hughes et al. 2003, Bellwood et al. 2004, Robbins et al. 2006) and shelf habitats (Auster 1998, Collie et al. 2000) to nearshore fisheries and species conservation. However, few have considered ecological linkages to nearshore habitats by mobile top-level predators despite their significant and often critical role in maintaining ecosystem function (Myers et al. 2007). While no-take MPAs have been shown to be effective for populations of highly site-attached sharks, such as the grey reef whaler, *Carcharhinus amblyrynchos* (Heupel et al. 2009), protection of endangered shark species that have lifecycles encompassing a range of habitats are less understood. An area of high tourist value has been protected in one known case in the Pacific, the Fiji Shark Reef Marine Reserve established in 2003, to ensure adult *C. leucas* that frequent this nearshore coral reef habitat are not fished (Brunnshweiler & Earle 2006).

The specific aims of this study were to investigate the size distribution, catch per unit effort (CPUE), pupping and diet of *C. leucas* in nearshore Queensland waters using biological information and historical catch data from the QSCP. Emphasis is placed on spatial and temporal differences in catches across a major tropical/sub-tropical latitudinal gradient and tested for ecological linkages to habitat characteristics along the east coast of Queensland. The shark’s biological characteristics and selectivity of gill nets and drumlines are examined in relation to habitat characteristics and their implications for the conservation and management of the species.
2.2 Methods

2.2.1 The Queensland Shark Control Program – study regions

The Queensland (QLD) coastline extends from a tropical climate in the north to subtropical conditions in the southeast. The north and central coastline (Cairns to Bundaberg) (Figure 3) are sheltered by the barrier system of coral reefs on the continental shelf, whereas the southeast (Rainbow Beach to Gold Coast) (Figure 4) has a narrow continental shelf and connects directly with the open ocean (Heap and Harris, 2008). At ten locations (Figure 3) along the QLD coastline between Cairns (17°S) and the Gold Coast (28°S), the QSCP deployed a series of gill nets and drumlines specifically designed to mainly target tiger (*Galeocerdo cuvier*), *C. leucas*, and other whaler species. While effort varied significantly between locations, differences are mostly due to the varying number of beaches (Short 1999) protected by the program in each location (Table 2).

![Figure 3](image)

**Figure 3.** The study area in Queensland, Australia, showing the ten locations of the Queensland Shark Control Program and tropical north and subtropical Queensland regions.
Table 2. Number of beaches and fishing equipment used by the QSCP at 10 locations along the east coast of Queensland, 1996-2006.

<table>
<thead>
<tr>
<th>Location</th>
<th>No. of beaches</th>
<th>Drumlines</th>
<th>Gill nets</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cairns</td>
<td>7</td>
<td>24</td>
<td>5</td>
</tr>
<tr>
<td>Townsville</td>
<td>8</td>
<td>54</td>
<td>0</td>
</tr>
<tr>
<td>Mackay</td>
<td>5</td>
<td>27</td>
<td>5</td>
</tr>
<tr>
<td>Capricorn Coast</td>
<td>9</td>
<td>54</td>
<td>0</td>
</tr>
<tr>
<td>Tannum Sands</td>
<td>1</td>
<td>12</td>
<td>0</td>
</tr>
<tr>
<td>Bundaberg</td>
<td>4</td>
<td>20</td>
<td>0</td>
</tr>
<tr>
<td>Rainbow Beach</td>
<td>1</td>
<td>12</td>
<td>3</td>
</tr>
<tr>
<td>Sunshine Coast</td>
<td>23</td>
<td>78</td>
<td>11</td>
</tr>
<tr>
<td>Point Lookout</td>
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<td>28</td>
<td>0</td>
</tr>
<tr>
<td>Gold Coast</td>
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<td>11</td>
</tr>
</tbody>
</table>

2.2.2 Fishing methods

C. leucas, as well as other large shark species, were captured using drumlines and gill nets. Drumlines usually consist of a single hook (Mustad shark hook size 14/0) baited with ~ 2 kg of mullet (Mugil cephalus) or shark flesh, while surface gill nets were 186 m in length with a 6-m drop and a 50-cm stretch mesh size. The drumlines and gill nets were deployed in an average of 8 m of water and positioned 300 to 1,000 m from the beach line. Soak times usually varied between one to three days depending on weather conditions, as nets and drumlines remained permanently in place and were checked and rebaited or replaced by contractors ~ 15 days out of every month. A total of 344 drumlines and 35 nets were used during the period for which catch data are analysed. All gear was removed from Cairns (29th January to 1st March) and the Capricorn coast (18th July to 26th August) each year for several reasons, including the reduced activity of sharks in these locations during this period. In addition, each year one gill net was temporarily removed from Mackay (1st October to 28th February) and the Sunshine coast (1st May to 10th October) and replaced with six drumlines.
2.2.3 Shark data collection
Data on *C. leucas* were collected by trained QSCP fishing contractors. Total length (TL) was measured in centimetres from the tip of the snout to tip of the tail (top lobe). Where possible, sharks were examined for stomach contents and presence of distinguishable prey items recorded. Gender was determined for all sharks via the presence of claspers in males. The gender and number of pups in pregnant females were also noted. Capture method along with prevailing weather, water temperature and sea condition were recorded by QSCP fishing contractors at time of capture.

2.2.4 Historical data validity
Reliable identification of whaler sharks has been a problem in the past and many commercial fishery log books aggregate sharks into a single catch category “shark” or at best “unidentified whaler” (Gribble et al. 2005). The Java or Pig eye shark, *Carcharhinus amboinensis*, is similar to *C. leucas* in its morphology and can only be distinguished with suitable training. Both species occur in QLD waters, although *C. leucas* is readily caught by the QSCP due to its tendency to frequent the nearshore environment. In 1992, a shark species identification training program was implemented within the QSCP, with particular emphasis on whaler identification. Our analyses focussed on data for which QSCP biologists were able to confirm consistent and correct whaler identification by the contractors and cover the period from 1996 to 2006.

2.2.5 Statistical analyses
Analyses were done using GenStat (2008) and SPSS v17 software, and the significance of all statistical tests was determined at the 0.05 probability level. Conditional generalised linear models (CGLMs) (McCullagh & Nelder 1989), combining the estimates of proportion (binomial distribution and logit link) and zero-truncated count (Gamma distribution and log link) models, were used to determine patterns of CPUE. CPUE was described as No. of bull sharks/No. of gears (drumline or gillnet)/day. Deviance or ANODEV, expressed as the sum of successes and failures of the grouped data, was used to describe the fit of the data to the systematic components of the model. Separate models were run for gill nets and drumlines as initial combined-gears models showed significant interactions with gear types, indicating the gears were not directly comparable within models. CGLMs were tested
for effects of year, location, month and gender on CPUE. Final CGLMs only
considered two-way interactions, as deviance ratio for three-way interactions tested
for nets and drumlines was > 0.5 (NS). A linear regression was fitted to annual trends
in drumline and net CPUE using Sigmmaplot v13. For further comparisons, locations
were grouped based on continental shelf characteristics (Heap & Harris 2008) and
separated into tropical (Cairns to Bundaberg) and sub-tropical (Rainbow Beach to
Gold Coast) regions (Figure 4). I included Bundaberg in the tropical region, as Fraser
Island creates a land bridge across the shelf separating it from other locations in sub-
tropical QLD (Figure 4).

Total lengths of *C. leucas* were analysed by general linear models (Normal
distribution and identity link) separately for gears, as the number of nets and
drumlines across locations was unbalanced (Table 2). Time-series means of predicted
TL for yearly catches from standard linear models were fitted using regression to
identify trends indicative of population shifts at individual locations. Size
distributions pooled over gender and locations were compared individually between
gear types and regions using the non-parametric Kolmogorov-Smirnov test (SPSS).
Size distributions for pregnant and non-pregnant *C. leucas* were combined for all
locations and both gears also compared using the non-parametric Kolmogorov-
Smirnov test.

Total CPUE and length data for the period of 1996 to 2006 for each location in the
QSCP were tested for ecological linkages derived from nine habitat characteristics
(Table 3). Spatial values assigned to habitat characteristics were partly derived from
Meynecke et al. (2008) identified by Queensland Primary Industries and Fisheries
(QPI&F) fish grids at QSCP locations. Habitat characteristics tested included distance
(km) to continental shelf (determined from a central point on the beach at each
location east (90°) to the edge of the continental slope), the number of estuaries at a
location, length of coastline (km), length of connecting river (km) and wetland area
(km²). Wetland patch density was defined as the number of wetland patches per 100
ha divided by the total landscape area in a location. Wetland length connected was
defined as the number of functional connections between all patches within a set
distance of the same patch type. This was then divided by the total number of possible
connections between these patches (Meynecke et al. 2008). I also considered the
number of patches in relation to *C. leucas* catch. Principal components (PCs) were then generated from these variables through principal components analysis (PCA) separately for drumlines and nets and eigenvalues > 2 were retained in final models. Individual regressions were run as there were no more than three PCs for each gear type. All subset regressions against PC predictors were tested selecting the best model based on significant betas.

### 2.3 Results

#### 2.3.1 Catch rates

Catch rates of bull sharks along the east coast of Queensland varied significantly among locations with both drumlines and gill nets, and regional differences were evident for drumline catches (Figure 4). During the 11 years, 1,060 bull sharks were reported from the QSCP, with gender information available for 1,046 sharks. Of these, 55.4 % were females and 44.6 % were males. While bull sharks caught in drumlines did not differ significantly in gender (*p* = 0.064), more females (n = 141) than males (n = 86) were caught in gill nets (*p* < 0.001). Annual trends in drumline CPUE differed significantly among locations and over years (deviance = 1.47, *p* = 0.003). Several locations in tropical QLD (Cairns, Townsville, Mackay, Tannum Sands) all exhibited a peak in drumline CPUE in 2004, whereas CPUE increased over the 11 years at Townsville (*r*² = 0.636, *p* = 0.003) (Figure 4). In contrast, in subtropical QLD annual drumline CPUE declined significantly at all locations except Rainbow Beach, which was data deficient due to the low sampling effort (*r*² = 0.533, *p* = 0.0087). Gillnet CPUE also varied significantly over years among locations (deviance = 1.93, *p* <.001) with gillnet CPUE on the Sunshine and Gold Coasts remaining stable over time and no trends were evident at the other two locations. Seasonal variation in drumline CPUE was most evident in tropical QLD where it was highest during summer months (Dec to Feb). Locations in sub-tropical QLD peaked during January, March and June (deviance = 1.74, *p* < .001). There was no evidence of monthly variation in gill net CPUE (deviance = 1.37, *p* = 0.053).
Table 3. Habitat metrics derived for locations of QSCP drumlines and gill nets. Refer to Meynecke et al. (2008) for further definitions of metrics.

<table>
<thead>
<tr>
<th>Location</th>
<th>Southern Latitude (decimal degrees)</th>
<th>QDPI&amp;F fish grids</th>
<th>Distance (km) to 50m contour</th>
<th>No. of Estuaries</th>
<th>Length of coastline (LCE)</th>
<th>Length of river (LR)</th>
<th>Wetland area in km² (CA)</th>
<th>Wetland patch density (PD)</th>
<th>Wetland length connected (WLC)</th>
<th>Number of patches (NP)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cairns</td>
<td>16.25</td>
<td>G15</td>
<td>68.56</td>
<td>7</td>
<td>34</td>
<td>37</td>
<td>52</td>
<td>0.36</td>
<td>25</td>
<td>19</td>
</tr>
<tr>
<td>Townsville</td>
<td>19.25</td>
<td>J21</td>
<td>124.68</td>
<td>10</td>
<td>59</td>
<td>71</td>
<td>119</td>
<td>0.29</td>
<td>179</td>
<td>34</td>
</tr>
<tr>
<td>Mackay</td>
<td>21.25</td>
<td>O25, O26</td>
<td>202.52</td>
<td>20</td>
<td>66</td>
<td>123</td>
<td>322</td>
<td>0.83</td>
<td>1568</td>
<td>133</td>
</tr>
<tr>
<td>Capricorn Coast</td>
<td>23.25</td>
<td>R29, R30</td>
<td>143.41</td>
<td>6</td>
<td>185</td>
<td>51</td>
<td>616</td>
<td>0.5</td>
<td>246</td>
<td>110</td>
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<tr>
<td>Tannum Sands</td>
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<td>S30</td>
<td>102.29</td>
<td>7</td>
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<td>98</td>
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<td>Bundaberg</td>
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<td>69</td>
<td>61</td>
<td>97</td>
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<tr>
<td>Rainbow Beach</td>
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<td>VW34</td>
<td>69.68</td>
<td>2</td>
<td>232</td>
<td>104</td>
<td>421</td>
<td>0.17</td>
<td>256</td>
<td>72</td>
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<tr>
<td>Sunshine Coast</td>
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<td>VW35, W36</td>
<td>59.7</td>
<td>5</td>
<td>150</td>
<td>82</td>
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<tr>
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<td>39.79</td>
<td>10</td>
<td>235</td>
<td>119</td>
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<td>0.02</td>
<td>960</td>
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</tr>
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<td>Gold Coast</td>
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<td>9</td>
<td>222</td>
<td>99</td>
<td>361</td>
<td>0.08</td>
<td>444</td>
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</tr>
</tbody>
</table>
**Figure 4.** Predicted mean annual drumline CPUE (No. of *C. leucas*/No. of gears/day) for the ten locations in the QSCP from 1996 to 2006. Significant temporal trends exist for Townsville (b) in tropical Queensland and sub-tropical Queensland (g). Locations for sub-tropical Queensland (Sunshine Coast, Point Lookout, and Gold Coast) were grouped as all displayed a significant decline in CPUE (refer to Table 4). The number...
of *C. leucas* caught at Rainbow Beach was too low to obtain yearly trends and as such this location was not included in the regression.

### 2.3.2 Length characteristics

*C. leucas* TL ranged from 0.6 to 4 m, with means of \(1.77 \pm 0.02\) (SE) m for males and \(1.81 \pm 0.01\) m for females in tropical QLD. In sub-tropical QLD, TL ranged from 1.0 to 4.0 m, with means of \(2.08 \pm 0.08\) m for males and \(2.2 \pm 0.05\) m for females (Table 3). For drumlines, annual mean length differed between regions \((p < 0.001)\) with larger males and females in sub-tropical compared to tropical QLD \((p = 0.042)\) (Figure 5). While male and female annual length followed similar trajectories in each region, the models indicated they were still significantly different within regions \((p = 0.011)\). Annual trends in sub-tropical QLD indicated a significant decline in mean length for sharks over the study period \(\left( r^2 = 0.488, p = 0.017 \right)\) with differences in the length of *C. leucas* among locations and months \((p < 0.001)\). Pooled along the entire east coast, females \((\text{TL} = 1.86 \text{ m} \pm 0.03)\) were significantly \((p = 0.020)\) larger than males \((\text{TL} = 1.73 \text{ m} \pm 0.03)\). Larger sharks were present in winter months (June, July and August). Townsville \((r^2 = 0.65, p = 0.005)\), and North Stradbroke \((r^2 = 0.457, p = 0.032)\) had significant declines in mean TL, but an increase occurred for Mackay \((r^2 = 0.45, p = 0.016)\) over the study period (Table 4). *C. leucas* caught on drumlines and in gill nets in the QSCP exhibited a wide range in size (Table 4), and included all life history stages (including likely neonates at Capricorn Coast and Tannum Sands (Table 4). The size distribution of *C. leucas* caught in tropical and sub-tropical QLD differed with larger males in the sub-tropical region, but not for females (Figure 6).
Table 4. Catch metrics for *C. leucas*, at 10 locations off the Queensland east coast based on data from the QSCP during 1996 to 2006. TL = total length (m). *r* = value of regression coefficient. **Bold**: significant (*p* < 0.05) fit highlighted with + and - for direction of slope.

<table>
<thead>
<tr>
<th>Location</th>
<th>Drumline CPUE</th>
<th>Net CPUE</th>
<th>Mean annual length</th>
<th>Mean annual catch</th>
<th>Gear Selectivity</th>
</tr>
</thead>
<tbody>
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</tr>
<tr>
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<td>-0.7710</td>
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<td>3.89</td>
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<td></td>
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</tr>
<tr>
<td>Mackay</td>
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<td>0.2730</td>
<td>+0.6361</td>
<td>11.27</td>
<td>1</td>
</tr>
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<td></td>
<td></td>
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<td></td>
<td>0.8</td>
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</tr>
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<td>Bundaberg</td>
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<td></td>
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</tr>
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<td>Sunshine Coast</td>
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<td>2.13</td>
<td>1</td>
</tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>4</td>
</tr>
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<td>Point Lookout</td>
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</tr>
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</tr>
</tbody>
</table>
Figure 5. Predicted mean (± SE) annual total length for *C. leucas* captured on drumlines, at ten locations in the QSCP from 1996 to 2006. Regression fitted for sub-tropical regions of Queensland from 2000 to 2006.

\[ y = -0.0775x + 157.17 \]

\[ r = 0.49 \]

\[ p = 0.0166 \]
Figure 6. Size frequency distributions of male and female *C. leucas* caught on drumlines in tropical and sub-tropical regions of Queensland in the QSCP between 1996 and 2006. Broken lines denote approximate divisions for maturity based on Branstetter & Stiles (1987).

### 2.3.3 Reproduction

Over the study period, 59 pregnant females ranging from 1.8 to 3.8 m TL were examined (Figure 7) with information on litter size and pups obtained from eight females. An additional female was also obtained from commercial fishers working off the Gold Coast in 2007 and examined. While no detectable relationship between litter size and the TL of females was evident, litter size recorded by the QSCP varied between 5 and 11, with a maximum of 15 pups (mean embryo size = 0.65 m) in the female (3 m TL) examined off the Gold Coast (Figure 8). Embryo size varied between 0.2 and 0.75 m TL. Pregnant females with pupping information were mostly caught in sub-tropical QLD (n = 6) and were caught by both gear types. Pregnant females were captured predominately between December and March with embryos at 0.5 to 0.7 m
TL, suggesting that pupping occurs during warmer months (Figure 9). Whilst pregnant females were captured during cooler months, the TL of their embryos indicated that they were not close to parturition. One pregnant female was captured during May on the Gold Coast with 0.3 m TL embryos and one female was captured in Mackay during September with 0.35 TL embryos. TL of pregnant females ranged from 1.6 to 3.8 m and comprised 15.3 % of all female sharks caught over 1.6 m TL (Figure 7).

**Figure 7.** Size frequency distribution of pregnant (including one 3-m TL female capture within the Gold Coast, independent of the QSCP) and non-pregnant female *C. leucas* caught in the QSCP between 1996 and 2006.
Figure 8. Front view (a) and side view (b) of pregnant *C. leucas* (3 m TL) with 15 pups (c, d).
Figure 9. Mean total length of embryos from pregnant female *C. leucas* caught in the QSCP throughout the year. Number of pregnant females examined shown above symbol.

2.3.4 Diet

53.2 % of the 1,036 *C. leucas* stomachs examined were empty. Benthic and demersal prey were present in stomachs, with bony fish (excluding schooling baitfish) the most abundant prey recorded at all ten locations (23.1 % of stomachs). Baitfish (4.3 %), rays (3.5 %), turtles (1.8 %) and other sharks (1.4 %) were the next dominant prey types.

2.3.5 Linkages with habitat characteristics

Linkages of habitat characteristics with bull shark CPUE were evident for drumline and gillnet catch. Principal component analyses provided three components (PCs) for drumlines whereas two components were generated for gill nets (Table 5). Eigenvalues for all drumline PCs were > 2 and together accounted for 88 % of the standard variance of the data set, whereas gill net PC eigenvalues were also > 2 and together accounted for 95 % of the variance. For drumlines, the first principal component contributed 32 % of the variation (eigenvalue = 2.92) and was dominated by distance to shelf edge, followed by wetland patch density and number of estuaries.
The second principal component contributed 28% (eigenvalue = 2.52) and was dominated by length of river, wetland length connected and wetland area. The final principal component comprised the number of patches and length of coastline and contributed 27% (eigenvalue = 2.45). For gill nets, distances to shelf edge and number of estuaries contributed 62% (eigenvalue = 4.93) for the first principal component. The second principal component was dominated by wetland area and length of coastline with a 33% contribution (eigenvalue = 2.64).

Specific analyses of drumline CPUE was best explained by PC 1 comprising distance to shelf edge, followed by wetland patch density and number of estuaries ($r^2 = 0.714$, $p = 0.001$). Further breakdown of drumline CPUE into gender and sharks > 2 m and < 2 m TL revealed strong relations with PC 1, with males and sharks > 2 m TL having the best fit ($r^2 = 0.789$, $p = 0.001$ and $r^2 = 0.841$, $p = 0.001$, respectively). Analyses with gillnet CPUE was best explained by PC 1 ($r^2 = 0.982$, $p = 0.001$). Pregnant sharks caught by gillnet were best explained by PC 1 ($r^2 = 0.907$, $p = 0.033$); however, no relationship was evident with drumline principal components. A relationship with TL of sharks caught by gillnet was evident with PC 1 ($r^2 = 0.821$, $p= 0.05$), however, males caught by gillnet were not significant ($r^2 = 0.295$, $p = 0.05$) whereas females were ($r^2 = 0.922$, $p = 0.009$). No relationships were significant for TL of sharks caught on drumlines. Proportion of bony fish, other elasmobranchs and turtles in the diet had no relationships with principal components for combined drumlines and gill nets.

2.4 Discussion

2.4.1 Biological catch characteristics
Shark control programs aim to reduce local populations of dangerous sharks and this has been observed for *C. leucas* in the KZN beach meshing program in South Africa (Cliff & Dudley 1991, Cliff & Dudley 1992, Dudley & Simpfendorfer 2006). In the QSCP, the trends in drumline CPUE may indicate reductions in the local *C. leucas* populations, but anecdotal evidence also suggests that dolphin scavenging may reduce the effectiveness of drumlines (particularly for the Sunshine Coast). Dudley and Simpfendorfer (2006) noted that declining CPUE may be the result of density-dependent mechanisms operating with populations and include space-limited coastal areas forcing periodic emigration of *C. leucas* to search for resources in other
locations outside the area of sampling. In this study, the strong relation of estuarine habitat density and number of estuaries to *C. leucas* CPUE indicated that *C. leucas* abundance is likely to be influenced by space-limited coastal areas. My study shows direct evidence of connectivity between estuarine juvenile habitat and near shore adult *C. leucas* habitats demonstrated by the variability in nearshore *C. leucas* catch explained by number of estuaries. This is a critical missing link in our understanding of the nursery role of specific marine habitats to top-level predators (Gillianers et al. 2003, Heupel et al. 2007). Declines in CPUE at the majority of the sub-tropical QLD locations, however, suggest a larger scale decline in the abundance of *C. leucas* at the regional level. A similar decline in large tiger shark, *Galeocerdo cuvier*, and an increase in Scalloped hammerheads, *Sphryna lewini*, over the same time period have also been observed (Wayne Sumpton pers. comm.).

Fishing effort for *C. leucas* is likely to provide a linear transformation as doubling of effort will likely double catch until the ‘local’ carrying capacity of sharks in the area is reached. The occurrence of *C. leucas* of different sizes in estuarine and nearshore habitats is likely driven by the need for large prey, hence their movements offshore from rivers, and available space in river and bay areas. Rivers and bays are limited in their volume and as such are in themselves a space-limited habitat. Larger *C. leucas* (> 2m in length) in nearshore beach areas have left the confines of space-limited river and bay nurseries and are utilising coastal habitat on the continental shelf. While the size of the available habitat in this coastal area has increased compared to that of rivers, my analyses suggest that large *C. leucas* are still space-limited by the amount of available continental shelf. This aspect was clearly demonstrated by significant increase in shelf width at sites in the GBR where large bull shark numbers were higher. Increasing effort in a nearshore area should provide an initial increase in catch, but the space-limited nature of the continental shelf in sub-tropical Queensland would mean once the "carrying capacity" of the area has been reached numbers of large bull sharks captured would be expected to decrease despite addition fishing effort. *C. leucas* have trophically driven and density-dependant population dynamics.

Data on the long-term trends in *C. leucas* population characteristics is scant, despite the species’ global distribution and growing concern for declines (Clarke et al. 2006). The fishery-independent insight of the QSCP catch data for *C. leucas* is highlighted
by the trend in Mackay where mean TL increased significantly over the 11 years (Table 3), suggesting a healthy increase in the local population. Conservation of top-level predators requires identification of areas of importance (Heupel & Simpfendorfer 2005) and Meynecke et al. (2008) noted a high CPUE for crab and bony fish (favoured prey for small *C. leucas*) in Mackay compared to other sections of the QLD east coast and this was attributed to the presence of a large number of estuaries (n = 10) and close proximity of different fish habitats (e.g. mangrove and seagrass areas). The ecological characteristics of the fish habitats in Mackay appear to favour high fish production and this is reflected in the characteristics of the QSCP *C. leucas* catch data. Meynecke et al. (2008) also suggested that fish habitats in subtropical Queensland were degraded and commercial fishing effort is substantially higher (i.e. by several orders of magnitude) than other areas of the Queensland coast, particularly for Moreton Bay. The effects of these pressures could be reflected in the QSCP catch statistics by the significant declines in *C. leucas* CPUE in subtropical QLD and mean TL at Point Lookout. Dudley and Simpfendorfer (2006), however, found a significant decline in the CPUE of *C. leucas* over a 26-year period in the KZN nets but the TL of animals remained stable over this time period. While they used independent life-history parameters to assess the impact of the netting program on *C. leucas*, they concluded that the potential effect of the program was more pronounced on this species than with many other local whaler populations, because of a moderate catch, a low intrinsic rate of growth and low ability to recover from fishing mortality.

While CPUE can provide an indication of the population trends, concomitantly overall catch metrics provide a clearer picture of population trends and these can also be related to the biological characteristics of the shark (e.g. ontogenetic feeding activity and reproductive capacity of sharks in nearshore habitat). Decline in mean TL is indicative of overfishing and potential pressure on the sustainability of localised *C. leucas* populations. These phenomena are being observed on a global basis (Clarke et al. 2006, Myers et al. 2007). Frisk et al. (2001) in his analysis of 36 elasmobranch species recommended that species over 2 m TL be subjected to only conservative fishing limits. Dulvy and Reynolds (2002) suggested species with a larger body size are more susceptible to local extinction. In this study, patterns of TL remained relatively constant over years for most tropical QSCP locations, with small annual fluctuations (Table 2). While Townsville had a significant decline in the TL of bull
sharks, drumline CPUE increased significantly. This pattern could indicate a shift in the characteristics of the local population due to natural conditions of the location rather than a change due to overfishing, with smaller sharks caught. Proliferation of small sharks (< 1 m) in the catches of KZN shore-based anglers in the late 1970’s was attributed to decreased predation by large sharks, in particular *C. leucas*, due to numbers of this species declining from the KZN shark nets (Elst 1979). Increase in local populations of smaller shark species due to the absence of large sharks has been noted in other recent studies (Myers et al. 2007). Factors driving this population change at Townsville could be depletion of cannibalistic large *C. leucas*. However, it could be argued that this change is independent of the QSCP, in view of the exponential increase in commercial coastal shark catch in the Great Barrier Reef reported by Gribble et al. (2005). This clearly warrants further investigation.

