Hammerhead sharks (*Sphyrnidae*) of southeast Queensland: habitat and movements

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Abstract

Hammerhead sharks (Sphyrnidae) are iconic and charismatic species that have received little attention until more recently, resulting in knowledge gaps about life histories, habitats, behaviours and migratory drivers, mostly in the southern hemisphere such as Australian waters. Globally, shark populations are declining as many species extinction risk has increased under the threat of fishing and habitat degradation. Hammerhead shark (Sphyrnidae) populations are highly susceptible to human-induced pressure such as long lines and are currently undergoing severe declines, especially in Australia. Recently, hammerhead sharks have been added to the International Union for Conservation of Nature’s (IUCN) Red List of Threatened Species, with scalloped hammerhead listed as critically endangered. Therefore, further information is needed to address the current shortfalls regarding hammerheads in Australia, for the management and conservation of these species.

Earlier research using catch data from the Queensland Shark Control Program (QSCP) showed a decline in numbers of caught hammerhead sharks since the start of the program in 1960. A review of the literature (CHAPTER 1) revealed that hammerhead sharks were understudied in Australia, with information shortfalls on movement, resource use, nursery areas and habitat use. The general aim of this thesis was to provide a better understanding of the movement, distribution, habitat use and resource use of scalloped hammerhead shark (Sphyra lewini) in Queensland, Australia to improve conservation and management strategies. I used multiple methodologies to determine (i) the distribution of suitable habitat for juvenile scalloped hammerhead sharks and the percentage of overlap with marine protected areas (CHAPTER 2); (ii) fine-scale movement of juvenile scalloped hammerheads within these habitats and determine behavioural states using high-resolution acoustic tracking (CHAPTER 3); (iii) thermal tolerance range “thermal niche” of hammerhead shark using historical catch records from the QSCP (CHAPTER 4); and (iv) resource overlap between hammerhead sharks species and with other co-existing large sharks using carbon and nitrogen stable isotopes (CHAPTER 5). This allowed me to build a solid baseline framework of the ecology of scalloped hammerhead sharks in Queensland.

The species distribution model identified 10,082.87 km² of suitable habitat characterised by low current velocities (< 0.5 m/s), warm sea surface temperatures (> 20°C), estuarine/oceanic salinities (25-35 PSU) and shallow bathymetries (< 20 m). Suitable habitats occurred in coastal areas within wetland and seagrass habitats. Highly suitable areas accounted for 1,784.33 km² of the total distribution and
occurred around highly developed areas, such as Moreton Bay, Hervey Bay, Townsville and Cairns. Coastal beach areas of the Gold Coast were also uncovered as highly suitable habitats and may be due to close proximity of the Gold Coast seaway and Tweed River connections to more sheltered estuarine habitats. The majority of the predicted suitable distribution occurred within the lower protection multi-use zones (6,291.20 km$^2$) and outside marine protected areas (3,791.67 km$^2$); where no-take zones protected only 11% and 8.56% of high and medium modelled suitable habitats. Within these habitats, continuous tracking of two juvenile scalloped hammerhead sharks uncovered highly active diving behaviours where both sharks continuously dove from water surface to the bay floor over 12- and 3-hour tracks. Two diving patterns were observed in both sharks and described as A-type: one long dive with multiple small dives at depth, and B-type dives: one long dive without extra dives at depth. The two-state behavioural model uncovered low activity (forage) and high activity (direction) states, which were influenced by distance to seagrass and coral habitats as well as habitat depth.

Quantile regression modelling determined catches of hammerhead sharks in relation to changes in seas surface temperatures changed with latitude along the Queensland coast. Scalloped hammerhead catches in the southern areas were most likely to occur between 20$^\circ$C - 25$^\circ$C and likely to occur throughout the year in the northern areas, as sea surface temperatures remained above 22$^\circ$C. Co-existing bull (*Carcharias leucas*) and tiger (*Galeocerdo cuvier*) sharks also occurred throughout this thermal range while white shark (*Carcharodon carcharias*) only occurred below 23$^\circ$C. Stable isotope analysis revealed scalloped and great hammerhead sharks overlapped 69% in isotopic space and with several large shark species. Both hammerhead species undertook a seasonal dietary shift, and scalloped hammerheads showed a wider $\delta^{13}$C and lower $\delta^{15}$N than the more specialised great hammerhead. Tiger sharks feed at a lower trophic level overlapping mostly with both hammerhead sharks. White and bull sharks competed with hammerhead sharks at higher $\delta^{15}$N.

Overall, results from my research make original contributions to the knowledge of hammerhead sharks by identifying previously unreported distributions of suitable juvenile habitats of the scalloped hammerhead, which occurred in developed areas and within multi-use protection zones. Additionally, the research described previously unreported diving patterns and state-switching of juvenile hammerhead sharks within highly developed areas, highlighting the importance of wetland and estuarine habitats for shark conservation. Furthermore, the research showed high overlap in resource use between two endangered hammerhead species with several large predatory shark species. In
summary, this thesis highlights the relevance of movement and habitat use information in the conservation and management of endangered iconic shark species.
Statement of Originality

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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1. Introduction

Hammerhead sharks (Sphyrnidae) are uniquely identifiable from other shark species due to the iconic flattened-shape of their head (see Gallagher and Klimley 2018). Presently, there are ten recognised species of hammerheads. The most known species are the two largest, great hammerhead (*Sphyrna mokarran*) and scalloped hammerhead (*Sphyrna lewini*). Recently, these large species have been listed as globally endangered in the International Union for Conservation of Nature’s Red List of Threatened Species, (IUCN redlist). Great and scalloped hammerhead sharks have a global distribution within tropical to temperate waters near coastlines and oceanic islands, and they also migrate between coastal areas and islands (Klimley and Nelson 1984, Bessudo et al. 2011a, Hoyos-Padilla et al. 2014, Ketchum et al. 2014a, Ketchum et al. 2014b, Spaet et al. 2017, Wells et al. 2018). This distribution also orientates hammerhead sharks in areas with high fishing activities creating anthropogenic pressure on hammerhead shark populations (Gallucci et al. 2006, Gallagher et al. 2014b, Queiroz et al. 2019).

Hammerhead sharks are reported to be sensitive to capture stress, with a post mortality rate higher when compared to other sharks species, if not handled correctly (Gallagher et al. 2014a, Gulak et al. 2015). Increased sensitivity, high overlap with anthropogenic pressures and habitats in close proximity to developed areas has led to global declines in their populations (Gallagher et al. 2014b, Queiroz et al. 2019). Until recently, both great and scalloped hammerheads have received little attention from the scientific community leaving limited information available for fisheries management and conservation efforts, especially in Australia were catches of hammerhead species within the Queensland shark control program (QSCP) have declined significantly since early 1960 (Roff et al. 2018). A review of the literature identified knowledge limitations relating to critical aspects of hammerhead shark ecology in Australia, which are necessary for effective management tools and marine park protections (Dwyer et al. 2020).

Recently, they have become a focus in research due to the limited information known about them globally. The majority of research on hammerhead sharks comes from the northern hemisphere, though in the southern hemisphere, Australia is a leader in marine research, yet an information deficit exits in terms of hammerhead sharks. Several studies focusing on adult scalloped (*S. lewini*) and great (*S. mokarran*) horizontal movements around a central residency area, from which they migrate from at night and return at first light (Ketchum et al. 2014a, Ketchum et al. 2014b). These studies also showed
connectivity between islands at varying ranges from the central refuge, revealing frequent small, moderate and long-distance journeys between islands. They exhibited homing behaviours often returning after long distance migrations. Passive acoustic telemetry also showed diel movement patterns of tagged sharks, with near shore daylight social, refuging behaviours and isolated foraging behaviours during the night. Night excursions occur at distance from the day refuge over deep waters, were archival tags have shown deep excursions of up to 1000 m, multiple times throughout the night (Jorgensen et al. 2009, Bessudo et al. 2011b). This behavioural trait infers that specific areas are vital for the species existence on the eastern coastline of Australia.

Shark meshing programs in Australia’s eastern coast have suggested the possibility of two distinct populations of hammerheads separated by temporal range: tropical and temperate. Harry et al. (2011) found a possible size segregation between hammerhead populations in northern and temperate waters of the east coastline, based on growth rate estimations. Findings suggested that tropical clusters grow and mature faster to an overall smaller length than hammerheads in the temperate cluster, where sharks grow and mature at a slower rate to an overall larger size. Though as the author states, the temperate sample size was small and the sampling method differed from the tropical site, possibly adding variance to the results and warrants further investigation.

Hammerhead sharks also exhibit locality affiliation, coined core habitats (Bessudo et al. 2011). These ranges appear to be important to local hammerhead populations throughout different seasons and are sites of high conservation value which may be attributed to ocean temperatures and currents. Along with core locations and residency around islands, two aggregation groups were found by Bessudo et al. (2011a) at the north and south areas of Malpelo island, Columbia, where aggregates found in the north occurred during the cold season (and southerly current), and sharks in the southern areas occurred in warmer water (and a north-easterly current). This indicates that not only temperature was influencing the distribution of hammerheads, but water currents may also be important; these distinct aggregations correlated with strong currents, and the only area dominated by slower currents was poor in shark detections.

Studies in Australia have shown broad sex segregation with males tending to be more common near shore than females, which were more common offshore. For the Gold Coast region of Australia, the East Australian Current (EAC) runs along the shelf in waters exceeding 100 m depth up to 15 nm from
shore. This irregular boundary current strongly influences the coastal environment and marine life. Eddies of the EAC can either warm or cool the coastal waters, alter the current speed and direction, and produce upwelling or down-welling (Nilsson and Cresswell 1980, Tranter et al. 1980, Cresswell and Legeckis 1986, Cresswell et al. 2016). It is possible that core habitats for hammerhead sharks may occur around the southeast coast, influenced by fluctuating water temperatures, varying ocean currents, productivity and access to breeding sites with ample resource availability. Noriega et al. (2011) found declining catch rates in the longer female scalloped hammerhead sharks and increases of catches within the QSCP at the Gold Coast, which may be a localised “hot spot” for scalloped hammerheads.

Shark and other marine species have been observed to exhibit a thermal preference (Etnoyer et al. 2006, Carlson et al. 2010, Froeschke et al. 2010). With the growing threat of ocean warming, ocean temperatures are expected to rise and directly influence the habitat preferences of multiple species, change ecosystems, change the ranges and core habitat areas of hammerhead sharks along the eastern coastline. This coupled with the expected declining population trend and the minimal information known about hammerheads in Australia, the species faces a bleak future.

Information on their movement patterns currently come from studies occurring from the U.S.A, South Africa, Brazil and Australia (non-tagging), showing that the species is highly mobile and possibly migratory (Maguire et al. 2006), moving around continental margins and oceanic islands (Hearn et al. 2010, Ketchum et al. 2014a). A comprehensive satellite study in the Gulf of Mexico discovered spatial segregation between males and female scalloped hammerhead where females occupied shelf-edge waters and males utilised mid-shelf areas. Habitat preferences indicated affinity to areas with hard substrate and artificial structures and restrictive long-distance movements (Wells et al. 2018).

Studies have also shown that hammerheads exhibit site fidelity where they tend to aggregate and travel around but always returning to ‘core/kernel’ habitat areas (Duncan and Holland 2006). Distances moved from these sites varied between studies and geographical locations, ranging from less than 100 km (U.S.A) (Kohler and Turner 2001), 147.8 km (South Africa) (Diemer et al. 2011) and 1.6 km (Hawaii) (Duncan and Holland 2006). It is important to note that these studies also focused on hammerheads of different sizes, where Hawaii reported on juveniles, South Africa reported on a range of size classes from neonates to adults over 1.5 m. This also implies differences in habitat types; habitat
usage and behavioural changes in response to environmental stimuli (i.e. sex aggregation, predation, and physical oceanographic variables).

In addition to movements around core habitat areas, they have also been observed to travel over much longer distances. Bessudo et al. (2011a) reported scalloped hammerheads (S. lewini) travelled between Malpelo and Cocos Island (627 km) and moving further to the Galapagos Islands, a further 710 km from Cocos Island totalling 1337 km. The study showed that scalloped hammerheads (S. lewini) moved over long distances before returning to their home location (Malpelo Island) with a maximum distance travelled of 1941 km. However, these long-distance movements were recorded for less than 7% of the tagged sharks. In terms of seasonal drivers, water temperature seems to have an influence on movements and residency times around the islands, with more sharks remaining closer to the islands during winter months compared to summer. Residency times also showed diel and seasonal drivers, with time spent near the islands was longer at night during the winter months but remained away from the islands during summer at night.

Hammerhead sharks also utilise different habitats throughout their life-stages including shallow estuarine nursery habitats (Cuevas-Gómez et al., Holland et al. 1993, Zanella et al. 2019) and coastal adult habitats (Ketchum et al. 2014a, Ketchum et al. 2014b, Wells et al. 2018), reducing predation on smaller life-cycle stages and increasing access to suitable prey abundance (Heupel et al. 2007). Understanding the separation of habitats coupled with their life-history traits can complicate effective management and conservation of the species as diet and habitat use change with growth, as well as movement patterns (Oh et al. 2017). Juvenile scalloped hammerhead nursery’s occur in shallow, turbid embayment’s with access to deep water, were juveniles have been recorded for multiple years (Holland et al. 1992, Holland et al. 1993, Zanella et al. 2019), as well as estuarine environments (Rosende-Pereiro and Corgos 2018). Therefore, a complete understanding of hammerhead ecology would need to include both juvenile and adult life-stages.

In Australia, movements of hammerhead sharks are unknown, however their occurrence is well documented along the eastern coastal thanks to the SCP and various fishing vessel logs. The QSCP is the only largest continual data set in Australia that has documented the abundance and seasonal occurrence of hammerheads (and other shark species), although many records do not contain species level identification and there has been changes in gear deployment (Reid and Krogh 1992, Reid et al.
From these records and those in Queensland, the numbers of hammerheads caught has decreased with time. Likewise, the size of the hammerheads caught has also decreased. Also, a strong seasonal signal pattern has been determined where hammerhead species are caught in high numbers during warmer waters.

It is important to note genetically, scalloped hammerheads (*S. lewini*) exhibit genetic discontinuity between oceans due to oceanic barriers, with male sharks possibly undertaking (very rare) oceanic migrations (Daly-Engel et al. 2012). Female scalloped hammerheads (*S. lewini*) have been theorised to travel along connected coastal habitats visiting various nursery grounds (Duncan et al. 2006). Chapman et al. (2009) however, found contrasting evidence theorizing that females display natal homing behaviours or remain close to their region of origin. However both studies were acquiescent to the rarity of oceanic dispersal by female scalloped hammerheads. Daly-Engel et al. (2012) ascertained evidence from biparentally inherited DNA suggesting male scalloped hammerheads may undertake oceanic migrations (at an unknown frequency) very rarely.

Soler et al. (2011) observed similar behaviours of nine indicator species around Malpelo Island between warm and cold-water seasons between and ENSO events. The study found most species relative abundance remained constant throughout the study period with scalloped hammerheads showing the only decline in numbers. Furthermore seasonal drivers for ENSO events showed no effect on scalloped hammerheads abundance, but their relative abundance was found to be significantly higher in the colder seasons, confirming the results in Bessudo et al. (2011a). These findings showed no statistical significance of scalloped hammerheads abundance with ENSO events; contrastingly these sharks tended to be in higher abundance in Malpelo Island when the waters were coolest, while in Cocos Island they were more abundance during the warmer season. Soler et al. (2011) also noted when SST were above the average, scalloped hammerheads numbers decreased (El Niño 1997-1998).

As mentioned above, hammerheads respond to seasonal changes in water temperature, generally, preferring warmer waters, however a strong correlation with the location of the thermocline has become evident (Bessudo et al. 2011a, Bessudo et al. 2011b, Soler et al. 2011, Ketchum et al. 2014a). They have been observed to follow the thermocline with depth as it moves vertically between seasons; with sharks in warmer waters recorded utilising deeper waters (deeper thermocline), and shallower depths in cooler waters (higher thermocline). Ketchum et al. (2014a) described a thermal niche of 23-
26°C, above the thermocline with occasional shark dives below the thermocline into temperatures of 4°C. Ketchum et al. (2014a) also determined a preference of sites in up-welling dominated areas by scalloped hammerheads (*S. lewini*) on the east-south-eastern area of Wolf Island, attributing it to a higher abundance of prey. However, a study by Bessudo et al. (2011a) showed tagged hammerheads in Malepelo Island preferred areas with a stronger water current, rather than areas with no current. Bessudo et al. (2011b) determined hammerheads dove to depths below 100 m almost exclusively at night and remaining equal times within the mixed layer (0 – 50 m) equally during the day and night. Because the thermocline moves with seasonal water temperatures, it deepens during summer and rises during winter, causing hammerheads to occupy deeper waters during summer (<50 m) and surface waters during winter (1 – 10 m). The most recent study on vertical diving behaviour was carried out by Hoffmayer et al. (2013) which recorded 76 repeated and consistent dives of scalloped hammerheads (*S. lewini*) over 27 days. They concluded that this behaviour maybe a common behaviour but with an unknown purpose, though feeding is the most cited hypothesis along with energy saving through oscillatory movements. The decent rates recorded in their study was 2.1 m/s and repeated for every dive to a maximum of 964 m, and a slow ascent rate, which does not support the energy saving hypothesis.