The wide range of TL of sharks caught indicates low selectivity of gill nets and drumlines. Juveniles (0+) remain within defined salinities in rivers and estuaries and are unlikely to be encountered in the nearshore areas of the QSCP (Heupel & Simpfendorfer 2008, Pillans et al. 2005). However, the difference in TL for male *C. leucas* between regions, suggests the gears may have a gender rather than size bias. Heithaus (2001) found more female tiger sharks in Shark Bay, Western Australia, amongst sharks of small size range and a 1:1 ratio for large sharks, but was unable to explain these observations. Cliff and Dudley (1991) found fewer male *C. leucas* in the nets of the KZN coast, a result consistent with that of the present study. Females may be aggregating and spend more time in nearshore habitats for reproductive and energetic benefits, whereas males may be more solitary and transitory in their movements. Aggregations of females have also been noted with the scalloped hammerhead, *Sphyra lewini* (Klimley 1985).

2.4.2 Ecological linkages with habitat

The clear linkages between *C. leucas* catch and habitat characteristics along the east coast of Queensland reflect the life cycle patterns of this top-level predator. Nearshore habitats are dominated by sub-adult (1.6 to 2 m TL) and adult sharks (> 2 m TL), with fewer juveniles in nearshore waters of subtropical QLD (Figure 4), which is probably a function of shelf width and the number of estuaries (Table 2). Linkages between estuarine habitats and nearshore fisheries have been established (Lee 2004;
Manson et al. 2005; Meynecke et al. 2008), including direct correlations with areas of mangroves (Staples et al. 1985) or the extent of the intertidal habitat (Lee 2004). Abundance of prey is likely to be greater with higher mangrove standing crop translating to greater abundance of juvenile *C. leucas* (Figure 4), e.g. mean annual catch at Mackay and Capricorn Coast (Table 3). Adult bull sharks are likely to be more directly influenced by the shelf characteristics and this is important in the design of top predator MPAs. Regional differences were evident with sharks (both sexes) in sub-tropical QLD being significantly larger than their counterparts in tropical QLD. Tropical QLD has an extended shallow lagoon fringed by the Great Barrier Reef whereas the continental shelf is narrow (< 70 km offshore) in sub-tropical QLD. This geomorphic difference provides the basis for delineation of these regions (Heap & Harris 2008) (Figure 3). As shown by PCA-regression, the shelf characteristics strongly influence the CPUE of *C. leucas* along the east coast of QLD. The shelf break beyond which the continental slope steeply drops away often marks the oceanographic front between coastal and oceanic water masses (Longhurst 1998). Fish faunas also often change rapidly with depth (Musick et al. 1996) and oceanographic fronts close to the nearshore environment probably space-limit the shelf environment in sub-tropical QLD, and may account for larger animals occurring more frequently in the nearshore QSCP in this region.

Small *C. leucas* are known to move down river during periods of high freshwater flow (Heupel & Simpfendorfer 2008). Low rainfall proceeding the study period (average annual fall 1991 to 1995 of 368.92 mm for Ross River) in Townsville followed by a substantial increase from 1996 to 2006 (average annual rainfall 995.4 mm for Ross River) may account for the increase in smaller bull shark catch over the period of the study. Higher catches during 2004 for Cairns, Townsville, Mackay and Tannum sands may also be attributed to a peak in annual rainfall this year, which was preceded by a severe El Niño event with little summer rain. Environmental parameters such as rainfall are likely to affect feeding and movement of bull sharks, particularly as they are closely tied to low-salinity environments as juveniles (Pillans et al. 2005).

Site fidelity in many shark species increases the impact of beach protection programs on shark populations, particularly in size-limited habitats. Cliff and Dudley (1991) suggested that *C. leucas* have high site fidelity and Brunnschweiler and Earle (2006)
observed seasonal site fidelity in a population of adult *C. leucas* in the coastal waters of Fiji. Heupel and Simpfendorfer (2008) also observed a pattern of site attachment in neonate and 0+ juvenile *C. leucas* using long-term telemetry in a river system in Florida. These patterns of distribution and movement have direct implications for local depletion of sharks and the effect of shark control programs. Large MPAs provide better protection for shark populations that are highly mobile (Heupel & Simpfendorfer 2005). However, the patterns of site fidelity have been poorly examined for larger size classes (2 to 4 m TL) of *C. leucas* that inhabit the nearshore environment. Point Lookout had a reduction in *C. leucas* TL and drumline CPUE, and these combined trends may indicate a local depletion of *C. leucas* possibly due to high site fidelity and philopatry rather than population-level changes in abundance. While the extent of bait scavenging from drumlines by dolphins needs to be determined, research determining the movement and habitat use of *C. leucas* (> 2 m) in this location is required to ascertain the drivers for these trends in abundance and to determine whether sharks display short and long-term site fidelity (e.g. Heithaus 2001).

The importance of habitat in determining the abundance and distribution of sub-adult and adult life stages of large marine predators is directly applicable for conservation planning (Simpfendorfer & Heupel 2004). A single beach in eastern Australia, for example, has been identified as an important area for juvenile white shark, *Carcharodon carcharias*, despite their ability to move thousands of kilometres along the east coast of Australia (Barry Bruce pers. comm.). Heupel and Simpfendorfer (2005) found that a large protected area provided less consistent levels of protection, but for a greater period of time, than a small reserve when taking into account excursions made by the sharks. Source estuarine habitat sites that show linkage to near-shore habitats with the greatest level of *C. leucas* catch could potentially be set aside as MPAs (Gillanders et al. 2003). This study clearly shows linkages with habitat characteristics for top-level predators with a life cycle closely linked to freshwater habitats can guide the design of MPAs despite the often nebulous spatial boundaries of near shore habitats.
2.4.3 Reproductive and pupping data
Female *C. leucas* caught in the QSCP included all size ranges. Pregnant females were caught from 1.6 m TL and occurred throughout the size range of pregnant females, however, most pregnant females captured were 2 to 2.1 m TL. This size range is consistent with other studies (Bransetter & Stiles 1987) that report maturity at 1.8 to 2 m TL. Large size at maturity increases the vulnerability of an elasmobranch species to exploitation (Cortes 2002). In the current study, I have the first known record of 15 pups at an average of 0.65 m TL in a 3 m TL pregnant female. Most pregnant sharks were captured during summer months and embryo TL of litters examined ranged from 0.5 to 0.7 m TL (i.e. close to size range at birth), which would suggest pregnant females were in shallow coastal areas for pupping over summer. Whilst some pregnant sharks were captured over winter, the small embryo TL (0.2 to 0.35 m TL) in the litters examined suggests pupping did not occur at that time.

2.4.4 Diet
The diet of most *Carcharhinus* species includes teleosts and neonate and juvenile *C. leucas* predominately target teleost prey in rivers and estuaries (Bass et al. 1973). Sub-adult and adult *C. leucas* commonly consume other elasmobranchs and a wide range of higher vertebrates in other regions of their natural distribution. Cliff and Dudley (1991) found 50.2 % of *C. leucas* stomachs containing food in the KZN were dominated by elasmobranchs such as batoids and the giant guitarfish (*Rhynochobatus djiddensis*), and smaller shark species were the second most important elasmobranch component in the diet. The ecological importance of large predators in coastal ecosystems has also been recognised in long-term studies with shifts in the composition of prey species in estuaries due to the chronic overfishing of *C. leucas* (O’Connell et al. 2007). The importance of large adult *C. leucas* in regulating food chain diversity is an important consideration for fisheries management. It is also not surprising that a marginal link with distance to shelf edge, wetland patch density and number of estuaries was evident for proportion of other elasmobranchs and rays in the diet. Larger estuarine habitat probably encourages greater nearshore productivity. Near-shore locations with a high number of adjacent estuaries should be considered in the design of MPAs for top predators.
2.4.5 Implications for management and conservation

Prince (2005) suggested shark fisheries are robust when long-lived adults remain in the fishery and remain stable over generations. Depletion in sub-tropical QLD suggests migration from other areas is not sufficient to offset the decline and that local area management is needed. Therefore understanding the connectivity of local *C. leucas* populations along the east coast of Queensland, in terms of gene flow, short-term movements and potential migrations of large adults between locations is important for assessing the longer-term effects of the QSCP on *C. leucas*. These data are also essential for the design and implementation of top predator MPAs. I recommend research to ascertain local population size and, in combination with a genetic study, determine whether serial depletions in CPUE and shark length are indicative of population level changes in abundance. Telemetry studies to provide information on habitat preference, their connectivity and site fidelity will be particularly useful in areas such as Point Lookout, where localised serial depletions may be an issue.

Rainfall variation as part of the overall effects of climate change is likely to be a key factor in the future dispersal of coastal organisms and requires important consideration for management and conservation initiatives (Meynecke et al. 2006). Interpreting CPUE patterns and hence patterns of occurrence in areas frequented by human co-users in relation to rainfall and other components of climate change are essential for assessing the effectiveness of the QSCP. This is particularly pertinent for *C. leucas*, which is able to freely move between fresh and salt waters (Pillans et al. 2005). Understanding these patterns may enable periods of net removal from local areas to reduce bycatch species.

The demonstrated link between habitat characteristics and *C. leucas* CPUE further highlights essential nursery and feeding habitats for *C. leucas* populations across the tropical and sub-tropical range of their natural distribution. Environmental parameters are likely drivers of *C. leucas* abundance and space-limiting habitat needs to be an important consideration in future conservation of *C. leucas*, particularly in sub-tropical areas with characteristic narrow shelf environments. Guidelines for future management and conservation of top-level predators should consider particular habitats linked to nearshore shark catch to ensure the design of top predator MPAs is
representative and ecologically effective (Almany et al. 2007, Gillanders et al. 2003, Robbins et al. 2006). Efficacious analyses of historical records from shark management programs may help guide these processes.
CHAPTER 3

INFLUENCE OF RAINFALL AND OTHER CLIMATE PARAMETERS ON BULL SHARK CATCH IN NEARSHORE HABITATS ON THE EAST COAST OF QUEENSLAND

3.1 Introduction
Understanding how large sharks use coastal habitats is increasingly important as sharks are among the most threatened species worldwide (del Monte-Luna et al. 2007). Significant insights into the habitat use by sharks in coastal areas have resulted from acoustic and satellite telemetry (e.g. Heupel et al. 2003, Dagorn et al. 2007) and long-term patterns of activity have been determined with historical fishery-independent data (e.g. Cliff & Dudley 1991). The effects of climate drivers on sharks, which have ‘K-selected’ life-history strategies (e.g. long-lived, slow growth, low fecundity), is an important consideration for their management and conservation, as their populations are particularly vulnerable to anthropogenic pressures (Baum et al. 2003, Martin 2005). Catches of important fisheries species such as mullet (Mugil cephalus) and barramundi (Lates calcarifer) are correlated with rainfall (Halliday et al. 2001) and have life cycles coupled to rainfall and temperature, making them particularly susceptible to shifts in climate (Meynecke et al. 2006). Sharks with similar life cycles and rely on food chains whose productivity is correlated to climate parameters are also likely to be susceptible to these pressures. Furthermore, the long-term survivorship of species that are reliant on particular habitats may be compromised as their habitats become less viable due to climate-driven pressures (Bellwood et al. 2004). Recent studies indicate sharks have suffered a significant worldwide decline, mostly due to illegal and unsustainable fishing practices (Baum et al. 2003, del Monte-Luna et al. 2007). The uncertain magnitude of climate change can potentially obscure the effects of fishing and other anthropogenic activities (Walker 2007). Sharks, with existing pressures, reduced populations and biological attributes that favour slow population growth, have increased risk to changes in climate (Chin & Kyne 2007).
The life history characteristics and habitat requirements of a shark determine its ability to respond and adapt to changes in climate. Consequently, understanding how sharks use coastal habitats is imperative to managing sharks in the face of climate change. Walker (2007) highlighted components of climate likely to impact sharks from a list of climate change impacts in coastal marine systems identified by Harley et al. (2006). These include: increased water temperature, altered rainfall, salinity and turbidity patterns, rising sea level, increased storm strength and frequency, coastal erosion, changed ocean currents and upwelling, increased ultraviolet light from reduced ozone, and ocean acidification. Changes in the value (i.e. food web viability) and biological productivity of river, estuarine and inshore coastal habitats as a result of rainfall and temperature drivers are likely to increase the vulnerability of chondrichthyan species that are top-predators in such habitats and alter their patterns of abundance and distribution (Chin & Kyne 2007, Martin 2005).

The bull shark, *Carcharhinus leucas*, is a tropical species with a global distribution and occurs in most tropical and some sub-tropical river systems (Last & Stevens 1994). Its life cycle is closely tied to freshwater and low saline environments, relying on river and estuarine habitats as nursery areas for neonate and juveniles, whereas adults readily occur in the nearshore environment (Cliff & Dudley 1991, Heupel & Simpfendorfer 2008). Recognised juvenile nursery grounds include coastal and inland waters in Louisiana (Blackburn et al. 2007), lagoons of the east coast of Florida (Castro 1993, Simpfendorfer et al. 2005) and the freshwater reaches of the Brisbane River, Queensland Australia (Pillans & Franklin 2004).

Previous studies have estimated *C. leucas* reach maturity at 6 to 8 years of age (Branstetter & Stiles 1987) and with females, this equates to a length of 1.8 m (Cliff & Dudley 1991) to 2.0 m total length (TL) (Branstetter & Stiles 1987, Jensen 1976). After a gestation period of 9 – 10 months, pregnant females are believed to pup litters of 1-13 live young (0.56 to 0.75 m TL) (Clark & Von Schmidt 1965, Cliff & Dudley 1991) in estuaries or at river mouths. The neonates then move upstream into freshwater (Thomas & Thorson 1972, Thorson et al. 1973) where they remain within defined low salinities, presumably for physiological benefits (Heupel & Simpfendorfer 2008, Pillans et al. 2005). The osmotic ability to utilise low-salinity
environments in juveniles likely decreases intra-specific competition with adults, providing safe haven from predators including conspecifics (Pillans & Franklin 2004, Martin 2005). These unique euryhaline abilities directly influence movement of different sized *C. leucas* in coastal habitats, as sub-adult and adult animals can readily move between fresh and oceanic waters (Thorson 1971, Pillans et al. 2006).

Determining the influence of climate parameters on *C. leucas* in coastal habitats is therefore essential for fisheries management and conservation concerns. In this chapter, I determined the influence of parameters of climate (particularly rainfall and temperature) on the catch of *C. leucas* in the nearshore environment of Queensland, Australia and to test the hypotheses that (1) catches of *C. leucas* varied according to ontogenetic factors; and (2) catches are influenced by climate parameters.

3.2 Methods

3.2.1 Study site

Historical catch data from the Queensland Shark Control Program (QSCP) (January 1996 to July 2007) was used to examine the influence of drivers of climate on *C. leucas* caught at ten locations from Cairns (17°S) to the Gold Coast (28°S) along the east coast of Queensland (QLD), Australia (Figure 2). At these locations the QSCP deployed a series of gill net (passive) and drumline (active) ‘sampling’ gears specifically designed to target *C. leucas* and other large shark species (Table 2). While active gears were present at all ten locations, passive gears were only deployed at five locations namely, Cairns, Mackay, Rainbow Beach, Sunshine Coast and the Gold Coast. The QLD coastline extends from a tropical climate in the north to a subtropical climate in the southeast (SEQ). Nearshore waters vary in Sea Surface Temperature (SST) from an average of 15°C in July to 28°C in January. Numerous rivers and catchments (n = 73) drain into the nearshore environment (Cairns to Gold Coast) and rainfall patterns are typically seasonal (Meynecke et al. 2006). The QSCP has maintained standardised fishing methods and locations for the period of the study and as such catches rates can be used to examine *C. leucas* relative abundance and feeding activity in relation to parameters of climate.
3.2.2. Size composition of catches

Daily catch per unit effort (CPUE) and the catch statistics for gill nets and drumlines were divided into groups of < 2 m and > 2 m TL individuals to determine differences in the influence of parameters of climate on juvenile and adult *C. leucas* (Branstetter & Stiles 1987, Cliff & Dudley 1991) activity patterns in nearshore habitats. I included an additional category for pregnant *C. leucas*. All data on *C. leucas* were collected by trained QSCP fishing contractors as per section 2.2.4 (Chapter 2). Analyses in this paper extend from 1996 onwards with data for 1044 *C. leucas*. CPUE was defined as the number of *C. leucas*/number of gears (drumline or gill net)/day.

TL of sharks was measured in metres from the tip of the snout to tip of the tail (top lobe) in its natural position. Gender was determined by the presence of claspers in males. The gender and number of pups for all pregnant females was also noted (Last & Stevens 1994). Passive or active capture method along with prevailing weather, water temperature and sea condition were recorded by QSCP fishing contractors at time of capture.

3.2.3 Catch and feeding activity

I used *C. leucas* catch on active gears (drumlines) as an indicator of feeding activity for the different ontogenetic stages of *C. leucas*. To further interpret the ontogenetic differences in presence of *C. leucas* in nearshore areas, stomach contents of *C. leucas* were examined for different sized *C. leucas*. I analysed only dominant food type recorded in the stomach contents and the proportion of teleost and higher vertebrates in the diet of juvenile and adult *C. leucas* was compared using a chi-square test. *C. leucas* catch on gill nets was used to determine both feeding and non-feeding related presence in the nearshore habitat.

3.2.4 Climatic Parameters

Daily climatic data on sea surface temperature (Bureau of Meteorology and Environmental Protection Agency), rainfall (Bureau of Meteorology), Southern Oscillation Index (http://www.bom.gov.au/climate/current/soihtm1.shtml) and fraction of the moon illuminated (lunar phase) (http://aa.usno.navy.mil/data/docs/MoonFraction.php) were obtained for QSCP
locations for the period January 1996 to July 2007. Rainfall was analysed in two ways: (1) as daily records; and (2) cumulative total rainfall for the eight-day period prior to when *C. leucas* was captured. Wind direction and speed at 0900 or 1500 hrs and surface water temperature were also recorded by QSCP fishing contractors when animals were captured.

3.2.5 Statistical analysis - Conditional generalized linear modelling

Daily CPUE data for *C. leucas* were analysed by stepwise forward conditional generalised linear modelling (CGLM, McCullagh & Nelder 1989), using the program GenStat™ 9.2 (GenStat 2008, McCullagh & Nelder 1989). To overcome analytical problems arising from numerous zero values, I used a binomial model for presence/absence, and a conditional gamma model for the numbers actually caught. Combining the means and standard errors of these binomial and conditional gamma models (Mayer et al. 2005) enabled more accurate and meaningful estimation of the main effects and interactions of statistical significance and were considered reliable as distribution of residuals in the binomial and gamma generalised linear models were close to normal. Variables that explained the greatest amounts of deviance were plotted. Binomial and gamma (truncated zero) models were screened to select the dominant variables to retain in the final models. If main effects or interaction term was significant in one model, then it was retained in the other model. This was done because the gamma model is conditional to the binomial model and the two models need to contain identical main effects and interactions when combined to estimate the overall adjusted means. The term “gear” was always included in the CGLM analyses. The justification for the distribution assumptions trends were from residual plots of the modelled trends (refer to Appendix 1 for examples). Rainfall on the day of capture and from one to eight days prior to capture were screened for significance and direction, and pooled as appropriate. Other terms screened included the Southern Oscillation Index (SOI), sea surface temperature (SST), lunar phase (Moon) and wind speed (at 0900 and 1500 hrs). *C. leucas* CPUE for gill nets and drumlines were also analysed separately for juvenile *C. leucas* (< 2 m), adult *C. leucas* (> 2 m) and pregnant females.

Daily wind speed data were also analysed separately using circular statistics to detect any potential relationships. Additional SST was recorded by shark contractors on the
day and at location of capture for *C. leucas*. Studies suggest that some chondrichthyan fishes have optimal temperatures for feeding and their physiology (Matern *et al.* 2000). In addition to CGLM of SST and all shark catch, I compared the catch data separately as tropical (Cairns to Bundaberg) and subtropical (Rainbow Beach to Gold Coast) to determine whether optimal temperatures was evident for passive gears in the respective nearshore habitats. Catches in relation to SST were best described by non-linear regression model after several models were tested for adequate fit to the data trends:

\[ y = ae^{-0.5(b(x-x_0))^2} \]

where \( a \) = maximum \( y \); and \( x_0 = x \) at \( y \) maximum; \( \beta \) = beta value to be estimated by regression.

### 3.3 Results

#### 3.3.1 Combined analyses

Relationships between climatic variables and *C. leucas* catch were evident for drumlines and gill nets and these relations varied for juvenile and adult sharks (Table 1). The final models indicated by the CGLM analyses were Season + Location + Year + Year \( \times \) Location + Climate Parameter. Rainfall had interesting effects, negative on relationship with the day of capture, but positive for all days prior to capture. For this reason, and to lessen the degree of autocorrelation, rainfall for days 1 to 8 prior to capture was pooled into ‘weekly rain’, which was fitted in the models as a single term. Prior rainfall was the only significant variable for *C. leucas* catch in both gears for which correlations were evident across different life history stages. Patterns indicate an exponential increase in catch after periods of 300 mm of rain or greater. These data also indicate a 2 to 9 % increase in *C. leucas* catch with previous rainfall one to eight days prior.
**Table 5.** Probability values for combined deviance (ANODEV) from Conditional General Linear Models analysing the effects of various factors on *C. leucas* catch in nets and drumlines. Significant values are highlighted in bold.

<table>
<thead>
<tr>
<th>Gear</th>
<th>Shark size</th>
<th>Rain</th>
<th>Weekrain</th>
<th>Southern Oscillation Index</th>
<th>Lunar phase</th>
<th>Sea Surface Temperature</th>
<th>WindSpeed 9:00</th>
<th>WindSpeed 15:00</th>
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<tr>
<td><strong>Drumline</strong></td>
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<td></td>
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<tr>
<td>All</td>
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<td>0.02</td>
<td>0.920</td>
<td>&lt;0.001</td>
<td>0.338</td>
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<td>0.001</td>
<td>0.793</td>
<td>&lt;0.001</td>
<td>0.609</td>
<td>0.98</td>
</tr>
<tr>
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<td>0.801</td>
<td><strong>0.028</strong></td>
<td>0.324</td>
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<tr>
<td>Pregnant F</td>
<td></td>
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<td>0.173</td>
<td>0.463</td>
<td>0.245</td>
<td>0.274</td>
<td>0.133</td>
<td><strong>0.03</strong></td>
</tr>
<tr>
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<td></td>
</tr>
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<td><strong>0.022</strong></td>
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<td>0.909</td>
</tr>
<tr>
<td>Large</td>
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<td>0.095</td>
<td>0.124</td>
<td><strong>0.035</strong></td>
<td>0.485</td>
<td>0.114</td>
<td>0.208</td>
<td>0.531</td>
</tr>
<tr>
<td>Pregnant F</td>
<td></td>
<td>0.542</td>
<td>0.193</td>
<td><strong>0.033</strong></td>
<td>0.382</td>
<td>0.167</td>
<td>0.581</td>
<td>0.696</td>
</tr>
</tbody>
</table>
3.3.2 Drumline catch

Differences in feeding activities between the two TL size groups were evident for *C. leucas* captured on drumlines. Importance of other vertebrates in the diet differed between juvenile and adults (*χ²* = 33, *p* = 0.034). CGLM analyses was positively related to prior rainfall and SST for juvenile and adult *C. leucas* and catch increased exponentially for both life history stages of the *C. leucas* after 300 mm of prior rainfall (Figure 10). Correlations with SST were significant for juvenile and adult *C. leucas* captured on drumlines and these patterns occurred with an interaction between years and locations with both life-history groups (*p* = 0.04 and *p* = 0.028 respectively). Capture on drumline increased with increasing SST for both juvenile and adult shark (Figure 11) with an optimum temperature for sharks in tropical QLD (Cairns to Bundaberg, 26°C) and subtropical QLD (Rainbow Beach to Gold Coast, 23°C) captured by passive gears (Figure 12). In tropical QLD the relationship showed a slower incline followed by steeper decline.
**Figure 10.** Plot for results from CGLM mean CPUE (± SE) for rainfall 1 to 8 days prior to capture for (a) combined small (< 2m TL) and large (> 2m TL) *C. leucas* caught on drumlines and (b) small *C. leucas* caught in gill nets.

**Figure 11.** Plot for results from CGLM mean CPUE (± SE) for sea surface temperature (SST) and combined catch of small (< 2m TL) and large (> 2m TL) *C. leucas* caught on drumlines.
3.3.3 Net catch

CPUE of adult *C. leucas* in gill nets varied significantly among locations and years ($p = 0.024$), and there was an interaction between year and location for juvenile *C. leucas* ($p = 0.019$). Results of the CGLM indicated a significant relationship with the SOI and the capture of adult *C. leucas* in nearshore habitat, with increase in catch during periods of positive SOI (Figure 13). Alternatively, CGLM indicated juvenile *C. leucas* CPUE was significantly correlated with rainfall on day of capture, prior rainfall and moon phase (Table 1, Figure 10 a, Figure 14). In this case, juvenile *C. leucas* catch also increased after a threshold of > 300 mm of rainfall. Juvenile *C. leucas* CPUE decreased linearly in nearshore habitats from no exposed moon (0%) to full moon (100%) (Figure 14).
Figure 13. Plot for results from CGLM mean CPUE (± SE) of Southern Oscillation Index (SOI) for (a) small (< 2m TL) *C. leucas* caught on drumlines, (b) large (> 2m TL) *C. leucas* caught in gill nets and (c) pregnant females in gill nets.
Figure 14. Plot for results from CGLM for lunar phase and small (< 2 m TL) *C. leucas* caught in gill nets.

### 3.3.4 Pregnant females

Circular statistics showed no significant (p > 0.05) relationships between wind speed and *C. leucas* catch rates on either gear type. However, CGLM indicated a positive relationship with decreasing wind speed at 1500 hrs for pregnant female CPUE (Table 1). While the error varied substantially at the outer extremes of the relationship, pregnant female CPUE increased exponentially during periods of positive SOI (Figure 13).

### 3.4 Discussion

The results from this study suggest that prior rainfall (> 300 mm) and sea surface temperature are significant climate parameters that influence the catch of both small (< 2 m TL) and large (> 2 m TL) *C. leucas* in nearshore areas on the east coast of Queensland. The response of different ontogenetic stages of the *C. leucas* to these physical drivers reflects the range of habitat use of this species throughout its life cycle. *C. leucas* distribution is closely tied to fresh and low-salinity environments as juveniles. This is followed by a transition into nearshore habitat as adults with a shift
in diet to target larger vertebrate prey (Cliff & Dudley 1991), which are more available in the nearshore habitat. The relationship between catch and prior rainfall was different for small and large sharks, which may reflect the pattern of use of nearshore habitats by different ontogenetic stages. The significant relationship between drumline catch for small and large *C. leucas* with prior rainfall suggests active feeding in nearshore areas after rainfall. A relationship with prior rainfall and catch in gill nets was only significant for small *C. leucas*, suggesting that small *C. leucas* may be moving into these areas specifically for feeding.