Data available in Australia originated from incidental catches by fishermen and the shark control programs. The shark control data in Australia provides a historical record of shark presence since the programs beginning in 1962, it has a steady data set of caught sharks for the entire Queensland coast, showing trends in catch abundance seasonally and yearly. This data set has shown seasonal abundance of hammerhead sharks around southeast Queensland, with a constant yearly presence, summer peak and a winter low. However, a yearly decrease in catch numbers with a declining trend has been seen to oscillate.

A lack of tracking data exists in Australia for hammerhead sharks, which in term can miss-inform conservation strategies in their effectiveness in managing conservation efforts. Data especially lacks for multiple life stages of hammerhead head including identification of pupping and nursery grounds for juvenile life stages, as well as adult life stages. Identifying juvenile habitats and understanding how these habitats are used and link juveniles to adult habitats are important to understand for informed conservation and management of the species.
1.1. Specific research aims

The general aim of this thesis was to increase the knowledge of hammerhead sharks in Queensland, particularly investigating habitat use and movement ecology of the scalloped hammerhead over multiple life stages. This is done by determining previously unknown juvenile habitats and their behaviours within these habitats, then linking the coastal distribution of adult sharks through their thermal tolerances and trophic ecology.

Chapter 2 investigated the spatial distribution of suitable habitats of juvenile scalloped hammerhead sharks, and whether these habitats fall under current protection strategies.

Chapter 3 describes fine-scale diving behaviours of juvenile scalloped hammerheads as well as habitat use and influences on behavioural states, using acoustic tracking data.

Chapter 4 utilised long-term catch data to determine a thermal response of hammerhead and co-existing sharks to sea surface temperatures at varying latitudes along the eastern coast of Queensland.

Chapter 5 investigated resource sharing between coastal hammerhead species and further competition with other sympatric shark species.

Chapter 6 provides an overall summary of the chapters within the thesis.

1.2. Content and thesis structure

This thesis is organised into six chapters: general introduction (Chapter 1), four results chapters (Chapters 2-5) and a general discussion (Chapter 6). Each result chapter is structured in a manuscript form specifically formatted to meet the requirements of the intended academic journal to which it will be submitted. Hence, there is some repetition (e.g. study site, study species, references) among chapters throughout the thesis.
1.3. Publications


1.4. Publications to be submitted

1.5. **Industry Reports**


1.6. **Media and outreach contributions**

- Interviewed by Newsreader for ABC North Coast NSW, Lismore, 12:00 News. Nov 2018
- Interviewed by Nicole Dyer for ABC Gold Coast, Gold Coast, Mornings. Nov 2018
- Interviewed by Cathy Border for ABC Gold Coast, Gold Coast, On Drive. July 2018
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1.7. Conference presentations

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1.8. References


2. Living in the city: Habitat suitability of juvenile scalloped hammerhead sharks (*Sphyrna lewini*) in Queensland coastal waters, Australia

This chapter is a co-authored paper that has been reformatted for this thesis. The bibliographic details /status of the co-authored paper, including all authors, are:

2.1. Abstract

Conservation of marine species is challenging, especially for threatened species with limited current data, and an abundance of knowledge gaps to inform accurate trends and condition of marine populations. The large marine shark, the scalloped hammerhead shark (*Sphyrna lewini*) is classified critically endangered (IUCN), though in the Australian national legislation it is only “conservation dependent” (EPBC Act 1999), allowing the species to be managed under commercial fisheries legislation. Available data suggests that continuing commercial fishing pressure, and additional pressure from shark culling in lethal shark control programs, continues to contribute to the decline of hammerhead sharks. Although conservation awareness for this species is increasing, there is little information to support conservation action, particularly for early life stages. To address one of the critical knowledge gaps for this species, we targeted the habitat use and distribution of juvenile scalloped hammerhead sharks across ~11,330 km² of the Queensland coastline. We modelled the species distribution using catch and sightings data in a maximum entropy algorithm (Maxent). Model projections of suitable habitat for juvenile scalloped hammerhead sharks were compared to the cover of Marine Protected Areas (MPA), assuming that some level of protection was afforded by the managed area. We separated low-level protection (the percentage of suitable areas within multi-use areas) to high-level protection (“no-take” zones). In low protection, multi-use MPAs fishing activities are still permitted with line fishing, trolling and bait netting allowed in all zones (Department of National Parks 2015). Although there is a “no-take” rule for recreational take of hammerheads in Queensland, mortality may still occur as accidental or bycatch mortality in gillnet and line fisheries in these areas. Approximately 1,800 km² of highly suitable habitat occurred in nearshore coastal areas, adjacent to coastal wetlands, and proximal to urban centres. The majority of the predicted suitable distribution (10,083 km²) for juvenile hammerheads has a low-level of protection (6,291 km²) or no protection (3,792 km² outside of MPAs). Only 11% of highly suitable habitats and 8.6% of medium suitability habitats occurred in high protection MPAs. This study identified that areas with best habitat suitability for juvenile scalloped hammerhead sharks in Queensland, fall short of MPA protections exposing juveniles of this endangered shark species to higher anthropogenic pressures.
2.2. Introduction

Marine conservation is challenging given the spatial extent of the world’s oceans. To date, anthropogenic influences are negatively impacting global biodiversity (Díaz et al. 2020), and conservation efforts are challenging, especially for highly mobile species, such as sharks. Globally, many shark populations are declining under the threat of increased fishing pressures (Baum et al. 2003, Baum and Myers 2004, Queiroz et al. 2019). In particular, hammerhead sharks (*Sphyrnidae*) are highly susceptible to fishing pressures (Dulvy et al. 2008, Dulvy et al. 2014, Gallagher et al. 2014b, Calich et al. 2018) and undergoing global declines, which is evident in Australian catch data (Roff et al. 2018).

Hammerhead sharks are an iconic and highly charismatic species easily identified by their flattened head (Gallagher and Klimley 2018). They are not a true pelagic shark, remaining near coastal land masses world-wide in tropical to temperate waters (Compagno et al. 2008). Satellite tracking of scalloped hammerhead (*Sphyrna lewini*) utilise a range of coastal area from the self-edge through to the inner-self waters (Wells et al. 2018). Ontogenetic segregation is also evident as juvenile scalloped hammerheads have utilise nearshore and estuarine habitats (Holland et al. 1993, Duncan and Holland 2006, Rosende-Pereiro and Corgos 2018, Zanella et al. 2019). As hammerhead shark populations continue to decline, identification of suitable habitats are critical for conservation strategies, especially for juvenile sharks (Gallucci et al. 2006). Sharks have a k-selected life history which include slow growth, long gestation periods and late maturation ages, which decrease the recovery of declined populations.

Marine protected areas (MPAs) are considered the standard tool for conservation and management of essential habitats utilising multiple zones to regulate various activities and offering levels of protection to marine habitats, including “take” and “no-take” zones (Ferretti et al. 2018, Speed et al. 2018, MacKeracher et al. 2019). Areas classified as “no-take” zones prohibit the use of activities that remove animals and offer the highest level of protection. Whereas, zones denoted “multi-use” allow various types of activities that remove animals, including net and line fishing (Department of National Parks 2015). As monitoring methods develop and further our understanding of how sharks utilise and interact with various habitats over time, the effectiveness of MPAs to protect critical habitats may change. Therefore, MPAs need to adapt to incorporate new information (Brooks et al. 2011, Dwyer et al. 2020).
Species distribution models (SDMs) have become a reliable tool to successfully determine a species distribution in relation to biologically relevant drivers of their habitats (Feitosa et al., Meyers et al. 2017, Calich et al. 2018, Báez et al. 2020, Udyawer et al. 2020). Their use has also been important in conservation and planning including MPAs, by overlapping highly suitable habitats with fishing pressures and implementing conservation strategies (Meekan et al. 2006, Hannah et al. 2007, Embling et al. 2010, Oh et al. 2017). Robust machine learning SDMs (i.e. MaxEnt) are also successful in determining suitable habitat distributions with environmental drivers when occurrence data is rare or difficult to obtain (Retana and Lewis 2017, Udyawer et al. 2020).

Coastal waters of Queensland, Australia, extend from tropical to temperate latitudes and include three marine parks: the world heritage listed Great Barrier Reef Marine Park (GBRMP) in northern Queensland; the Great Sandy Marine Park (GSMP) and Moreton Bay Marine Park (MBMP) in southeast Queensland (SEQ). Multiple shark species occur throughout these marine parks including scalloped hammerhead sharks; however, suitable habitats for juveniles have not been described. Studies have noted the occurrence of juvenile scalloped hammerheads in northern Queensland and they have been caught within the Queensland shark control program (QSCP) (Simpfendorfer and Milward 1993, Taylor et al. 2011, Yates et al. 2015). Juvenile scalloped hammerhead shark nursery grounds have been studied in the northern hemisphere, determining small core areas of 1.26 – 2.5 Km² were used by juveniles in nursery areas (Clarke 1971, Holland et al. 1992, Holland et al. 1993, Zanella et al. 2019). Therefore, identification of areas that are used by juveniles are restricted in area and maybe sensitive to habitat changes and identifying these habitats is critical for conservation policy.

In this study, we aim to identify suitable juvenile scalloped hammerhead habitats along the Queensland coast and further determine the current level of protection afforded by MPAs. Due to scarce available data, species distribution models were used to identify suitable habitats and determine suitable habitats overlapping with “take” and “no-take” zones of all MPAs along the Queensland coast.

2.3. Methods

2.3.1. Study region

The study region was restricted to the eastern Queensland coast of Australia, due to the limitation of available environmental data encompassing the entire range of occurrence data, but also had an
appropriate fine-scale resolution to include shallow nearshore environments. The final extent of the study area was between Cape York in northern Queensland to Kingscliff in New South Wales (NSW) and included coastal islands (Figure 2-1). The extent transects tropical to temperate latitudes and includes multiple marine habitat types including coral reefs, coastal bays and vegetated wetlands. The extent of the study captured three highly iconic marine protected areas (MPAs): Great Barrier Reef Marine Park (GBRMP), Great Sandy Marine Park (GSMP) and Moreton Bay Marine Park (MBMP).

Coastal habitats vary along the eastern coast of Queensland latitudinally, with the Great Barrier Reef Marine Park (GBRMP) in the mid to north latitudes, and various Ramsar listed wetland areas in the south Great Sandy Marine Park (GSMP) and Moreton Bay Marine Park (MBMP). Southern Queensland is also heavily influenced by oceanographic features such as upwelling by direct access to unprotected oceanic waters of the Pacific Ocean.
Figure 2-1. Extend of the study region along the Queensland east coast of Australia, and the extent of the study area based on the eReefs environmental data set (blue) (reefs.org.au). Three MPAs occurring within the study area were grouped into “no-take” (green) and “multi-use” (yellow) IUCN listed zones in the CAPAD database.

2.3.2. Species occurrence data

Juvenile scalloped hammerhead (*Sphyra lewini*) occurrence data is rare in Australia; due to the difficulty in catches, and the lack of available catch data from formal monitoring. Therefore, citizen
science was employed by utilizing catch records from online fishing groups and the fishing app, FishBrain (https://fishbrain.com). Catch records were limited to the eastern coastline of Queensland, Australia. Records were filtered to include reports with GPS location, photo ID, length between 30 cm – 100 cm, date of each catch; which resulted in 63 records. The remaining records were further filtered to catches below 90 cm, resulting in 47 reliable records of juvenile scalloped hammerheads between 2017-2019 and spanned from northern to southern Queensland. Occurrence records were plotted in ArcGIS 10.8.1 (ESRI) to determine if occurrences clustered within 1 km radius of each other which may introduce bias to certain areas (Phillips et al. 2006, Phillips et al. 2009). After removing clustered occurrence points, 37 spatially unique records remained to build the species distribution model.

2.3.3. Environmental covariates

Juvenile scalloped hammerheads have been reported to occur in shallow bay and near shore environments, generally in estuarine habitats, therefore continuous data that spanned the entire area of Queensland was needed. Fine scale eReefs model data (ereefs.org.au) was provided environmental data at a high resolution (1 km grid), thus allowing improved estimates in shallow coastal habitats. The eReefs model included the following environmental variables: yearly aggregated Sea Surface Temperature (SST), water velocity (mean along-coast (V, m/s) and easterly flow (u)), Practical salinity (PSU) and bathymetric depth (m). These variables are the most significant predictors of shark distribution (Calich et al. 2018, Fourcade et al. 2018); in particular, SST and PSU are major drivers affecting shark distribution and occurrence behaviours by influencing strong physiological constraints on a majority of shark species including scalloped hammerhead sharks (Schlaff et al. 2014, Ward-Paige et al. 2015, Yates et al. 2015).

2.3.4. Habitat suitability Model

A stepwise maximum entropy (MaxEnt [version 3.4.1]; (Phillips et al. 2006)) species distribution model (SDM) was used to identify suitable habitat areas in Queensland coastal waters. MaxEnt is a complex machine learning model that uses presence data without true absence, small samples sizes and has shown to outperform other algorithms (Pearson et al. 2007, Elith et al. 2011). MaxEnt has also successfully been used to predicted several marine species distributions, and is a proven tool for modelling the habitat suitability of species and environmental variables (Friedlaender et al. 2011,
Bombchosch et al. 2014, Gomez and Cassini 2015, Udyawer et al. 2020). MaxEnt model was fitted with 85% occurrence data for training and 15% for testing, 10 000 randomly generated pseudo-absence background points, 5000 iterations and generating 15 models. The area under the curve (AUC) metric is used to determine the performance of the model incorporated on the receiver operating plot (ROC). AUC values below 0 indicates the model cannot align projected and observed occurrence data; AUC of 1 indicates perfect model alignment between projected and observed data. For this study, the averaged model was used as all individual model AUC were > 85.

Suitable habitat probability threshold was determine using the 10% training logistic threshold determined by the model, indicating the minimum value determining “suitable” habitat, values under this threshold represent less than 10% of occurrence data occurred. In this study, we identified three categories of habitat suitability as high (>75%), medium (50-75%) and low (threshold – 50%) habitat probability maps were created using this threshold and jack-knife tests are a measure of environmental variable importance on occurrence projections, by removing one variable at a time and comparing it to a model with the remaining variables (Phillips et al. 2006, Elith et al. 2011).

2.3.5. Marine park conservation assessment.

Conservation and management of critical marine habitats are done through Marine protected areas (MPAs) which alter the level of human activity within the parks via certain zones. We use the Collaborative Australian Protected Area Database (CAPAD 2018) using IUCN zones to incorporate “multi-use” (IV and VI) and “no-take” (IA, IB and II) zones (Department of Agriculture 2018). This data base integrates commonwealth and state MPAs that meet the IUCN definitions of marine protected areas. “No-take” zones provide high level protection by prohibiting all fishing activities and multi-use zones provide the least protection by allowing various fishing activities (Day et al. 2012). We overlayed all three habitat suitability categories with MPAs to determine the areas of suitability inside “take” and “no-take” zones along the east Queensland coast MPAs. This area overlap can be used as a proxy to determine anthropogenic influences on various levels of suitable habitats of juvenile scalloped hammerhead sharks and the level of protection afforded to them through MPAs.
2.4. Results

2.4.1. Habitat suitability model

All models performed well using the trained occurrence data (AUC = 0.95), suggesting high reliability in the model’s predictive performance. Water current, SST, bathymetry and salinity contributed most to the model with current and SST having the most influence on habitat suitability model (Figure 2-2). Jackknife model results showed that bathymetry was the most important individual environmental variable that contributed to the model in isolation. This suggests habitat depth strongly influenced suitable habitat selection. Response curves generated by the model indicated juvenile scalloped hammerhead sharks were more likely to occur in habitats with reduced currents (< 0.2 m/s), salinity approximately 30 PSU and a range of SST up to 25°C and restricted to shallow habitat areas (Figure 2-3). Habitat suitability projection maps showed many suitable habitat areas along the coast and within estuarine systems (Figure 2-4). Southeast Queensland (SEQ) identified many highly suitable habitat areas, particularly within the Moreton Bay and Hervey Bay marine protected areas (MPAs). Shallow near coastal waters of the Gold Coast were highly suitable, with decreasing suitability further offshore. Similar suitable habitats were predicted around river mouths and national park areas at the Sunshine coast. The estuarine system between Rainbow Beach and Bundaberg was also predicted as suitable habitat, with highest suitable areas located within small estuarine systems and along the western banks, like the southern bays. Northern areas had suitable habitats in areas in similar areas as SEQ, generally highest suitable habitats occurring around island and cove/bay areas.
Figure 2-2. Variable relative contribution for environmental variables used in the MaxEnt model (top) and relative variable importance calculated by the jackknife iteration model within the maxent model.
Figure 2-3. Response curves of environmental variables on juvenile scalloped hammerhead shark habitat suitability. Mean current and Velocity are tidal which include directional influence, u = east, v = north.
Figure 2-4. Habitat suitability projection of the overall threshold (left maps) and high suitable category (right maps) within MPA “multi-use” (yellow) and “no-take” (green) zones for north Queensland (top) and southeast Queensland (bottom).
2.4.2. Suitable habitats protected by marine protected areas

Suitable habitat occurred throughout the Great Barrier Reef Marine Park (GBRMP), Great Sandy Marine Park (GSMP) and the Moreton Bay Marine Park (MBMP) (Figure 2-3). Suitable areas were also identified outside of the MPAs including coastal beach areas of the Gold Coast and Sunshine Coast. High suitability 15.75% (1784.33 km²) of the total projected suitable habitat (11328.48 km²), whereas medium and low suitable habitats accounted for 35% and 49.24% of suitable habitat area. In relation to MPA zones, the majority high suitability areas (0.75% occurrence) occurred in “multi-use” and outside MPAs (41.93% and 46.98 %) with 11.09% were protected by “no-take” zones. In fact, most of all levels of suitable areas occurred in “no-take” zones. A similar pattern was identified for medium and low suitable habitats (Figure 2-5).
Figure 2-6. Percentage of suitable habitat protected by MPAs in Queensland. High protection zones are indicated by “no-take” zones, low protection by “multi-use” zones, and no protection outside MPAs.