Mechanisms underpinning relationships of climate parameters and shark catch are likely influenced by changes in distribution from altered habitats and changes in population dynamics, i.e. recruitment, growth, survival, abundance, transitions between nursery and adult foraging habitats and migration behaviour (e.g. Meynecke et al. 2006). Adult and juvenile *C. leucas* in nearshore habitats are influenced by rainfall and sea surface temperature, as suggested by the analyses and these patterns of catch reflect ontogenetic activity and movement responses to these physical drivers. I suggest that *C. leucas* are moving into nearshore areas, possibly from deeper coastal waters (> 25 m deep) (Brunnshweiler & Van Buskirk 2006), to feed in the freshwater plumes extruding from river mouths (Figure 15). Lagged responses of shark catch to rainfall reflect changes in availability of food and foraging effectiveness with changes in salinity after sufficient rainfall (> 300 mm). Lagged responses to rainfall have been recorded on scales of days to years for other nearshore species such as mud crabs (*Scylla serrata*), mullet (*Mugil* spp.) and barramundi (*Lates calcarifer*) (Hill et al. 1982, Williams 2002, Staunton-Smith et al. 2004).
Several estuarine sharks are influenced by a range of temperatures (Heupel & Heuter 2002, Simpfendorfer et al. 2005). Species that are able to tolerate and exploit warming conditions are likely to move poleward in their range (Chin & Kyne 2007). However, some cartilaginous fishes have been shown to feed in higher water temperatures and rest in cooler waters and as such sharks may move to new areas where optimal temperatures for their physiology prevail (Matern et al. 2000). Drumline catch increased exponentially for *C. leucas* in the current study and optimal temperatures for *C. leucas* in gill nets suggest use of nearshore habitat differs between tropical north Queensland (28°C) and sub-tropical southeast Queensland (23°C). *C. leucas* appear to be larger in size at colder extremes of their natural distribution (McCord & Lamberth 2009) and the results of this study suggest an optimal temperature adaptation for *C. leucas* populations according to the prevailing SST of the area. Further, these different optimal temperatures could be due to geographically separate populations that have adapted to the range of prominent temperature fluctuations within each region.

A significant impact of rainfall on fish catch is reflected in a significant relationship with the Southern Oscillation Index (SOI). El Niño or dry years in eastern Australia lead to reduced fish catch and wet years translated to higher catches (Meynecke et al. 2006) and these patterns were also consistent for *C. leucas* in the current study. Pregnant *C. leucas* catch also increased significantly with a positive (wetter) SOI.

**Figure 15.** Conceptual model of the two size classes of *C. leucas* in relation to previous rainfall. The model represents the hypothesised movements of small (<2 m TL) and large (> 2m TL) *C. leucas* from opposing habitats into beach areas after sufficient rainfall 1 to 8 days prior to capture in QSCP areas.
(Figure 13), suggesting better neonate recruitment during wet years when nearshore fisheries catch is higher. SOI appears to be correlated to rainfall patterns driving the movement of *C. leucas*. SOI, however, is a useful indicator of potential rainfall patterns not detected directly in other *C. leucas* categories such as pregnant females. While it is difficult to prove underlying environment-recruitment correlations, Meynecke et al. (2006) expect rainfall and temperature to alter fish species composition. In addition, disruption of ecological process that drive biological productivity and prey availability modulated by climate (e.g. rainfall) are likely to influence *C. leucas* catch and long-term trends in populations. Many sharks are 3rd or 4th trophic level consumers and as such regulate lower trophic levels (Cortes 1999). Reduction in *C. leucas* recruitment due to increase in frequency or severity of dry years may affect lower trophic levels as reduced *C. leucas* abundance has cascading and long reaching flow-on effects in an ecosystem (O’Connell et al. 2007).

Lunar phases have been shown to play a role in food availability, activity, stress, temperature and salinity ‘choices’, for lemon sharks (Brown & Gruber 1988), diving behaviour of whale sharks (Graham et al. 2006). Depth preferences of juvenile whites (Weng et al. 2007b) and CPUE of blue shark, *Prionace glauca*, and shortfin mako shark, *Isurus oxyrinchus*, are suggested to both be due to associated movement of prey species (Lowry et al. 2007). Moonlight avoidance has been recorded in other large predators, including the Galápagos fur seal, *Arctocephalus galapagoensis* due to (1) predator (shark) avoidance and (2) varying feeding efficiency of the fur seals due to the influence of moonlight on the vertical distribution of prey (Trillmich & Mohren 1981). I hypothesize that juvenile *C. leucas* may be moving into nearshore areas with greater frequency during periods of reduced moonlight to avoid predation from adult conspecifics.

### 3.4.1 Implications for management
This study has demonstrated specific links of *C. leucas* catch and presumably feeding activity to parameters of climate. Predictions of future rainfall and SOI trends are possible and can be monitored for informed adaptive management in fishing and shark control measures. Meynecke et al. (2006) suggest positive effects of rainfall such as availability of food and negative effects such as higher mortality of juveniles and reduction in useable nursery habitat from changes in salinity and/or turbidity infer
linked mechanisms between productivity, rainfall and catchability. Management policies that ensure sustainability of shark populations under conditions of environmental pressure, such as reduced rainfall patterns from more frequent El Niño, should be enabled. For the east coast of Queensland, differences in catch for small (< 2 m) and large (> 2 m) C. leucas suggest different feeding activity patterns in nearshore habitat in response to climate parameters (Figure 14). Whilst these differences probably reflect transition from estuarine nursery habitat into larger foraging areas incorporating the nearshore region as part of the lifecycle of the C. leucas, they highlight the importance of individual management and conservation strategies for juvenile and adult C. leucas populations. Shark fisheries remain stable when long-lived adults remain in populations to ensure sufficient recruitment (Prince 2005). While a ‘gauntlet’ fishery that only targets neonates, juveniles and sub-adults has been shown to be sustainable for school shark (Galeorhinus galeus) and gummy shark (Mustelus antarcticus), adequate protection of habitats used by each stage of a species lifecycle is necessary (Gillanders et al. 2003; Prince 2005; Punt et al. 2005). Management strategies that incorporate protection of rivers and estuaries in addition to nearshore habitats will ensure conservation of near-threatened C. leucas populations (IUCN 2008) in the face of expected climate change.

Understanding stock-recruitment relationships in elasmobranchs is important for fisheries management (Cortés 1998) and these relations have been suggested to be linear (e.g. dogfish) (Holden 1977) or density-dependent, with constant recruitment over a range of high parental stock levels (e.g. gummy shark) (Walker 1994). However, no studies have identified climate parameters as drivers. Sufficient rainfall may be an important element of the recruitment processes for C. leucas, due to their lifecycle relying on euryhaline environments. The significant relationship between SOI and pregnant C. leucas catch in passive gears suggests pupping may be timed with appropriate environmental conditions for neonates and this warrants further investigation.

Estuarine and coastal systems are likely to exhibit earlier regional changes in species loss from shifts in climate as many species in these habitats live near their tolerance levels (Carlton 1996). Given the ability of the C. leucas to tolerate a wide range of salinities and environmental conditions, this species may be capable of sustaining
greater fluctuations in environmental extremes. The clear link of rainfall to *C. leucas* catch and feeding activity in nearshore habitats illustrates management and conservation strategies need to consider these effects. Measuring the movement of *C. leucas* < 2 m TL and > 2 m TL is critical to better understand the responses of *C. leucas* to climate parameters in nearshore habitat and to determine the connectivity between nursery habitats and those used by adults. *C. leucas* are highly adaptable (Ortega et al. 2009) and acoustic and satellite telemetry will better determine the movement and depth preferences of adults in shelf environments and the importance of connectivity of nearshore habitats to the shark’s life cycle. Determining which specific habitats or sites contribute more per unit area to the production of individuals that recruit to adult populations will enable management efforts to focus on habitats that make the largest contribution to adult populations and potentially have these sites set aside as marine protected areas (Gillanders et al. 2003). Conserving these habitats may provide buffers for *C. leucas* populations in the face of climate change.
CHAPTER 4

SHORT-TERM MOVEMENT OF THE BULL SHARK WITH PARTICULAR REFERENCE TO THE INFLUENCE OF HYDROLOGY

4.1 Introduction
Understanding fine-scale patterns of habitat use by sharks is important to gaining an insight into the distribution of top-level predators and is essential to predicting the consequences of human disturbance and environmental changes on these species. Top-level predators often have low population densities and large home ranges, making studies of their habitat use a challenge. Previous studies of top-level predators have relied on tracking data to identify broad-scale movement patterns (Holland et al. 1999). However, reliable data on the fine-scale patterns are scant, yet necessary for understanding the dynamics of habitat use in spatially heterogeneous ecosystems (Heithaus et al. 2002). One way of tagging, acoustic tracking, has been used to follow animals and determine their fine-scale movements over short periods and this technology proves useful, for example, for identifying habitats that optimise survival and growth (Sundstrom 2001, Gowan & Fausch 2002). Further, some analysis of shark habitat use has been enabled using crittercam, an attached underwater video camera with an integrated time-depth recorder, which provides continuous fine-scale movement data and insight into the shark’s behaviour (Heithaus et al. 2001).

Coastal wetlands fulfil important functions through providing habitat and food sources for associated organisms. This value of wetlands is, however, influenced by the main physical drivers of hydrological and sedimentation regimes (Hughes et al. 1998, Clynick & Chapman 2002, Faulkner 2004). Rapid global trends towards urbanisation of coastal environments can impact the ecological processes of these habitats, largely through the alteration of hydrology and sedimentation, as the impervious surfaces can concentrate run-off from rainfall increasing loadings of sediment, nutrients and pollutants (Lee et al. 2006). Furthermore, changes in
hydrology have been hypothesised to disrupt wildlife migration routes (Lee et al. 2006). Sharks that rely on riverine environments during their life cycle may be especially vulnerable to changes in coastal environments (Martin 2005, Ortega et al. 2009). Euryhaline elasmobranchs, such as juvenile *C. leucas* (Pillans et al. 2005), and the spear tooth shark, *Glyphis* spp. (Pillans et al. 2009), rely on riverine and estuarine environments throughout their life cycle. The limited extent of riverine areas suggests euryhaline elasmobranchs may be particularly influenced by changes in the hydrological regime. Therefore, it is essential to gain a better understanding of the fine-scale habitat use of riverine sharks in relation to hydrology to inform both conservation and management of the species.

Environmental variables, such as salinity (Heupel & Simpfendorfer 2008), temperature, diel period (Ortega et al. 2009) and correlations with tide (Pillans et al. 2009), have been shown to influence the movements of euryhaline elasmobranchs. However, short-term tracking studies measure the physical variables at the location of the research vessel following the animal being tracked or infer correlations with measured parameters at a single or from several fixed locations in the study site. To date, no studies have related short-term movement of sharks to fine-scale hydrology at the inferred location of the animal as it moves through time and space. Southern Moreton Bay (Australia), including the Gold Coast with the adjoining Nerang River and numerous man-made canals is an area used by *C. leucas* (Zeller 1999, Pillans & Franklin 2004). In addition, state-of-the-art hydrodynamic numerical models, e.g. MIKE HD, a computer modelling program developed by DHI (Danish Hydraulic Institute), have been extensively ground-truthed, providing a strong ability to determine current velocity and direction down to a scale of 1 m$^2$ throughout this system (Mirfenderesk & Tomlinson 2009). These models can be related to the fine-scale movements of juvenile *C. leucas* that occur throughout this area, providing a powerful examination of the hydrological regime at the location of a tracked shark and can be used to predict shark movement.

In order to gain an understanding of the fine-scale movements of juvenile *C. leucas* in relation to hydrological processes, the present study aims to (1) identify the short-term movement patterns of juvenile *C. leucas* in the Nerang River, adjoining man-made canals and the connecting southern Moreton Bay; and (2) determine how fine-
scale movement patterns of *C. leucas* are related to hydrology and other physical parameters.

### 4.2. Methods

#### 4.2.1 Study site

Sampling for *C. leucas* was carried out from February 2007 to March 2008 in Southern Moreton Bay at the entrance to Coomera River and in the Gold Coast canals system (Figure 16). The entrance to Coomera River connects to the Broadwater and the open ocean at the Seaway (Figure 16 D). This area has large stands of mangrove vegetation (mainly *Avicennia marina*) and is characterised by tidal sand flats and deep channels. South of the Seaway and connecting to the Broadwater is the Nerang River which has numerous adjoining man-made canals with trophodynamics that differ to areas with more mangrove and natural vegetation (Waltham & Connolly 2006). The top reaches of the Nerang River are tidal and salinity fluctuates from 6 to 25 ‰ (Figure 16 A). Most of the artificial man-made canals connect to the middle reaches of the Nerang River (Figure 16 B). The Nerang River and estuary responds non-linearly to tidal forces, with a predominately semi-diurnal and flood-dominant regime (Mirfenderesk & Tomlinson 2009). Depth ranges from < 1 m to an average of 2 - 3 m, with several distinct deep holes 5 – 10 m in the Nerang River and adjoining canals. Bathymetry in the Broadwater and Southern Moreton Bay ranges from 1 – 20 m.

#### 4.2.2 Capture and tagging of juvenile *C. leucas*

The majority of *C. leucas* were captured using modified longlines of 1000-pound monofilament. Traces were attached to the main line and set mid water. Traces consisted of 1 m of 300-pound monofilament with 1 m of stainless wire and an 8/0 tuna hook. Freshwater eel fillets and mullet (mostly *Mugil cephalus*) were used as bait. Lines were set in each of the study areas and checked every two to three hours. Captured *C. leucas* were restrained in a specially designed harness next to the research vessel (Figure 17), measured (TL), sexed, and tagged with a single barbed plastic external stream tag next to the dorsal fin for identification (Figure 18) and a fin clip sampled for genetic analysis. For those animals to be tracked, acoustic tags (V16 and V16P, Vemco) were attached with dissolving galvanic release to the dorsal musculature. In this method, acoustic tags were embedded in a small float and were
retrieved and detached from the animal after 6 to 18 hrs. This method was used for tracking *C. leucas* in the Southern Moreton Bay and lower reaches of the Nerang River (Figure 16 B and D) immediately after release.

**Figure 16.** Study area in sub-tropical Queensland, Australia, showing the sites (A to D) of the short-term tracking and crittercam deployments. A - the top reaches of the Nerang River; B - mid-ranges of Nerang River and adjoining man-made canals; C - man-made canals of Mermaid waters and Bond University lake; and D - southern Moreton Bay at the entrance to Coomera River south to the Gold Coast Seaway.
In addition, five *C. leucas* were captured in the Nerang River and Gold Coast canals and an acoustic tag was attached via a roto tag to the dorsal fin (Figure 19). These sharks were then released and periodically tracked two to six weeks after release.

**Figure 17.** Captured *C. leucas* in specially designed harness (a) with water flow maintained over the gills (b) by positioning the shark facing the current.

**Figure 18.** Orange barbed plastic external stream tag next to the dorsal fin for identification.

### 4.2.3 Telemetry

Short-term tracking was done using a Vemco VR60 acoustic receiver and a Vemco V22tp-01 hydrophone. Acoustic tags were Vemco V16 transmitters with a battery life of ~ 36 to 48 d. Transmitters pulsed continuously (every 1.03 s) on one of five acoustic frequencies (51, 54, 57, 60, 78 kHz) (Figure 19). Tracking was carried out using a 4.5-m aluminium boat or 5.9-m Stabicraft research vessel. The hydrophone was mounted on an aluminium pole that was rotated manually in order to maintain accurate signal strength and ascertain the direction of the shark from the boat. The
tagged animal was followed from a boat and its approximate location determined and plotted on GPS. Every 10 minutes the boat GPS location and direction to the shark was recorded. Estimated distance to the shark was based on distance-signal strength calibration conducted prior to tracking, which indicated position ± 5 m with the Nerang River and adjoining man-made canals and ± 10 to 15 m in southern Moreton Bay. In general a distance of 50 – 100 m was maintained from the shark in the Nerang River and canals, as in most cases the engine was not used and the boat was manoeuvred using oars or simply remained free floating. A distance of 50 - 300 m was maintained in southern Moreton Bay depending on the weather conditions or if the motor was engaged. Several of the sharks for which acoustic tags were attached via roto tag were tracked once during night (1800 to 0559 hrs) and day (0600 to 1759 hrs) each for a 6-hr period. Tracks of these sharks were done by randomly selecting a tagged individual and sequentially driving the Nerang River and the adjoining canal system until the chosen shark was located.

![Roto tag through dorsal fin of a juvenile C. leucas with attached acoustic tag.](image)

**Figure 19.** Roto tag through dorsal fin of a juvenile *C. leucas* with attached acoustic tag.
4.2.4 Crittercam

Crittercam is an animal-borne recorder that enables continuous monitoring of the shark by video in addition to integrated temperature, salinity and depth data collection (Heithaus et al. 2002). In this study crittercam was used as a fine scale pressure sensor in order to describe the minute by minute vertical and horizontal movements. These units have been successfully deployed on large *G. cuvier* and *C. leucas* and are attached via a soft clamp on the dorsal fin with a timed release (Heithaus et al. 2001). Heithaus et al (2002) reported that *G. cuvier* show no obvious behavioural changes to crittercam attachment and their movements remain similar to those tracked with standard acoustic telemetry. In this study, large *C. leucas* (~ 1.5 m TL) that were swimming strongly were tracked with crittercam in southern Moreton Bay only. An acoustic tag was also attached to the unit to enable the shark to be followed until the dorsal fin clamps disengaged the crittercam. Crittercam is positively buoyant and floats to the surface. The camera was then recovered using a TR-4 VHF receiver (Telonics) that detected a signal from a built-in VHF transmitter. Crittercam were left attached for 2 hr as initial short-term tracks acoustic tracking showed *C. leucas* of 1.5 m or larger return almost immediately to normal movements in this study site when released quickly after release (unpubl. data).

4.2.5 Physical parameters

Depth, current direction, tide (flood or ebb) bearing and temperature and salinity readings were recorded using a TPS kit in conjunction with the shark’s position every 10 min. To relate detailed knowledge regarding the temporal and spatial variations in depths and flows to the movement of *C. leucas*, a state-of-the-art hydrodynamic model, MIKE HD (Danish Hydraulic Institute for water and environment) (Mirfenderes & Tomlinson 2009), was used. Current velocity, direction and water depth for each position of the shark during its track were extracted from modelled simulations. For the Nerang River and adjoining canals, a single simulation was run for this area one month before and after each shark track over the period of the study. A separate simulation was done for tracks obtained at the southern Moreton Bay site.
4.2.6 Statistical analysis

Statistical tests were performed using Genstat (v.11) and SPSS (v.17) with significance set at the 0.05 level. Recorded positions of the boat were plotted using ArcGIS (v.9.3) and the positions of *C. leucas* were then plotted based on signal-strength recordings and direction from the boat. Distance between consecutive points was calculated using the ‘measure distance’ tool following the contours when the sharks were in the Nerang River or adjoining canals. The rate of movement (ROM) in m s\(^{-1}\) was determined by dividing the distance in metres between consecutive points by the sampling interval and initially compared to current velocity using chi-square analysis. Current velocity and direction were plotted at the location of individual *C. leucas* through time using MatLab R2007b. Activity space of *C. leucas* was determined by plotting the shark positions in ARC GIS v.9 using the home range extension. The total activity space used by each animal in each location was determined using minimum convex polygon analysis, with the smoothing factor calculated via least-squares cross validation and regions of the study site at which most detections occurred were visually identified. Relative sizes of kernels (50, 90, and 95 %) were compared across locations by one way-ANOVA after natural log transformation. A Tukeys test was done to determine where differences occurred. In order to determine the influence of the hydrological regime on the sharks, circular statistics (Mardia 1972) were used to compare the sharks’ ROM and heading (degrees) with current velocity, direction (degrees) and still water depth. A polar plot was used to represent the proportions of *C. leucas* movement in relation to the current direction after Rayleigh’s test of uniformity (0.141). Categorised direction difference of *C. leucas* was then done to investigate shark speed as instantaneous representations of distances. All physical parameters were incorporated in a univariate generalised linear model (GLM) and comparison of diel period was done based on time periods of tracks in day and night. To stabilise skewness and variances, variables were log\(_{10}\) transformed. Regression analysis was used to compare the relationships of current velocity and salinity with *C. leucas* ROM.
4.3 Results

4.3.1 Acoustic tracking of *C. leucas*

Eleven *C. leucas* were captured in this study and ten *C. leucas* were tracked, with three successful crittercam deployments (Table 7). Shark TL ranged from 0.78 to 1.98 m, with tracks from 2 to 18-hr duration and a total of 400 detections. One *C. leucas* to which an acoustic tag was attached via roto tag was not able to be located two weeks after release. Based on other movement data (unpubl. data) and the size of this *C. leucas*, it was considered that this animal left the study site and was unable to be tracked. Sharks were tagged in all locations other than the top reaches of the Nerang River (Figure 16, region A), although animals subsequently moved into this area. *C. leucas* moved from 5.2 to 18 km over 6-hr periods and up to 31.2 km for the 0.92 m TL male tracked over 18 hr (Figure 20). ROM varied from 0.03 to 0.92 m s$^{-1}$ with an average of 2.7 ± 2.5 m s$^{-1}$ across all animals (Table 7). The largest *C. leucas* (1.8 m TL) that was tracked moved 18 km at an average of 0.92 ± 0.93 m s$^{-1}$ and this movement was often with the ebb tide (Figure 20 D). Tracking data revealed that 0.33 of shark movements did not correlate with current flow conditions, with equal probabilities with, against or indifferent to the current (Figure 21).
Table 6. Morphometrics, catch and track details and physical parameters at capture for individual C. leucas. * indicates crittercam deployments.

<table>
<thead>
<tr>
<th>Shark No.</th>
<th>Gender</th>
<th>Total Length (m)</th>
<th>Date</th>
<th>Site</th>
<th>Capture Length (hr)</th>
<th>Length (km)</th>
<th>Mean shark heading (degrees)</th>
<th>Mean ROM (m s$^{-1}$) ± SD</th>
<th>Mean Temp. (°C)</th>
<th>Salinity range</th>
<th>Absolute water depth range (m)</th>
<th>Mean Current Velocity (m s$^{-1}$) ± SD</th>
<th>Mean current direction (degrees)</th>
</tr>
</thead>
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<td>0.85</td>
<td>1/04/2008</td>
<td>B</td>
<td>6</td>
<td>18</td>
<td>177</td>
<td>0.1 ± 0.1</td>
<td>21.3</td>
<td>17.2 - 19.4</td>
<td>1.5 - 3.4</td>
<td>0.04 ± 0.01</td>
<td>178</td>
</tr>
<tr>
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<td></td>
<td></td>
<td>23/04/2008</td>
<td>A</td>
<td>day</td>
<td>8</td>
<td>191</td>
<td>0.13 ± 0.2</td>
<td>21.2</td>
<td>15.8 - 18.1</td>
<td>1.1 - 3.3</td>
<td>0.03 ± 0.01</td>
<td>234</td>
</tr>
<tr>
<td>2</td>
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<td>0.78</td>
<td>1/04/2008</td>
<td>B</td>
<td>6</td>
<td>15.9</td>
<td>0.14 ± 0.1</td>
<td>22.5 – 19.7</td>
<td>12.2</td>
<td>16.1 - 19.7</td>
<td>1.2 - 3.2</td>
<td>0.04 ± 0.01</td>
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</tr>
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<td>166</td>
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<td>0.23 ± 0.12</td>
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<td>3/04/2008</td>
<td>C</td>
<td>6</td>
<td>14</td>
<td>172</td>
<td>0.19 ± 0.27</td>
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<td>17.8 - 24.4</td>
<td>2.1 - 9.9</td>
<td>0.04 ± 0.06</td>
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<td>day</td>
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<td>17.4 - 26</td>
<td>2.3 - 6</td>
<td>0.05 ± 0.07</td>
<td>124</td>
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<td>25/04/2008</td>
<td>C</td>
<td>2</td>
<td>3</td>
<td>172</td>
<td>0.04 ± 0.08</td>
<td>22</td>
<td>22.3 - 26.1</td>
<td>3 - 10</td>
<td>0.02 ± 0.01</td>
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<tr>
<td>5</td>
<td>M</td>
<td>1.18</td>
<td>3/04/2008</td>
<td>B</td>
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<tr>
<td>6*</td>
<td>F</td>
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<td>21/01/2008</td>
<td>D</td>
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<td>1.8</td>
<td>186</td>
<td>0.19 ± 0.03</td>
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<td>4.8 - 5.4</td>
<td>0.21 ± 0.09</td>
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<td>23/02/2007</td>
<td>D</td>
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<td>22</td>
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<td>21.4</td>
<td>23.1 - 26.1</td>
<td>3.3 - 10</td>
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<td>23 - 33</td>
<td>2 - 7.7</td>
<td>0.4 ± 0.1</td>
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Figure 20. Bathymetry and *C. leucas* individual short-term tracks for the period of the study at sites A to D (refer to Figure 14). Arrows indicate the direction of *C. leucas* movement.
These results indicated that sharks moved both with and against the current during tracks. A consistent direction difference factor by current speed interaction was found (deviance = 2.74, p = 0.005), with the main contrast being between proportion of shark tracks heading directly into the current versus those moving with the current (Figure 21). *C. leucas* heading with or against the current was not consistent with current speed.

**Figure 21.** Deviation of mean *C. leucas* movement in relation to current direction. Region of proportion of total movements with the current (-45 to 0 and 0 to + 45) and against the current (-45 to 0 and 0 to + 45) are indicated by grey arcs and broken lines. Areas in-between the arcs indicate movement neither with nor against the current. Circles correspond to proportions indicated at the -90 mark to the centre of the plot.
C. leucas showed overall movements both upstream and downstream and as indicated by the GLM, movements constituted significant periods of both movement with and against the current in addition to periods of movement irrespective of the current (Figure 21, 22 a, b, c). C. leucas ROM decreased with increasing current velocity (p = 0.026) (Figure 23 a), but increased when C. leucas were moving both independent of the current and with the current (Figure 23 b, c). The magnitude of C. leucas ROM in relation to with current (0.09 to 0.4 m s⁻¹) (Figure 23 c) was substantially greater than when C. leucas moved against the current (0.062 to 0.086 m s⁻¹) (Figure 23 a). However, overall ROM trends was greatest during periods of movement irrespective of the current (~ 0.1 to 1 m s⁻¹) (Figure 23 b).
Figure 22. Velocity vectors and direction at individual *C. leucas* position detections for the top reaches of the Nerang River (A), man-made canals of Mermaid Waters (B) and southern Moreton Bay at the entrance to Coomera River south to the Gold Coast Seaway (C). Numbers indicate sequence of detections. Strength of flow is illustrated by size of arrows (scale $\times 1000$ cm s$^{-1}$).
Further, GLM indicated that salinity was correlated with *C. leucas* ROM, with increasing speed in higher salinities. This was best described by an asymptotic relationship (double-log transformation, $r^2 = 0.9$, $p < 0.0001$). While all physical parameters were considered in the model, no other factors (including diel period) were detected as having an effect on the movement of *C. leucas*.

### 4.3.2 Movements in relation to depth

*C. leucas* for which swimming depth were obtained from acoustic tags ($n = 2$) exhibited a pattern of remaining predominantly in the mid to bottom layers of the water column (Figure 24). *C. leucas* with crittercam deployments ($n = 3$) displayed finer scale movement. While still remaining in the mid to lower levels of the water column (average depth $2.8 \pm 1.6$ m) and on occasion coming to the surface, *C. leucas* would swim with a small, but relatively rapid, descent with intermittent rapid ($16 \pm 3$ s) deep dives ($8.5 \pm 2$ m) characterised by both rapid descent and ascent (Figure 25).
Figure 24. Swimming depth and bottom depth throughout the track of a 95-cm TL *C. leucas* male (Shark 3) in the mid-section of the Nerang River (Site B). Corresponding salinity is shown beneath the bottom depth.

Figure 25. Vertical movements of *C. leucas* (Shark No. 9) as recorded by crittercam (24 hr time). The thick line beneath the depth profile indicates the sea floor.
4.3.3 Activity space
Relative activity space of *C. leucas* between locations varied significantly (F = 14.312, df = 3, p = 0.001), but in all locations most 50% kernels were centred over deep holes (Figure 26 A). Tukeys test indicated the top and mid section of the Nerang River formed a subset, the mid section of the Nerang River and the man-made canals a second subset and a third subset occurred between the man-made canals and southern Moreton Bay. Movements of *C. leucas* between the deep holes were generally directed from one deep hole towards the next in that study site. Kernels of 50% and 95% were confined over deep holes in a tight area of 0.036 km$^2$ and 0.042 km$^2$, respectively, in the top reaches of the Nerang River. Kernels in the mid reaches of the Nerang River were also centred over areas of deep holes in the study site for an area of 0.257 km$^2$ (50%) and 0.273 km$^2$ (95%) (Figure 26 B). *C. leucas* movements were further detected predominately over deep holes in the man-made canals, with 1.05 km$^2$ at the 50% kernel (Figure 26 C). 50% kernels (with 1.78 km$^2$) for *C. leucas* in southern Moreton Bay occurred over deep holes at the entrance of Coomera River and the Seaway.
Figure 26. Kernel estimates per site of combined *C. leucas* short-term movement across the study sites. Red colour indicates area enclosing 50% of detections.
4.4 Discussion

Short-term movement patterns of *C. leucas* showed that they were capable of moving up to 18 km during an ebb tide. *C. leucas* display a pattern of foraging in deep holes followed by a cyclic up or downstream movement towards other deep holes, a similar pattern displayed in mulloway, *Argyrosomus japonicus* (Taylor et al. 2006). This pattern resulted in *C. leucas* repeatedly using small sections of available habitat, with patterns of movement between holes repeated across all size ranges of shark and locations studied. Directional movements can indicate avoidance of an area (Bergman et al. 2000). Directional movements to particular habitats have been observed in tiger shark, *Galeocerdo cuvier* (Heithaus 2001), scallop hammerhead, *Sphyrna lewini* (Klimley 1993) and related to the tide in leopard shark, *Triakis semifasciata* (Ackerman et al. 2000) and juvenile sandbar whalers, *Carcharhinus plumbeus* (Medved & Marshall 1983). Riverine sharks in other studies moved in the same direction as strong tidal currents in order to assist movements upstream or downstream (Pillans et al. 2009). This phenomenon was observed in tracked sharks in the current study. The fine scale at which current velocity was able to be determined, however, indicated that while *C. leucas* may use tidal current to assist movement, periods of movement against current readily occurred. Observations in the field indicated that *C. leucas* moved against the tide or maintained a position usually during slack tide or in an eddy, a phenomenon also observed in *Glyphis* spp. (Pillans et al. 2009). *C. leucas* maintained positions against the current generally over deep holes. This behaviour may help detect prey that are upstream. ROM against the current declined with increasing current velocity, which probably indicated higher level of energy required to maintain movement and in many cases the sharks would increasingly turn with the current when velocity increased over 0.6 m s\(^{-1}\). *C. amblyrinchos*, however, have been observed to swim against strong currents (> 0.6 m s\(^{-1}\)) by moving slowly close to the bottom (pers. observ., Osprey Reef, Australia), possibly in bottom layers where the substrate decreases the current speed and drag. Juvenile *C. leucas* in the upper areas of the Nerang River experienced a mean current velocity of 0.04 ± 0.01 m s\(^{-1}\), as compared to a ten-fold average increase in flow in the lower reaches of the Nerang River and southern Moreton Bay. In these two locations of higher flow, *C. leucas* displayed periodic movement against the current in areas of
deep holes and eddies. Flow was greater in the sections of the man-made canals where *C. leucas* were detected compared to the top of the Nerang River.

Several estuarine species, such as penaeid shrimp, mangrove jack (*Lutjanus argentimaculatus*) and barramundi (*Lates calcarifer*), have been noted to selectively use tidal currents as a transport means to maintain positions in the estuary or selectively facilitate movements into and out of inshore waters (Hughes 1969, Williams 2002). Further, grey nurse shark, *Carcharhinus taurus*, are often noted maintaining their position in the water column facing the current in sand gullies (Pollard et al. 1996). Bathymetry is believed to be one of the major influences on the dynamics of tidal currents and water velocities (Egbert 1997) and may assist organisms to remain in preferred foraging habitats. Kernel estimates for *C. leucas* in this study indicated a consistent association with deep holes, with directional movement between holes. *C. leucas* may be using these areas as refuge areas to maintain position against the current in order to conserve energy. Depth profile of shark 3 also indicated periods in holes were spent in the mid to bottom layers of the water column.

The significant periods of time in which all *C. leucas* congregated in areas of limited deep holes suggests this species may be particularly susceptible to fishing pressures (Martin 2005). Recreational fishing for *C. leucas* is a popular sport in the Gold Coast area (pers. observ.). Given the limited volume of the river and estuarine habitat and frequent movement between deep holes suggests targeted fishing in these holes could significantly influence the local *C. leucas* population. It was noted that tagged *C. leucas* (shark 2) that were tracked over a two-week period in the top reaches of the Nerang River were also detected approximately two weeks later in the deep holes in the man-made canal system (Figure 16 C). In addition, one shark tracked in the man-made canals was subsequently detected in the mid reaches of the Nerang River approximately two weeks later. While neither of these sharks were tracked over time after their additional detections, their subsequent occurrence in these adjacent habitats suggests *C. leucas* move between deep holes between the study site locations, possibly over two week cycles. This further illustrates their particular vulnerability to fishing.
Optimal selection of a foraging habitat by a predator can increase the probability of encounter with prey (Heithaus 2004). Diving patterns of sharks have been observed with crittercam for example, which illustrated a stereotypical swimming pattern referred to as ‘bouncing’ by Heithaus et al (2002) in tiger sharks, Galeocerdo cuvier. This pattern of movement was characterised by a rapid descent followed by a slower ascent which reflected power-swimming. Heithaus et al (2002) hypothesise that this behaviour is a strategy of stealth, enabling stalking of both surface breathing and benthic prey. Rapid distinctive deep dives of C. leucas illustrated using crittercam in this study occurred with both rapid descent and ascent. C. leucas may be moving into deeper and cooler waters, but quickly returning to shallower waters on the surrounding intertidal banks of the study site as a foraging tactic to optimise targeting of both benthic and midwater prey. Deep dives most likely occurred when C. leucas was moving away from shallow intertidal areas and along banks adjacent to a deep channel. Observation of crittercam video suggests the deep dives of C. leucas occurred at the edge of the channel.

How sharks hunt their prey is perhaps the least understood aspect of their feeding biology (Motta 2004). However, rays and sharks have been observed hunting and chasing down chokka squid, Loligo vulgaris reynaudii, to capture them off South Africa (Smale et al. 2001). Further, white sharks, C. carcharias, will stalk prey downstream in tidal currents (Pyle et al. 1996), and sevengill sharks, Notorynchus cepedianus, move within striking distance before making a quick dash at the prey (Ebert 1991). The magnitudes of increase in C. leucas ROM during periods of movement independent of the current compared to movement with or against the current suggest C. leucas are undertaking short bursts of speed during these periods. When moving with the current, C. leucas are probably gliding, but using energy to swim when moving against the current explaining the reduced ROM during these periods. However, bursts of speed irrespective of the current could indicate foraging activities or opportunistic pursuit of prey. Furthermore, this pattern of increased ROM was consistent across C. leucas tracked suggesting a strategy of quick dash at prey is readily used by this species in river and estuarine habitats.

Niche partitioning between shark species in estuarine and river conditions has been observed in other studies. Pillians et al. (2009), for example, noted a niche partitioning
amongst Glyphis spp. and C. leucas, with C. leucas further upstream and in less turbid waters in rivers of north Australia. Competition between C. leucas, however, is likely to be sized-based as larger C. leucas prey on smaller conspecifics. Competition for food sources has been noted between sympatric species of sharks (Carrasson et al. 1992), between co-occurring teolosts and sharks and sharks and marine mammals and between consecutive size classes of sharks of the same species. Simpfendorfer et al. (2005) noted some partitioning among 0+ and 1+ yr C. leucas in a survey in a southwest Florida nursery in the USA. Within the current study site, the size-limited habitats could force periodic emigration of C. leucas to search for suitable habitat and prey further downstream, as predation risk from conspecifics decreases. It was interesting to note that two tagged sharks (No. 4, and 10) of 1.13 m and 1.6 m TL, respectively, co-occurred over a two-hour period in the same deep hole in the man-made canals during the tracking of shark 10. This co-occurrence further highlights the importance of these deep hole areas to C. leucas and illustrates the potential size classes of C. leucas that can co-occur.

Salinity is one of the major physical changes associated with changes in tide that elicits a corresponding behaviour in marine organisms (Rowe & Dunson 1995, Heupel & Simpfendorfer 2008), enabling organisms to use a tide for placement and avoiding displacement by alternative tides. This study revealed an effect of salinity on the ROM of C. leucas and salinity has been shown to have an important effect on the displacement of this species in relation to TL along the length of a river (Pillans & Franklin 2004). Responses to salinity may contribute to directional movement with tide by C. leucas in combination with asynchronous opportunistic feeding on abundant prey using similar movement strategies. Freshwater flows into tropical estuaries and coastal rainfall have been shown to influence hydrological regimes and trigger spawning in king threadfish, Polydactylus macrochir, and barramundi, Lates calcarifer, and seasonal blooms in prey such as Ascetes spp. (Halliday et al. 2008). These authors suggest that reduction in flows from development of water infrastructure or long-term climate change may reduce the population of estuarine fish and this will have a direct effect on shark populations.

Natural wetlands have a hydrological regime of diffuse flow during non-flood periods and concentrated flow to estuarine areas during flood events. However, urbanisation
alters this regime to further concentrate rain-fall runoff and create hydraulic modification of tidal flows (Lee et al. 2006). The implication of this for euryhaline top-level predators may be reduced value of coastal habitat to these species. The type of vegetation cover is critical to balancing hydrology in estuaries and urbanisation may alter conditions above the preferred tolerance range to the velocity and duration of inundation for *C. leucas*. Movement of some estuarine eels is not directly correlated with tide, e.g. cownose ray (*Rhinoptera bonasus*), which remained in very small areas for long periods of time (Collins et al. 2007). When estuarine systems are inundated by rainfall (e.g. during floods), these species may, however, be displaced to lower reaches of rivers (Heupel & Simpfendorfer 2008) and nearshore environment (see Chapter 3). Further, the influence of turbidity on the short-term movements of *C. leucas* is unknown.

The influence of hydrology with associated bathymetry and salinity play a key role in the distribution and short-term movements of *C. leucas*. Movement between deep holes occurs with selective use of tide and water velocity. Deep holes provide refuge and probably enable *C. leucas* to maintain their position against prevailing currents. These areas are possibly important feeding grounds and sharks frequently remain or return to these “hotspot” areas for extended periods. *C. leucas* are directly influenced by the limited availability of their habitat and are susceptible to urban influences on habitat hydrology, increased pollution and potential targeted fishing pressures (Martin 2005, Lee et al. 2006). Periods of reduced flow are important for foraging in *C. leucas*. Management needs to consider the ramifications of natural habitat modification and its effects on the hydrological regime to top-level consumers such as *C. leucas* and recognise areas of deep holes represent important areas to the species. Data in this study on foraging behaviour and short-term movement supports the potential effectiveness of “no take” protection zones for *C. leucas* in these areas.
CHAPTER 5

ONTOGENETIC PATTERN OF MOVEMENT AND HABITAT USE OF THE BULL SHARK: THE VALUE OF URBAN HABITAT TO LIFE CYCLE

5.1 Introduction

Estuaries are biologically diverse and productive ecosystems that provide essential habitats for many flora and fauna particularly through their role as nurseries in the life cycle of many commercially important species, including prawns, crabs, fish and sharks (Staples & Vance 1985, Ishikawa et al. 2003, Nagelkerken et al. 2008). Studies of sharks have largely focussed on the importance of natural habitats in their life cycles, feeding and general ecology. Physical conditions such as water depth, temperature and salinity in coastal habitats may play an important role in determining the ontogenetic pattern of use by sharks for feeding and nutrition. Several studies suggest that organisms select their habitat on the basis of available food sources (Micheli 1997, Rangley & Kramer 1998). Nursery habitats usually abundant with prey resources should enhance the survival and growth of juvenile sharks (Simpfendorfer & Milward 1993) and provide refuge from cannibalistic large conspecifics (Heupel & Heuter 2002). Rapid anthropogenic modification of coastal habitats and the global ‘sea change’ phenomenon may have considerable implications for shark species that rely on estuaries as nursery areas (Cohen et al. 1997, Maxted et al. 1997, Ortega et al. 2009). In contrast, the value of alternate habitats, such as urban canal systems, is however, poorly known.

The bull shark, *Carcharhinus leucas*, often regarded as a cosmopolitan species, is one of the few elasmobranchs that is truly euryhaline and freely migrates between freshwater and saltwater environments. This species uses low saline areas as nursery habitats (Jensen 1976, Montoya & Thorson 1982). Within Australia, *C. leucas* is reported from most tropical and sub-tropical estuaries and waterways, having been recorded far upstream in the freshwater reaches of southern Queensland waters (Thomson 1957, Thomson 1978, Last & Stevens 1994). In the Brisbane River,
juveniles are abundant in freshwater environments (Pillans & Franklin 2004), whereas adult *C. leucas* (1.8 – 3.5 m TL) frequent nearshore habitat (Brunnshweiler & Earle 2006). Sightings of *C. leucas* in the Gold Coast canal system are often reported by the media and Gold Coast residents (Zeller 1999). The ability of *C. leucas* to use a range of salinities throughout its life cycle makes them one of the most likely species to regularly use coastal urban habitats (Martin 2005). Ontogenetic changes in habitat use by sharks can result from changes in vulnerability to predation, with more susceptible juveniles selecting safe habitats and shifting into more productive, but dangerous areas as their vulnerability to predation decreases (Werner & Hall 1988, Bouskila et al. 1998, Heithaus et al. 2005). Juvenile *C. leucas* inhabiting nursery areas (sheltered estuarine areas) are likely to delay use of connected habitats if predation risk outside nurseries increases, as adult *C. leucas* are known to consume elasmobranchs, including conspecifics (Snelson et al. 1984, Bouskila et al. 1998, Cliff & Dudley 1991).

Urban canals may operate as extended nursery grounds for neonate and juvenile *C. leucas* outside the range of conventional natural estuaries. Therefore, understanding how *C. leucas* use urban waterways and how use differs ontogenetically is essential for the effective conservation of this species and management of adverse interactions with humans. The aims of this study were to (1) determine the influence of urbanisation on *C. leucas* occurrence in river nursery areas using stable isotope analysis; (2) determine the patterns of movement for *C. leucas* of different ontogenetic stages in the Gold Coast canal system; (3) whether the movements of *C. leucas* of different ontogenetic stages were related to particular key physical factors.
5.2 Methods

5.2.1 Study site
Sub-tropical Queensland is characterised by a combination of mangrove-fringed river systems and estuaries and areas of intense urbanisation, where removal of mangroves and the construction of canal systems adjoining the natural causeway of rivers has occurred (Figure 27). The Gold Coast is the fastest growing city in Australia where increasing urbanisation has largely modified and extended the natural habitats of the Nerang River with extensive canal systems. My main study site was the Nerang River and its adjoining artificial man-made canals (Figure 27 insert). The Nerang River has a mean tidal range of 1.2 m at the mouth, 0.72 m in the upper estuarine region and hence tidal forcing conditions now predominately prevail through a man-made seaway (Morton 1989). Mesohaline (5 – 18 ppt) conditions commence ~ 8 km from the river mouth (Figure 26). The artificial canals provide ~ 200 km of additional waterway to the system (Morton 1989, Waltham & Connolly 2006). Several freshwater areas of the system are landlocked through the construction of weirs and these areas were not included in the study. For the purposes of this study, I divided the Nerang River into four habitats/regions, namely, (1) upper river (UR); (2) lower river (LR); (3) canals on the north side (NC) of the Nerang River; and (4) canals on the south side (SC) of the river. UR and NC are connected with 1.24 and 0.56 km$^2$ of available waterways respectively. UR and LR are also connected with SC (2.34 km$^2$) connected to LR (2.53 km$^2$) but not to UR. NC and SC are also separated by a length of approximately 2.5 km of the Nerang River.
Figure 27. Study area in southeast Queensland, Australia, showing the locations of the VR2 and VR2W acoustic receivers in the Nerang River and the adjoining Gold Coast canal system (insert). One receiver was also deployed at the Seaway (see main map). Broken line (insert) indicates approximate delineation of salinity during non-flood periods. During these periods salinity ranges from 6 to 25 ppt on the west of this divide and 18 to 35 ppt on the east. This salinity delineation was used to identify the upper (UR) and lower (LR) reaches of the Nerang River and the northern canal (NC) and southern canal (SC) habitats. Numbers indicate sampling sites for quarterly surveys of *C. leucas*. Pairs of natural (N) and urban (U) rivers and creeks sampled for *C. leucas* in southeast QLD are also shown.
5.2.2 Capture of sharks

*C. leucas* were captured using modified long lines set throughout the entire Gold Coast canal system and rivers in southeast Queensland (Figure 27). Lines were set with freshwater eel, *Anguilla reinhardtii*, and mullet, *Mugil cephalus*, as bait using 8/0 tuna hooks and checked approximately every two hours. Captured sharks were restrained in a water-filled stretcher that maintained sufficient water flow over the shark’s gills, permitting tagging and the recording of various morphometric measurements (Figure 17, 28). Morphometrics were taken and tagging took place while the shark remained in the water. I ensured a range of *C. leucas* of different ontogenetic stages were tagged, including neonate (young of the year), small juvenile and large juveniles.

![Restraint of large juvenile C. leucas in harness with external acoustic tag attached to dorsal fin.](image)

**Figure 28.** Restraint of large juvenile *C. leucas* in harness with external acoustic tag attached to dorsal fin.

5.2.3 Stable isotope analysis

The signature of urban nitrogen sources ($\delta^{15}\text{N}$) are distinct from those of nitrogen sources in natural coastal systems and can provide an indication of feeding by a consumer within an urban system (Waltham & Connolly 2006). In this study, *C. leucas* captured using modified long lines were also sampled for stable isotope signatures of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. In order to ascertain if sharks inhabiting natural and
urban estuaries derive their nutrients from different sources, long lines were set simultaneously or within several days of each other in three pairs of a natural (N) and urban (U) rivers in subtropical Queensland (Figure 26). Urban and natural rivers within a pair were defined based on area of mangrove and/or urban development along the river compared to surface area of water. Small juvenile sharks (< 1 m TL) only were sampled for tissue and I ensured sharks in each pair of rivers were collected in the mesohaline regions, as salinity is known to affect at least the N isotopic signature. A small piece of tissue was taken from the dorsal fin of three *C. leucas* from each river and frozen until analysed for its isotopic signature. The shark tissue was dried (60°C) and ground prior to analysis on an Isoprime continuous flow isotope ratio mass spectrometer. Isotopic abundance of C and N were expressed as the relative difference (‰) between the sample and recognised standards. Stable isotope analysis uses an ‘isotopic signature’ (e.g. δ\(^{15}\)N) based on the ratio of a heavy, rare isotope (e.g. \(^{13}\)C or \(^{15}\)N), to a light, common isotope of an element (e.g. \(^{12}\)C or \(^{14}\)N) when compared to recognised standard. Isotopic signatures are reported in standard delta notation (δ) and calculated according to the difference between the isotopic ratio and a recognised standard, as follows:

\[
\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000
\]

where \(\delta X\) refers to \(\delta^{13}\)C or \(\delta^{15}\)N, and R is \(^{13}\)C/\(^{12}\)C or \(^{15}\)N/\(^{14}\)N. This signature can clarify food sources for a consumer when the isotopic signatures of available producers are distinct from one another. Differences in producer signatures result from differences in the source of nutrients, and fractionation (i.e. differential retention) of the isotopes of an element during their uptake and assimilation. The signature of a consumer generally reflects that of its food and a comparison of the isotopic signatures of consumers and producers can reveal the source of organic matter over multiple trophic transfers (Peterson et al. 1986), after adjusting for fractionation across trophic levels. An organism’s preference for one food source over another will be reflected in its \(\delta^{13}\)C signature (Werry & Lee 2005), which remains relatively constant (~ +1‰ fractionation) throughout successive steps of the food chain (Lajtha & Michener 1994, McCutchan et al. 2003). Organisms will also take on the \(\delta^{15}\)N signature of the nitrogen in food sources; however, there is an average +2 to +3 ‰ shift (i.e. enrichment) in the value of \(\delta^{15}\)N across each trophic level which may
be species specific (McCutchan et al. 2003). A consumer that has assimilated tissue originating from two distinct prey species has a signature that lies between those of its prey, depending on the relative contribution of each source to the assimilated diet. In addition, consumers that feed within a single habitat will most likely reflect the isotopic signature of the autochthonous producers and prey that feed in that habitat, unless significant allochthonous production is available. In this manner, comparisons of consumer isotopic signatures from different habitats can indicate from which habitat nutrition is sourced. Concurrently the short-term residency or transitory nature of a consumer’s presence within a specific habitat can be determined through lack of correlation of prey and consumer signatures.

5.2.4 Quarterly long-line surveys
To determine the size and distribution of *C. leucas* in each of the four defined habitats/regions in the Gold Coast canal system, lines were set in a random sequence at 16 sites throughout the Gold Coast canal system (Figure 27 insert) on a quarterly basis from 2006 to 2008. Each line contained one baited trace beneath a surface float and a second trace approximately one metre from the sea floor. Sites were sampled over three consecutive nights within each quarter. All sharks captured were stream-tagged to identify recaptures (Figure 17) and selected individuals were tagged with acoustic tags. In order to increase the number of acoustic-tagged neonates in my study, I used gill net sets (8 cm stretched mesh) in the top-most reaches of the Nerang River beyond my quarterly sampling sites.

5.2.5 Acoustic tracking of sharks
The application of acoustic technologies to monitoring animal movement has seen this approach rapidly become a powerful tool for observing animals in coastal and shelf environments (Lacorix & McCurdy 1996, Voegeli et al. 1998, Lacorix & Voegil 2000, Heupel et al. 2006). This method has been successfully applied to determining broad-scale habitat use and movements of sharks that remain in or return to a restricted area for a prolonged period (e.g. nursery or feeding areas) (Heithaus et al. 2001, Bruce et al. 2005). In this study, I used submerged, fixed, independent single-channel acoustic monitors (VR2 and VR2W, Vemco Canada) to test hypotheses regarding the occurrence and movement of *C. leucas* of different ontogenetic stages in urban habitats. An array of 10 underwater receivers were deployed at strategic
locations throughout the Nerang River and adjoining canals of the Gold Coast canal system to record the movements of tagged sharks. Receivers were deployed on existing navigation markers using large grip ties and oriented to ensure full reception of acoustic tags in an area. Receivers with an approximate detection range of 800 m recorded the time and date for individual sharks fitted with acoustic tags (V16 and V13P). The narrow (100 – 300 m wide) Nerang River and adjoining canals enabled each receiver to operate as a ‘curtain’ detecting the presence of sharks with acoustic tags. Salinity and water temperature were recorded in conjunction with the shark’s movements via Greenspan CTD profilers deployed with acoustic receivers. Juvenile sharks are also known to respond to large-scale storm events (Heupel, et al. 2003). To record atmospheric pressure, I also used a Greenspan pressure gauge that was attached above the high water mark at site 5 (Figure 26). Each acoustic tag was attached via a roto tag to the first dorsal fin of the shark (Figure 27). Tags were attached externally to enhance subsequent resighting as there is substantial recreational fishing activity in the system, including targeting of *C. leucas*. Acoustic tags were individually coded with a random signal transmission between 30 and 60 s (V16) and 45 and 75 s (V13P), enabling a battery life of up to 18 mo. Over the study period (1/2/2007 – 30/12/2008), 24 *C. leucas* comprising ten neonates as indicated by the presence of a fresh umbilical scar, six small juveniles (0.67 – 0.72 m fork length (FL)) and eight large juveniles (0.94 – 1.33 m FL), were tagged.

5.2.6 Statistical analysis

All analyses were done using SPSS v17 and Genstat v 13 software. To investigate differences in the catch per unit effort (CPUE) of *C. leucas* during the quarterly surveys, I used a Generalised Linear Model (GLM, binomial with a logit link function) procedure. The model was CPUE + Year + Season + Habitat. Size of *C. leucas* from quarterly surveys was investigated using pairwise comparison of t probabilities comparing location and FL of sharks. Differences in the FL of sharks captured on top or bottom baits of modified long lines were compared using a regression model. Average stable isotope signatures of *C. leucas* from urban and natural rivers in sub-tropical Queensland were plotted for comparison pair-wise comparisons done using paired t-tests.
The presence of individually tagged *C. leucas* via detections on the receivers deployed within the Nerang River and adjoining canals were plotted for the period of the study. Detections of tagged sharks were standardised into a single present or absent score at 15-min intervals, to account for differences in random signal transmission for the different tags (V13P and V16). Simpfendorfer et al. (2005) noted that segregating neonate (< 1 year old) juveniles (> 1 year old) significantly reduces the potential for cannibalism. A 2-way ANOVA of shark size and habitat was used to examine possible differences in the proportion of time spent by tagged neonate (< 1 year old) and juvenile (small and large juvenile, > 1 year old) for shark ontogenetic stages in the river and the canals. The proportion of time spent in mesohaline (6-18 ppt) or polyhaline (19-32 ppt) salinity zones for neonate and *C. leucas* > 1 year old was determined individually for all sharks and compared using t-test of log-transformed data.

To further determine if the different ontogenetic stages of tagged sharks (neonate, small juvenile and large juvenile) exhibited a preference among the four available habitats in the Gold Coast canal system, the proportion of standardised time individuals were recorded was assessed relative to the available area of each habitat (km\(^2\) of water surface) using electivity analysis (Ivlev 1961):

\[
E_i = \frac{r_i - n_i}{r_i + n_i}
\]

Where \(E_i\) = electivity measure, \(r_i\) = percentage of tagged population recorded in habitat \(i\), \(n_i\) = percentage of total habitat \(i\) available in the respective study site. The value of \(E_i\) can range from -1 to 1, with 0 indicating no preference, 1 indicating strong preference and -1 indicating strong avoidance. During the study period, two flood events occurred in the Gold Coast canal system (22/10/2007 - 15/12/2007 and 6/1/2008 - 15/2/2008) and these were recorded on the CTD profilers. Electivity analyses were done separately for flood and non-flood periods, defined according to rainfall and recorded drop in salinity by Greenspan CTDs.