2.5. Discussion

Scalloped hammerhead shark (*Sphyrna lewini*) populations are reported as declining globally and within Queensland (Roff et al. 2018), and habitat use information about this species is still lacking in many localities including Australia (Gallagher and Klimley 2018). Scalloped hammerheads occur globally in warm to temperate waters often near coastlines and island (Compagno et al. 2008, Hearn et al. 2010, Bessudo et al. 2011, Ketchum et al. 2014, Gallagher and Klimley 2018) where adults occupy specific habitats at the shelf edge and inner-self coastal waters (Wells et al. 2018). Recently, hammerhead populations have been declining globally leading them to be listed as endangered, with many anthropogenic factors driving their decline (Baum and Myers 2004, Dulvy et al. 2008, Dulvy et al. 2014, Calich et al. 2018, Queiroz et al. 2019). With global declines in mind, identification of suitable

This study was the first to use MaxEnt modelling to determine suitable habitats and the influence of several biologically important environmental variables in Queensland. Our results determined that highly suitable habitats occurred in several places along the coast within shallow estuarine areas as well as nearshore coastal habitats (Figure 2-3 and 2-4). Our results further finding from previous studies on juvenile scalloped hammerheads movement, where sharks occurred shallow coastal and estuarine habitats (Holland et al. 1992, Holland et al. 1993, Simpfendorfer and Milward 1993, Adams and Paperno 2007, Rosende-Pereiro and Corgos 2018, Zanella et al. 2019). Shark distribution is often influenced by environmental, biologically relevant variables including depth, turbidity and temperature, which can strongly influence shark occurrence by acting on their physiology and behavioural patterns, in turn directing use of certain habitats (Schlaff et al. 2014, Ward-Paige et al. 2015, Yates et al. 2015). Juvenile scalloped hammerheads occur along the eastern coast of Queensland and often found in sheltered, turbid environments in the north (Simpfendorfer and Milward 1993, Yates et al. 2015), however our study expanded suitable habitats along the east coastline and determined highly suitable areas with heavily developed areas, including Brisbane, Gold Coast, Fraser Coast, Townsville and Cairns. Furthermore, high and medium suitable habitats were seen to occur within coastal wetlands which are also critical to many juvenile marine megafauna (Sievers et al. 2019). Turbid waters could reduce predation (Blaber and Blaber 1980) while the wetlands provide abundance prey resources. Suitable habitats were characterised mainly by low current flows and since swimming can be an energetically costly behaviour (Lowe et al. 1998, Lowe 2001, Lowe 2002) for smaller sharks in areas exhibiting wide ranging water velocities (i.e. tidal flows). Therefore juvenile sharks would seek out areas of low velocities for resting and conservation of energy (Bouyoucos et al. 2018) or swim with the tidal changes or behavioural patterns (Payne et al. 2016). Sea surface temperature was also a strong influencing variable on habitat suitability indicating suitable habitats would range between 20 °C - 25 °C. Scalloped hammerheads have been found in north Queensland where higher SST occur and have been associated with SST above 25 °C (Yates et al. 2015) and even above 30 °C (Ward-Paige et al. 2015). Occurrence preferences related SST was not as important as current velocities, and other studies showed turbidity was also important in localised areas (Yates et al. 2015). Our study identified many high and medium suitable areas which overlapped well with coastal wetland areas (Figure 2-5), which characteristically have turbid waters (i.e. Gold Coast Broadwater, south and western Moreton
Bay). Many of the high suitable habitats were occurred in densely populated areas which was also characterised by extensive river/estuarine systems opening to coastal waters. Urbanisation is known to affect marine life through habitat loss and fishing resulting in ecosystem disruptions (Beninde et al. 2015, Concepción et al. 2015). Therefore, protection of juvenile habitats becomes crucial for overall species population recruitment potential.

Marine parks are considered an effective tool in conserving species diversity and critical habitats (McCook et al. 2010). Our study indicated that of the three marine parks within Queensland, less than 10% highly suitable habitats are afforded protection with the majority of this habitats falling within multi-use zones or outside of the MPA, even though these MPAs cover large areas (Figure 2-5). This suggests that juvenile scalloped hammerheads are exposed to potentially high levels of anthropogenic stress through fishing and habitat disturbances. Hammerhead sharks are especially prone to capture stress, especially in nets, with a high attrition rate if not handles appropriately (Gallagher et al. 2014a, Gallagher et al. 2014b, Queiroz et al. 2019). A study of juvenile scalloped hammerheads in Florida (USA) determined a nursery ground at Cape Canaveral is successfully protected area for neonate scalloped hammerheads, due to human-access closure by the NASA space centre, acting like a “no-take” protected area (Adams and Paperno 2007). In contrast, juvenile scalloped hammerhead shark habitats are not well known in Queensland, Australia and occurrence data is difficult to collect. Through citizen science platforms, a reliable occurrence data was collected for the east coast of Queensland and suitable habitats were determined through MaxEnt modelling. Our study determined high suitable habitats were located near highly developed cities and a small percentage of these habitats were protected by “no-take” zones. We present the first account of suitable habitat modelling of juvenile scalloped hammerheads in Queensland and identified several if highly suitable habitats exposed to high levels of urbanisation. These results are relevant for fisheries management, conservation and urban development policies to help mitigate anthropogenic impacts on this charismatic species. Further research into the use and residency of this habitats is needed to understand the need of increased habitat protection.
2.6. References


Day, J., et al. (2012). Guidelines for applying the IUCN protected area management categories to marine protected areas, IUCN.


3. Fine-scale continuous tracking and state-switching of juvenile scalloped hammerhead sharks in the southern hemisphere

This chapter is a co-authored paper that has been reformatted for this thesis. The bibliographic details/status of the co-authored paper, including all authors, are:

3.1. Abstract

Scalloped hammerhead shark (*Sphyrna lewini*) inhabit coastal waters and islands throughout warm-temperate regions and pup within estuarine/bay environments. Their specialised behaviours and habitat preference directly places them with dense urbanised areas and fishing hotspots. This has led to scalloped hammerheads to be recently listed as threatened globally. Successful implementation of management strategies requires adequate information on the movement and habitat use, not only for adult but also juvenile sharks. Juvenile hammerheads are relatively understudied in Australia and fine-scale movement information is scarce. This study aimed to determine fine-scale movement patterns of juvenile hammerhead sharks in southeast Queensland, using continuous acoustic telemetry. We used Hidden Markov Modelling (HMM) to uncover space-state behaviours and determine if habitat characteristics influences behavioural states. Two juvenile scalloped hammerhead sharks (SHH1 0.30 and SHH2 0.53 m) were tagged and continuously tracked for 12 and 3 hours (respectively) before the tag prematurely detached. Both tagged sharks displayed high levels of repetitive “Yo-Yo” diving throughout the entire track and displayed two distinctive types of diving patterns. A-type dives were characterised by multiple small dives at depth before returning to the surface, and B-type dives resembled U-shaped dives. In general, all dives observed from the surface to the bay floor and tracked individuals did not show preference for a specific depth. A two-state movement model determined forage (low activity) behaviours were more probable in shallow waters closer to seagrass beds. Directional movements (high activity) were likely to occur over deeper water. SHH1 undertook foraging behaviours at a refuge point crossing a depth contour whereas SHH2 showed mostly directional movements due to strong tidal velocities. Our finds provide first insights to fine-scale vertical movements of juvenile scalloped hammerhead and behavioural state-switching in relation to local environmental factors. These results highlight the importance of shallow estuarine environments as usable habitats for endangered scalloped hammerhead sharks, furthering the need of habitat conservation.
3.2. Introduction

Movement of sharks in the horizontal and vertical environment has greatly increased our understanding of shark ecology and habitat use including their influence on behaviour (Speed et al. 2010). Collecting movement data can be expensive and labour intensive, often with associated issues, however acoustic telemetry technology has allowed researchers to collect fine-scale movement information to infer how sharks use different habitats and both horizontal and vertical distribution. These cutting edge technology has been used on several shark species, including white (*Carcharodon carcharias*) (Harasti et al. 2017), bull (*Carcharhinus leucas*) (Werry et al. 2011), tiger (*Galeocerdo cuvier*) and scalloped hammerhead (*Sphyrna lewini*) sharks (Bessudo et al. 2011, Bessudo et al. 2011, Ketchum et al. 2014), revealing patterns of habitat use, diel behaviours, residency and seasonal movements.

Recently, scalloped hammerhead sharks have been the focus of attention due to data deficiency in many areas, and global reports of population declines leading to the IUCN listing hammerheads as endangered (iucnredlist.org). Scalloped hammerheads are commonly caught off the eastern coast of Australia, inhabiting inner bay and coastal environments (Harry et al. 2011, Taylor et al. 2011, Wells et al. 2018). Adult scalloped hammerhead sharks occupy tropical - temperate coastal waters globally (Compagno et al. 2008, Gallagher and Klimley 2018) as well as oceanic islands (Hearn et al. 2010, Bessudo et al. 2011, Ketchum et al. 2014, Ketchum et al. 2014), where they are also known to school in large numbers (Klimley and Nelson 1981, Klimley 1983, Klimley 1985). This species of shark is also highly susceptible to fishing threats, especially long-line and gill net fisheries, due to its sensitive physiology (Gallagher et al. 2014, Gallagher et al. 2014, Gulak et al. 2015, Queiroz et al. 2019). Therefore, baseline information on its movements and habitat use is critical for establishing conservation and also fisheries management strategies (Roff et al. 2018, Queiroz et al. 2019).

Many sharks display ontogenetic partitioning in the way they use habitats, often using dedicated areas separating juveniles and adults, and survival of juveniles is known for effective management of shark species, particularly coastal sharks (Cortés 2002, Kinney and Simpfendorfer 2009). For example bull sharks are known to pup in brackish estuarine environments where they spend several years maturing before migrating to coastal adult habitats (Werry et al.). Wells et al. (2018) used satellite tagging to show adult scalloped hammerheads occupied shelf waters within the 200 m isobath at the Gulf of
Mexico, while other studies have shown juveniles to occur in nearshore bays and estuarine habitats (Holland et al. 1992, Holland et al. 1993, Simpfendorfer and Milward 1993, Duncan and Holland 2006, Hoyos-Padilla et al. 2014, Rojas et al. 2014, Brown et al. 2016, Sievers et al. 2019, Zanella et al. 2019). Within juvenile scalloped hammerhead habitats, information on horizontal and vertical movements are still needed. Zanella et al. (2019) determined that juvenile scalloped hammerheads remained within the Golfo Dulce area (2.5 km²) for up to one year and use the area as a connection to offshore habitats, through the use of passive telemetry but did not report vertical movement. Holland et al. (1993) tracked several juveniles in Kaneohe Bay using force-fed acoustic transmitters and reported sharks remained within a small core area of 1.26 km², hovering off the bay floor at an estimated 1.5 m in approximately 9 m of water. Rosende-Pereiro and Corgos (2018) determined juveniles remained in nearshore areas close to a river mouth in water depths less than 30 m and less than 1.5 km from shore. However, fine-scale movements of juvenile hammerheads have not been reported, particularly in Australia. This study uses continuous acoustic telemetry of juvenile scalloped hammerhead sharks to determine fine-scale horizontal and vertical movements in southeast Queensland, Australia. We aimed to uncover behavioural state-switching and influences of habitat features (benthos and depth) on state transitions. This information is important for conservation and fisheries management strategies in coastal areas that are highly urbanised adding to the population strain of juvenile scalloped hammerhead.

3.3. Materials and Methods

3.3.1. Study site

Juvenile scalloped hammerheads were captured within the Moreton Bay Marine Park (MBMP) at Brisbane and the Gold Coast within southeast Queensland (SEQ) (Figure 3-1). These sites were chosen based on the highly suitable habitat results from chapter 2. from. SEQ has an abundance of coastal wetlands of international significance (Ramsar, https://www.ramsar.org/). Moreton Bay and the Gold Coast Broadwater are semi-enclosed bays, which open to the Pacific Ocean. Being tidal, the Broadwater tidal flow transfers estuarine water offshore through several open coastal bars along the coastline, connecting oceanic and estuarine habitats. The connectivity (via movement of both water and animals) between the coastal wetlands, shallow water environments and open ocean, supports marine biodiversity and the survival of higher order species, such as sharks and rays. The Gold Coast
Broadwater is an intricate estuarine system linking rivers and wetlands through many mangrove islands and connected to the Pacific Ocean by Jumpinpin Bar. Moreton Bay consist of a mix of mangrove and seagrass mudflats and islands on the south and western banks, corals and sandbanks on the eastern (closer to the ocean bars). Both mangrove and seagrass habitats are characterised with mud/sand substrata, seagrass and mangrove fringes. Depths also vary from 25 m to 1 m throughout this system.

Figure 3-1. Location of study area in southeast Queensland showing capture sites of scalloped hammerhead (SHH) 1 and 2.

3.3.2. Tagging

Juvenile sharks were captured using rod and reel from the Griffith University research vessel, over multiple days from morning to night during the Austral summer. Two juvenile hammerheads were captured, one in each location (SHH1 from Moreton Bay, SHH2 from Jumpinpin Bar), after exhaustive 12 hours of fishing. Caught sharks were brought onboard and a saltwater hose placed into the mouth to maintain waterflow over the gills and relax the animal. Morphometric details were taken for each shark including total length (TL, cm), sex, and condition of the animal. Continuous acoustic tags fitted
with temperature and pressure sensors (V13-TP, Vemco) were attached to the base of the dorsal fin and then released. Both sharks exhibited strong swimming movements and healthy release. Each shark was followed from the vessel using a directional hydrophone (VH-110) and receiver (VR-100). During tracking, signal strength was maintained above 70 db and zero gain. Heading, direction, signal readings and observations were recorded at five-minute intervals for 12 hours (SHH1) and three hours (SHH2). Tracking of SHH1 occurred in Moreton Bay during early morning to the afternoon in shallow water with a low water current and adjacent deeper dredged channel and a slope entering the wider bay (Figure 3-2). The substrata consisted of silt flocculated mud with algae and seagrass meadows, soft corals and fringing mangroves. In contrast, SHH2 was tracked in a river channel surrounded by dense mangrove and mud systems with low visibility, during the afternoon and strong water velocity.

### 3.3.3. Statistical Analysis

Movement patterns and behavioural states were determined using Hidden Markov Models (HMM) in the R package *momentuHMM* (McClintock and Michelot 2018). HMM are state-space models which use characteristics of time series data, in this case individual animal tracking data, to determine distinct underlying behavioural states (Patterson et al. 2008, Towner et al. 2016, Leos-Barajas et al. 2017). HMM can be used to estimate the probability of animals switching between states (state transition probability) and link changes in behavioural state probabilities to environmental or physiological drivers. We used a two-state HMM defined as a less active “foraging” and a high activity “directional” state, by subsampling each data set over a 5 minute and a 30 second mean time step parameter for SHH1 and SHH2 respectively. A shorter time step used for SHH2 was due to the significantly smaller dataset compared to SHH1. A smaller time step allowed for a better fitting model while still reducing the temporal autocorrelation in the data set. We used two variables, step length (meters) and turning angles (radians) to determine basic behavioural states, where small step lengths (small distances in locations) within an area and time indicate “foraging” behaviour and higher step lengths indicate “directional” movement. Turning angles (bearing) is calculated as the changes in bearing between location intervals (around ‘0 radians’ indicate persistent movement in that direction), therefore peaks in turning angles around the mean (‘0 radians’) indicates clustering compared to peaks at ‘0 radians’ which indicate uninterrupted movement in the travel direction. State-dependent probability distributions were set to gamma and Von Mises and considered many sets of initial values in order to
find the optimum likelihood function. We also tested the influence of environmental factors on behavioural states by adding tag depth (m), tag temperature (°C), bathymetry depth (m), distance to seagrass (m) and distance to coral (m). Seagrass and coral datasets were obtained from Seamap Australia (seamapaustralia.org) and 30 m resolution bathymetry was obtained from Deep Reef (deepreef.org).

3.4. Results

3.4.1. Description and diving behaviour

3.4.1.1. Scalloped hammerhead 1 (SSH1)

During the track, SSH1 moved from the tagging site directly to the channel slope, where it remained for a five-hour period (refuge point). At the refuge point, SSH1 was continuously active, constantly diving thorough the water column and moving around an area of 0.52 km². After five hours at the refuge point, SSH1 undertook a sudden rapid and directional movement northward where it became stationary and reported a single depth on the seafloor, indicating the tag shed early (Figure 3-2). During this directional movement, SSH1 swum in a brief circular pattern (denoted as forage) before continuing in the initial direction. During this track, SSH1 remained within the shallow confines of the bay diving to a maximum of 4 m spending little time at any depth but displayed a constant well-defined ‘Yo-Yo’ swimming pattern (Nakamura et al. 2011, Iosilevskii et al. 2012). The acoustic transmitter prematurely detached after 12-hours into the track of SSH1.
The vertical movement profiles showed two types of diving patterns, multiple dives at depth (type A) and short U-shaped dives (type B) (Figure 3-3). Type A dives were differed from type B by multiple short dives times at depth, were the shark spent less time at the sea floor before returning to the surface. In type B dives, the shark did not perform multiple dives and dived for longer before returning to the surface. These diving behaviours occurred through the entire track with type B dives occurring almost
twice as frequent as type A. Bottom times during type A dives were generally twice as long than type B. Time at depth for type B generally lasted for 1 minute while time at the surface (> 0.5 m) was generally the same. These bottom and surface times increased with track time.