To provide an indication of the maximum displacement at which the tagged sharks moved, the greatest distance between different receivers that detected a tagged shark
was plotted for individual *C. leucas* and linear regression used to describe the relationship between movement and *C. leucas* size during flood and non-flood periods. Detections of individual *C. leucas* were further investigated using generalised linear models (GLM) to determine hourly patterns in detections with tide for the different ontogenetic groups of tagged *C. leucas*. GLM was used to determine patterns in *C. leucas* detections standardised to 15-min intervals and CTD measurements. Atmospheric pressure and daily rainfall patterns were also examined in relation to *C. leucas* movement using GLM. Initial models indicated temperature and salinity interacted whereas tidal effects could be analysed independently of temperature and salinity.

5.3 Results

5.3.1 Stable isotope analysis

Eighteen *C. leucas* were sampled for stable isotopes in three pairs of adjacent urban and natural river systems (Figure 27). Each triplicate $\delta^{13}$C and $\delta^{15}$N *C. leucas* sample attained a distinct signature for each urban (U) and natural (N) river. Urban rivers had a more depleted $\delta^{13}$C signature compared to their corresponding ‘natural’ rivers (e.g. Maroochy (U1) and Noosa Rivers (N1)) and $\delta^{15}$N also differed significantly between natural and urban river pairs. Urban $\delta^{15}$N values were more enriched typically by 1 – 2 ‰ (Figure 29). Paired t-tests were run on the SIA data for juvenile *C. leucas* sharks from the different rivers (natural and urban). $\delta^{13}$C was non-significant between pairs, whereas Maroochy (U1) and Noosa (N1) $\delta^{15}$N differed significantly ($p = 0.014$). However the Gold Coast canals (U2) to Coomera River (N2) ($p = 0.641$), Tweed river (N3) to Tallebudgera creek (U3) ($p = 0.521$) were not significant. Whilst differences in $\delta^{13}$C and $\delta^{15}$N did not all differ significantly between the urban and natural river pairs, a general trend in depletion of $\delta^{13}$C and an enrichment in $\delta^{15}$N occurred for *C. leucas* urban river SIA samples.
Figure 29. Mean $\delta^{15}$N and $\delta^{13}$C (‰) values for juvenile *C. leucas*, from pairs of natural (N) and urban (U) rivers in southeast Queensland. Pairs of corresponding natural (N) and urban (U) rivers sampled are numbered. Arrows indicate the direction of general shift in signatures for the N-U pairs. Means are the average of three replicates +/- SE.

5.3.2 Seasonal surveys

A total of 59 *C. leucas* was captured during quarterly surveys and gill netting in the Gold Coast canal system. Eighteen *C. leucas* (< 1.1 m FL) were captured in the upper reaches of the Nerang River on baited lines and a further nine with gill nets (Figure 30). Sixteen small and large juvenile, sub-adult and one pregnant female *C. leucas* were caught in the lower reaches of the Nerang River. *C. leucas* captured during surveys in the northern canals (n = 9) were 0.5 - 0.9 m FL, whereas *C. leucas* captured in the southern canals were 0.5 - 1.3 m FL (Figure 30). The CPUE of *C. leucas* differed significantly among habitat types (deviance = 11.86, df = 3, p = 0.008) and season (deviance = 12.3, df = 3, p = 0.006). However, patterns of CPUE were consistent across years (deviance = 0.13, df = 2, p = 0.935). CPUE was greatest in the upper (0.73 ± 0.10) and lower reaches (0.46 ± 0.12) of the Nerang River followed by
the southern (0.28 ± 0.10) and northern (0.18 ± 0.10) canals. Highest CPUE also occurred during autumn and summer with only one *C. leucas* captured in winter during the survey period. Fork length of the 59 *C. leucas* differed significantly among habitats (deviance = 8531, df = 3, p = 0.006). Pairwise comparisons indicated a difference between FL of sharks captured in the northern and southern canals (p = 0.013) and upper and lower river (p = 0.003). Northern canals differed from the lower river (p = 0.014), but not the upper river (p = 0.659). Further, the size of sharks caught on top and bottom baits differed (p = 0.008) with larger sharks occurring on bottom baits (0.91 ± 0.40 m FL) compared to top baits (0.71 ± 0.6 FL) during quarterly surveys.

![Figure 30](image-url)

**Figure 30.** Comparison of the sizes of the *C. leucas* caught on surface or bottom lines baited with freshwater eel, *Anguilla reinhardtii*, during quarterly survey and opportunistic gill netting in the Gold Coast canals 2006-2008. Size distributions of *C. leucas* are given as % of total catch (n = 59) for the entire Nerang River and adjoining man-made canals and are divided into regions of upper and lower reaches of the river and man-made canals north and south of the Nerang River. n represents the total number of *C. leucas* captured at each region.
5.3.3 Long-term movements of *C. leucas*

Twenty-four *C. leucas* were tagged with V16 and V13P acoustic tags between February 2007 and March 2008 (Table 8) and > 100,000 detections were obtained from the ten receivers strategically placed in the system (Figure 27). Ten neonates spent the majority of their time in the upper reaches of the Nerang River in salinity ranges of 6 to 18 (p < 0.001), making excursions into adjoining flow-through canals with mesohaline salinities (Figure 31). During flood periods the neonates exhibited a preference for the upper reaches of the Nerang River and the northern canals (Figure 32). Fourteen juveniles (Table 8) were tagged (0.67 to 1.33 m FL) with acoustic tags and these sharks ranged further than the neonates but most detections occurred in the main river channel (p < 0.001) (Figure 31). However, an interaction between habitat type (Nerang River and adjoining canals) and *C. leucas* ontogenetic category (neonate and juvenile) was evident (2-way ANOVA, p = 0.028). The neonates spent significantly more time in the river than adjoining canals, whereas the time spent by juveniles in the Nerang River and canals did not differ significantly. However, small juveniles showed a preference for the upper Nerang River and northern canals during non-flood periods (Figure 32). The distance moved by sharks through the system increased with increasing shark FL, although these patterns differed between flood and non-flood periods (Figure 33, 34). Large juvenile *C. leucas* moved further than small juvenile conspecifics. Several large juveniles disappeared from detections for up to six-week periods, with one large *C. leucas* detected in the Gold Coast Seaway. These sharks left the Nerang River presumably moving into estuarine or nearshore waters beyond the study site, but returned on several occasions (Figure 35).
Table 7. Biological data for individuals of *C. leucas* at different ontogenetic stages monitored within the Gold Coast Canal system. Year refers to the year in which the *C. leucas* were tagged. N, neonate; SJ, small juvenile; LJ, large juvenile.

<table>
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<th>Ontogenetic stage</th>
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<th>TL</th>
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<tr>
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<td>153</td>
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</table>
a) Upper River

Northern Canals

b) Upper Reaches of Nerang River
c) Northern Canals

Date
01/11/2007  01/01/2008  01/03/2008  01/05/2008  01/07/2008  01/09/2008

Transmitter Number
218
4660
209
4659
4664
4655
c) Northern Canals
4665
4663
4654
d) Lower Reaches of Nerang River

Date
01/11/2007  01/01/2008  01/03/2008  01/05/2008  01/07/2008  01/09/2008

Transmitter number
218
4663
216
217
218
d) Lower Reaches of Nerang River
4660
20
Figure 31. Plots of individual detection at acoustic receivers deployed at key locations in the four sections of the Gold Coast canal system between 1/01/2007 and 1/09/2008. Transmitter numbers above the broken line are neonate *C. leucas*, between the broken and solid lines are small juveniles and below the solid line are large juveniles. The solid line in (a) divides the habitats tagged neonate and small juveniles occurred in the study site during the initial acoustic tagging in early 2007.
**Figure 32.** Electivity of habitat types by neonate, small and large juvenile *C. leucas* with acoustic tags. The left columns (a, c) show the relative area of the available habitat types and the relative distribution of the tagged population during flood and non-flood periods in 2007 and 2008. The right column shows the electivity plots.
Figure 33. Maximum displacement between detections during non-flood (closed circle) and flood (open circle) periods for *C. leucas* of varying sizes on receivers deployed throughout the study site.
Figure 34. Linear distance from river and canals to the ocean in relation to % of total detections of acoustically tagged *C. leucas* during flood and non-flood periods for neonate (a), small juvenile (b) and large juvenile (c).
The proportions of detections of all ontogenetic stages of *C. leucas* differed between flood and non-flood periods. Neonates and small juveniles increased their range throughout the system during flood periods, moving downstream into the lower Nerang River and southern canals (Figure 35). A significant relationship between daily rainfall and shark detection was found (deviance = 1523, df = 2, p < 0.001), with frequency of detection of same shark at different locations increasing with 0 to 2.95 mm rainfall and then decreasing at 35 mm rainfall within the Gold Coast canal system. An interaction between barometric pressure and rainfall for neonates was evident (deviance = 750.54, df = 3, p = 0.004) and affected their location within the canal system (p < 0.001). There is no influence of barometric pressure on small (p = 0.197) or large juveniles (p = 1). Detections of tagged *C. leucas* with CTD measurements differed between ontogenetic stages in relation to salinity (Figure 36). During non-flood periods, peak detection of neonates occurred at 17 – 22 ppt, 24 - 26 ppt for small juveniles and 24 ppt for large juveniles, decreasing during floods to 4 ppt for neonates, 6 ppt for small juveniles and 16 ppt for large juveniles (Figure 36).
Figure 35. Excursion pathways of different ontogenetic life history stages of acoustic-tagged *C. leucas* based on detections from acoustic stations (see Figure 27 for acoustic station locations) 2007-2008 for non-flood (A) and flood periods (B). Note insert (B) with salinity readings of CTD meter at site 5 (Figure 27) during a flood period. Salinity ranges indicate non-flood fluctuations (15 minute intervals) and drop in overall salinity level during flood, before returning to non-flood levels.
Figure 36. Occurrence of different ontogenetic groups of *C. leucas* in relation to salinity during non-flood (a) and flood (b) periods (+ SE) from the GLM.
Tide was a significant factor influencing the hourly presence and absence of all *C. leucas* (deviance = 826, df = 4, p < 0.001). Shark no. 21 (tagged with a V13P) remained within a deep hole (Lake Wonderland in Figure 27 insert) during the weekends over a three-week period (Figure 37) regardless of tide. The depth of the shark at time of detection on weekends ranged from 4 to 8 m, whereas the depths for detections outside these periods ranged from 0 to 10 m (Figure 37). During survey periods boating activity in the canal systems occurred on the weekend was almost absent during the weekdays.

![Figure 37. Detection of *C. leucas* (ID No. 21) in relation to tide at Lake Wonderland for the period 25/03/2007 and 17/04/2007. Arrows indicate weekend time periods when recreational boating occurs in this area.](image)
Figure 38. Hourly occurrences of ontogenetic groups of *C. leucas* at low tide (0.4 m, a), mid tide (1.3 m, b) and high tide (1.8 m, c) from the GLM.
Hourly detections of tagged *C. leucas* differed across low, mid and high tides and peak detections occurred around dusk and dawn periods for all ontogenetic stages (Figure 38). Detections of all ontogenetic stages increased at 1500 hrs and large juveniles increased detections at 1000 hrs particularly during corresponding high tides (Figure 38 c). Peak hourly detections of large juvenile *C. leucas* were out of phase with peak detections of neonate and small juvenile *C. leucas*.

5.4 Discussion

5.4.1 Ontogenetic distribution pattern of *C. leucas*

*C. leucas* is a predator in coastal and urban environments and understanding how long-term movement patterns vary for different sized *C. leucas* that use urban or peri-urban habitats is essential for their effective management and conservation. Juveniles of various shark species commonly display strong site-fidelity (e.g. Holland et al. 1993), whereas older and larger sharks tend to range over much wider areas (Gruber et al. 1988). This pattern was evident with the small and large juvenile *C. leucas* in the current study. In the Gold Coast canal system, the larger juvenile *C. leucas* moved further through the whole canal and river system and appeared to leave the study site on occasion, returning and moving along the entirety of the Nerang River. Whilst the neonates and small juveniles were consistently found in areas that had low salinity, the neonates appeared to prefer the main river course (i.e. a more natural habitat) over the adjoining canals. However, the canals used by the neonates were all in the upper reaches of the Gold Coast canal system and had similar salinity ranges as the region of the Nerang River that had higher use by the tagged *C. leucas*.

The segregation in size distribution of *C. leucas* throughout the study site supports the findings of Heithaus et al. (2009) who found the use of Shark River Estuary (USA) by *C. leucas* varied with body size and physical characteristics of the environment. Further, these authors suggested the long-term use of the upper reaches of the Shark River Estuary by *C. leucas* was influenced by a need to avoid predation rather than access to food resources, whereas the probability of the presence of sharks at smaller spatial scales and over shorter time periods is driven by abiotic conditions. In the current study, larger *C. leucas* occurred further downstream in the lower reaches of
the Nerang River and neonate *C. leucas* clearly remained in a confined area in the top reaches of the Nerang River. Juvenile and young-of-year (YOY) *C. leucas* move to remain with optimal salinity and temperature in the Caloosahatchee River of southwest Florida, USA, whereas size of *C. leucas* increase with increasing salinity in the Brisbane River, Australia (Heupel and Simpfendorfer 2008, Pillans and Franklin 2004). Alternatively, the abundance of YOY and juvenile *C. leucas* was influenced by site and abiotic factors such as dissolved oxygen and not salinity in the Shark River Estuary, USA (Heithaus et al. 2009). While the patterns of small juvenile and YOY *C. leucas* occurring in the top reaches of river systems and concentrated at one location appears to be consistent across different studies, the likely drivers of size-based segregation of *C. leucas* may differ between river systems. These differences are likely to be influenced by the spatial variation in the physical structure and hydrological dynamics of the estuary or river and further extrapolated by urbanisation in these habitats (Martin 2005, Heithaus et al. 2009).

### 5.4.2 Urban nurseries for *C. leucas*

Shark nurseries are thought to be areas that provide an abundance of food for which neonate sharks have a tendency to remain or return for extended periods (Branstetter 1990, Heupel et al. 2007). The movement of *C. leucas* at different ontogenetic stages throughout natural and urban habitats in the Gold Coast canal system could be due to greater energetic requirements with increasing size or age. Neonates and juvenile *C. leucas* use estuaries as nursery grounds where mullet (*Mugil* spp.), a major component of the diet of *C. leucas* in this size range, readily occur (Zeller 1999, Pillans et al. 2005). *C. leucas* also exhibits ontogenetic changes in diet and prey size (chapter 6) (Cliff & Dudley 1991), which commonly accompanies changes in foraging tactics and habitat. This change in habitat is probably a strategy to increase net rate of energy gain with increase in size or age. *C. leucas* are top-level consumers as Cortes (1999) has shown, using Ecopath II modelling (Christensen and Pauly 1992), that they have a trophic level > 4. Their significance as a predator probably increases as their ability to consume larger and more varied prey increases with size. While Simpfendorfer et al. (2005) and Pillans and Franklin (2004) suggested that it may be physiological benefits that retain neonates and small juveniles in low-salinity waters, it could be argued that *C. leucas* may be more restricted by the size range of their accessible prey particularly before the onset of observed ontogenetic shifts in diet.
Carbon isotope values of fish are known to vary in response to dietary shifts and environmental conditions (Gaston et al. 2004). The carbon isotope values for *C. leucas* (-15 to -19.4 ‰) were similar to those of teleost fishes in the same area (e.g. Waltham & Connolly 2006). These values are less depleted than terrigenous C (e.g. mangroves or terrestrial plants, ~ 28 ‰, Nagelkerken et al. (2008) but more typical of estuarine microphytobenthos (MPB) (Oakes et al. 2010), probably a reflection of the use of herbivorous prey such as mullet in the diet of small juvenile *C. leucas*. As the top-level predators in river systems, the key ecological role of *C. leucas* in regulating food chain diversity means this species could be a natural indicator of the health of a waterway. Although attributed to overfishing, correlations in the decline in *C. leucas* have been observed in areas with declines in biodiversity in estuarine areas (O’Connell et al. 2007). Dietary switching as a response to trophic requirements not provided by a single food source can alter the C and N stable isotope ratios. However, distinct signatures between southeast Queensland rivers, further support the theory that *C. leucas* remain within single defined rivers as small juveniles, making them particularly susceptible to anthropogenic influences and especially in urbanised environments (Heupel & Simpfendorfer 2008, Ortega et al. 2009). Waltham and Connolly (2006) also noted in their comparative study of the isotopic signatures of garfish, *Arrhamphus sclerolpis*, a depletion in $^{13}C$ in the artificial urban waterways of the Gold Coast canal system compared to natural wetlands. Detection of depleted $\delta^{13}C$ signatures in urban rivers compared to natural rivers is only possible if the sharks do not cover the two rivers equally as habitats.

While no other shark species were caught on long-line sets at the entrance to the Nerang River or throughout the study site, size-based intra-specific competition and potential predation is likely to be a significant factor for ontogenetic partitioning amongst *C. leucas* in this system (Simpfendorfer et al. 2005). Small juvenile *C. leucas* moved further in the study site than neonates and did show a preference for the northern canals in addition to the top of the Nerang River. These canals occur in the mesohaline section of the study site, are characterised by a large deep hole and have direct flow from the Nerang River. The non-preference for this area by large juveniles could explain the electivity for these canals by small juveniles as these areas still retain abiotic conditions similar to the top reaches of the Nerang River.
5.4.3 Environmental conditions and habitat preference

Habitat preferences and social organisation can influence the spatial distribution of fishes (Kane et al. 2009). Habitat complexity (i.e. available underwater structure for refuge), water depth and turbidity are factors that can define the intrinsic habitat risks for a predator and prey (Hugie & Dill 1994). Lack of underwater structure in the canals could explain the preference of *C. leucas* for the upper reaches of the Nerang River, with its small stands of mangroves, over man-made canals and reduced numbers of prey. It is unlikely that juvenile sharks will leave an estuarine nursery unless a threat within a nursery exceeds the intrinsic risk, for example, cyclonic conditions (Heupel et al. 2003). Heupel and Simpfendorfer (2008) noted that during periods of low flow and higher salinity, greater proportions of their acoustically-tagged *C. leucas* population (< 1 yr old) occurred within the Caloosahatchee River. Moreover, fewer *C. leucas* were detected during periods of high flow and low salinity.

In this study, results indicated differences in the preferred salinities for sharks of different sizes/ages. Neonate *C. leucas* were detected in 17 to 22 ppt during non-food periods, which coincides with the salinity preferences for neonate and young of the year *C. leucas* in other studies (Heupel et al 2008, Ortega et al. 2009). Occurrence in this salinity can explain the increased displacement of individuals during flood periods, as salinity can strongly influence the distribution of 1+ *C. leucas* (Pillans & Franklin 2004, Simpfendorfer et al. 2005).

This study provided evidence of ontogenetic habitat segregation within the Gold Coast canal system during non-flood periods. It is interesting to note that during flood periods, however, the predicted salinity range for occurrence of neonate *C. leucas* dropped to 4 ppt, a level that Heupel and Simpfendorfer (2008) found to be avoided by *C. leucas* in their study. Large juvenile *C. leucas* penetrated further upstream into the top reaches of the Nerang River during flood periods in the current study, an opposite movement to the other smaller *C. leucas* size classes during flood periods. Nonetheless, large *C.leucas* still occurred in a predicted salinity range of 19 ppt and electivity analyses suggested they avoided the study site during floods. While neonates concurrently occurred in the lower reaches of the study site and in the southern canal system, *C. leucas* of different ontogenetic stages were utilising salinity ranges that increased with *C. leucas* size class. These data suggest *C. leucas* of
different ontogenetic stages are using salinities differently and segregation amongst size classes was still evident during flood periods. The low salinities for occurrence of neonate *C. leucas* during floods could be due to avoidance of large juvenile *C. leucas*, which were penetrating further upstream, or neonate *C. leucas* maintaining preferred positions within the study site. Avoidance of predation may be a likely factor to override the habitat preferences of neonates, forcing them to remain in salinities lower than those of other studies. Movement further downstream of neonate and juvenile *C. leucas* during floods, however, could be enabled by large juveniles migrating into nearshore areas following freshwater plumes (as per Chapter 3). It is difficult to explain the prevalence of detections upstream during flood periods for large *C. leucas*; however, this size range of shark moved substantially greater distances on short time scales, with several large *C. leucas* moving to the top of the Nerang River and into the southern canals in one tidal cycle. Larger *C. leucas* readily occur in more marine waters (Pillans & Franklin 2004). It is interesting to note that while large juveniles were detected in polyhaline salinity ranges throughout all habitats in the Gold Coast canal system, their movements did not indicate a preference for the man-made canals. The need to search for larger and more varied prey could explain the movement of these individuals beyond the study site into the Broadwater.

Tidal data revealed distinct hourly patterns in detections for all ontogenetic stages of *C. leucas* around dusk and dawn, with movement of neonate and small juveniles often occurring in addition at one or two hours post and prior to the movements of large juveniles. These results also highlight the periods of potentially increased risk to swimmers in canals. Most activity of *C. leucas* during short-term tracking in the Gold Coast canals system occurred during periods of less flow (Chapter 4). Concurrently, in this study of the long-term movements of *C. leucas* in the same system, most activity of *C. leucas* occurred during mid tides (i.e. ~ 1.3 m). Periods of activity at mid tide occurred at all hours of the day for neonates, but were restricted during periods of high flow to late afternoon/evening at low tide and the morning at high tides. Determining whether these movements were correlated with feeding, particularly for large *C. leucas* which pose an increased risk to humans, warrants further investigation.
5.4.4 Value of urban habitats to *C. leucas*

Increasing pressure from encroaching coastal urban development in sub-tropical Queensland has resulted in emphasis on the conservation of estuarine habitats and the importance of these habitats to recreationally and commercially important fish species. Humans frequently exert rapid, large-scale influence on their immediate environment in coastal areas, such as the modification of waterways including construction of canal systems (Ehrlich et al. 1973). With the recent ‘sea change’ phenomenon and the increased growth of urban populations in coastal areas, human interactions with co-users of coastal habitats, such as *C. leucas*, are likely to increase. The osmoregulatory ability of *C. leucas* enables this species to use a wider variety of coastal habitats than can most other sharks, making it one of the most likely shark species to be involved in attacks on humans. When in estuaries, *C. leucas* are potentially more vulnerable to urban habitat modifications compared to their oceanic counterparts (Moyle & Leidy 1992, Compagno & Cook 1995, Martin 2005). River and estuarine habitats have more limited volume and their physio-chemical properties vary widely (Martin 2005). These habitats are also often highly modified for agriculture and urban developments. The long-term movements of *C. leucas* at different ontogenetic stages in urbanised coastal habitats such as the Gold Coast canals suggest that the movements of large *C. leucas* should be of particular significance for managing possible adverse interactions. The patterns of *C. leucas* movement differ between sharks of increasing size. Larger sharks range further and increase their potential for interaction with humans through covering more area. Alternatively, humans that frequent areas at the top of rivers are using areas where neonate and small juvenile *C. leucas* are most concentrated. Therefore, *C. leucas* face a collision between the effects of increasing human population and their own inherent biological adaptability to estuarine ecosystems (Compagno & Cook 1995, Zeller 1999).

The current study illustrates the changing abilities of *C. leucas* of different ontogenetic stages to use urban canal systems and highlights the value of the Nerang River as a nursery habitat. As a result of this study, it is recommended that the transitional movements of large juvenile *C. leucas* from river, and estuarine (including urban habitats) habitats into nearshore environments be further investigated. This
would permit a better understanding of the return of large *C. leucas* (> 1.5 m TL) to rivers and estuaries. Whilst *C. leucas* use man-made canals, these are not preferred habitats in the life cycle of *C. leucas*. The value of urban habitats to *C. leucas* will, however, increase with continual destruction of their natural, preferred habitats. The potential impact of continued urbanisation of natural riverine habitats that are used as nurseries for neonate and small juvenile *C. leucas* should be of concern for their long-term conservation.
CHAPTER 6

ESTUARINE-NEARSHORE HABITAT TRANSITION OF THE BULL SHARK

6.1 Introduction

Linkages between animal populations in freshwater and nearshore coastal waters are most often viewed in terms of larval recruitment process but rarely considered at the level of highly mobile top-level predators such as sharks. Understanding patterns of usage of habitat by top-level predators is important to understanding the consequences of environmental and human disturbances on these species, their linkages between habitats and the potential ecological ramifications for the communities they inhabit (Heithaus et al. 2002, Gillanders et al. 2003). Habitat selection may occur in response to abiotic factors such as temperature and salinity (Bräger et al. 2003), ecological factors such as prey availability or changes in intra and inter-specific competition (Heithaus 2004). Moreover, these factors are likely to be crucial for species in transition between their nursery and adult foraging grounds. Past studies suggest ontogenetic shifts in habitat use by sharks can result from decreased vulnerability to predation enabling the use of a wider range of habitats (Wetherbee & Cortes 2004, Ebert 2004, Heithaus 2004). These changes also result in shifting ecological roles of the species in marine communities, which may be mediated by the ability to consume larger and more varied prey (Werner & Hall 1988, Nagelkerken et al. 1998, Simpfendorfer et al. 2001, Ebert 2002, Heithaus et al. 2005). Consequently, the timing of habitat shifts is a critical feature in the life cycle of marine animals. Many of the inhibiting factors to increased utilisation of habitats are thus influenced by an animal’s size and life history organisation, meaning larger sharks are able to range further (Werner & Hall 1988).

Much effort has been spent with traditional methods such as stomach content analysis (SCA) which, by necessity, requires the examination of numerous individuals to identify trophic shifts at different stages of maturity (Cortes 1997, 1999). Despite
these analyses, the natures of estuarine-nearshore shifts for many sharks are still obscure. Further, it is often difficult to obtain data on top-level predators that are threatened, elusive, have large home ranges, and/or have low population densities. Complementary methods of chemical analysis and acoustic tracking, however, may be particularly useful for identification of ontogenetic shifts in the trophic ecology and habitat of sharks (Heupel & Hueter 2002, Hale et al. 2006). Recent studies have shown that stable isotopes are a useful tool for examining trophic links between estuarine production and the pelagic food chain (e.g. Lee 1995, Werry & Lee 2005) and ontogenetic trophic shifts such as in white shark, *Carcharodon carcharias*, (e.g. Estrada et al. 2006). The utility of laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS) as a means of studying the spatial distribution of elements in the vertebrae of sharks also provides an insight into habitat shifts, as differential deposition of elements in the vertebrae is influenced by environmental factors such as temperature and salinity, thus revealing histories of habitat use (Hale et al. 2006, Kerr et al. 2006).

A recent surge in acoustic monitoring has allowed researchers to better define the occurrence and movements of sharks. This technology is particularly useful for large juveniles that potentially increase home ranges (Yeiser et al. 2008). Recent studies suggest that it is critical to measure the movement of individuals from juvenile to adult habitats (Beck et al. 2001). However, relatively few studies document movements between different habitats and this is likely due to the potentially large spatial scales (tens to hundreds of kms) over which shifts in habitat usage can occur.