The sharks’ initial movement after tagging was to head to deeper water which was also where a dredged shipping channel opened into the wider Moreton bay area, taking roughly 1-hour. After this movement, SHH1 remained in this ‘refuge’ spot and consistently undertook vertical dives like the initial swim (Figure 3-4) but performed more (12) type A dives then type B (9). Before some deeper dives, a shallower dive reaching 1.5 m often occurred (Figure 3-4). Within the refuge area, SHH1 moved over the 3 m contour and the shipping channel, constantly moving throughout the area. The benthos was roughly characterised as fine flocculated sediments, low visibility, algae with soft corals, warm temperature and low water currents. Since the start of the track, SHH1 occupied the upper water column above 1 m, and towards the end of the time in the refuge area, SHH1 occupied vertical space below 1 m (Figure 3-5). Suddenly, SHH1 moved in a northerly direction totalling 2.6 km in 1.5 hours before the tag shed (Figure 3-7). Dive profile showed multiple type A dives occurred during the swim with multiple small dives at depth, which may be related to foraging behaviours (Figure 3-6). A particularly extended bottom time in a type A dive can be seen during the directional swim at 11:03 in and lasting for 11 minutes with a very short surface interval before continuing the dive. This foraging behaviour also changed the direction of the swim and seen in Figure 3-2. After this event, SHH1 swum in the regular yo-yo pattern until the end of the swim where surface intervals became longer, and increased bottom time occurred again before tag shedding.
Figure 3-3. Swimming behaviour of SHH 1 after tagging swimming to the refuge point. Two diving patterns were observed with type A being more frequent with time.

Figure 3-4. SHH1 vertical movement profile while at the refuge point. Arrows indicate shallow dives before type A dives.
Figure 3-5. Example hourly dive profiles of SHH 1 during the five-hour period spent at the refuge point. After 0930, SHH1 remained under 1 m depth before the directional movement.

Figure 3-6. SHH1 directional vertical movement profile from refuge area towards Manly Harbour.
Figure 3-7. Movement profile of the sudden highly directional swimming behaviour from the refuge point to Manly Harbour. The end of the movement indicated the tag shedding from the animal.

3.4.1.2. Scalloped hammerhead 2 (SSH2)

SHH2 was caught within a main channel within the Jumpipin Bar estuarine area dominated by mangroves and seagrasses and fine to sand sediments (east) with turbid waters. This area was deeper and narrower compared to Waterloo Bay, experiencing strong tidal currents from the nearby coastal bar reaching 3 kts (Figure 3-8). Due to shallow depths and mudbanks, the track lasted 3 hours before the hydrophone mount assembly hit a mud bank and needed repairs. After 1-hour of searching, SHH2 was not able to be detected, search continued over five days throughout the Gold Coast, Moreton Bay and offshore coastal area without detecting SHH2. SHH2 was noted to be swimming with the tidal current west into the wetland system with the incoming tide.
Figure 3-8. Track location of SSH 2 in southern Moreton Bay, northern Gold Coast.

Vertical swimming behaviour were similar to SHH1 with type B dives being more frequent than type A and generally preceded by fast shallow dives (Figure 3-9 and Figure 3-10). SHH2 surface and deep dives were generally longer than SHH1 averaging 3 – 5 minutes. The first hour of tracking was undertaken at the start of the incoming tide. During the track, SHH2 remained along the channel slopes making vertical dives along the slope during the as the water current increased.
Figure 3-9. Hourly plots of SHH 2 vertical movement for the first hour (top) and second hour (bottom). Arrows indicate type B dives (U-shaped) and type A dives (extra dive at bottom).
The second hour of tracking occurred in the main channel heading up-river with shallower banks, where SHH2 dived along the channel edges. The last hour of tracking (Figure 3-10) occurred at night but did not last long enough to determine a night diving pattern different to the daytime. Diving remained along the channel edge with frequent longer bottom times through extended A-type dives (Figure 3-10).

![Figure 3-10. Third hour vertical movement profile of SHH2 showing increased bottom time and A-type dives.](image)

### 3.4.2. Behavioural States

#### 3.4.2.1. SHH1

Autocorrelation function (ACF) of the model step predictions shows that the subsampling of positions to one every 5 minutes reduced the temporal autocorrelation in the dataset (Figure 3-11).
Figure 3-11. Autocorrelation function determine the best fit model using a 5-minute time step.

Figure 3-12. Step length and tuning angle distributions for SHH1 track over a 5-minute time step.
Step length and turning angles showed the model described the behavioural states adequately, with small step lengths accounts for most of the forage behaviour and lager length comprising the directional movement behaviour, which accounted for the bulk of the data set (Figure 3-12). Turning angles were also described well for each behavioural state with directional movements encompassing near “0” angles and forage behaviours spread across larger angles.

Figure 3-13. Behavioural states during the 12-hour track of SHH1. Orange indicated forage and blue indicates directional behaviours.

Behavioural states during the track showed SHH1 undertaking directional movements from the tagging site to the refuge point, where more centred movement was concentrated (Figure 3-13). During time sent at the refuge site, several directional behaviours were also seen, mainly at the eastern side of the refuge site, which also coincided with deeper channel waters of Moreton Bay. The second directional behaviour also occurred with the observed directional swim before the tag shed.
Tag depth related to extrapolated bathymetry depth showed forage behaviours occurred more at depth while directional movements occurred at depth and surface. Tag depth overlayed with estimated bathymetry showed behavioural states differed with depth, where directional movements occurred near the surface during the initial swim across the shallow flat. At the refuge site, forage behaviours occurred more often and directional movements occurring at various depths. Directional movements in between forage behaviours may indicate hunting/escape-like movements. The last directional swim was comprised entirely by directional movements at various depths before the tag shed.

Figure 3-14. Behavioural states at shark depth overlayed with habitat depth, at 5-minute time step for the 12-hour track. Vertical blue lines differentiate time segments from the release swim to the refuge point (left) and the end of the refuge point to the direction swim (right).

Environmental influences on behavioural state switching showed the probability of transitioning between forage and directional movement decreased with SHH1 depth, where foraging was more likely to occur when the SHH1 was deeper water than when SHH1 was higher in the water column. Likewise,
directional movements were more likely when SHH1 was nearer the surface. Similarly, foraging was more likely in deeper habitats than shallow with the probability of foraging transitioning to directional movements increasing in shallower environments (Figure 3-14). Changes in habitat also effected changes in behavioural states, as SHH1 was closer to seagrass habitats increased the probability of changing to foraging from directional movements and SHH1 was more likely to remain foraging closer to areas with seagrass. Interestingly, more directional movements were likely closer to corals, and a low probability of transitioning to forage was likely closer to corals and may reflect patrolling behaviours (Figure 3-15).

![Graphs showing stationary state probabilities of environmental variables on behavioural state switching for SHH1. All units are in meters.](image)

Figure 3-15. Stationary state probabilities of environmental variables on behavioural state switching for SHH1. All units are in meters.
3.4.2.2. **SHH2**

Step lengths and turning angles for SHH2 showed a significant density of very small length in and directional turning angles near 0 radians indicating a strong single directional state behaviour (Figure 3-16), justified by observations during the track. This may have been influences due to the strong flood current experienced in this area. However, two states were determined by the model with foraging behaviour occurring coinciding to lower tidal currents.

![Graphs showing step length and turning angle distributions](image)

*Figure 3-16. Step length (left) and turning angle (right) distribution for a 30-second time step over a 3-hour track of SHH2.*
Figure 3-17. SHH2 behavioural states during the three-hour track.

Forage behavioural states rarely occurred and SHH1 mainly showed highly directional movements in a westerly direction swimming with the tidal current upriver, though several forage behaviours were noted near the eastern end of the track and further upriver near then the track end (Figure 3-17).

Behavioural states occurring at the depth of the shark related to habitat depth showed directional behaviours occurred more often than forage throughout the water column. Interestingly, at 1600 hours, forage behaviour occurred in a clump with no directional behaviour. This occurred when SHH2 was near a connecting shallower creek mouth and a central sand bank with steep bank, creating a well-defined deep intersecting channel to the creek. Environmental variables influenced SHH2 behaviours.
in contrast to SHH1, as directional behaviours were more likely in deeper waters and the probability of foraging was high in shallower waters (Figure 3-18). The probability of SHH2 foraging was high closer to seagrass areas and transition to directional behaviours further from seagrass habitats. Seagrass in this area was observed to occur closer to shallower banks, mostly likely due to the high turbidity in the area (Figure 3-19).

Figure 3-18. Depth profiles of SHH2 showing behavioural states with habitat depth during the track.
3.5. Discussion

This study used active acoustic telemetry to describe fine-scale movement of two juvenile scalloped hammerhead sharks in two locations within southeast Queensland (SEQ), Australia. Furthermore, we used Hidden Markov Modelling (HMM) to describe two behavioural states associated within the acoustic data and identify environmental variables influencing these behavioural states. Behaviours were interpreted as “foraging” and “directional” and these behaviours were influenced by depth, habitat bathymetry as well as distances to seagrass and coral habitats. Our results further the literature and report the first fine-scale movement and habitat use of juvenile scalloped hammerhead sharks in Australia. These results will aid in conservation and management of the endangered scalloped hammerhead shark.
Globally, juvenile scalloped hammerheads are found in warm, shallow, muddy estuarine habitats usually with access to ocean waters (Holland et al. 1992, Holland et al. 1993). In this study, juveniles were also caught in turbid waters in areas characterised by dense fringing wetlands and seagrass habitats, however, SHH1 occupied an area fringed by corals while SHH2 did not. These near shore shallow water presences were also seen in juvenile sandbar sharks (*Carcharhinus plumbeus*) and white sharks (*Carcharodon carcharias*) where these sharks remained away from adult areas and patrolled a warm shallow habitat (Rechisky and Wetherbee 2003, Hoyos-Padilla et al. 2016).

Early studies on scalloped hammerhead movement showed high site fidelity to a core area, during the day in which they returned after a wider night-time range, generally remaining near the bay floor patrolling reef and bank edges (Holland et al. 1999). The core area was also the area in which all sharks in the study were captured and used a total core of 800 m². SHH1 in our study showed a similar movement behaviour as in Holland et al. (1993) where the shark moved from the mudbank tagging site to an area where it remained for 5 hours before patrolling for the night and returned back to this 5 hour area. Unfortunately, the tag on SHH1 detached after its similar 5-hour 540 m² refuging area, and SHH2 was not found after entering a maze of channels.

Rosende-Pereiro and Corgos (2018) also noted juvenile scalloped hammerheads used a near shore area within proximity to a river mouth totalling a 14 m² area in the Mexican Central Pacific and confirmed site fidelity for this species. Their study described the habitat as soft bottomed and shallower than 30 m with two kernel area in front of the river mouth most used. Our study reports fine-scale diving behaviours of juvenile scalloped hammerhead sharks within their habitats, and showed these sharks constantly swim throughout the water column spending equal time at the surface and seafloor, unlike other shark species which utilised a preferred depth range (Hoyos-Padilla et al. 2016). Both juvenile scalloped hammerheads showed two dive patterns, a single dive with multiple dives at depth (A) and a single U-shaped dive (B). These dive types occurred throughout the track and were more closely spaced during directional swims. Andrzejaczek et al. (2018), Andrzejaczek et al. (2019) described U-shaped dives of adult tiger shark (*G. cuvier*) and sandbar sharks (*C. plumbeus*) as benthic foraging behaviours due to high number of fine-scale turning movements and may explain the smaller-scale U-shaped dives seen in both juvenile hammerhead sharks.
Common features found in both habitats were depth contours and channel slopes of shallow to deeper water, which both sharks utilised. SHH2 occupied an area with defined deep channels and very high tidal currents in contrast to SHH1, which had lower turbidity and occupied areas near dredged channels. Forage behavioural states were more likely to occur at shallow depths changing into directional behaviours as depth increased for both SHH1 and SHH2, but as habitat depth increased foraging behaviours had a higher probability to transition into directional movements. This may be due to prey type changes or predation by larger sharks in deeper waters. The section of Moreton Bay with deep channels is also pathways for larger predatory shark species including bull (*Carcharhinus leucas*) and tiger (*Galeocerdo cuvier*) sharks, but also a change in prey species may also occur. Juvenile scalloped hammerheads predate on small benthic prey such as shrimps, squid and small fish (Torres-Rojas et al. 2010, Torres-Rojas et al. 2015), which may become harder to obtain in deeper environments experiencing stronger water currents. Therefore, directional movements over deeper areas may be more transitional or exploratory. Areas close to seagrass showed a higher probability of forage behaviours high for up to 400 m from seagrass habitats, after which transitioning to directional movement had a 50% probability (SHH1). Seagrasses are a well-known habitat supporting diverse crustacean and fish abundance (Zarco-Perello and Enríquez 2019), therefore foraging behaviours would be more likely to occur.

In contrast, SHH2 described different patterns explaining its behavioural states, most likely due to strong tidal current experienced during this track. SHH2 was caught on the low tide near the coastal bar and tracked moving east towards the ocean. As the flood tide flows increased, SHH2 begun to move west with the tide direction, towards the dense estuarine habitats. Throughout SHH2 track all forage behaviours occurred near channel entrances, dive patterns during forage times occurred with the increased A-type dives with extended benthic times and may relate to prey searching movements.

Our study reported the fine-scale movement of two juvenile hammerhead sharks in southeast Queensland and the first to report diving profiles in this species. Juvenile scalloped hammerheads showed extensive use of estuarine environments and preferred areas with sloping depth contours, such as dredged channels and steep banks. Behavioural state models uncovered foraging behaviours occurred in shallow waters near seagrasses and transitioned into directional movements over deep waters. Our result also showed directional behaviours occurred close to coral habitats for SHH1 which
may indicate patrolling behaviours. SHH2 occupied a high tidal velocity channel in which the track showed directional movement in the following the direction of tidal flow. SSH2 also showed affinity for shallower areas of the channel and remained near the bank slope where it constantly dived. The strong tidal current may have prevented SHH2 from foraging in preferred habitats and may be the reason for low forage behavioural detections. These results further indicate intricate usage of estuarine habitats containing seagrass and fringing mangroves, which warrant further investigate to support conservation and management strategies of these areas.

3.6. Funding

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3.7. References


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4. Thermal limits for hammerhead (*Sphyrnidae*) shark and coexisting large shark catches in Queensland, Australia

This chapter is a co-authored paper that has been reformatted for this thesis. The bibliographic details/status of the co-authored paper, including all authors, are:

4.1. Abstract

Environmental variables influence how marine organisms can optimise the use of their environment. Understanding this influence is important for management, conservation efforts and predicting future response of sharks to shifting climate. As shark populations continue to decline globally, efforts are required to better understand and manage crucial habitats that support these elusive creatures. Water temperature is an important species habitat marker that can inform scientists and policymakers of shark occupancy and movement, including coastal habitats where water temperatures experience large diurnal and seasonal fluctuations. Quantile regression was used to estimate the response of five large sharks to sea surface temperature along the Queensland coast in Australia. We tested the fitness of simple to complex models at the highest quantile of shark catch density. The most complex model and best fitting model indicated the most likely response of temperature on shark catch. We found that hammerhead sharks had a smaller thermal tolerance (5 °C change) and were most likely to occur between 20 °C - 25 °C, while co-occurring tiger and bull sharks had the widest tolerance (9 °C and 7 °C, respectively). White sharks were also most likely to occur in the same environment when cooler waters (<19 °C) occur during winter and spring. Southern Queensland areas had larger seasonal sea surface temperature (SST) variations compared to more stable northern Queensland areas. Our results indicate bull and tiger sharks have a wider temperature range and may be present throughout more of the year compared to the cooler water-dependent white shark. Our results provide the ability to predict periods of peak occurrence of potentially hazardous shark species at different latitudes, which in turn will help to inform public safety and conservation efforts along increasingly urban coastlines. As the world’s oceans continue to warm, the expanding thermal limits of hammerhead sharks may force them into new territories.
4.2. Introduction

Hammerhead sharks occur throughout tropical and temperate environments, often close to land, and therefore are not considered truly oceanic (Hammerschlag et al. 2011, Gallagher and Klimley 2018). Recent studies have shown declines in abundances of many shark species including both large hammerhead shark species: Great hammerhead (*Sphyrna mokarran*) and the scalloped hammerhead (*Sphyrna lewini*) (Roff et al. 2018). Hammerhead sharks are under threat due to their unique specialisation and response to global fishing pressures (Gallagher et al. 2014, Gallagher et al. 2014, Queiroz et al. 2019). Hammerhead sharks have been found to move between nearshore and oceanic habitats with frequent excursions into deep pelagic zones (Bessudo et al. 2011, Hammerschlag et al. 2011, Roemer et al. 2016). A recent comprehensive satellite tagging study showed the scalloped hammerhead occupied shelf waters in the Gulf of Mexico, United States, within the 200 m isobath. Within this area, scalloped hammerheads showed a preference for hard bottom or artificial substrates, presumably linked to higher prey abundance (Wells et al. 2018).

With increasing ocean temperatures (Wernberg et al. 2011), distribution and abundance of many shark species may change. Coastal habitats are integral habitats for coastal shark species (Sievers et al. 2019); however, they are also highly developed in Australia adding additional pressures to shark populations (Stevens et al. 2000, Dulvy et al. 2008, Werry 2010, Werry et al. 2011, Dulvy et al. 2014, Queiroz et al. 2019) as well as increasing shark-human interactions (McPhee 2014). Sea temperature is one of the most influential factors that affects marine species distribution due to the physiological limitations, e.g. ectothermy (Speed et al. 2012, Vianna et al. 2013).

This can impact horizontal movements and vertical diving behaviour, where pelagic blue (*Prionace glauca*) and white (*Carcharias carcharodon*) sharks have been observed to use oceanic warm-core eddies to dive deeper into cooler waters, increasing their foraging times in deeper waters (Gaube et al. 2018, Braun et al. 2019). Tiger sharks (*Galeocerdo cuvier*) in Australia have also shown a thermal preference in relation to abundance at New South Wales (NSW) beaches, where higher occurrences were associated with sea surface temperatures of 22 °C and white sharks associated with temperatures below 19 °C (Payne et al. 2018).

Other large shark species co-occurring in Queensland (QLD) coastal waters, such as the bull shark, were also influenced by environmental factors, with bull shark occurrence in coastal and estuarine
systems increasing with >100 mm of rain and higher sea surface temperature (SST) (Werry et al. 2018). Therefore, it can be assumed that fluctuations in sea temperatures likely influences shark occurrence seasonally and may vary between other species (i.e. tiger versus white shark) co-occurring with hammerhead sharks depending on their thermal niches.

The effect of temperature on the occurrence of hammerhead shark species has been reported in the literature. For example, in Columbia, the average swimming depth of the scalloped hammerhead varied monthly, which was attributed to the seasonal shift in the local thermocline (Bessudo et al. 2011). More scalloped hammerheads were also found closer to land during winter compared to summer and generally at shallower depths when the thermocline was deeper (Klimley and Nelson 1984, Hearn et al. 2010).

The eastern coastline of Queensland, Australia spans tropical and subtropical climatic zones experiencing a change in sea surface temperatures. The east coast is also dominated by the Western Boundary Current (WBC), the East Australian Current (EAC), which has a strong influence on the circulation of shelf waters (Ridgway and Dunn 2003, Suthers et al. 2011). The EAC is fed with warm nutrient poor waters from the north and intensifying into a southward flow along the continental shelf (Ridgway and Dunn 2003), with a strong flow in the autumn-summer periods and retracting in the winter.

Earlier studies have investigated temperature influences on shark occurrences using linear modelling, such as Generalised Linear Models (GAMs); however, this may not best describe ecological responses that are non-linear. If a species tolerance is limited in two directions (upper and lower limits), the response can typically be unimodal and can be mis-represented when modelling the mean (Westman 1980, Meents et al. 1983, Austin 2007, Austin 2013). Thus, this study investigates the thermal niche of great and scalloped hammerhead sharks in relation to co-occurring bull shark, tiger shark, and white shark in southern and northern Queensland coastal areas. The primary aim was to determine whether each species has a separate thermal niche and if this affects occurrences both spatially (north to south) and temporally (seasonally).
4.3. Methods

4.3.1. Queensland Shark Control Program catch data

Numbers of sharks caught on a series of drumlines and gillnets along the Queensland coastline were sourced from the Queensland Government’s Shark Control Program (QSCP), managed by the state government’s Department of Agriculture and Fisheries. Gear type varied with location and mainly consists of baited drumlines and surface mesh nets. Surface gill nets are 182 m long by 6 m deep and are comprised of a 50 cm mesh net, held at the surface by a floating headline and three A3 polypropylene floats. Each net is stretched and anchored at each end by a 32 kg Danforth of Clyde Quick Release anchors. Each net was set ~500 m from and orientated parallel to the shoreline in 5 and 12 m of water. No nets are installed in Townsville and nets are removed from the water during February in Cairns. Baited drumlines consisted of a single A3 float with a baited hook suspended by 2 m of galvanised chain. The A3 float is connected to rope and two smaller floats to keep the hook away from the Danforth anchor. Contractors collect daily logs and record species information (total length, species, etc) and species identification was considered reliable since 1996 following identification training. Catch Per Unit of Effort (CPUE) was calculated on the number of sharks caught in each gear type per month, and then summed for each location to give the total CPUE for each area. Catch data was analysed between 1996 and 2018 due to the QSCP implementing species identification training in the early 1990’s. Areas were then classified into northern areas (Cairns and Townsville), mid-latitude (Mackay) and southern areas (Sunshine and Gold Coasts). Catch data was then summed for each day for each species in order to coincide with mean daily SST.

4.3.2. Sea Surface Temperature

Sea surface temperatures was collected by wave monitoring buoys at each location from Cairns to Tweed Heads (Queensland Department of Science). SST data were quality controlled to exclude outliers (e.g. -99°C, 0°C and 99°C) and averaged into daily and monthly averages. Daily mean SST were then matched to sum daily shark catches from each location.
Table 4-1. Wave rider buoy location and SST date range.

<table>
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<th>Location</th>
<th>Wave Rider</th>
<th>SST Date Range</th>
<th>Drumlines</th>
<th>Gillnet</th>
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<td></td>
<td>E: 145.715167</td>
<td></td>
<td></td>
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<tr>
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<td>S: -19.159167</td>
<td>1996 – 2018</td>
<td>54</td>
<td>0</td>
</tr>
<tr>
<td></td>
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<td></td>
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4.3.3. Quantile Regression Modelling

Quantile regression, QR, (Koenker and Bassett 1978) was used to determine the thermal niche of the great hammerhead and scalloped hammerhead sharks. This was performed using the daily summed catch data associated with a mean daily SST for each area tested. QR (Koenker and Bassett 1978) can determine a more reliable maximum response to a limiting factor by modelling response quantiles (Cade et al. 1999, Guisan et al. 2006, Shuker et al. 2016). QR models used included simple models (no response and straight line) and logistic S-shaped (estimates point of inflection, X-mid) as well as complex models. Complex models included the unimodal Gaussian and generalised bell curve, which estimate optimal X-peak SST as well as the upper and lower limits from the standard deviation (σ). These models were used as the distribution of catch data and temperature was non-linear, therefore nonlinear models were used. QR is recognised to better predict biological response to a single environmental variable (like SST) and determines the species maximum response to the variable by modelling the highest possible quantile, rather than the average (Cade et al. 1999, Cade and Noon 2003, Guisan et al. 2006, Austin 2007). The best model was chosen based on the Akaike’s Information Criteria (AIC), with the best model being lower by 2 from the previous. Parameters of each model were also assessed for significance (α = 0.05). QR was undertaking in R (v3.6, R development Core Team) using the package quantreg (v5.54).
4.4. Results

4.4.1. Sea Surface Temperature

The annual SST mean from 1996 to 2018 showed surface waters were warmer at higher latitudes (Cairns and Townsville) and cooler at mid- to lower-latitudes (Mackay, Sunshine Coast and Gold Coast) (Figure 4-1). Mean SST were 4 °C warmer at the northern sites compared to the southern sites. There was also a difference in heating cycles between regions, where the northernmost areas reached lowest temperatures one month earlier than the southern regions. The Gold Coast and Sunshine Coast showed a greater change in monthly SST means with winter reaching 19 °C and summer > 26 °C. Northern areas were generally warmer with winter monthly mean SST only reaching 23 °C and summer mean SST reaching 29 °C.

Figure 4-1. Annual long-term (left) and monthly (right) mean sea surface temperatures taken from the wave rider buoy in each area from 1996 - 2018.
4.4.2. Catches in the Queensland Shark Control Program

Scalloped hammerhead catches exhibited a seasonal, cyclical trend, with highest numbers recorded in summer and lowest in winter for the southern areas (Figure 4-1). CPUE peaked at various times of the year for all areas except Townsville where no nets were deployed. Catches at the Gold Coast were highest during late spring and summer when SST were above 21 °C, almost double compared to catches in other months. This pattern occurred at a lesser extent for catches at the Sunshine Coast. The Sunshine Coast showed a similar trend as the Gold Coast with peak catches occurring in September and November, whereas Mackay peaked before both the Sunshine and Gold Coasts in June declining until the spring peak in November. In the northern areas, Townsville showed little fluctuations with scalloped hammerheads being constant through the year, but highest catches recorded during the winter months, contrasting to the southern areas. The great hammerhead catches were generally high in summer decreasing through Autumn and winter for the Gold Coast (Figure 4-2). High catches on the Sunshine Coast occurred before the Gold Coast from August to December with low periods in Autumn to the beginning of winter. Similarly, Townsville had higher catches during winter with lower numbers.
at the end of summer and Autumn, again peaking before the southern areas. Cairns showed similar variability in catches, with the highest catches at the start of the year.

Cairns showed a major decrease in CPUE in February across all species due to the removal of shark nets during this month. Similarly, Townsville shows a consistently low CPUE for all sharks due to no netting gear deploying throughout the year. Total catches for Townsville did show high numbers of tiger shark caught by drumlines throughout the year and maximum numbers caught during autumn and winter. Differences in catches between northern and southern areas were evident for each species (Figure 4-4 and Figure 4-5). Bull shark CPUE (Figure 4-4) at Mackay were caught throughout the year exhibiting a near unimodal trend, with lowest catches occurring in winter. In the southern areas, Gold Coast and Sunshine Coast, high bull shark catches occurred between March and July and lowest during spring. Bull sharks were caught throughout the year in the northern areas, though total catch numbers at Townsville decreased during autumn and winter. Tiger shark catches were more prominent in the northern areas consistently through Autumn and winter (Figure 4-4). Catches declined first in Cairns (from June), followed by Townsville (July), Mackay (September). Catches in the southern areas increased from October, coinciding with the low catch periods for the northern areas. Tiger shark catches were generally lowest in October-January in Townsville, November-May in Mackay and February-October in the southern areas. White shark catches in the QSCP were restricted to the southern areas and showed a distinctive cold-water trend (Figure 4-4). White shark catches peaked rapidly from April to November on the Gold Coast, and June to September on the Sunshine Coast. Catches were more prominent on the Gold Coast than the Sunshine Coast.
Figure 4-3. Total CPUE of each species per month per location, in the shark control gear. Total CPUE is inclusive of drumline and net CPUE for each area averaged from 1996-2018.
Figure 4-4. Total mean monthly number of sharks caught in the QSCP at each study location, with the long-term monthly averaged SST from 1996-2018.
4.4.3. Thermal tolerance

Scalloped hammerhead had a thermal range best described by the generalised bell model with significant catches were most likely to occur within 20.3 ± 1.2 °C and 24.9 ± 1.2 °C at the Gold Coast (Table 4-2 and supplementary 1). Further north, no influence on catches was seen for Townsville or Cairns as the no response model indicated the SST in these areas were always high enough (SST > 22 °C) for scalloped hammerheads to occur (Table 4-2 and supplementary 1). Catches at Mackay were best described by the generalised bell model which determined a significant influence of temperature on catches between 24.3 ± 0.3 °C and 28.3 ± 0.3 °C, where catches were most likely to occur within this range at mid latitudes. These results suggest a 5 °C small thermal niche for catches of scalloped hammerhead sharks in southeast Queensland and 4 °C niche at Mackay (Table 4-2 and supplementary 3). A response to temperature was not determined at the Sunshine coast due to a low sample size.

Great hammerhead catches were best described by the logistic model indicating great hammerheads were most likely to occur when SST were above 20.3 ± 0.2 °C and 19.9 ± 1.3 °C at Gold Coast and Sunshine Coast. No response model best described catches at Townsville. The thermal niche for the great hammerhead was determined to be above 20 °C and which is evident in catches at the Gold and Sunshine Coasts (supplementary 1 and 2).

White shark results were only reported for the Gold Coast which had the largest sample size, and catches were not reported further north in the data set. White sharks at Gold Coast showed temperature threshold of 23.4 ± 0.5 °C best described by the logistic model, suggesting white sharks were most likely to be caught below 23.4 °C (supplementary 1).

Tiger shark showed a wider 8.5 °C temperature range than both hammerhead species at Gold Coast and Sunshine Coast (18.5 ± 0.8 °C and 26.9 ± 0.1 °C) described by the generalised bell model (supplementary 1 and 2). In comparison, the no response model was the best fit for tiger shark catches in Cairns. Mackay and Townsville showed a marginal decline in catches with increasing temperatures (x = -0.1 and -0.12, p = < 0.001).

Bull shark catches had a small thermal range compared to tiger shark and higher than the scalloped hammerhead in southern Queensland (supplementary 1 and 2). Catches were likely to occur below 27.0 ± 0.01 °C (Gold Coast) and a 6 °C range between 20.6 ± 0.8 °C and 26.4 ± 0.8 °C (Sunshine Coast)
(supplementary 2). Similarly, bull shark catches at Mackay were higher above $18.2 \pm 4.0 ^\circ C$, and no response model described catches at Cairns which has higher mean monthly SST. Generalised bell model described a $6 ^\circ C$ temperature range for bull sharks caught at Townsville ($23.8 \pm 0.26 ^\circ C$ to $30.2 \pm 0.26 ^\circ C$), and more catches occurred in the higher temperatures than below the lower calculated limit (supplementary 4).
Table 4-2. Quantile regression models of best fit ($\Delta$ AIC > 2) from the no response model at the highest $\tau$ value.

<table>
<thead>
<tr>
<th>Area</th>
<th>Species</th>
<th>Model</th>
<th>$\tau$</th>
<th>AIC</th>
<th>P</th>
<th>X-peak or slope (x)</th>
<th>SD (σ)</th>
<th>St. Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gold Coast</td>
<td>SHH</td>
<td>Generalised bell curve</td>
<td>0.99</td>
<td>3832.597</td>
<td>0.000</td>
<td>22.6</td>
<td>2.3</td>
<td>1.2</td>
</tr>
<tr>
<td>Sunshine</td>
<td>SHH</td>
<td>Small sample</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Mackay</td>
<td>SHH</td>
<td>Generalised bell curve</td>
<td>0.95</td>
<td>1978.58</td>
<td>0.000</td>
<td>26.0</td>
<td>2.3</td>
<td>0.3</td>
</tr>
<tr>
<td>Mackay</td>
<td>GHH</td>
<td>Logistic curve</td>
<td>0.97</td>
<td>2277.746</td>
<td>0.000</td>
<td>Min 20.3</td>
<td>-</td>
<td>0.02</td>
</tr>
<tr>
<td>Mackay</td>
<td>GHH</td>
<td>Logistic curve</td>
<td>0.97</td>
<td>1568.735</td>
<td>0.000</td>
<td>Min 19.9</td>
<td>-</td>
<td>1.3</td>
</tr>
<tr>
<td>Mackay</td>
<td>GHH</td>
<td>Small sample</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Townsville</td>
<td>GHH</td>
<td>No response</td>
<td>0.97</td>
<td>2126.084</td>
<td>0.000</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Cairns</td>
<td>GHH</td>
<td>Small sample</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Gold Coast</td>
<td>WS</td>
<td>Logistic curve</td>
<td>0.99</td>
<td>1853.716</td>
<td>0.000</td>
<td>Max 23.4</td>
<td>-</td>
<td>0.5</td>
</tr>
<tr>
<td>Sunshine</td>
<td>WS</td>
<td>NA</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Mackay</td>
<td>WS</td>
<td>NA</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Townsville</td>
<td>WS</td>
<td>NA</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Cairns</td>
<td>WS</td>
<td>NA</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Gold Coast</td>
<td>TS</td>
<td>Generalised bell curve</td>
<td>0.99</td>
<td>2808.96</td>
<td>0.000</td>
<td>22.7</td>
<td>4.2</td>
<td>0.8</td>
</tr>
<tr>
<td>Sunshine</td>
<td>TS</td>
<td>Generalised bell curve</td>
<td>0.80</td>
<td>1014.992</td>
<td>0.000</td>
<td>22.7</td>
<td>2.1</td>
<td>0.1</td>
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<td>Mackay</td>
<td>TS</td>
<td>Straight line</td>
<td>0.97</td>
<td>3610.177</td>
<td>0.000</td>
<td>X = -0.1</td>
<td>-</td>
<td>0.04</td>
</tr>
<tr>
<td>Townsville</td>
<td>TS</td>
<td>Straight line</td>
<td>0.91</td>
<td>2964.811</td>
<td>0.000</td>
<td>X = -0.12</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Cairns</td>
<td>TS</td>
<td>No response</td>
<td>0.90</td>
<td>1196.572</td>
<td>0.000</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Gold Coast</td>
<td>BS</td>
<td>Logistic curve</td>
<td>0.99</td>
<td>2389.754</td>
<td>0.000</td>
<td>Max 27.0</td>
<td>-</td>
<td>0.01</td>
</tr>
<tr>
<td>Sunshine</td>
<td>BS</td>
<td>Gaussian bell curve</td>
<td>0.98</td>
<td>1685.503</td>
<td>0.000</td>
<td>23.5</td>
<td>2.9</td>
<td>0.8</td>
</tr>
<tr>
<td>Mackay</td>
<td>BS</td>
<td>Logistic curve</td>
<td>0.99</td>
<td>3635.038</td>
<td>0.000</td>
<td>Min 18.2</td>
<td>-</td>
<td>4</td>
</tr>
<tr>
<td>Townsville</td>
<td>BS</td>
<td>Generalised bell curve</td>
<td>0.85</td>
<td>2150.279</td>
<td>0.000</td>
<td>27.0</td>
<td>3.2</td>
<td>0.26</td>
</tr>
<tr>
<td>Cairns</td>
<td>BS</td>
<td>No response</td>
<td>0.99</td>
<td>690.5613</td>
<td>0.000</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

$^a$ Tau indicates the quantile of data used in model.  
$^b$ Akaike’s Information Criteria with the difference ($\Delta$AIC) ≥ 2 indicating model superiority of the lower AIC model (Shuker et al. 2016).  
$^c$ Significance p < 0.05.  
$^d$ Gaussian and generalised bell curve minimum and maximum values determined by subtracting/adding the standard deviation. Logistic curve min or max temperature threshold. Straight line model indicated by X value, (+) increasing or (-) decreasing with temperature.  
$^e$ Standard deviation of the gaussian and generalised bell curve models.  
$^f$ Standard error of the temperature threshold. Gaussian and generalised bell curve models’ error are additive of the Centre point and SD errors.
4.5. Discussion

The Queensland coastline showed defined temperature differences between the southern areas (Gold and Sunshine Coasts), mid (Mackay) and the northern areas (Townsville and Cairns) in mean monthly SST (Figure 4-1). Monthly temperature means showed a delay in seasonal SST between the northern and southern areas. The SST in the northern areas warmed around approximately one month before the southern areas. This temperature delay may be due to the ramping time of the EAC before its effects are seen in the southern areas (Figure 4-2), effectively delaying temperature influenced movement of sharks. Occurrences of both hammerhead species showed no response to SST in both northern areas, and typically, both species are caught throughout the year in small numbers. The mean monthly SST in the northern areas was always higher than 22 °C and suggests this is warm enough year-round for hammerhead occurrence. A strong thermal niche indicated that the scalloped hammerhead preferred warmer waters and occurred mostly during the months with SST > 20 °C. The thermal niche in Mackay was also a 5 °C range, warmer than southern areas, which may be a result of the number of sampling points at this wave rider buoy or intrusions of warmer waters from irregularities in the EAC.