The bull shark, *C. leucas*, occurs circum-globally in rivers, estuaries, river mouths and shallow coastal waters and yet has received relatively little attention in the scientific literature, particularly in regards to its movement and occurrence in habitats at the interface between fresh and marine environments (Yeiser et al. 2008). Its life cycle is closely tied to movement between freshwater and marine environments (Pillans et al. 2006) and involves significant periods in both habitats with adults occurring in nearshore marine areas (Brunnshweiler & Earle 2006). Thorson (1971) described their unique ability to navigate rapids and move between Lake Nicaragua and the Caribbean Sea. However, despite these extraordinary shifts in habitat, the scientific literature is still speculative in relation to when these shifts occur in the life cycle of
C. leucas. A recent tracking of a female 4-m adult C. leucas found that this shark moved 20 km upstream in a river and 2 km offshore over a 43-hr period (McCord & Lamberth 2009). This shark was suggested to be pregnant (but not definitely confirmed) and possibly searching for suitable pupping grounds while foraging, thus explaining its presence upstream rather than in nearshore waters. Adult C. leucas are notorious for consuming other sharks including conspecifics (Vorenberg 1962), with one record of white shark, Carcharodon carcharias, in the stomach of a large C. leucas (Cliff & Dudley 1991). One hypothesis is that predation from conspecifics is a major driver of size-based shift to marine habitats for C. leucas. Influence of intra-specific interactions between intermediate size ranges and maturity classes may define smaller scale shifts in addition to predation, but investigation of interactions between individual C. leucas are almost non-existent. Agnostic, size-based encounters have been observed in C. carcharias (McCosker 1985) and also occur with C. leucas (Chapter 4). Furthermore, risk of predation from other large shark species in nearshore and neritic habitats may also influence the size of C. leucas in transition into nearshore areas in addition to cannibalism.

While small juvenile (< 1.3 m TL) C. leucas inhabiting nursery areas (sheltered estuarine areas) are likely to delay expanding habitat range because of increased predation risk outside nurseries, large juveniles and sub-adult C. leucas are less vulnerable to predation (Bouskila et al. 1998, Cliff & Dudley 1991). Understanding how C. leucas use transitional habitats between river and nearshore environments is essential for the effective conservation of these species and management of possible interactions with humans. The aims of this study were to (1) determine the patterns of occurrence of large juveniles (up to 1.6 m TL) and sub-adult C. leucas (1.6-2 m TL) at the transition between nursery and nearshore adult habitats; (2) identify shifts in diet with habitat transition; and (3) whether the elemental composition of C. leucas vertebrae can provide a history of habitat transition and movement with size.
6.2 Methods

6.2.1 Study site
This study was done in sub-tropical Queensland where extensive forests of *Avicennia marina* occur along tidal river courses and in estuaries (Figure 39). Though not supporting *C. leucas* densities comparable to tropical NE Queensland, significant populations of *C. leucas* still occur in the local rivers, estuaries and nearshore areas. To examine the transition of *C. leucas* from rivers and estuaries to nearshore habitat, passive, long-term tracking and chemical techniques were used. Sub-tropical Queensland is characterised by a narrow shelf (Heap & Harris 2008) and is influenced by tropical currents flowing from the north mixing with cooler temperate waters from the south. Numerous rivers provide nursery habitat for young-of-the-year (YOY) and juvenile *C. leucas* and these connect with the nearshore areas (Pillans & Franklin 2004).

Southern Moreton Bay, the location for passive tracking of *C. leucas* movement, is characterised by two major seaways connecting to the nearshore environment (Figure 39). Mangrove (mainly *A. marina*), sand banks and seagrass between several channels (~ 5 to 15 m deep) characterise entrance to the Coomera River and Jumpinpin section. The Gold Coast Seaway and Broadwater area has an urbanised shoreline, with adjoining urban canals and connects with southern Moreton Bay. Substantial water flow occurs through Jumpinpin and the Gold Coast Seaway, resulting in substantial mixing at the entrance to Coomera River. Flows from Jumpinpin also proceed north into greater Moreton Bay. Salinity reflects nearshore waters (~ 35 ‰) and drops to 10-20 ‰ after substantial rainfall (Bureau of Meteorology (BOM)).
Figure 39. Study area in southeast Queensland, Australia, showing the locations of the VR2 and VR2W acoustic receivers in the river (including the Gold Coast canal system that feeds from Nerang River), estuarine, southern Moreton Bay, seaways and nearshore environments. Urban canals can also be seen in the figure connected to the natural waterways.
6.2.2 Field methods

An array of 12 VR2 and VR2W receivers (Vemco, Canada) was designed to collect presence-absence and long-term movement data of large juvenile (< 1.6 m TL) and sub-adult (1.6-2 m TL) *C. leucas*. Receivers (*n* = 11) were deployed in transitional estuarine habitat at the interface between river and the nearshore environment (Figure 39) at key locations to detect movement of tagged *C. leucas* between the habitats. Receivers were attached mid-water to existing navigational markers by divers on SCUBA. Receivers were deployed at Coomera river entrance in December 2008 and at all other locations in February 2009. The receivers were continuously deployed for the duration of the project, except for the entrance to Coomera River, which was absent from the water for three weeks in August due to a large recreational vessel crashing into the navigational pole. The unit was redeployed when the navigation pole was replaced. Receivers were single-frequency and omnidirectional with an approximate detection range of 400-700 m for V16 tags. Receivers recorded the time, date and identity of sharks fitted with acoustic transmitters. Data were downloaded on an opportunistic basis throughout February to August 2009 and all receivers were downloaded in September 2009. In conjunction with the deployed receiver units, Odyssey probes, New Zealand, were deployed in Nerang River, the Seaway, and Tallebudgera Creek to record temperature and salinity at 10-min intervals. Daily rainfall (BOM) was also used to assist with the interpretation of the movements of *C. leucas*.

Sampling of *C. leucas* was done using modified long-lines with floats and setlines. Lines consisted of 1000-pound line with traces of 2-3 m of 5-mm braided cord and a 1-m stainless steel wire leader. I used large bricks as mobile anchors to allow the lines to drag if a large adult *C. leucas* were captured. Tuna hooks 8/0 were baited with fresh eel (*Anguilla australis*) and mullet (*Mugil cephalus*). Long-lines were set for periods of 30 min to 2 hr and setlines were checked approximately every 2 hrs. Sets were made during February 2009 and March 2009. Captured sharks were then transferred into a non-abrasive harness and water flow was maintained over the gills by a small pump within the holding tanks. The shark was then moved via crane to an onboard holding tank on a large mother ship (Figure 40). *C. leucas* caught were identified and sexed. Measurements of length (to the nearest 0.5 cm) were taken: precaudal length, fork length and total length (TL). Height of the first and second dorsal fins and a
tissue sample for DNA analysis was also taken to further confirm the species identification. A V16 (Vemco) acoustic transmitter was surgically implanted in each captured shark. Each transmitter is coded with a unique pulse series on 69.0 kHz at randomly spaced intervals between 60 and 120 s. Each transmitter had a battery life of about five years. Twelve *C. leucas* were internally tagged and their movements recorded, including two sharks that were captured on an opportunistic basis in the field site in November 2008 during a short-term fine scale movement study (Table 9). Internal tagging was done using sterile equipment. A small incision (~ 2 cm) was made in ventral surface of the shark while it was maintained in tonic immobility (Heithaus et al. 2007) and the acoustic tag was inserted after being sterilised. The incision was sutured and antiseptic applied to the closed incision. *C. leucas* were also externally tagged with a single-barb plastic dart tag.

**Figure 40.** *C. leucas* in holding tank on board the mother ship.

### 6.2.3 Archival satellite tagging

Catch statistics from the QSCP confirm that adult *C. leucas* readily occur in the nearshore environment of the study site. To obtain an estimate of the potential extent of movement beyond the receiver locations, a female *C. leucas* was tagged with a Wildlife Computers MK-10 archival pop-off tag (PAT) attached to the dorsal fin via a cattle ear tag in addition to an internal acoustic tag (Figure 41). The release time was set for two months from the date of deployment. Location estimates of the PAT tag were determined using the ARGOS satellite system.
Figure 41. Attachment of archival pop-off satellite tag to dorsal fin (a, b) of sub-adult *C. leucas* using a roto tag.

### 6.2.4 Chemical analyses

#### 6.2.4.1 Vertebrae preparation

Vertebrae have a high organic component that can be used to interpret diet and habitat shifts, and thus, reflect the life-history of an individual organism (Compana et al. 2002). Vertebrae were obtained from 32 *C. leucas* comprising juvenile, sub-adults and adult (Table 10) collected from 2005 to 2008. Rivers from Noosa to Tweed (Figure 27, Chapter 5) were sampled for juvenile *C. leucas* and vertebrae from sub-adult and adult *C. leucas* were obtained from commercial fishers and the Queensland Shark Control Program in the nearshore areas between Rainbow Beach and Tweed Heads (Gribble et al. 1998). Vertebrae were taken immediately anterior to the first dorsal fin and were sagittal-sectioned using a Buehler isomet saw and then mounted on a glass slide (25 x 45 mm). Growth increments were counted in relation to the vertebrae radius (mm). One age band (1 yr) was determined by one light and one dark band on the vertebrae.
6.2.4.2 LA-ICPMS

The sensitivity of the LA-ICPMS for studying the spatial distribution of elements across the vertebrae is the major advantage of this technique (Hale et al. 2006). The *C. leucas* vertebrae sections were analysed for elements using a Coherent GeolasPro 193 nm laser unit coupled to a Varian 820-MS inductively coupled plasma mass spectrometer (LA-ICPMS) through a 2-m Tygon LEP-lined tubing and a 3-way mixing bulb. Sectioned vertebrae were mounted on glass slides and inserted into the ablation chamber of the laser system. Samples were pre-ablated with the laser to remove surface contamination, and the specimen chamber and transmission lines were then purged with high quality helium (He) gas prior to analysis. For sample ablation, the Step and Repeat Scanning Mode was used. A laser spot size of 32 µm was used to ablate the sample and the laser was operated at the repetition rate of 10 Hz. The ablation distance was set at 32 µm, therefore each spot was ablated 10 times. The laser energy fluence was at 6 J cm$^{-2}$. Measurements were carried out along a linear transect from the focal region to the edge of the vertebral centrum. Elements monitored included calcium ($^{43}$Ca and $^{44}$Ca), magnesium ($^{24}$Mg and $^{26}$Mg), copper ($^{63}$Cu), strontium ($^{88}$Sr), barium ($^{137}$Ba and $^{138}$Ba), phosphate ($^{31}$P) and manganese ($^{55}$Mn).

There is no matrix-matched standard (apatite standard) available for the shark vertebrae. Hence the widely used synthetic glass standard (NIST 610 or 612) was used for instrument calibration, and to correct for the matrix effects mainly due to the difference between the calibration standard and the sample matrix composition. An internal standard was used (Ca in this case) to correct for instrument drift. The NIST glass standard was ablated immediate prior to and after the sample ablation. In each analysis, 80 s of gas blank reading was done prior to the standard and sample ablation. These blank data were subtracted from the standard and sample reading in the data processing. The detection limits were calculated based on the gas blank readings. Response from the NIST was typically < 1 µg g$^{-1}$ as reported by others. Plasma gas flow was set to 18 L min$^{-1}$ and auxiliary gas flow was set at 1.8 L min$^{-1}$, sheath gas flow operated at 0.24 L min$^{-1}$ with sampler gas flow at 0.95 L min$^{-1}$. Peak jumping scan ICPMS was used with one point per peak and a dwell time of 10 ms.
6.2.4.3 Tank trials
To ground truth the time period taken for the *C. leucas* vertebrae elemental composition to reflect moves from estuarine (mesohaline) toward a nearshore signal, controlled tank trials were done. Six juvenile *C. leucas* (0.85-0.9 m TL) were caught from their mesohaline estuarine habitats, with two from the Nerang River, two from Caboolture River and two from Pumistone passage, and transported to a holding facility and placed in individual circular flow-through tanks (9m radius × 1.5 m ht). Each tank was maintained with a constant flow and exchange of water pumped directly from the polyhaline nearshore environment and filtered by a sand filter. *C. leucas* were maintained for two time periods, firstly for three weeks (n = 3, with one shark from each river sampled) and secondly for five weeks (n = 3, with a second shark from each river sampled) before being euthanised. Vertebrae (n = 3) from similar sized *C. leucas* obtained from commercial fishers in the rivers (i.e. not maintained in tanks) were used as a 0 week control. Vertebrae were extracted and prepared for LA-ICPMS as described above.

6.2.4.4 Isotope readings across the vertebrae
Stable isotope analysis reflects the isotopic composition of a predator’s diet and has been successfully used to verify ontogenetic trophic shifts in white shark (Estrada et al. 2006). δ¹³C values have a typical enrichment of ~ +1 ‰ per trophic level whereas δ¹⁵N isotopes have a +2-3 ‰ enrichment per trophic level, although this may vary with species and tissue (McCutchan et al. 2003). *C. leucas* vertebrae (n = 5) samples were used from sub-adult and adult sharks only (Table 10). I removed ~4 mg dry weight of powdered vertebral tissue for isotope analysis in 1-mm increments across a single vertebral column from each shark. δ¹⁵N and δ¹³C were measured using a continuous-flow isotope-ratio mass spectrometer, with the appropriate standards. Standards were introduced at regular intervals to provide quality control as well as to give an indication of the level of precision.

6.2.5 Queensland Shark Control Program diet data
Estrada et al (2006), in their study in the ontogenetic diet shift in white sharks, verified their isotopic data with stomach content data. To verify trends in δ¹⁵N across the vertebrae, I compared stomach content data of *C. leucas* of different TL at ten locations along the QLD coastline, between Cairns (17°S) and the Gold Coast (28°S).
(Figure 3, Chapter 2). The Queensland Shark Control Program (QSCP) deployed a series of gill nets and drumlines specifically designed to target *C. leucas*. Data on stomach contents from 1036 *C. leucas* caught from 1996-2006 were examined. Only dominant food type was recorded in the stomach contents to identify ontogenetic shifts in diet with TL.

**6.2.6 Statistical Analysis**

Statistical analyses were carried out using the Primer 6.0, SPSS 17.0 and Genstat 13 software packages. Non-metric multidimensional scaling (nMDS) was used to visually represent the elemental composition pattern across the vertebrae of *C. leucas* of different sizes. Data were square root transformed and resemblance was determined by the Bray Curtis similarity index. Results of the stable isotope signatures were analysed by linear regression for $\delta^{15}$N and sigmoid regression for $\delta^{13}$C, following initial exploratory data analysis of the likely pattern. Regression was used to describe the relationship between TL and the proportion of elasmobranchs, reptiles, and birds in the diet of *C. leucas* captured by the QSCP. Results of the stable isotope signatures for shark species co-occurring with *C. leucas* were compared using one-way ANOVA for differences in $\delta^{15}$N and $\delta^{13}$C among species, after data were tested for normality and homogeneity of variances. A Tukey's post-hoc test was used to determine where the differences between samples occurred, where appropriate.

Presence of tagged *C. leucas* was assessed on a daily basis for each receiver location. Excursion pathways of large juvenile and sub-adult *C. leucas* were plotted, based on detections at different receiver sites. To investigate physical factors that may influence the presence of *C. leucas* at different locations, data were compared to daily rainfall (BOM) and salinity and temperature readings. A generalised linear model (GLM) was used to investigate the relationships between *C. leucas* presence and factors considered to influence the presence of *C. leucas*. The GLM was tested as location + rainfall and separately for physical parameter readings from the probe, as salinity + temperature. Final models identified factors and interactions that had a significant influence on the proportion of *C. leucas* at each of the locations. In the GLM analyses, detections of salinity and temperature were analysed based on the range of detections that occurred. Pop-off location of the MK10 PAT tag was
compared to the capture location of the shark to provide an estimate of the extent of the adult *C. leucas* movement in nearshore waters beyond the receiver locations.

### 6.3 Results

#### 6.3.1 Shark occurrence and excursion pathways

The total amount of time sharks were detected at each of the receiver locations was variable, with most sub-adult *C. leucas* detections occurring at the Jumpinpin bar (Figure 42 a). Sub-adult *C. leucas* were consistently present from March to June 2009 at this receiver location, occasionally detected at the entrance to Coomera River (Figure 42 b) and periodically detected in both the Gold Coast Seaway (Figure 42 c) and the Jumpinpin bar from May to August 2009. Both large juvenile and sub-adult *C. leucas* exhibited movement between Jumpinpin bar and the Gold Coast Seaway via southern Moreton bay (Figure 43), but detections only of large juveniles occurred in the entrance to Nerang River and the Gold Coast canal system (Figure 42 d, 43). No detections of any tagged *C. leucas* occurred in the nearshore environment receiver stations. The large juvenile *C. leucas* tagged in Tallebudgera Creek was detected on the receiver station at the entrance to Tallebudgera creek, but not at the receiver station beyond the river mouth in the nearshore environment (Figure 43). It is interesting to note that the 1.92 m adult *C. leucas* that was also acoustic tagged was not detected on the receivers in southern Moreton Bay or receivers in the nearshore habitat south of the Gold Coast seaway. The MK 10 archival pop-off tag detached from this shark after 12 days, substantially earlier than programmed. The PAT tag, however, indicated that this shark remained in the nearshore area and moved northward, remaining at 20 m depth for three days before returning to shallower water (5 to 10 m) prior to the early release (Figure 43).
**Table 8.** Biological data for large juvenile and sub-adult *C. leucas* monitored within the Gold Coast river, bay and nearshore environment

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<td>122</td>
<td>143</td>
<td>M</td>
<td>7913</td>
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<tr>
<td>2009</td>
<td>Tallebudgera Creek Canal</td>
<td>107</td>
<td>127</td>
<td>M</td>
<td>55421</td>
</tr>
</tbody>
</table>
Figure 42. Plots of individual detection at acoustic receivers deployed at key locations in the study site between February and September 2009. Transmitter numbers above the broken line are large juvenile *C. leucas*, and below the solid line are sub-adults.
Figure 43. Excursion pathways and proportion of detections of acoustic-tagged large juvenile and sub-adult *C. leucas*, based on detections from acoustic stations 2009. The pathway of the pop-off tagged adult *C. leucas* is also shown.
6.3.2 Effect of temperature and salinity

GLM indicated that the proportion of detections differed significantly for large juvenile (p < 0.001) and sub-adult *C. leucas* (p < 0.001) in relation to salinity and temperature at the receiver location. Presence of large juveniles peaked at 17.8 and 36 ‰ and 23.5 °C. Sub-adults were present through a range of salinities (< 5 to 36 ‰); however, the GLM indicated increased proportions of sub-adults present at 28 and 36 ‰ and 21 and > 23.5 °C (Figure 44). A significant relationship between previous daily rainfall (one to eight days prior) was evident for large juveniles (p < 0.001) and sub-adults (p < 0.001).
**Figure 44.** Proportion of sub-adult *C. leucas* present at various salinity (a) and water temperature (b) levels at Jumpinpin bar for the period of the study.

6.3.3 Habitat transition

Vertebrae showed a linear relationship between centrum radius and *C. leucas* total length (Figure 45). The number of rings corresponded to length of the shark and habitat transition into bay/estuary appeared to correspond to approximate age of 4 to 6 years for *C. leucas* (Figure 46). For the five large *C. leucas* sampled for isotopes across the vertebrae, a strong relationship occurred ($r^2 = 0.937$, $p = 0.002$) where $\delta^{13}C$ migrated from seagrass dominated signature (-12.3 ‰ ± 0.4) during the bay/estuarine period, to a more typical oceanic plankton based signature (-15.5 ‰ ± 1.1) with transition to nearshore habitat (Figure 46 a). The signature for the large pregnant female (shark no. 23, Table 10) extended beyond 10 mm from the centrum of the vertebra and began to decline back towards a more estuarine/seagrass signature of -12 ‰ (Figure 46 b). Following ordination of the LA-ICPMS across the vertebrae of 32 *C. leucas*, a relatively tight group of *C. leucas* from rivers formed in the top section of that plot (Figure 47 a). Sub-adult and small adult *C. leucas* radiated further from the river sample, however a difference with between male and female adult *C. leucas*
was also evident. The two large adult males (2.6 and 2.7 m TL respectively) were more distant from the samples from small *C. leucas*. The elemental signature of the pregnant female *C. leucas* returned close to that of the river samples (Figure 47 a).

**Figure 45.** Relationship between centrum radius (mm) of *C. leucas* of different total length (mm).
Figure 46. Change in $\delta^{13}$C (‰) values with distance from the centrum of *C. leucas* shark vertebrae as an approximate age for the first 10 yrs for *C. leucas* (a). The rapid transition at the 4 to 8 yr corresponds to *C. leucas* of approximate size 1.5 m TL. Data points are means of five replicates ± SE. (b) illustrates the return of *C. leucas* females to a bay/estuary signature after 10 yrs.

MDs Ordination of the LA-ICMPS signatures of *C. leucas* in the tank trial indicated a separation of sharks maintained for three weeks in nearshore waters (from the left of the plot) to those maintained for five weeks in the nearshore water (right of the plot) (Figure 47 b). Size of all *C. leucas* captured in this study increased from river to southern Moreton Bay and coastal areas with a clear partitioning of size of *C. leucas* caught in nearshore/shelf, southern Moreton Bay and river habitats (Figure 48).
Table 9. Biological data for different ontogenetic stages of *C. leucas* sampled for LA-ICMPS. Refer to Figure 26 (Chapter 5) and 37 for sampling locations * indicate samples used for $\delta^{15}$N and $\delta^{13}$C, p indicates pregnant female (see Chapter 2, Figure 8).

<table>
<thead>
<tr>
<th>shark No.</th>
<th>location</th>
<th>TL (cm)</th>
<th>gender</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Coomera River</td>
<td>55</td>
<td>F</td>
</tr>
<tr>
<td>2</td>
<td>Coomera River</td>
<td>57</td>
<td>M</td>
</tr>
<tr>
<td>3</td>
<td>Coomera River</td>
<td>58</td>
<td>F</td>
</tr>
<tr>
<td>4</td>
<td>Tweed River</td>
<td>74</td>
<td>F</td>
</tr>
<tr>
<td>5</td>
<td>Tweed River</td>
<td>79</td>
<td>M</td>
</tr>
<tr>
<td>6</td>
<td>Maroochy River</td>
<td>80</td>
<td>M</td>
</tr>
<tr>
<td>7</td>
<td>Maroochy River</td>
<td>82</td>
<td>M</td>
</tr>
<tr>
<td>8</td>
<td>Gold Coast canals</td>
<td>83</td>
<td>M</td>
</tr>
<tr>
<td>9</td>
<td>Noosa River</td>
<td>84</td>
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<td>Noosa River</td>
<td>90</td>
<td>M</td>
</tr>
<tr>
<td>11</td>
<td>Maroochy River</td>
<td>91</td>
<td>M</td>
</tr>
<tr>
<td>12</td>
<td>Noosa River</td>
<td>93</td>
<td>F</td>
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<td>Gold Coast canals</td>
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<td>F</td>
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<td>112</td>
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</tr>
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<td>181</td>
<td>F*</td>
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<td>Burleigh Heads</td>
<td>187</td>
<td>M*</td>
</tr>
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<td>Tweed Shelf</td>
<td>195</td>
<td>M*</td>
</tr>
<tr>
<td>20</td>
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<td>200</td>
<td>F*</td>
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<tr>
<td>23</td>
<td>Tweed Shelf</td>
<td>300</td>
<td>pF*</td>
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Figure 47. Non-metric multidimensional scaling of the elemental composition across the *C. leucas* vertebrae for different sized sharks (increasing bubble size for shark size) with open (males) and closed bubbles for females (a) and controlled experiment in tanks trials (b).
Figure 48. Proportion of *C. leucas* caught in rivers (solid bars), southern Moreton Bay (light grey bars) and nearshore/shelf waters (dark grey bars) during this study. Numbers at the top of the bars indicate the sample size. Nearshore/shelf samples were obtained from QSCP and as an observer on commercial fishing vessels; southern Moreton Bay samples were from tagging efforts in the current study and river samples are from samples collected from commercial and recreational fishers (Table 10). Size class (m) is based on TL.

### 6.3.4 Ontogenetic shifts in diet

In adult *C. leucas*, δ¹⁵N values were described by linear relationship with increasing distance from the vertebral centrum (Figure 49). This same trend occurred in the stomach content analysis of *C. leucas*, with composition of the diet in nearshore habitat changed with increase in size from juvenile to adult *C. leucas* (Figure 50). An ontogenetic shift in diet ($r^2 = 0.573$, $p = 0.003$) from crabs, prawns, octopus, squid, baitsfish and fish to larger and more varied prey such as rays, other sharks, sea snakes, turtles and birds (Figure. 50) was apparent for sharks over 1.2 m in length, with shark and ray being the most common diet items in large *C. leucas*. Larger prey items made up to 22% of stomachs with prey items for juvenile sharks and up to 100% of
stomachs with prey items for adult *C. leucas*. The δ¹⁵N and δ¹³C signatures, during the bay/estuarine period of the *C. leucas* life history reflected a seagrass dominated signature (-12), compare to a more typical oceanic plankton based signature with transition to nearshore (-15/-16). (Figure 46, 49).
c) Shark 19, 195 cm TL, Male

\[ y = 9.85 + 0.11x \]
\[ r = 0.82 \]
\[ p = 0.0001 \]

\[ d) \text{Shark 20, 200 cm TL, Female} \]

\[ y = 10.96 + 0.14x \]
\[ r = 0.75 \]
\[ p = 0.0038 \]
**Figure 49.** Change in $\delta^{15}$N (‰) with distance from the centrum of *C. leucas* shark vertebrae for individual sharks (a) shark No. 17, (b) shark No. 18, (c) shark No. 19, (d) shark No. 20, (e) shark No. 23 (Table 10). The ontogenetic relationship for the large female is only taken for the first 10 years, after which she returns to an estuarine environment.

**Figure 50.** Relationship between *C. leucas* size class and percentage of stomachs with rays, sharks, sea snakes, turtles and sea birds in relation to all *C. leucas* with identifiable stomach contents within each size class. Numbers indicate *C. leucas* with stomach contents dominated by elasmobranchs, reptiles and birds.
6.4 Discussion

Spatial partitioning of ontogenetic stages has been used to indicate movement between juvenile estuarine and adult offshore habitats in lutjanids and serranids (Sheaves 1995). Large juvenile *C. leucas* in the Pine Island Sound, a large semi-enclosed lagoon in lower Charlotte Harbour, Florida, USA, which indicated that this estuary probably provides important habitat during the late juvenile portion of this species’ life history (Yeiser et al. 2008). Data from this study suggest frequent occurrence of sub-adult *C. leucas* at the marine and estuarine interface and at the river and estuarine environment for large juvenile *C. leucas*. The results also suggest direct connectivity of the Jumpinpin and Gold Coast seaways for large juvenile and sub-adult *C. leucas*, with presence-absence data indicating the vast proportion of detections occurring at Jumpinpin. Sub-adult *C. leucas* were not detected in any of the river or canal systems during the study, suggesting they may only be using habitats at the interface between estuarine and the nearshore environment, before moving into adult habitats. Large juvenile *C. leucas* detections indicated connectivity of southern Moreton Bay with the Gold Coast canal system. However, they did not occur at other river sites that were accessible. The Logan River is one of the most productive rivers for mud crabs (*Scylla serrata*) in sub-tropical Queensland (Loneragan & Bunn 1999). While crabs are prey of juvenile *C. leucas* (Cliff & Dudley 1991), no tagged *C. leucas* moved into this river system. This could be due to the period over which movement data was collected (10 months). Sharks may move have been detected moving into this area if the study continued for a long period (yrs).

Factors that drive a species to investigate habitats beyond their natal grounds are still poorly understood. The results of this study suggest a gradual transition from natal grounds to intermediate habitats and tagged sharks were not detected moving back into the river systems. This suggests a preference or need to leave neonate habitat, possibly driven by the need for larger and more varied prey. The role that gradients in prey abundance may play in structuring the short-term distribution of predators remains largely unknown (Hart 1997, Sims 2003). Sims (2003) suggested that productive habitats with abundant and available prey are likely to be selected over poorer ones, as one of the main factors determining animal distribution patterns. The clear shift in diet to larger prey in this study suggests pursuit of larger prey is a clear
driver of transition into intermediate habitats along the estuarine-nearshore continuum. The presence of juvenile Carcharhinus limbatus in various portions of the Terra Ceia Bay (USA), however, could not be correlated with the abundance of prey species within the geographical zones of the study site (Heupel & Hueter 2002). These authors suggested that water temperature may play a larger role and that habitat choice or predator avoidance was more critical than prey capture. Maturity-specific segregation has been suggested for C. leucas along the Florida Gulf Coast (Simpfendorfer et al. 2005, Yeiser et al. 2008). The hypothesis of predator avoidance suggests this factor drives ontogenetic habitat segregation. Habitat segregation by maturity has been observed in other species (Klimley 1985) and is also a possible influence of the life cycle stage of C. leucas that move into nearshore habitats. This could explain the presence of tagged sub-adults in southern Moreton Bay and the larger satellite-tagged C. leucas remained in the nearshore environment and did not move into the Bay.

Some studies suggest smaller juvenile sharks prefer shallow areas as a means of avoiding predation, whereas larger and older sharks occupy deeper areas (Merson & Pratt 2001). This study showed that C. leucas > 1.2 m TL began to exhibit a shift in diet that included larger and more varied prey, reflecting movement of C. leucas from nursery grounds to other habitats. Predator avoidance in sub-adult and large juvenile C. leucas, however, may still be a factor contributing to their use of transitory habitats at this stage of their life cycle. Larger elasmobranch predators are less likely to initiate attacks on vigilant prey (Heithaus 2004), which may explain the frequent movement by large and sub-adult C. leucas between the Gold Coast and Jumpinpin seaways (> 20 km apart) as a predator avoidance mechanism. In transitory habitats, large juvenile and sub-adult C. leucas may be the dominant top-level predators. This may explain their residency in these habitats until it is more advantageous for them to move more frequently into nearshore and shallow coastal habitats. The pursuit of larger prey or mating may then outweigh the benefits of transitory habitats and drives their movement into the nearshore areas. The PAT tag on the single mature female C. leucas indicated movement within the nearshore habitat, with no movement back into the estuarine environment. Movement of adult C. leucas into nearshore areas may provide additional benefits through increased opportunity for mating and larger and more varied prey. However, the trade-off for adult C. leucas is that they will then
need to share resources with other large shark species such as the tiger shark, *G. cuvier*, and this warrants further investigation.

### 6.4.1 Ontogenetic habitat shift

LA-ICPMS analysis of elemental signatures indicates habitat transition with increasing size of shark. Analysis of soft tissues can distinguish short-term movement of juvenile *C. leucas* from individual estuaries. Several studies suggest that juveniles from individual estuaries can be distinguished using elemental signatures, potentially enabling natal origins of adult fish to be determined (Gillanders & Kingsford 2000, Thorrold et al. 2001) (Chapter 5). Subtle changes in elemental isotopic signatures have been suggested as a tool to reveal movements from estuarine to nearshore habitats (Gillanders 2005). The pattern of spreading of the mean elemental signature of larger *C. leucas* samples in this study suggests this tool can provide an indication of transition into adult habitat. Further, the signature of the pregnant female (S23) similar to that of a large juvenile in estuarine conditions (which was also separated from male adults - S21 and 22) could indicate a return to estuarine conditions possibly as a result of frequent searching for pupping grounds (McCord & Lamberth 2009). Literature suggests *C. leucas* pupping occurs at river mouths; however, this is based on the capture of pregnant females at these locations (Jensen 1976). During seasonal long-line surveys in the Gold Coast canal system, however, I caught a 3.2 m TL pregnant female *C. leucas* at site 3 (Figure 27, insert, Chapter 5), 6 km along the Nerang River from the river mouth, indicating that pregnant females may actually pup in waters of optimal salinity for neonates. This study indicated that turnover in the elemental signature is likely to occur in the order of weeks, as evidenced through the results of tank-based experiments with *C. leucas*. The shift in the signature of pregnant female *C. leucas* back to δ¹³C values of -12 ‰ more reflective of earlier life history stages also indicates this as a potential explanation. Caution should be exercised; however, as this result was from a single pregnant female and the shift in elemental signature could be due to other factors including a possible reproductively–coupled hypocalcaemia previously postulated by Urist and Van de Putte (1967).

Few studies have tracked animals for long enough periods to actually detect direct ontogenetic shifts in habitat use. However, this study has illustrated the powerful combination of chemical tracing techniques, acoustic and satellite telemetry with
distribution data in order to decipher such movement in animals. For some fishes, movement into deeper waters is very often associated with ontogenetic habitat shift, as site fidelity to shallow waters diminishes with body size (Macpherson 1998). Further, many marine fishes exhibit directional and long-range migrations (Bruce et al. 2006) associated with changing environmental parameters such as rainfall and sea surface temperature (Chapter 3) or stimuli such as temporarily abundant food sources and mating requirements (Pittman & McAlpine 2001). Adult mating and breeding grounds may also require migrations to specific locations where sexually mature individuals congregate, driving ontogenetic habitat shift. For example, Bolden (2000) found Nassau grouper, *Epinephelus striatus*, migrated 220 km to a spawning aggregation. Further, Mazeroll and Montgomery (1998) proposed that individual fish learn routes to spawning sites before reproduction begins. Data in this study suggest *C. leucas* use specific routes, probably moving between deep holes (Chapter 4) before moving offshore, probably also following learned routes. Further, this study found that *C. leucas* remained primarily within southern Moreton Bay and sub-adults tagged were not detected in the Gold Coast canal system or other adjoining river systems to the Bay. This supports the hypothesis that *C. leucas* remain within the bay in preference to the adjoining urban canal systems.

6.4.2 Ontogenetic diet shift

Varying degrees of diet overlap have been described for co-occurring elasmobranchs and teleosts. However, diet overlap is most often encountered between pairs of consecutive size classes or adjacent geographical locations (Wetherbee & Cortes 2004). The sequential δ¹⁵N isotopic analysis of *C. leucas* vertebrae probably indicates a shift in trophic level, as mediated by an ontogenetic shift in diet towards large and more varied prey. These results are supported by results of the stomach content analyses. The excursions and range of movements of large juveniles and sub-adult *C. leucas* throughout the study site probably provided expanded foraging areas. Ontogenetic shifts in diet have been established for *C. leucas* in South Africa, *G. cuvier* in Australia and *C. carcharias* in the USA (Cliff & Dudley 1991, Simpfendorfer et al. 2001, Estrada et al. 2006). The onset of ontogenetic changes in diet with size observed in *C. leucas* is indicative of an ontogenetic shift in habitat from estuarine nursery grounds towards coastal nearshore habitats. For sharks in general, gender (most likely due to different sizes of male and females), habitat type

Estrada et al. (2006) found a significant enrichment in δ¹⁵N values at a consistent sampling location along the vertebrae of *C. carcharias*, which coincided dietary shifts confirmed by stomach contents analysis. While the shift of diet from primarily fish to marine mammals is distinct for *C. carcharias*, this shift also coincides with distinct ontogenetic changes in tooth morphology (McCosker 1985). Although all relationships between δ¹⁵N and TL were described by a linear regression, there are variations in the dietary shifts among individuals, as some of the animals showed patterns resembling the sigmoidal relationship similar to that for δ¹³C. This could also be due to the often generalist diet of *C. leucas* (Wetherbee & Cortes 2004). *C. carcharias* have a life cycle that remains wholly in coastal shelf and pelagic waters, whereas *C. leucas* use habitat encompassing the entire range of inshore-offshore habitats involved in the ‘trophic relay’ concept of transport of production (Levin et al. 2001).

### 6.4.3 Influence of physical parameters

Species vary in their response to environmental conditions due to functional differences related to dietary requirements, habitat specialisation and body size (Pittman & McAlpine 2001). A clear relationship between environmental variables (such as flood frequency and temperature) and density and emigration rates in fish populations was observed from marsh habitats in New Jersey, USA (Hunter et al. 2009). Emigration of *C. leucas* into nearshore/shelf habitat is likely to occur according to both dietary requirements, inter- and intra-specific competition and influenced by physical variables. Further, Brunschweiler and Von Buskirk (2006) found that while adult *C. leucas* use shallow coastal areas with distinct temperature preferences, they can also cross deeper oceanic waters and alternate their behaviour accordingly. The extraordinary abilities of *C. leucas* to use diverse habitats, their euryhaline capability and generalist diet suggest this species is highly adaptable and may be able to exploit this ability in order to maximise use of resources in all of its life cycle habitats. When adequate size is reached and threat of predation reduced, movement of *C. leucas* into nearshore habitat may occur in relation to, but not restricted to, preferred environment requirements.
Salinity is likely to have less of an influence on *C. leucas* with increasing size (Pillans & Franklin 2004), as large *C. leucas* can rapidly move between fresh and salt waters. Rainfall, however, had an influence on catch of sharks in nearshore habitats. Reduced levels of occurrence of sub-adult *C. leucas* during peak rainfall (prior levels of 149 mm) also indicates *C. leucas* were moving from these areas, possibly into the nearshore waters. Catches of *C. leucas* increased substantially after periods of high rainfall in the nearshore catch of the QSCP (Chapter 3), which further supports this hypothesis.

*C. leucas* is considered near-threatened on the IUCN Red List (IUCN 2008) and thus, an understanding of their occurrence in different habitats throughout their life cycle is essential for their conservation and management. Occurrence in transitional habitats at the interface between riverine nurseries and nearshore habitats suggests these areas are all important to sub-adult *C. leucas* before moving offshore to adult habitats. Transition habitats represent a key period in the life cycle of *C. leucas* before maturity and these movements are associated with a shift in diet towards larger prey. Conservation efforts for sub-adult *C. leucas* should be directed more appropriately towards these “hot-spots” within *C. leucas* transitory habitats.
CHAPTER 7

SUMMARY AND GENERAL DISCUSSION: A CONCEPTUAL MODEL OF THE LIFE CYCLE AND HABITAT ECOLOGY OF THE BULL SHARK ON URBAN COASTS

7.1 Important habitats to *C. leucas* in the marine-estuarine continuum

This data-rich study has demonstrated strong new evidence to support the importance of space-limited natural estuarine and shelf habitats to the different life cycle stages of *C. leucas* and insight into how they use habitats in the marine-estuarine continuum. The concept of critical habitats has received much attention in both terrestrial and marine ecology (Takekawa & Beissinger 1989, Gregr & Trites 2001, Jones 2001). While frequency-dependent distribution models provide a basis for assessing the role of specific habitats to sharks (e.g. Chapter 2), it is necessary to understand the overall habitat-related distributions of fish species at particular life history stages, in order to assess the importance of a particular habitat. Examining the landscape for ecologically equivalent habitats is one approach to determining the importance of a habitat to fishes and has been used, for example, for assessing the value of deep-water corals to fish assemblages (Auster 2005) and estuaries to commercial fish production (Meynecke et al. 2008). The ‘outwelling’ hypothesis suggests that passive transport of nutrients and organic material from estuaries (which are important habitats to the life cycle of many fish) is a key driver of coastal fish production (Odum 1984, Staunton-Smith et al. 2004). Most studies have focussed on benthic transfer of mangrove-derived material (Lee 1995), although Werry and Lee (2005) demonstrated export to zooplankton of the pelagic food chain via grapsid crabs acting as shredders. Migration of fish and crustaceans from estuarine nursery habitats to nearshore habitat also exports biomass to nearshore areas (Lee 1995), but the importance of this transport is largely overlooked and can complicate interpretation of important habitats. The findings in this thesis, however, strongly support the model that estuaries are important habitat to key ontogenetic stages of *C. leucas*. Further, the size of available estuarine habitat directly influences *C. leucas* populations in adjacent nearshore areas, as *C. leucas* undertakes ontogenetic migrations within and uses the production
available from the marine-estuarine continuum throughout their life cycle. Estuaries, however, do not contribute equally to coastal production or *C. leucas* populations (Chapter 2) as they vary in their importance as nurseries (Beck et al. 2001), which may in part be due to their degree of urbanisation or habitat characteristics, e.g. mangrove density.

Estuarine habitats are usually inter-connected and dynamic habitats that are influenced by geomorphic and hydrological features (Lee et al. 2006) and their importance to *C. leucas* can vary. Outcomes in this thesis support the hypothesis that the spatial extent/area of natural estuarine habitat significantly influences adjacent nearshore *C. leucas* populations and these patterns are also influenced by the spatial extent of available shelf habitat (Chapter 2). Estuaries are critical habitats and transition zones that link the freshwater nursery habitat (Levin et al. 2001) of juvenile *C. leucas* with the nearshore marine adult habitat (Chapter 6). The temporal scale of ontogenetic habitat use and the space-limitation of estuarine and nearshore habitats are an important consideration for the conservation of *C. leucas* as they rely on a range of habitats throughout their life cycle (Figure 51). Urbanisation of coastal habitats does not increase available critical habitat to the life cycle of *C. leucas*, as this species shows a preference for river and areas of dense stand of mangroves over urban canal systems (Chapter 5 and 6). The rapid destruction of natural mangroves in coastal areas is therefore a major concern for *C. leucas*.

One of the aims of this thesis was to gain insight into the drivers for movement of *C. leucas* of different ontogenetic stages and thereby enhance current understanding of the biology and habitat ecology of this top-level consumer to better inform conservation and management of the species. Although difficulty in obtaining sufficient numbers for study is expected due to its elusive nature and often low natural abundances, it is still surprising that data on the habitat ecology and biology of *C. leucas* is scant. Given the accelerating global population decline of sharks, largely due to overfishing, and the concern for the ecological ramifications of cascading effects on marine ecosystems is particularly concerning (Myers et al. 2007). This thesis has provided a conceptual view of the ontogenetic importance of different habitats on an urban coastline to *C. leucas*. The major environmental variables and habitat characteristics influencing historical spatial patterns in immature (< 2 m TL) and
mature (> 2 m TL) C. leucas catch have been identified along ~ 2000 km of the east coast of Queensland, Australia. The outcomes of this thesis support the notion that rainfall patterns and the amount of available and connected estuarine/mangrove and shelf habitats, at a large spatial scale, play a key role in the distribution and abundance of C. leucas. Furthermore, novel and innovative telemetry and chemical analysis methods used to investigate the small-scale and long-term movements of C. leucas showed (1) the importance of river and natural habitat over urban canal systems; (2) the influence of current velocity and depth of water on the behaviour of C. leucas; and (3) the importance of transitional habitats to sub-adults and an ontogenetic shift in diet accompanying C. leucas migration with increasing size into nearshore habitat. Additional survey work in the nearshore environment illustrated little evidence for partitioning of terrigenous nutrient sources by adult C. leucas with other large coastal shark species (> 2 m TL as adults) (Appendix 4). These investigations contributed to the broader knowledge of the biology and habitat ecology of C. leucas on urban coastlines, with significant implications for their conservation and management.

Figure 51. A conceptual model of temporal and spatial habitat use by the life cycle stages of C. leucas based on results of this study and existing literature. Circles represent areas of majority of ontogenetic habitat activity and arrows indicate extent of potential movement. Size of C. leucas given in bubbles for each life cycle stage is indicated as TL. Large black arrow indicates a long-term driver of habitat use.
7.2 Ontogenetic phases of *C. leucas*

At least two important features relating to *C. leucas* habitat use are apparent in the temporal-ontogenetic habitat use model (Figure 51). Firstly, the range of habitat use expands over time in the life cycle, with the animal’s ‘footprint’ defined by its ontogenetic stage (Chapter 5). Secondly, as has been shown in other estuarine dependent species such as the yellowfin bream (*Acanthopagrus australis*) (Pittman & McAlpine 2001), *C. leucas* requires different resources and access to different habitats at different ontogenetic stages. Therefore, the composition, spatial arrangement and timely availability of those resources will be critical for achieving life cycle closure.

Increase spatial use of habitats and movement downstream in rivers for neonate and small juvenile *C. leucas* during flood periods probably occurs as the balance between the drivers of ontogenetic habitat segregation are disrupted. Neonate and small juvenile *C. leucas* appear to maintain specific salinities ranges they are physiologically suited to, rather than expend energy to acclimate to the altered salinity in during flood periods. The driver of predation from large sharks (reducing movement into more saline habitats) versus the driver of need for more varied and larger prey is altered, as the preferred salinity conditions of YOY and small *C. leucas* move downstream. The activity space of small juvenile *C. leucas* increased during the wet periods in a lagoon on the east coast of Florida, USA (Curtis 2008). YOY are hypothesised to avoid areas with higher densities of juvenile *C. leucas* while choosing habitats with optimal salinity (Simpfendorfer et al. 2005).

Short and long-term movements of *C. leucas* in this study indicate that this species is limited to comparatively small and consistent activity spaces that vary ontogenetically in importance and location in the marine-estuarine continuum. The size and distance of migrations between activity spaces increase with later ontogenetic stages (i.e. larger sizes). Similar phenomena have been observed in other sharks that use estuarine areas, for example, in lemon sharks, *Negaprion brevirostris*, which show a correlation between body size and home range size (Morrissey & Gruber 1993). Alternatively, white sharks, *Carcharodon carcharias*, in eastern Australia show seasonal co-occurrence in coastal areas with juveniles occupying relatively small ‘hot spots’ in nearshore beaches, with directed and long range migrations of often over 1000 km between these locations (Bruce et al. 2006, Werry et al. 2010). Ontogenetic driver of habitat segregation, however, is most easily observed in connected but highly variable
habitats in the marine-estuarine continuum. Estuarine habitats are essential to the early life cycle phase of *C. leucas* and this thesis has identified the following key life cycle phases corresponding to different size groups of *C. leucas*:

**Nursery phase:** The nursery phase firstly involves a neonate stage (0.45 to 0.84 m TL) in freshwater habitat primarily in the upper reaches of river systems (Chapter 5 section 5.3.2, Figure 49). In this study, I found evidence that pregnant *C. leucas* may pup within the riverine habitat (McCord & Lamberth 2009), possibly at the preferred salinity range of neonates, rather than at the river mouth as suggested by previous studies (Jensen 1976). *C. leucas* neonates remain within defined low salinity (17 – 22 ppt, mesohaline) areas (as low as 3 ppt during flood periods), in the top reach of rivers, which function as nurseries, and attain isotopic signatures distinct to their nursery. Long-term data from this thesis indicated that movement of the small juvenile stage (0.85 to 1.15 m TL) of the nursery phase then involves increased spatial extent of habitat use, incorporating movement further down river and a shift in salinity preference to 24 – 27 ppt. Competition and threat from predation (primarily cannibalism) restricts the extent of movement for this size range of *C. leucas* (Simpfendorfer et al. 2005). Flood events (consistent rainfall > 300 mm) enable periodic emigration further downstream, as larger conspecifics also alter movements to downstream and into intermediary *C. leucas* habitat during these events.

**Intermediary/Transitional phase:** Large juveniles (1.16 to 1.6 m TL) use increasingly larger spaces, with salinity preference shifting to 19 – 33 ppt as they move between upstream and downstream habitats within rivers. Tidal excursions into urban canal systems and to the top reaches of rivers are, on occasion, accompanied by movement into the lower reaches of estuaries and bays. Preference of this ontogenetic stage is also for top reaches of river systems and not for urban canal systems. This thesis identified that *C. leucas* move between deep-water foraging areas and regularly into sub-adult *C. leucas* (1.6 to 2 m TL) habitat at the interface between estuaries and the nearshore environment. Detailed analyses in the thesis indicate sub-adult *C. leucas* remain primarily within the lower estuary and within southern Moreton Bay, with its dense stands of mangrove, compared to the adjoining urban canal systems, rarely returning to river systems. Evidence from movement data in this study showed sub-adult *C. leucas* regularly occur at the interface with oceanic habitats. Large juveniles
and sub-adults make more use of deeper water than small juveniles through an overall broader extent of movement.

_Coastal phase_: Lagged responses to rainfall events are most evident in _C. leucas_ ontogenetic life cycle stages < 2 m TL. However, sub-adult transition into adult (> 2 m TL) nearshore habitat is accompanied by an ontogenetic shift in diet to incorporate larger and more varied prey (Figure 50, Chapter 6). Evidence in this study from chemical markers (LA-ICPMS and stable isotope analyses) showed that _C. leucas_ > 2 m TL remain in nearshore areas, although females may periodically return to upper estuarine habitat possibly in search of pupping grounds. Results from this thesis using LA-ICPMS analysis indicated males remain offshore. Further, archival pop-off tagging of a _C. leucas_ (1.92 m TL) showed this shark remained in the nearshore environment and did not return to the estuary over a 12-day tracking period (Chapter 6). Little overlap of ocean physical conditions during capture and source of nutrients of adult _C. leucas_ with other large co-occurring coastal shark species were evident in the nearshore and shelf habitats (Appendix 4). Interspecific differences in isotopic signatures are largely due to dependence on terrigenous versus oceanic sources of nutrients.

### 7.3 Movement between ontogenetic habitats and disruption to life cycle strategy

Migration allows _C. leucas_ to take advantage of resources available from different habitats as life-history requirements alter, environments change seasonally and adjustment to unfamiliar or urbanised habitats. The ability to use a diversity of connected habitats is integral to the life history strategy of _C. leucas_ and this thesis has provided an insight into these patterns as required for the effective conservation and management of this dangerous wildlife species on urban coasts. A multipartite life cycle with stage-specific occupation of distinct neonate, juvenile, sub-adult and adult habitats illustrates the dependence of this species on multiple and connected habitats (Figure 51 and 52), a feature also seen in many estuarine plants and animals (Pittman & McAlpine 2001, Sheaves 2009). Large juveniles and sub-adults, which have smaller-scale movements such as migrations from upper into lower river habitat and migrations to join adult populations through a variety of patterns and ecological relationships, depend significantly on the connectivity of these habitats in the life-cycle of _C. leucas_. These larger scale trends incorporate small-scale factors, such as
changing foraging behaviours with affinity for specific flows and increasing water depth for refuge and foraging. Preference for deeper habitat, often at the entrance of tributaries, in the short-term movements of neonate and small juvenile *C. leucas* occurred in a Florida estuary (Curtis 2008). He noted that orientation in the water column at these locations was not influenced by tidal movements and that the tracked animals were influenced by artificial thermal outflows from industry in the area. The current study illustrates that disruption to the life history pattern occurs through:

1. Urbanisation of habitats important to the life cycle of *C. leucas* through the removal of biological structural and/or functional components (e.g. mangroves) and alteration of the hydrological regime (Morton 1989, Lee et al. 2006). Urbanisation alters fish assemblages in estuarine waterways (Morton 1992) and creates significantly altered trophic food webs (Waltham & Connolly 2006). Urban canals are not preferred habitats by *C. leucas* (Chapter 5).

2. Climate-scale alteration in sea surface temperature and the frequency and volume of rainfall. Climate has a significant influence on movement, abundances, body-size distributions, and latitudinal life span of fish (Lehodey et al. 2003, Peltonen et al. 2007, Genner et al. 2009, Munch & Salinas 2009). I have found that sea surface temperature and rainfall (lagged effects) have significant effects on the catch of immature (< 2 m TL) and mature (> 2 m TL) *C. leucas* in nearshore habitats of eastern Queensland (Chapter 3). Climate change may, therefore, affect the abundance of *C. leucas* in nearshore habitats.

3. Overfishing from recreational and commercial targeting of *C. leucas* in space-limited habitats could lead to local depletion of populations, given the specific salinity preferences of neonates and small juveniles (Martin 2005). There is a risk of overfishing if knowledge on the biology of a species is lacking and this is further exacerbated if the biology and mobility, and thus habitat requirements, of a species are not considered in management decisions (Field et al. 2009a). Intensive fishing in nursery and space-limited important habitats or over-exploitation of the breeding population of nearshore *C. leucas* can
push shark populations to unsustainable levels (Reynolds et al. 2005, Field et al. 2009b).

This thesis investigated relationships between movement and *C. leucas* TL on a variety of scales: a broad scale using historical QSCP *C. leucas* nearshore catch (Chapters 2 and 3) and on a small scale using acoustic telemetry and innovative chemical tracing techniques (Chapters 4, 5 and 6). A range of estuarine and coastal shelf characteristics were expressed as habitat metrics in addition to historical trends in climate parameters and the historical catch data were split into capture gears (gill nets and drumlines) and according to *C. leucas* maturity (< 2m and > 2m TL). Linkages of *C. leucas* catch with habitat characteristics and climate parameters were measured using shelf and estuarine metrics and physical parameters of rainfall, sea surface temperature, SOI, and lunar phase. Distance to shelf and number of estuaries explained a significant portion of the CPUE for *C. leucas* in both gill nets and drumlines. Lagged effect (one to eight days prior to *C. leucas* capture) of rainfall (> 300 mm) and sea surface temperature explain significant variations in the CPUE data. The demonstrated effect of such factors on catch of *C. leucas* reflects some important considerations of fishery management in the face of climate change. Climate change impacts are long-term and may take years or decades to come into major observable effect on *C. leucas* populations. Physical attributes of estuarine habitats such as water quality, hydrological regime and freshwater input, however, can alter on short-term scales of days or months and are of immediate influence to how *C. leucas* use coastal habitats. Both types of influences need to be considered in the approach to sustainably managing *C. leucas* and other threatened organisms with similar habitat requirements and environmental sensitivity.

Detailed analyses of movement for four ontogenetic stages of *C. leucas* support the broad outcomes of nearshore CPUE trends, indicating differing habitat use with increasing size (Figure 51) and influence of salinity and large rainfall events (Figure 52). Trends of occurrence in relation to four available habitats, namely, upper reaches of river, lower reaches of river and two adjoining urban canal systems distinguished by meso and polyhaline conditions in the Gold Coast canal system, were demonstrated using acoustic telemetry and partitioned among habitats by ontogenetic salinity preferences (Chapter 5). The distribution and abundance of different
ontogenetic stages of \textit{C. leucas} in estuarine waters may be governed by a trade-off between the costs and benefits of moving between alternate feeding or refuge habitats in the marine-estuarine continuum (Sheaves 2009).

7.4 A conceptual model of the life cycle of \textit{C. leucas}

A conceptual model is constructed to illustrate the life cycle of \textit{C. leucas} in relation to urbanisation and significant physical parameters identified in this study (Figure 51). Habitat shifts as well as migrations within a life cycle often occur with predictable sequence and duration (Pittman & McAlpine 2001) and the results of this study illustrate a life cycle that has predictable patterns and drivers of movement in space and time. The proposed conceptual model (Figure 50) of the \textit{C. leucas} life cycle suggests conservation efforts for freshwater and estuarine-dependent \textit{C. leucas} should emphasise the intrinsic value and importance of natural estuarine habitats over the low value of urban canal systems to the life cycle of this species.