Little environmental information exists for the great hammerhead apart from this species preferring warmer waters. In this study, we were able to determine that great hammerhead sharks are less likely to be caught when sea surface temperatures are below 20 °C in the southern areas. Hammerschlag et al. (2011) suggested that a tagged great hammerhead off the northwest Atlantic followed the northeast pathway of the Gulf Stream where SST average 21.9 °C and nearshore waters were < 18 °C during the same tracking period. This information fits with the lower thermal limit determined in this study. This pattern of great hammerheads utilising offshore warmer boundary current waters during cooler months would be expected along the Queensland Coast, as the EAC waters can reach up to 5 °C warmer than surrounding waters during cooler months. Movement of the EAC can also change due to formation of localised eddies off the Gold Coast, either bringing warmer waters closer to the shore or pushing warm waters off the coast (Cresswell et al. 2016, Azis Ismail et al. 2017).

Tiger sharks showed high occurrences in northern areas during winter and decreased as SST increased above the thermal limit of (27 °C). As the northern SST approached the thermal limit, catches decreased but started to increase in southern areas two months late as SST rose in those areas. A similar trend was seen by Payne et al. (2018) where the highest catches of tiger sharks occurred at a mean SST of
22 °C, along the east coast of Australia. This occurred in the southern most areas when SST were warmer and peaked in the northern areas during cooler months. In this study, we determined a wide thermal response for the tiger shark occurrence and a similar thermal preference; however, our study determined tiger shark catches occurred over an optimal range between 18.5 – 26.9 °C. Movement of tiger sharks was demonstrated by Holmes et al. (2014) and Werry et al. (2014) where tiger sharks remained in warmer surface waters ranging from 18 – 28 °C. Similarly, in this study, the thermal niche we determined in the quantile regression where the majority of catches occurred within 20-23 °C.

Bull sharks are common along the east Australian coastline migrating along the coast and frequenting estuarine habitats (Werry et al. 2011, Haig et al. 2018). Thermal ranges determined in this study showed the bull shark can tolerate a range of temperatures with the majority of catches occurring between 20 – 26 °C in southern QLD and up to 30°C in Townsville. Though bull sharks were always present in the northern areas, bull shark occurrences at the Gold and Sunshine Coasts were between 20 – 24 °C during Autumn, with lower occurrence at SST < 20 °C. Our results determined an optimal thermal range compared to Lee et al. (2019) where the highest probability of shark abundance was at 24 °C.

The EAC also interacts in southeast Queensland to form the cyclonic Fraser Gyre, which transports nutrient rich shelf waters towards to coast influencing biodiversity (Azis Ismail et al. 2017). The seasonality of the EAC is more prominent in the southern Queensland areas which experience cooler ocean temperatures and warmed by the autumn-summer EAC flow and cooled through winter. However, short-term oceanic conditions can generate favourable up-welling conditions in these areas increasing biological productivity and bringing cooler waters onto the shelf waters, even during summer periods (Cresswell et al. 2016, Spencer et al. 2019). These changes may also have a localised driving effect on shark occurrence by altering local water temperatures, though more direct studies detailing this are needed.

In Queensland, the EAC can dramatically change the thermal environment of coastal waters through upwelling, eddy formations and seasonal flow. The long-term average annual SST showed cooler SST in the southern QLD areas but can experience maximum SST up to 25 °C. Townsville showed lower variability in SST annually and most species showed no variability due to temperature, except for the bull shark.
Northern areas are located within the Great Barrier Reef and closer to shore, whereas southern sites do not have a complex barrier reef system and are more exposed to EAC variability by eddies and wind driven events, which may alter the SST within these areas in each month, further influencing monthly catches of sharks. For example, between Moreton and Fraser Islands (Brisbane and Hervey Bay), a recently described gyre, The Fraser Gyre, induces upwelling events by bringing cool shelf waters closer to the coast, changing chlorophyll levels and effecting biodiversity; therefore, it is reasonable this may influence shark movement around these areas (Brieva et al. 2015, Azis Ismail et al. 2017). More recently, SEQ marine areas are exposed to marine heat waves lasting up to 64 days which may increase with increased climatic change (Heidemann and Ribbe 2019).

The aim of this study was to describe thermal niches of five large sharks along the east coast of Queensland using the sea surface temperature shark catches in the QSCP. Quantile regression was used to model the response of the highest quantile in catch data to predict the thermal limits. The results showed that catches of both hammerhead shark species were more likely in SST above 20 °C and below 28 °C. We also determined catches of white sharks were likely up to a maximum SST of 23.4 °C in SEQ, several degree’s warmer than previous studies. Tiger and bull sharks showed a wider optimal thermal range of 20°C – 30 °C.

4.6. Funding

The study was funding by the Queensland Department of Agriculture and Fisheries (DAF), Queensland Australia, as part of the project “Hammerhead Sharks of southeast Queensland”.

4.7. References


Brieva, D., et al. (2015). "Is the East Australian Current causing a marine ecological hot-spot and an important fisheries near Fraser Island, Australia?" Estuarine, Coastal and Shelf Science 153: 121-134.


4.8. Supplementary material

supplementary 1. Quantile regression models for each species catch with SST caught at the Gold Coast.
supplementary 2. Quantile regression models for each species catch with SST caught at the Sunshine Coast.
supplementary 3. Quantile regression models for each species catch with SST caught at Mackay.

supplementary 4. Quantile regression models for each species catch with SST caught at Townsville.
supplementary 5. Quantile regression models for each species catch with SST caught at Cairns.
5. Resource overlap among hammerhead sharks and sympatric large sharks off eastern Australia

This chapter is a co-authored paper that has been reformatted for this thesis. The bibliographic details /status of the co-authored paper, including all authors, are:

5.1. Abstract

Large shark species commonly coexist and often share food-web resources, which may further strain already declining shark populations. Both scalloped (*Sphyrna lewini*) and great (*Sphyrna mokarran*) hammerhead shark coexist in the coastal waters of southeast Queensland, Australia, and competition for resources between hammerheads and other large sharks is poorly understood. To address this, we sampled multiple tissues from scalloped (*n* = 17) and great (*n* = 8) hammerheads, tiger (*Galeocerdo cuvier*, *n* = 8), white (*Carcharodon carcharias*, *n* = 8) and bull (*Carcharhinus leucas*, *n* = 3) sharks caught in the Gold Coast Shark Control Program. Stable isotope analysis of δ$^{13}$C and δ$^{15}$N was then used to determine isotope resource overlaps, dietary changes and any ontogenetic shifts determined between tissue types. Our results suggested both hammerheads undertook a seasonal dietary shift, however scalloped hammerhead utilised a wider δ$^{13}$C and lower δ$^{15}$N than the more specialised great hammerhead. Longer-term patterns inferred both hammerheads shared similar coastal resources where great hammerhead shared 69% of scalloped hammerhead isotopic space. All large sharks displayed seasonal δ$^{13}$C dietary changes with hammerheads and also showed consistent resource overlap. Tiger shark feed at a lower δ$^{15}$N overlapping mostly with both hammerhead sharks. White and bull sharks competed with hammerhead sharks at higher δ$^{15}$N. Overall, results of this study suggest both hammerhead sharks compete for resources between themselves and with other large co-existing sharks throughout their seasonal dietary shifts. Hammerheads also overlap more with bull and tiger sharks during spring and summer, and white sharks in spring. Isotope overlaps showed both hammerhead shark species competed for resources in eastern Australian waters.
5.2. Introduction

Large sharks play an important ecological role as apex predators in marine habitats, from inshore coastal systems (Sievers et al., 2019) to oceanic environments (Queiroz et al., 2019). Hammerhead sharks have been recognised as declining globally yet ecological data in the southern hemisphere remains deficient (Gallagher and Klimley, 2018). Southeast Queensland (SEQ), Australia, is home to many threatened shark species, including several listed on the IUCN Red List: *Carcharhinus leucas* (bull shark), *Sphyrna mokarran* (great hammerhead), *Sphyrna lewini* (scalloped hammerhead) and *Carcharodon carcharias* (white shark). Of these species, only white shark is listed as vulnerable in Australian legislation (EPBC, 1999), and thus is offered some level of protection. Other shark species, including the globally endangered hammerhead species, remain at risk from both commercial, recreational and illegal fishing pressures (Gallagher et al., 2014; Queiroz et al., 2019).

Scalloped hammerhead is an apex predator that feeds on benthic and higher order prey throughout coastal and pelagic habitats (Torres-Rojas et al., 2010; Galván-Magaña et al., 2013a; Rojas et al., 2014; Torres Rojas et al., 2015). In the Americas, scalloped hammerheads exhibit ontogenetic diet shifts when they migrate to pelagic habitats at maturity (Klimley and Nelson, 1984; Klimley, 1987; Klimley et al., 1988). Although top predators overlap spatially, scalloped hammerhead was found to partition food resources with both bonnethead shark (*Sphyrna tiburo*) (Bethea et al. 2011) and silky shark (*Carcharhinus falciformis*) (Estupinan-Montano et al. 2017) by occupying a higher trophic position.

Ontogenetic habitat shifts are common in large sharks and are often driven by a change in prey requirements, for example, juvenile sharks moving from hunting smaller prey in inshore estuarine habitats to hunting larger fish in offshore, pelagic habitats as they grow (Werry et al., 2011). Scalloped hammerhead sharks and bull sharks utilise similar habitats and prey across the estuarine-marine continuum, potentially placing them in direct competition for food resources at different times. Great hammerhead shark utilises nearshore and shelf habitats (Hammerschlag et al., 2011; Calich et al., 2018) potentially sharing food resources with other large shark species, such as tiger shark (*Galeocerdo cuvier*) and great white (Heithaus et al., 2002; Heithaus et al., 2007; Matich et al., 2010; Matich and Heithaus, 2014; Meyer et al., 2017). Though it’s not clear if access to food resources are partitioned in space, species or time. Understanding the resource use patterns and determining where, and if, direct
competition is occurring between endangered hammerhead sharks and other large shark species will be important information to assist in large shark conservation strategies.

In Queensland, Australia, scalloped and great hammerhead shark occur along the extent of the coastline, with seasonal patchiness in their occurrence patterns (Noriega et al. 2011). Within southern Queensland, scalloped and great hammerheads coexist with numerous large predatory shark species (Taylor et al., 2011; Haig et al., 2018; Roff et al., 2018; Werry et al., 2018; Sievers et al., 2019). In New South Wales, great hammerhead primarily predates on rays and shark species spanning coastal and pelagic environments (Raoult et al., 2019). Yet information on feeding patterns of hammerhead sharks coexisting with other large predatory species is lacking and both large hammerhead species (scalloped hammerhead and great hammerhead) are present in QLD waters and experiencing population declines (Roff et al., 2018).

Stable Isotope Analysis (SIA) is an established method used to determine patterns in various isotopes within tissues. Carbon (C\text{\textsuperscript{14}} to C\text{\textsuperscript{13}}) and Nitrogen (N\text{\textsuperscript{15}} to N\text{\textsuperscript{14}}) isotopes fractionate at different rates and vary between species; displaying distinct signatures between freshwater, estuarine and pelagic habitats. Nitrogen increases with trophic level, hence information on the trophic position and carbon signatures are enriched in estuarine habitats and depleted in oceanic habitats, therefore nitrogen isotopes can inform of habitat use and movement patterns. For this reason, stable isotopes are used to determine ontogenetic and seasonal dietary shifts, indicating habitat change with age for large sharks (MacNeil et al., 2005; Werry et al., 2011; Estupiñán-Montaño et al., 2019).

Isotope analysis of multiple tissue types from an individual shark is useful as δ\text{\textsuperscript{13}}C and δ\text{\textsuperscript{15}}N turnover rates vary between tissues. This variable turnover between tissues is used to determine ontogenetic dietary shifts or seasonal migration patterns in large sharks. Fast turn over tissues (blood and liver) can indicate days to weeks, slow turn over tissue (muscle) indicate months to one year and very slow turn over tissues (cartilage and fin) describe >1 year but are biased to juvenile feeding habits (Hobson and Clark, 1992; MacNeil et al., 2005; Malpica-Cruz et al., 2012). When isotope data is compared between species, caught from similar locations at the same time, it is possible to determine if species are in direct competition for similar food resources. This knowledge may be useful to understand the drivers behind changes in shark behaviour or migration; when the prey and the abundance of those particular prey items are also known.
Hammerhead sharks show different seasonal movements compared to white sharks therefore spatial sharing of dietary resources would occur for a limited time period. Hammerhead sharks are also bottom feeders exploiting different prey resources compared to other large sharks including tiger and white sharks. However, great and scalloped hammerheads share similar seasonal patterns and habitats and are more likely to compete for prey over longer periods of time. This study uses $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis to investigate the dietary resource partitioning between scalloped and great hammerhead sharks and other co-existing large shark species. We test the hypotheses that hammerhead sharks undertake dietary shift over time and exhibit dietary overlap with other large sharks which varies temporally.

5.3. Materials and Methods

5.3.1. Study site

Gold Coast is a coastal city located within southeast Queensland, Australia (Figure 5-1). Throughout this area there is an abundance of coastal wetlands, some of international significance (Ramsar, https://www.ramsar.org/). Moreton Bay and the Gold Coast Broadwater are semi-enclosed bays, which open to the Pacific Ocean and are part of the Moreton Bay Marine Park. Being tidal, the Broadwater ebbing flow transfers estuarine water offshore through several open coastal bars along the coastline, connecting oceanic and estuarine habitats. The connectivity (via movement of both water and animals) between the coastal wetlands, shallow water environments and open ocean, supports marine biodiversity and the survival of higher order species, such as sharks and rays.

Since the early 1960’s, the Queensland Government has deployed 27 surface gill nets and 383 baited drumlines along the length of the east coast of Queensland to control shark numbers (known as the Queensland Shark Control Program (QSCP) (Sumpton et al., 2011). QSCP gear has remained permanently in place and only removed for short periods of time due to harsh weather events. Surface gill nets are 182 m long by 6 m deep and are comprised of a 50 cm mesh net, held at the surface by a floating headline and three A3 polypropylene floats. Each net is stretched and anchored at each end by a 32 Kg Danforth of Clyde Quick Release anchors. Each net was set ~500 m from and orientated parallel to the shoreline in 5 and 12 m of water. Baited drumlines consisted of a single A3 float with a baited hook suspended by 2 m of galvanised chain. The A3 float is connected to rope and two smaller floats to keep the hook away from the Danforth anchor. Contractors collect daily logs and record
species information (e.g. total length, species and sex) and species identification was considered reliable since 1996 following identification training. This information was then used to determine the long-term monthly, raw total catch numbers for each shark species and estimate probable temporal overlap of species catches within the Gold Coast area.

Figure 5-1. Location of the Queensland Shark Control Program equipment throughout the coastlines of Gold Coast, Australia.
Using opportunistic sampling of deceased sharks caught in the QSCP between 2013 and 2019; samples of three tissue types (i.e. liver, muscle and cartilage) were collected from five species of pelagic sharks caught in southeast Queensland. Species sampled included white shark (*Carcharodon carcharias*), tiger shark (*Galeocerdo cuvier*), great hammerhead (*Sphyrna mokarran*), scalloped hammerhead (*Sphyrna lewini*) and bull shark (*Carcharhinus leucas*) caught between 2013 and 2019. Benthic primary producers and prey samples were obtained within the SEQ regions from rivers to offshore waters. Each shark caught in the QSCP was measured for total length (TL), sex, condition, date and location. Tissue samples of liver (centre), white muscle (lateral), cartilage and dorsal fin were taken, placed into separate sealed bags and frozen at -20 °C until processed. Fish species were caught and collected from representative locations of river (Blue catfish, *Neoarius graeffei*), estuarine (Sea mullet, *Mugil cephalus*, Estuarine stingray, *Dasyatis fluviorum*, Common pike eel, *Muraenesox bagio*) and marine (Tregalin, *Atractoscion aequidens*, Mackeral Tuna, *Euthynnus affinis*, and Snapper, *Pagrus auratus*) habitats. Seagrass samples were also taken at ten locations from the Gold Coast Broadwater to Moreton Bay, and pooled together. Long-term sea surface temperature (SST) was also calculated from hourly SST data collected from the Tweed wave rider buoy (https://www.qld.gov.au/environment/coasts-waterways/beach/monitoring/waves-sites/).