Predator avoidance and the need for larger and more varied prey are hypothesised to be major factors driving the ontogenetic habitat use by \textit{C. leucas} along the marine-estuarine continuum. Transition of sub-adults into habitats at the interface between estuarine and oceanic habitats occurs with distinct shift in diet and movement from rivers and under non-flood conditions. These life cycle stages appear to rarely move into adult nearshore habitat. This further illustrates the space-limited and specific habitat use of different ontogenetic \textit{C. leucas} stages along the marine-estuarine continuum and their vulnerability to exploitation at all life cycle stages. Temporary disruption in the segregation of ontogenetic stages into separate habitats along the marine-estuarine continuum is driven by prior rainfall patterns, whereas long-term patterns of movement occur with the need to pursue larger and more varied prey with increasing body size. Patterns of movement into nearshore areas correlate with lunar phase, which could indicate both abundance of prey and avoidance of larger conspecifics even at the sub-adult size. Further, urban canals are not ideal habitat, but may become more valuable to the species in the form of alternate habitats, as rapid degradation of coastal areas occurs globally.
7.5 Implications for C. leucas conservation and management

Empirical evidence suggest that large body size and late maturity are the best life history trait predictors of vulnerability to fishing and for developing indicators of human impacts on a species (Reynolds et al. 2005, Genner et al. 2009). Regardless of whether differences among taxa in fishing mortality are controlled, Reynolds et al. (2005) suggest that there is no evidence that high fecundity confers resilience to fishing pressures. C. leucas are top-level predators and like many other elasmobranchs, they are particularly vulnerable to exploitation with their relatively late maturity and slow growth rates (Cliff & Dudley 1991, Musick et al. 2000). These biological characteristics reflect a strong K-selected life history pattern with an intrinsic slow rate of population increase (Pratt & Casey 1990, Cortes 2000). As such,
C. leucas are vulnerable to direct fishing pressure as emphasised by results of this study, which illustrated the concentrated use of specific areas within space-limited habitats. Despite the danger they pose to the safety of humans that use coastal areas (the last human fatality from a shark attack in Queensland is attributed to C. leucas and occurred in 2006 (ASAF)), ecologically sound management strategies need to take into consideration the biology and the habitat ecology of these animals along the marine-estuarine continuum, to ensure sustainability of localised C. leucas populations (Figure 53) on the premise of sharing such habitats between humans and dangerous megafauna.

Estuarine sharks such as C. leucas are potentially highly vulnerable to urban habitat modification, as they are subject to not just the same biological constraints as their oceanic counterparts but also additional habitat constraints not faced by their stenohaline relatives (Moyle & Leidy 1992, Compagno & Cook 1995, Martin 2005). River and estuarine habitats have more limited volume and their physiochemical properties vary widely (Martin 2005, Lee et al. 2006). As a result, C. leucas, is more likely to be in competition with humans for coastal resources and hence more vulnerable to their activities. Furthermore, throughout their distribution, C. leucas have long been regarded as highly dangerous and thus to be much feared (Zeller 1999, Martin 2005). Conservation of dangerous urban wildlife is a challenge for management bodies as biodiversity ‘erosion’ has become a major political, economic and ethical issue (Leveque & Mounolou 2003). Further, the concern for people’s safety requires a comprehensive understanding of how potentially dangerous wildlife species such as C. leucas use and value urban canal developments, in order that a balance between conservation and management of shark-human interactions may be reached. The results of this thesis support the notion that swimmers should avoid entering riverine and coastal water after significant periods of rain (Chapter 3) and particularly during period of increased C. leucas activity at dusk and dawn (Chapter 5).

The process of developing an effective conservation strategy needs to ascertain the impact of human activities upon species and their associated habitat to make concrete proposals for averting degradations not only at the habitat and species level, but considering ecosystem impacts (networks of habitats) (Martin 2005). The results of
this study suggest that when considering management and conservation issues relating to major urban wildlife species that pose a risk to humans, a range of factors encompassing different spatial and temporal scales including the climatic, physical and chemical elements of a habitat and the temporal pattern of use of space and resources, need to be considered. This approach seeks to ensure sustainability of wildlife populations. The model provides consideration for the scale at which process upon which *C. leucas* populations rely (i.e. ecosystems) and the habitats across the marine-estuarine continuum of varying ontogenetic importance to *C. leucas* (Figure 51). Further, Ley et al. (2002) found evidence that abundance of *C. leucas* was 4.4× greater in estuarine areas closed versus areas open to targeted *C. leucas* fishery along the Queensland coast.

**Figure 53.** Model approaches for balancing conservation of dangerous urban wildlife and their associated important habitats with urban human population needs (i.e. minimising harmful shark-human interactions) in managing coastal *C. leucas* populations. Adapted from Leveque & Mounolou (2003) and Martin (2005).
My findings provide valuable information on how to manage *C. leucas* in urban canal systems and suggest that these are not preferred habitats to *C. leucas* populations. Turning natural estuarine waterways into urban canal systems may alter estuarine fishes community structure; however, this habitat is not as useful as their natural counterparts to the life cycle of *C. leucas*. Urban canals, therefore, are not likely to increase natural *C. leucas* populations, but probably have an inverse effect that contributes to reduction in natural populations through the devaluing and reduction in available primary natural habitats. Managers should consider the ramifications of removal of natural waterways to the local ecology of estuarine and nearshore ecosystems. My findings further suggest that public perception of “thousands of bull sharks” in highly urbanised areas, in the Gold Coast canal system for example, is misinformed and probably based on multiple sightings of few individuals, providing a false impression of many sharks using these areas. Tracking results indicate that *C. leucas* are able to move from one end of the Gold Coast canal system to the other in short (hours) and medium (weeks) time frames, varying with size. Further, the limited volume of the river and the narrow sections of the canal habitats along with a high residential human population increase the likelihood of a shark being sighted.

This thesis found a dependence of *C. leucas* on habitat configuration and movement patterns influenced by rainfall throughout its life cycle. These factors should be considered in future management of shark control and in the establishment of potential marine protected areas (MPAs) for this species. Strong site fidelity (Chapter 4, 5 and 6) in estuarine habitats of *C. leucas* at key ontogenetic stages indicates the importance of targeted habitat protection so as to avoid the forced emigration (as a result of unavailability of preferred habitat) of *C. leucas* to less favourable, alternate, urbanised habitats (Figure 51). Furthermore, the results of this thesis on the ranging and migration/movement patterns of *C. leucas* suggest a network of MPAs at “hotspots” along the marine-estuarine continuum would help buffer the impacts of further urban canal developments. Data in this study on foraging behaviour and short-term movement supports the potential effectiveness of “no take” zones, e.g. sections of the Nerang River that serve as a nursery to neonates. Management zones, however, should encompass the home range of the most vulnerable (i.e. neonate) of ontogenetic stages in the *C. leucas*. 
For neonate and small juvenile *C. leucas*, MPAs should be focused on the limited sections of the upper reaches of rivers where the neonate and young juveniles aggregate. Further, deep holes in transitory habitats, such as at river mouths and junctions in bays between estuarine and nearshore habitats should be areas considered for reduction in fishing pressures for large juvenile and sub-adult *C. leucas*, particularly in urban areas. Nearshore locations with a high number of adjacent estuaries should be considered in the design of top-level predator MPAs. Relationships with rainfall also suggest *C. leucas* may be more vulnerable to fishing during seasons with very high rainfall. Activity of both immature (< 2 m TL) and mature (> 2 m TL) *C. leucas* in nearshore areas increases by several orders of magnitude during wet periods and beach users should avoid areas close to river mouths one to eight days after a major rainfall and particularly in summer months.

The protection of strategic habitats for conservation of *C. leucas* and to enable replenishment of populations through spill over and recruitment processes may counteract impacts of further alteration of estuarine habitats into urban canal systems and fishing pressures (Ley et al. 2002). For optimisation of management of *C. leucas* populations, a combination of habitats should be considered based on specific selection criteria of habitat value to its life cycle, bathymetry and available adjacent habitats (Figures 49 – 51). Regional differences in the nearshore adult *C. leucas* populations between sub-tropical and tropical Queensland suggest region-specific approaches to MPA designation. Regional implementation of a network of MPAs could also protect important habitats and conserve *C. leucas* populations by providing replenishment and recruitment to targeted, controlled (QSCP) and depleted (Chapter 2) nearshore *C. leucas* populations. MPAs covering a large space in addition to identified ‘resting areas’ or ‘hotspots’ in coastal areas provide protection for temporal periods as they take into account small foraging excursions by sharks outside ‘hotspots’ (Heupel & Simpfendorfer 2005). These have proved successful for other carcharhinid species with both high and variable site fidelity and subjected to varying fishing pressures (Garla et al. 2006, Heupel et al. 2009).

### 7.6 Limitations of the current study and directions for future research

The scarcity of studies on *C. leucas* available for comparative analysis with this thesis accentuates the unique and important contribution of this study to current understanding of the habitat ecology of *C. leucas*. While this thesis has identified
habitats of various ontogenetic importance to *C. leucas*, it has also identified further critical gaps in the understanding of the movements and population dynamics of *C. leucas*. Population abundance estimation is an important aspect for ensuring sustainable fishing practices (both recreational and commercial), determining a recruitment index and for assessing whether, over generations, abundance remains stable within a population (Prince 2005). This is particularly useful for management of *C. leucas* populations in river and nearshore habitats in eastern Queensland.

Movement data incorporated into mathematical models (e.g. agent-based modelling) may provide further predictive ability to model *C. leucas* habitat use by utilising the outcomes of this study and under scenarios of varying modelled physical stressors. The range of movement of *C. leucas* increases substantially with increasing TL, making study of adult *C. leucas* a necessary but challenging prospect, particularly for differences in gender-specific habitat use. The reduction in long-lived breeding females is a concern in nearshore areas and warrants further investigation (Chapter 2). Further archival satellite tagging of adults (> 2 m TL) in nearshore areas would help determine adult home ranges and, coupled with genetic analysis, elucidate the extent of connectivity between tropical and sub-tropical Queensland *C. leucas* populations on the eastern coast of Australia. Some tagging studies suggest movements of adults for several hundred kilometres, for example from one bay or estuary to another, although the reasons and ecological significance for these movements remain unknown and little information is available on the frequency of broad-scale inter-population movements (Brunnshweiler & Van Buskirk 2006). Satellite telemetry may confirm patterns of varying adult movements and habitat use according to gender, as has been suggested from LA-ICPMS in the current study, to guide management and conservation of adult *C. leucas* populations.
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APPENDIX 1

RESIDUAL PLOTS AS EXAMPLES FOR THE DISTRIBUTION ASSUMPTIONS OF THE MULTI-FACTORED PHYSICAL PARAMETER MODELS IN RELATION TO BULL SHARK CPUE

a)
Residual plots for the modelled trends of small *C. leucas* (< 2 m TL) in relation to lunar phase and caught on QSCP drumlines (a) and, modelled trends of SOI for pregnant female *C. leucas* caught on nets (b).
APPENDIX 2

DEDICATED BULL SHARK DISPLAY – SEA WORLD, GOLD COAST, AUSTRALIA

Substantial in-kind support from Sea World enabled significant tagging efforts for the research outlined in this thesis. Based on the findings of this study, a dedicated public display was subsequently constructed by Sea World to illustrate the research and to dispel many of the myths surrounding the *C. leucas*. Juvenile *C. leucas* are kept in a 220,000 L oceanarium on display. Larger individuals are released and internally tagged as part of my ongoing research efforts on the long-term movements and habitat-use of the species in southeast Queensland. Two *C. leucas* (1.3 and 1.65 m TL) were subsequently tagged and released in December 2009.

Plan view of the *C. leucas* display (Permission given by Sea World for use in this thesis).
Key facts to dispel many of the common myths surrounding *C. leucas* in coastal habitats

Display placing fear of shark attack in context.
SHARK RESEARCH

Imagine a career working with Bull Sharks, studying their behaviours, tracking their movements and trying to figure out exactly why these extraordinary creatures do the things they do!

Jonathan Werry

Jonathan Werry does exactly that. He is a shark research scientist studying sharks not only here in Queensland but as far afield as New Caledonia.

Jonathan often works with the team at Sea World...

Both Jonathan and Sea World are committed to learning more about Bull Sharks in order to conserve these remarkable creatures.

Jonathan’s ongoing research program is examining the movement patterns of Bull Sharks in the Gold Coast canal system and Broadwater areas. This isn’t as easy as it sounds. Sharks often travel underwater so it’s not as if Jonathan can just watch them swim past and see where they’re going!

QUESTIONS

Jonathan knows that natural habitats such as estuaries provide protection and food sources for the Bull Sharks and are very important to their life cycle.

However very little is known about how the man-made urban canal systems are affecting the Bull Sharks.

1. Do the canals provide the same benefits as natural habitats?
2. Do the Bull Sharks even hang out in the canals?
3. Do all the Bull Sharks frequent the same places or do they spend time at different locations depending on their age?

Jonathan, with help from the team at Sea World, is looking for answers!
TARGETED FORAGING

When people see a Bull Shark in a canal they often presume that the poor shark has somehow ‘lost its way’ within the twisting canal system and can’t find a route out to the open ocean.

JONATHAN’S RESEARCH HAS SHOWN THIS IS SIMPLY NOT THE CASE!

Short term tracking has shown that Bull Sharks have a two week cycle with clear patterns of movement from one key location (often a deep hole where fish hang out) to another. This behaviour is known as targeted foraging.

Just as Mum may drive directly to the supermarket, then the bakery and then the butchers – Bull Sharks do the same – moving directly from one familiar fishing spot to the next.

THEY'RE NOT LOST – BULL SHARKS KNOW EXACTLY WHERE THEY ARE GOING!
NATIONAL GEOGRAPHIC CRITTERCAM DEPLOYMENT ON SUBADULT BULL SHARKS

Deployment of crittercam on a sub-adult *C. leucas*

National Geographic crittercam with attached acoustic tag
APPENDIX 4

CO-OCCURRENCE OF OTHER LARGE SHARK SPECIES WITH ADULT BULL SHARKS IN COASTAL AND SHELF WATERS

Introduction
Little is known of adult *C. leucas* ecology in sub-tropical coastal and shelf habitats and their co-occurrence with other large shark species. In this exploratory study, I examined isotope ratios and catch of six large shark species (including *C. leucas*) in shelf waters of the Gold Coast. Preliminary results are presented and provide some insight into co-occurrence of key large shark species in adult *C. leucas* habitat.

Methodology

In this study, data were collected from captured sharks as an observer on a commercial fishing vessel in addition to *C. leucas* samples from the QSCP. A series of set lines were used by commercial fishers at distances of ~ 500 to 2000 m apart, starting several km from the entrance to the Tweed River (28°10'S), south of Currumbin Creek (Figure 37) out to depths of 60 m (~20 km from the shoreline). Lines consisted of a concrete anchor with 8-mm rope attached to a 20-L float at the surface, which then adjoined a second 20-L float set at 5 to 8 m apart (Figure 40). A single large trace of 4 m of braided cord connected to an 800 pound swivel with 2 m of stainless wire and an 8/0 tuna hook were used to capture sharks. Freshwater eel and bonito were used as bait and traces were set from the surface on rope between the two 20-L floats.
Study site illustrating the (A) Gold Coast/New South Wales (B) continental shelf.

Data on sharks was collected by an observer on the commercial fishing vessel one day out of each calendar week for the period of the study (2006 to 2008). Other than during periods of rough weather conditions that prohibited access to the set lines or boat maintenance, data were collected on a weekly basis. Captured sharks were measured (total length), sexed and maturity was determined by clasper calcification. Total length measurements were estimated from marks along the vessel for restraint of sharks during rough weather. Position of shark capture was recorded using GPS. A range of shark species were recorded during observations in addition to *C. leucas*. For
the purposes of this study, analyses on five common large shark species (> 2 m TL as adults) that were captured in adult *C. leucas* habitat: (1) Scallop hammerhead (*Sphyrna lewini*); (2) Short fin mako (*Isurus oxyrinchus*); (3) Sand bar whaler (*Carcharhnius plumbeus*); (4) Dusky whaler (*Carcharhinus obscurus*); and (5) Tiger shark (*Galeocerdo cuvier*).

Set lines used with floats (a) for capture of large *C. leucas* and other large shark in nearshore and shelf waters of the study site (28°10′S). Capture of *S. lewini* (a), *C. leucas* (b) and *C. obscurus* (c).

In addition to morphometric data on the sharks, daily climatic data on sea surface temperature (Bureau of Meteorology and Environmental Protection Agency), average daily rainfall (Bureau of Meteorology), current direction and velocity (CSIRO) and chlorophyll a levels at 4 km from the shore and at the continental shelf edge (http://poet.jpl.nasa.gov) and fraction of the moon illuminated (lunar phase) (http://aa.usno.navy.mil/data/docs/MoonFraction.php) were obtained for locations of shark capture for the period January 2006 to December 31 2008.
Stable isotope analysis
A tissue sample was randomly collected from the dorsal fin of captured sharks for the six species of sharks over a four-month period from October 2006 to February 2007. Samples were immediately frozen before being dried, ground and processed for stable isotope analysis. Tissue samples were analysed for isotope signature ($\delta^{15}$N and $\delta^{13}$C, ‰) and were taken from six individuals each for S. lewini, I. oxyrinchus, C. plumbeus, C. obscurus and G. cuvier and three for C. leucas.

Statistical analysis
Statistical analyses were carried out using the Primer 6.0, SPSS v17 and Sigmaplot 2000 software packages. Results of the stable isotope signatures were compared using one-way ANOVA for differences in $\delta^{15}$N and $\delta^{13}$C among species after data were tested for normality and homogeneity of variances. To determine where the differences between samples occurred a Tukeys post-hoc test was used. One-way analyses of similarity (ANOSIM) were employed to determine whether the catch per unit effort (CPUE) for shark species differed significantly in relation to the physical parameters.

Results
Catch of adult C. leucas (n = 14) from observer trips occurred primarily during summer months. Average stable isotope values of the six sharks ranged from -15.3 to -17.5 ‰ for $\delta^{13}$C and 12.5 to 14.8 ‰ for $\delta^{14}$N. Both $\delta^{13}$C and $\delta^{15}$N differed significantly between species (F = 11.93, p = 0.002). Tukeys post-hoc tests indicated that I. oxyrinchus $\delta^{13}$C values were grouped with all species except G. cuvier, whereas $\delta^{15}$N of S. lewini and I. oxyrinchus were grouped with all other species except G. cuvier. Partitioning of CPUE amongst the six large shark species in relation to physical parameters occurred, with ANOSIM indicating that the conditions under which the six species were captured were significantly different overall (p = 0.002, R statistic = 0.069). Pairwise comparisons indicated that I. oxyrinchus differed to all other species. Conditions under which captures occurred for C. plumbeus and G. cuvier differed (p = 0.006) while those for C. obscurus and C. leucas were marginally different (p = 0.06).
Numbers of six shark species caught by set line in the nearshore/shelf study area in each calendar month during observer trips for the sampling period 2006-2008.

<table>
<thead>
<tr>
<th>Species</th>
<th>Summer</th>
<th>Autumn</th>
<th>Winter</th>
<th>Spring</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Dec</td>
<td>Jan</td>
<td>Feb</td>
<td>Mar</td>
</tr>
<tr>
<td><strong>Sphyra lewini</strong></td>
<td>5</td>
<td>1</td>
<td>5</td>
<td>-</td>
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<tr>
<td><strong>Isurus oxyrinchus</strong></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>Carcharhinus plumbeus</strong></td>
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<td>-</td>
<td>2</td>
<td>-</td>
</tr>
<tr>
<td><strong>Carcharhinus obscurus</strong></td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td><strong>Carcharhinus leucas</strong></td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td><strong>Galeocerdo cuvier</strong></td>
<td>8</td>
<td>-</td>
<td>9</td>
<td>-</td>
</tr>
</tbody>
</table>

Results of one-way analysis of similarity (ANOSIM) of CPUE for adult *C. leucas* and five other large sharks species caught in nearshore and shelf waters of the study site during observer trips on commercial fishing boats and in relation to six physical parameters (global $p = 0.002$). Numbers are the $p$ values of pairwise tests, with significant values indicated in bold.
Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (‰) values for dorsal fin tissue of adult *C. leucas* and five other large shark species collected from nearshore and shelf habitats of the study area. Data are the average of three replicates ± SE

**Discussion**

Examination of dietary overlap among sympatric species of elasmobranchs is scant, although some studies have examined the degree of feeding specialization for several species (Bethea et al. 2004). Nonetheless, some overlap in the isotope analyses in this study would suggest little partitioning among adult *C. leucas* and the other shark species in nearshore and shelf habitat. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotope signatures indicated a distinct signature for each shark species and these may reflect the different sources of nutrients as a result of their dependence on terrestrial vs oceanic nutrient sources. The influence of diet on the isotopic signatures of top-level predator tissue is unknown; however, turnover rates in animal tissues can be affected by environmental disturbances (Perga & Gerdeaux 2003, Waltham & Connolly 2006). The grouping of the Carcharhinae with close signatures is interesting given their similar morphologies and life cycle traits. Alternatively, *S. lewini* have a very different head structure and squid are suggested to form a significant part of their diet (Stevens & Lyle 1989), which could explain their close proximity to that of *I. oxyrinchus* (a more oceanic species). *G. cuvier* have a broad diet when mature, are considered generalist...
feeders along with *C. leucas*, and may be important regulators of higher vertebrate populations (Simpfendorfer et al. 2001, Wetherbee & Cortes 2004). *G. cuvier* often target their favoured prey in shallow habitats (Heithaus et al. 2002), but are also recorded to transverse long distances over oceans as large individuals (Heithaus et al. 2007).

This study used multivariate analyses of catch data for six large shark species in shelf waters in each season of the year to explore the spatial and temporal patterns of catch of the top-level predators. The composition of species differed in seasons, for example, *I. oxyrinchus* were almost exclusively caught in July, August and September and of these most were small, immature and < 1.5 m TL. Large *C. leucas* were also almost exclusively caught during summer months and while the number of individuals captured over the study period was low, a clear pattern of increasing size with distance from shore was evident, with the majority of these sharks being mature, i.e. over 2 m TL (Branstetter & Stiles 1987). While all the carcharhinid species sampled in this study co-occurred across the shelf, *C. leucas* and *C. obscurus* were marginally different in terms of physical parameters when caught (pairwise comparison, p = 0.06). Almost all *C. leucas* catch occurred less than 12 km from the shoreline, whereas most *C. obscurus*, including all size ranges (< 0.5 m to 4 m TL) (Figure 4 d), occurred > 14 km from the shoreline. *C. leucas* are notorious for consuming other shark species and this separation may represent a partitioning of habitat amongst these two species with similar morphology, but different lifecycle strategies. *C. obscurus* pup in shelf waters as opposed to the strategy of using rivers as nursery areas in *C. leucas* (Pillans et al. 2005). In addition, *C. plumbeus* were well spread across the shelf in all size ranges, which could indicate their use of habitats between *C. leucas* closer to the shelf and *C. obscurus* on the outer shelf. The catch of *G. cuvier* across all seasons and physical parameters suggests that this species is unlikely to be influenced by the other shark species in this study except when small (< 2m TL), although this pattern could also be evidence for size-specific habitat partitioning within *G. cuvier*.

The significant difference between *C. plumbeus* and *G. cuvier* in terms of CPUE with physical parameters is interesting in that both species were caught throughout most months of the year. Coastal habitats represent a more unstable and unpredictable environment than the open ocean and the life history characteristics of sharks that
appear as adults in the coastal environment often correspond to the environment in which they occur (Cortes 2004). Catch of *C. plumbeus* and *I. oxyrinchus* occurred with a number of individuals at once, suggesting movement of numbers of individuals into the shelf area at the same time period. The unpredictable patterns of the shelf environment could be reflected by the sudden co-occurrence of groups of these species, with *I. oxyrinchus* moving in over the shelf from the open ocean to very specific temporal cues. These catch patterns have particular ramifications for fishery management and the sporadic occurrence of *C. plumbeus* across the months of sampling could also reflect the long-range movements of this species.

Recent studies have suggested that *I. oxyrinchus* are sexually segregated across the Pacific Ocean, presenting major implications for management of this species (Mucientes et al. 2009). In this study, however, I found both sexes were present, although all individuals were immature other than three males > 1.8 m TL (Francis & Duffy 2005). Size of individuals in the catch of *C. plumbeus* were larger than those recorded by other studies with a much larger sample size and up to 50% of *C. plumbeus* females are considered mature at 1.5 m TL (Sminkey & Musick 1995, Brewster-Geisz & Miller 2000, McAuley et al. 2007). McAuley et al. (2007) suggested *C. plumbeus* population on the west coast of Australia had apparently limited capacity for density-dependent compensation through changes in fecundity, somatic growth and longevity population with exploitation of older sharks. Nevertheless, harvest levels of mainly neonates of *C. obscurus* and *C. plumbeus* by the target fishery were considered sustainable. In this study, the presence of early life-stages of all shark species other than *C. leucas* suggests that this shelf area is used for purposes of breeding or pupping, further supported by the capture of pregnant females of all carcharhinid species. Because commercial exploitation of sharks for food (fins, meat) is increasing globally including along the east coast of Australia, more intensive and informed fisheries management may be required in this region. Further research into the movements and population biology of these species, particularly the adult size ranges, should be conducted to determine the range of movement and residency of these species, particularly for the carcharhinids. The movement of adult *C. leucas* is largely unknown and warrants further investigation.
In this study, I have investigated the co-occurrence of six large shark species in a shelf environment and determined these patterns with particular reference to *C. leucas*. The use of shelf environments is both beneficial for larger and older shark species in terms of a dynamic and productive environment providing immensely alternating conditions, which may favour individual species in time and space. These factors probably contribute to the particular use of habitat and reflect slight differences in diet and lifecycle strategy of these species. The benefits of the use of shelf environment for adult *C. leucas* outweighs the continued use of juvenile river habitats, but illustrates the advantage of a lifecycle strategy that enables this species to utilise river systems as the top-level predator in its juvenile phase.
Monogeneans on the dorsal surface of *C. leucas*, commonly between the first and second dorsal fins. Parasites frequently occurred on *C. leucas* in both natural and urban rivers.
APPENDIX 6

A LIST OF PRESENTATIONS ARISING FROM THIS THESIS

Conference Presentations

Werry JM, Sumpton W, Lee SY, Mayer D (2009) Influence of rainfall on catch of the bull shark, *Carcharhinus leucas*, in nearshore habitat. 8th Indo-Pacific Fish Conference, Fremantle, Western Australia

Werry JM (2009) Ontogenetic movement patterns of the Bull shark, *Carcharhinus leucas*, in the Gold Coast canal system. Guest presentation at the Australasian Regional Association of Parks and Aquaria, Gold Coast, Australia

Meynecke J-O, Werry JM, Olivier S (2009) On track! Using PIT tags and stable isotopes to reveal the movement of estuarine fish. Oceans 09, Bremen, Germany


Werry JM (2008) An overview of findings into the habitat use and movement of the bull shark, *Carcharhinus leucas* in the Gold Coast canal system. Invited speaker at the Shark Marine Advisory Group, Gold Coast, Australia, 10th April

Werry JM, Lee SY, Sumpton W, Gribble N, Otway N (2006) Management of large sharks on urbanising coastlines with a primary focus on the bull shark, *Carcharhinus leucas*. Australian Society for Fish Biology, Hobart, Australia. Received the John Glover travel award

Werry JM, Lee SY, Gribble N (2005) Sharks as cleaners of the ocean? Feeding strategies and habitat association of sharks in Queensland waters. Inaugural southeast Queensland Elasmobranch forum, Nth Stradbroke Island