### 5.3.2. Stable isotope analysis

Shark muscle and liver samples were cut into fine pieces, and cartilage samples were cleaned of remaining tissues. Only muscle samples were used for prey fish species. Samples were then oven dried at 60 °C for 24hrs before being ground into a fine powder. Lipid extraction was carried out on all samples to reduce the influence of lipids by agitating samples in 2:1 chloroform/methanol for 24hrs, drained and dried at 60 °C for 24hrs. Only 1 mg of sample was used for δ¹³C and δ¹⁵N measurements. SIA was carried out on an elemental analyser (Europa EA-GSL, Sercon) coupled to an isotope ratio mass spectrometer (Hydra 20-22, Sercon) at the stable isotope laboratory, Griffith University. Vienna PeeDee Belemnite (VPDB) and atmospheric air (AIR) were used as standards for C, and N, respectively. Stable isotope values are reported in δ-notation (‰), i.e. δ¹³C or δ¹⁵N = (R_sample/R_standard - 1) x 1000, where R is respectively ¹³C/¹²C or ¹⁵N/¹⁴N. Elemental compositions (%C and %N) of samples were also generated. The C:N ratio of each sample was checked if lipids were removed. Mathematical corrections were carried out on samples that still showed a C:N ratio higher than 3.5 to estimate lipid free δ¹³C following the method described by Fry (2002) and Skinner et al. (2016).
5.3.3. Statistical analysis

Isotopic niche is defined as an area in $\delta$-space with $\delta$-values as coordinates (Newsome et al., 2007) effectively creating a measurable area. Isotopic niche and overlap between shark species were estimated using SIBER (Stable Isotope Bayesian Ellipses in R, (Jackson et al., 2011)) from the SIAR (Stable Isotope Analysis) package in R. SIBER statistics were produced from estimates of corrected standard ellipse areas (SEAc, $\%\delta^2$) and total area (TA, $\%\delta^2$) of ellipse area.

Significance in shark total length versus nitrogen and carbon isotope values was tested using linear regression analysis in R for each tissue type. One-way Analysis of Variance (ANOVA) was used to determine if there was a significant difference in carbon and nitrogen values between species, tissue type or sex using the statistical package SigmaPlot 13 (SysStats). Temporal overlap for each species was determined by calculating the catch per month greater than 30% of the maximum monthly catch for that species (Table 5-3). Months of each species where catch was greater than 30% of the maximum monthly catch were used to compare months of species occurrence overlap (Table 5-4).

Table 5-1. Long-term catch overlap of shark species per month since 1996. X indicates presence in the Gold Coast QSCP catches $\geq$ 30% of the maximum total catch of that species occurred. 0 indicates $\leq$ 30 % of total catch occurred. Colours indicate season, where summer = red; autumn = orange; winter = blue and spring = yellow.

<table>
<thead>
<tr>
<th>Month</th>
<th>Bull shark</th>
<th>Scalloped Hammerhead</th>
<th>Great Hammerhead</th>
<th>Tiger shark</th>
<th>White shark</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>0</td>
</tr>
<tr>
<td>February</td>
<td>X</td>
<td>0</td>
<td>X</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>March</td>
<td>X</td>
<td>0</td>
<td>0</td>
<td>X</td>
<td>0</td>
</tr>
<tr>
<td>April</td>
<td>X</td>
<td>0</td>
<td>0</td>
<td>X</td>
<td>0</td>
</tr>
<tr>
<td>May</td>
<td>X</td>
<td>0</td>
<td>X</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>June</td>
<td>X</td>
<td>0</td>
<td>0</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>July</td>
<td>X</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>X</td>
</tr>
<tr>
<td>August</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>X</td>
</tr>
<tr>
<td>September</td>
<td>0</td>
<td>X</td>
<td>0</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>October</td>
<td>X</td>
<td>X</td>
<td>0</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>November</td>
<td>0</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>December</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 5-2. Percentage of shark species catches from the QSCP since 1996 which estimate possible overlap in the coastal waters adjacent to the Gold Coast, Queensland. (BS – bull shark, GH – great hammerhead, SH – scalloped hammerhead, TS – tiger shark, WS – white shark).

<table>
<thead>
<tr>
<th></th>
<th>BS</th>
<th>GH</th>
<th>SH</th>
<th>TS</th>
<th>WS</th>
</tr>
</thead>
<tbody>
<tr>
<td>BS</td>
<td>44</td>
<td>44</td>
<td>67</td>
<td>33</td>
<td></td>
</tr>
<tr>
<td>GH</td>
<td>80</td>
<td>60</td>
<td>83</td>
<td>20</td>
<td></td>
</tr>
<tr>
<td>SH</td>
<td>67</td>
<td>50</td>
<td>67</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TS</td>
<td>75</td>
<td>38</td>
<td>63</td>
<td></td>
<td></td>
</tr>
<tr>
<td>WS</td>
<td>50</td>
<td>33</td>
<td>67</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

5.3.4. Ethics statement

This study was carried out in accordance with the principals of a General Fisheries permit issued by the Department of Agriculture and Fisheries (194795) Queensland, Australia. The protocol was approved by Griffith University Animal Ethics Committee (ENG/01/15/AEC).

5.4. Results

A total of 39 samples were collected from five shark species collected from the QSCP (bull shark = 3, great hammerhead = 8, scalloped hammerhead = 17, tiger shark = 9, white shark = 8), and samples of liver, muscle and cartilage were collected (Table 5-1). Muscle samples from common pelagic (n = 12), estuarine (n = 9) prey species and seagrass (n = 10) were also taken (Table 5-2). Sharks maturity levels ranged from sub-adult to adult for most species varying in sizes from 1.2 m (TL) to 3.65 m (TL) and were sampled throughout the year (Figure 5-1). Catches of each shark species in the Gold Coast QSCP fluctuated monthly between 1996 – February 2019 but were usually caught through the year and approximate periods of higher catches can be seen (Figure 5-2). Scalloped, great and tiger shark catches were highest in the Austral summer and a secondary smaller peak before winter, whereas white shark catches were highest during the austral winter. Between the warmer water periods (months November-May) and cooler water periods (months June-October), seasonal co-occurrences were evident for all species except white shark, which declined in the warmer period.
Table 5-3. Isotopic compositions (‰ mean ± SD, range) and size (m mean ± SD, range) of sharks.

<table>
<thead>
<tr>
<th>Species</th>
<th>Liver δ¹³C</th>
<th>Liver δ¹⁵N</th>
<th>Muscle δ¹³C</th>
<th>Muscle δ¹⁵N</th>
<th>Cartilage δ¹³C</th>
<th>Cartilage δ¹⁵N</th>
<th>Size</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Carcharhinus leucas</em></td>
<td>-20.8 ± 4.4</td>
<td>11.9 ± 0.3</td>
<td>-17.2 ± 0.8</td>
<td>13.5 ± 0.6</td>
<td></td>
<td></td>
<td>3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(-17.7 - 24.0)</td>
<td>(11.7 - 12.2)</td>
<td>(-18.2 - 16.7)</td>
<td>(12.9 - 14.1)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Sphyra mokarran</em></td>
<td>-20.0 ± 0.7</td>
<td>13.0 ± 2.9</td>
<td>-16.5 ± 0.8</td>
<td>12.5 ± 1.3</td>
<td>-14.6 ± 1.6</td>
<td>10.8 ± 1.9</td>
<td>2.81 ± 0.98</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>(-21.4 - 19.3)</td>
<td>(10.6 - 18.9)</td>
<td>(-17.4 - 15.2)</td>
<td>(11.1 - 13.8)</td>
<td>(-16.5 - 12.7)</td>
<td>(8.4 - 13.3)</td>
<td>(2.0 - 2.49)</td>
<td></td>
</tr>
<tr>
<td><em>Sphyra lewini</em></td>
<td>-20.6 ± 3.3</td>
<td>13.0 ± 1.6</td>
<td>-16.9 ± 0.5</td>
<td>13.3 ± 1.0</td>
<td>-15.2 ± 1.4</td>
<td>11.9 ± 1.8</td>
<td>1.59 ± 0.33</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>(-23.9 - 13.6)</td>
<td>(9.2 - 15.0)</td>
<td>(-18.0 - 16.1)</td>
<td>(12.3 - 15.1)</td>
<td>(-18.4 - 13.1)</td>
<td>(8.8 - 15.2)</td>
<td>(1.2 - 2.39)</td>
<td></td>
</tr>
<tr>
<td><em>Galeocerdo curvier</em></td>
<td>-20.2 ± 2.5</td>
<td>13.3 ± 1.1</td>
<td>-16.5 ± 1.3</td>
<td>11.3 ± 0.7</td>
<td>-15.4 ± 2.6</td>
<td>11.4 ± 1.3</td>
<td>2.64 ± 0.67</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>(-25.0 - 17.7)</td>
<td>(10.1 - 13.5)</td>
<td>(-18.3 - 14.8)</td>
<td>(10.2 - 12.3)</td>
<td>(-19.0 - 12.5)</td>
<td>(9.9 - 14.0)</td>
<td>(1.9 - 3.65)</td>
<td></td>
</tr>
<tr>
<td><em>Carcharodon carcharias</em></td>
<td>-18.4 ± 3.0</td>
<td>13.4 ± 0.6</td>
<td>-17.1 ± 0.6</td>
<td>13.2 ± 1.1</td>
<td>-16.0 ± 0.9</td>
<td>12.6 ± 0.9</td>
<td>2.75 ± 0.37</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>(-21.9 - 14.6)</td>
<td>(12.8 - 14.2)</td>
<td>(-18.0 - 16.2)</td>
<td>(11.5 - 14.7)</td>
<td>(-14.9 - 15.1)</td>
<td>(11.3 - 14.2)</td>
<td>(2.1 - 3.2)</td>
<td></td>
</tr>
</tbody>
</table>

Table 5-4. Isotope composition and metrics of common prey and seagrass from southeast Queensland.

<table>
<thead>
<tr>
<th>Common prey muscle</th>
<th>Number</th>
<th>δ¹³C</th>
<th>δ¹⁵N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pelagic Fish</td>
<td>8</td>
<td>-17.2 ± 0.4</td>
<td>12.5 ± 0.7</td>
</tr>
<tr>
<td>Catfish</td>
<td>3</td>
<td>-20.2 ± 0.3</td>
<td>13.0 ± 0.26</td>
</tr>
<tr>
<td>Estuarine ray</td>
<td>3</td>
<td>-17.0 ± 0.4</td>
<td>11.4 ± 0.4</td>
</tr>
<tr>
<td>Eel</td>
<td>3</td>
<td>-16.2 ± 1.4</td>
<td>11.0 ± 0.5</td>
</tr>
<tr>
<td>Sea Mullet</td>
<td>4</td>
<td>-15.3 ± 1.8</td>
<td>9.3 ± 1.3</td>
</tr>
<tr>
<td>Seagrass</td>
<td>10</td>
<td>-11.8 ± 2.5</td>
<td>3.2 ± 1.6</td>
</tr>
</tbody>
</table>
Catches of hammerhead species appear to increase during the same seasons; though scalloped hammerheads were consistently caught in greater numbers (Noriega et al., 2011), compared to great hammerhead sharks. Overlap in temporal occurrence was higher during spring and summer for most species except white shark which was caught during winter and spring. Tiger and bull sharks were caught throughout the year compared to hammerhead species which were only caught between spring and summer. Temporal overlap of hammerhead catches showed great hammerhead occurred mostly with bull shark (80%, summer), scalloped and tiger shark overlapped 60% of great hammerhead occurrence during summer and spring. Scalloped hammerhead sharks occurred most of the year with tiger shark (83%, summer and spring) and 67% with bull (summer) and white (winter and spring) shark.

Scalloped and great hammerheads co-occurred in catches 50% of the time during the summer months. Tiger sharks were caught throughout most of the year with bull (summer and autumn) and scalloped hammerhead (summer and spring) shark being present 75% and 63% of the same time. White shark
occupied the same area evenly with scalloped hammerhead (spring) and tiger (winter and spring) shark (67%) and bull shark occurred 50% of the time during winter.

5.4.1. Stable Isotopes

Ellipses of all shark and prey muscle suggest estuarine sea mullet and sea grass do not constitute shark diet however, coastal eel, ray and pelagic fish (snapper and tunas) overlap with all shark species (Table 5-1 and 5-2). Liver was the most $^{13}$C depleted (-20 ‰) compared to longer-term muscle (-17 ‰) and cartilage (-15 ‰). Total ellipse area (TA) was highest for scalloped hammerhead (liver, 34.42 ‰) and the least for great hammerhead and white shark (6.75 ‰ and 4.97 ‰, respectively) (Table 5-5). TA were similar across all shark species for muscle and cartilage and showed the highest TA of all three tissue types for all shark species. White shark constantly showed the lowest total area across all tissue types (Table 5-6).
Figure 5-3. Stable isotope ellipses of shark liver (a), shark muscle (b) and shark cartilage (c). Each tissue type is representative of a different time period, liver (recent) to cartilage (years).
Liver $\delta^{13}C$ showed scalloped hammerhead varied the most ($\Delta^{13}C = 10.3 \%$) and great hammerhead varied the least ($\Delta^{13}C = 2.1 \%$), other shark species showed less variations in liver $\delta^{13}C$ (Figure 5-3). Liver $\delta^{15}N$ showed high trophic variability for great hammerhead ($\Delta^{15}N = 8.3 \%$) and scalloped hammerhead ($\Delta^{15}N = 5.8 \%$), whereas the bull and white shark showed the least variation ($\Delta^{15}N = 0.5 \%$ and $\Delta^{15}N = 1.4 \%$). Muscle $\delta^{15}N$ varied less for both hammerhead species but white shark showed the highest variation and bull shark varied the least ($\Delta^{15}N = 3.2 \%$ and $0.5 \%$, Figure 5-3.)

Great hammerhead liver overlapped mostly with scalloped hammerhead (57.49 %) and tiger shark (37.35 %) for most of its lower trophic $\delta^{15}N$ range, while 24.61 % was overlapped with the white shark at higher trophic positions (Figure 5-3). Scalloped hammerhead overlapped 84.09 % of tiger shark isotopic niche and tiger shark overlapped 48.71 % of scalloped hammerhead. White shark overlapped predominantly with scalloped hammerhead (35 %) and great hammerhead (18 %).

Muscle $\delta^{13}C$ showed a shift of $+4 \%$ from liver for all sharks (Figure 5-3). Tiger shark had the widest $\delta^{13}C$ range ($\Delta^{13}C = 3.5 \%$) followed by great hammerhead ($\Delta^{13}C = 2.2 \%$). White shark and scalloped hammerhead showed a narrow $\delta^{13}C$ range ($\Delta^{13}C = 1.8 \%$ and 1.9 %). Muscle $\delta^{15}N$ indicated the tiger shark predated on the lowest trophic group compared to white and great hammerhead, which predated on the highest range of trophic groups. Out of the prey species, tiger and great hammerhead sharks

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Table 5-5. Ellipses metrics for each tissue samples, liver (A), muscle (B) and cartilage (C). (TA = total area; SEA = standard ellipse areas; SEAc = standard ellipse areas corrected).

<table>
<thead>
<tr>
<th></th>
<th>Tiger shark</th>
<th>Great hammerhead</th>
<th>Scalloped hammerhead</th>
<th>White shark</th>
<th>Bull shark</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TA</td>
<td>11.48</td>
<td>6.75</td>
<td>34.42</td>
<td>4.97</td>
<td></td>
</tr>
<tr>
<td>SEA</td>
<td>8.07</td>
<td>4.84</td>
<td>15.33</td>
<td>5.30</td>
<td></td>
</tr>
<tr>
<td>SEAc</td>
<td>9.68</td>
<td>5.81</td>
<td>16.72</td>
<td>7.95</td>
<td></td>
</tr>
<tr>
<td>B</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TA</td>
<td>4.75</td>
<td>3.08</td>
<td>3.57</td>
<td>2.4</td>
<td>0.41</td>
</tr>
<tr>
<td>SEA</td>
<td>2.42</td>
<td>3.16</td>
<td>1.54</td>
<td>1.62</td>
<td>0.74</td>
</tr>
<tr>
<td>SEAc</td>
<td>2.83</td>
<td>4.21</td>
<td>1.65</td>
<td>2.02</td>
<td>1.49</td>
</tr>
<tr>
<td>C</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TA</td>
<td>14.9</td>
<td>13.58</td>
<td>12.18</td>
<td>4.19</td>
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</tr>
<tr>
<td>SEA</td>
<td>8.86</td>
<td>7.83</td>
<td>4.99</td>
<td>2.54</td>
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<tr>
<td>SEAc</td>
<td>10.34</td>
<td>9.13</td>
<td>5.44</td>
<td>3.05</td>
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</tr>
</tbody>
</table>
overlapped with coastal eel and ray species, where scalloped hammerhead, bull and white sharks overlapped more with pelagic fish species. Bull sharks were similar to white and scalloped hammerhead sharks. Resource overlap shows white sharks only overlap resources with great hammerhead (37.89 %), whereas great hammerhead isotopic niche was shared evenly with all species (Table 5-6). Scalloped hammerhead mostly overlapped with white (89.20 %) and great hammerhead (69.17 %).
Table 5-6. Percent of isotopic niche overlap of shark liver (A), muscle (B) and cartilage (C) tissues; representing different feeding periods over time, where liver < muscle < cartilage.

<table>
<thead>
<tr>
<th></th>
<th>Tiger shark</th>
<th>Great hammerhead</th>
<th>Scalloped hammerhead</th>
<th>White shark</th>
<th>Bull shark</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tiger shark</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Great hammerhead</td>
<td>37.35</td>
<td></td>
<td></td>
<td>24.61</td>
<td></td>
</tr>
<tr>
<td>Scalloped hammerhead</td>
<td>48.71</td>
<td></td>
<td></td>
<td>16.70</td>
<td></td>
</tr>
<tr>
<td>White shark</td>
<td>0.00</td>
<td>17.99</td>
<td></td>
<td>35.09</td>
<td></td>
</tr>
<tr>
<td>Bull shark</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>100.00</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Tiger shark</th>
<th>Great hammerhead</th>
<th>Scalloped hammerhead</th>
<th>White shark</th>
<th>Bull shark</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tiger shark</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Great hammerhead</td>
<td>25.43</td>
<td></td>
<td></td>
<td>24.94</td>
<td>17.34</td>
</tr>
<tr>
<td>Scalloped hammerhead</td>
<td>0.00</td>
<td>69.17</td>
<td></td>
<td>89.20</td>
<td>40.05</td>
</tr>
<tr>
<td>White shark</td>
<td>0.00</td>
<td>51.93</td>
<td>72.52</td>
<td></td>
<td>30.20</td>
</tr>
<tr>
<td>Bull shark</td>
<td>0.00</td>
<td>49.56</td>
<td>44.59</td>
<td>41.22</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Tiger shark</th>
<th>Great hammerhead</th>
<th>Scalloped hammerhead</th>
<th>White shark</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tiger shark</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Great hammerhead</td>
<td>70.87</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Scalloped hammerhead</td>
<td>75.00</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>White shark</td>
<td>63.63</td>
<td>29.49</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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Cartilage $\delta^{13}C$ showed the highest $\delta^{13}C$ enrichment (Table 5-1). Tiger sharks had the highest TA (14.8) followed by great hammerhead (13.58) where white shark has the smallest TA (4.18). Overlap was highest for great hammerhead and scalloped hammerhead with tiger sharks (70.87 \% and 75 \%). White sharks overlapped mostly with scalloped hammerhead and tiger sharks (73.79 \% and 63.63 \%). Great hammerhead $^{15}N$ showed predation on the lowest trophic prey sharing benthic prey with tiger and scalloped hammerhead sharks. The majority of tiger shark niche was shared with scalloped and great hammerheads (62.63 \% and 39.49 \%).

Muscle $\delta^{15}N$ ANOVA showed that tiger shark was significantly lower to scalloped hammerhead ($t = 4.843, P < 0.001$), white ($t = 3.725, P < 0.004$) and bull shark ($P = 0.019$). No differences were found between $\delta^{13}C$. Great hammerhead $\delta^{13}C$ liver showed significant difference to scalloped hammerhead ($Q = 3.898, P < 0.005$) and tiger shark ($Q = 3.175, P < 0.005$). Liver $\delta^{15}N$ showed differences between white and great hammerheads ($t = 41.857, P < 0.001$), scalloped hammerhead and great hammerheads ($t = 31.899, P < 0.001$), tiger and great hammerheads ($t = 31.262, P < 0.001$). Cartilage showed no statistical differences in $\delta^{13}C$ ($P = 0.217$) or $\delta^{15}N$ ($P = 0.444$) between species.

### 5.4.2. Isotope difference between tissue types

Differences between shark tissue types show a small enrichment of $\delta^{15}N$ in white shark liver over muscle (+0.3 \%), whereas scalloped hammerhead liver and cartilage were similarly $\delta^{15}N$ depleted over muscle (-1.4 \%). Great hammerhead liver was more depleted in $\delta^{15}N$ than tiger shark which was similar to muscle. However, great hammerhead cartilage was more depleted in $\delta^{15}N$ than muscle and liver, and at a steady state with scalloped hammerhead cartilage. There were significant differences between all shark species tissue $\delta^{13}C$ values, with cartilage being significantly enrichment in $\delta^{13}C$ to muscle and liver ($P = 0.001$), liver was significantly depleted in $\delta^{13}C$ across all species. All species tissue types were consistently different to muscle indicating possible dietary changes seasonally (Table 5-1).

### 5.4.3. Shark size and tissue stable isotopes

Linear regression analysis of shark $\delta^{13}C$ and $\delta^{15}N$ between tissue types and shark length (TL) was only significant for scalloped hammerhead $\delta^{13}C$ liver ($R^2 = 0.33, p = 0.04$) and muscle tissues ($p = 0.047$, $R^2 = 0.25$) indicating a positive relationship with depleted $\delta^{13}C$ source with increasing shark length (Figure 5-4). No significant relationships were found for any other shark species tissue types with $\delta^{15}N$
with length. Scalloped hammerhead liver tissues from sharks 1.6 m and smaller correlated with inshore δ¹³C (average = -22.4 ‰, river) whereas sharks 1.6 m and larger correlated more with an oceanic δ¹³C source (average = -16.5 ‰). Slower metabolic rate muscle values showed sharks 1.5 m and less correlated with narrower coastal δ¹³C (average = -17 ‰) and over 1.5 m changed by 1‰ (average = -16.6 ‰ to -17.3 ‰).

![Graphs showing correlation between total length and δ¹³C values for liver and muscle tissues.](image)

**Figure 5-4.** Significant linear regression results for scalloped hammerhead δ¹³C liver and muscle tissues with total shark length (TL).

### 5.5. Discussion

Large shark species frequent the eastern Australian coastal waters often at similar times, placing them in competition for resources and the potential for intra-species predation (Reid and Krogh, 1992; Noriega et al., 2011; Reid et al., 2011; Sumpton et al., 2011; Taylor et al., 2011; Roff et al., 2018). Multiple large shark species co-occurrence may drive individual large shark niche specialisation, however studies on resource sharing and dietary overlap are still under reported for many of these shark species in southeast Queensland (SEQ) waters. SEQ habitat is conducive to juvenile and adults of several shark species that utilise various habitats along the regional river-estuarine-marine continuum.

In this study, we reported five common large shark species to the SEQ that coexist seasonally and share prey resources most of the year (Figure 5-2). Great and scalloped hammerhead occur within the warmer months with tiger and bull sharks. Cooling water temperatures may trigger these species catch decline
coinciding with white shark increase in occurrence. Studies have also indicated that $\delta^{13}C$ values vary depending on oceanographic variables and latitude as upwelling events and proximity to deeper shelf waters can alter base carbon source (Oke and Middleton, 2000; Bird et al., 2018). SEQ has strong connections between inshore habitats and close shelf proximity and experiences upwelling events dominated by the east Australian current (Cresswell and Legeckis, 1986; Cresswell et al., 2016). These species of sharks are commonly observed and caught within all of these habitats (Werry et al.; Werry, 2010; Werry et al., 2014; Harasti et al., 2017; Haig et al., 2018; Zanella et al., 2019).

As these species are migratory and move over large distances, thus sampling multiple tissue type can help determine feeding habits over time, due to the varying metabolic turnover rates in relation to incorporating prey and habitat signatures (Bruce et al., 2006; Hammerschlag et al., 2011; Holmes et al., 2014; Werry et al., 2014; Queiroz et al., 2019). Our results show a substantial $\delta^{13}C$ shift for all shark species between tissue types likely suggesting changes in feeding habits over time. Our results also showed reliance on prey such as pelagic fish, eel and rays.

### 5.5.1. Hammerhead coexistence

Previous studies on hammerhead behaviour and resource use have described the foraging ecology of scalloped hammerhead, compared to smooth, bonnethead and other shark species (Torres-Rojas et al., 2010; Bethea et al., 2011; Galván-Magaña et al., 2013b; Rojas et al., 2014; Loor-Andrade et al., 2015; Torres Rojas et al., 2015; Estupinan-Montano et al., 2017). Our results show the first comparison of great hammerhead and scalloped hammerhead niche partitioning in SEQ waters and they shared isotopic space. Great hammerhead is the largest of the hammerhead species and fast turnover tissues indicated a strict $\delta^{13}C$ range reflecting predation on a higher trophic prey in the oceanic environments compared to scalloped hammerhead. Hammerhead liver tissue indicated both species predated in pelagic waters, however recent feeding by scalloped hammerhead sharks indicated a preference for benthic prey over a wider coastal-pelagic range compared to great hammerhead. Scalloped hammerhead sharks had the largest isotopic niche which overlapped 57.49% of great hammerhead’s more specialised niche. This overlap occurred at the lower trophic level of great hammerhead’s niche, suggesting that recent resource sharing only occurred on lower trophic levels between these species. Previous movement studies have shown scalloped hammerheads move from coastal to oceanic habitats around oceanic islands in diel patterns with frequent dives to 1000 m, presumably for foraging (Bessudo et al., 2011a; Bessudo et al., 2011b; Ketchum et al., 2014). These studies also showed
seasonal movement of scalloped hammerheads during cooler seasons to warmer waters which indicate a seasonal feeding transition. At Malpelo Island Colombia, scalloped hammerheads occur close to the coastline but were found to have a stronger oceanic signal (muscle $\delta^{13}C -16 \%$) suggesting feeding occurred further offshore rather than closer to the island. In our study however, scalloped hammerheads showed a lower $\delta^{15}N (13.3 \%)$ than scalloped hammerhead caught in Malpelo Island study (15.9\%) (Estupinan-Montano et al., 2017). Information on great hammerhead feeding behaviour is largely deficient compared to scalloped hammerhead, and dietary information comes from observations indicating a reliance on rays, teleosts and other shark species (Cliff, 1995; Mourier et al., 2013; Roemer et al., 2016). A recent study by Raoult et al. (2019) showed great hammerhead significantly preferred Australian cownose ray and the blacktip shark off the east coast of Australia, but liver samples suggested a small portion of sampled sharks fed on cephalopods and teleosts, spanning across coastal and pelagic environments.

The slow metabolite tissue (representing long-term patterns) cartilage showed scalloped hammerhead niche overlap of great hammerhead’s prey range was reduced by 30.32 %. This reduction in resource overlap can be attributed to great hammerhead feeding on different trophic prey than scalloped hammerheads. The isotopic niche area (SEAc) for scalloped hammerheads was reduced to a smaller isotopic niche compared to great hammerhead. This change suggests that over a longer time period (>1 year), scalloped hammerhead may undergo a dietary change, maybe due to seasonal cues. This change is reflected in $\delta^{13}C$, where liver (-20.6 \%) is greatly depleted compared to muscle (-16.9\%). This may represent a seasonal movement further offshore during winter periods, as the water cools and the influences of the warmer EAC current reduces to an offshore area. When the coastal waters warm, scalloped hammerhead return closer to the coast for pupping in shallow nursery grounds (Gustafson unpublished data). A similar trait is seen in the great hammerhead but to a lesser extent. Wells et al. (2018) satellite tagged 33 scalloped hammerheads in the Gulf of Mexico showing these sharks preferred areas closer to deep shelf waters. The northern and south ends of the Gold Coast are also close to deep shelf waters and may facilitate this movement, as sharks are often seen more during the warmer months.

Interestingly, long-term cartilage $\delta^{15}N (11.9\%)$ was similar to short-term liver $\delta^{15}N (11.9\%)$ indicating that scalloped hammerheads were consistently feeding on seasonal prey items over time and may represent juvenile seasonal feeding from coastal to oceanic habitats over a much longer time period.
(cartilage). Similarly, great hammerhead cartilage being much more depleted in $\delta^{15}$N than liver may also indicate nearshore-oceanic feeding during juvenile years, however more replicates are required to confirm these movements. Differences between tissues for $\delta^{13}$C show consistent enrichment of cartilage to muscle and liver and depletion in liver values for both hammerhead species. This consistent $\delta^{13}$C pattern suggests both species have a similar feeding behaviour between coastal and oceanic habitats. MacNeil et al. (2005) observed a similar trend between short-fin mako shark liver and muscle, suggesting that these differences may be due to a similar inshore dietary source. Further studies on the movement of hammerheads in this area is needed to determine the seasonal and ontogenetic feeding patterns of both species.

Surprisingly the length-$\delta^{13}$C relationship showed smaller scalloped hammerheads (< 1.5 m) were more depleted than larger sharks (> 1.5 m), whereas the opposite was expected. Given that the relationship was only weakly significant, the close proximity and flushing of oceanic waters may explain these values.

It was surprising that no relationship was found between $\delta^{15}$N and total length as smaller shark species tend to feed on lower order organisms, climbing the trophic ladder as they grow (Dicken et al., 2017; Matich et al., 2019; Raoult et al., 2019). Similarly, bull sharks show a unique and clear pattern of ontogenetic shift from estuarine to coastal environments as they grow in length and feed on higher trophic prey (Werry et al., 2011). However, tiger shark muscle showed a shift to enriched $\delta^{13}$C with increasing length, whereas fast turn over tissues showed the opposite, and may be due to a seasonal dietary shift (Ferreira et al., 2017). Our results show a similar pattern in both tissue types and is different to the $\delta^{13}$C depleted with increasing size we expected. This result may also be due to the relevant sizes of the sampled scalloped hammerhead, which included only a small number of larger sharks compared to shorter animals.

5.5.2. Hammerhead and other apex predators

Other large shark species inhabit SEQ with hammerhead sharks. Tiger and bull sharks occur year-round and catches peak during the spring and summer months (Figure 5-2). In contrast, peak catches of white sharks occur during the cooler months and declined as the waters begun to warm. Thus, all sharks co-occurred during spring and early summer. White sharks consistently inhabited a narrow isotopic area (Table 5-5).
Liver samples showed that in recent feeding events tiger sharks overlapped largely with scalloped hammerhead (84%), and since tiger shark is caught 83% of the time scalloped hammerheads are in the same area, a strong resource competition may exist between these species. Scalloped/great hammerhead overlap is lower (37.35%) and may be due to these two species potentially interacting only within several months of the year and indicating limited resource partitioning for lower trophic level prey during the summer months. Tiger shark is a known generalist feeding throughout the food web including birds, terrestrial and marine mammals and our result confirm previous studies that tiger sharks in SEQ occupy a lower trophic position compared to other large shark species with a wide coastal-oceanic distribution (Dicken et al., 2017; Ferreira et al., 2017). In our results, tiger sharks showed no substantial differences between all three tissue types suggesting a steady state feeding throughout the year. Over a longer period, muscle tissue showed the great hammerhead was the only species to overlap isotopic niche with tiger sharks (37.89‰) 60% of the time and is due to feeding at the same δ¹³C location but at the lower trophic level of great hammerheads, a similar pattern seen in liver.

These diet changes between species and differences in occurrence times indicates the possibility that hammerhead species coexisting with other large shark species and have high resource sharing in the summer and spring seasons and less for other periods. Further studies, including movement studies would provide more evidence into the resource use of multiple coexisting large sharks in the south eastern Queensland area.

5.6. Conclusions

Our results show the first comparison of the two largest hammerhead species which coexist in SEQ sharing dietary resources. Scalloped hammerheads showed a greater seasonal variability in feeding compared to great hammerhead which was more specialised to coastal mid to high trophic prey. During a seasonal shift, scalloped hammerhead predates mostly on lower trophic prey where great hammerhead exploited a larger prey range inshore. During this feeding period, both hammerhead species shared resources with tiger sharks and a lesser extent, white sharks. Over longer time periods, both hammerheads occupied a smaller oceanic-coastal niche where scalloped hammerhead specialised in higher trophic prey (teleosts and squid), competing with white and bull sharks. Great hammerhead shared benthic prey with tiger sharks and higher-level trophic fish species with scalloped hammerhead,
white and bull sharks. Resource interactions between species varied through the year with white sharks only occurring during cooler months, but other species interacted mostly during the warmer months. This indicates that resource competition occurs at different times of the year and these apex sharks may show seasonal dietary shifts which may be influenced by the seasonality of the EAC.

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5.9. References


6. General Discussion and Conclusion

6.1. Overview

The aims of my research were to determine baseline ecological information for threatened hammerhead shark species across juvenile and adult life-stages, that can be used by local and national governments. The structure and approach of the thesis aimed to reveal previously unknown ecological information of hammerhead sharks in Australia by using a whole of life-cycle approach. The thesis has identified previously unknown highly suitable areas for juvenile sharks and how they utilise habitat types within these areas. Furthermore, the thesis also investigated adult hammerhead shark occurrence and movement in northern and southern Queensland coastal waters driven by ocean temperatures in addition to their trophic ecology with other large shark species. Relevant agencies would be able to adapt current management strategies for effective protections, suitable regulations, as well as furthering the knowledge of hammerheads in Australia across juvenile and adult life-stages.

The research presented in this thesis outlines knowledge limitations regarding movement and habitat use (CHAPTER 1) from juvenile hammerheads. I determined the spatial distribution of suitable habitats (high, medium, and low) of juvenile scalloped hammerheads and the level of protection afforded to them in existing marine protected areas (MPAs) (CHAPTER 2). Fine-scale movements and behavioural state-switching was uncovered within high suitability habitats in south east Queensland, describing limited use of these areas and the first descriptions of diving behaviours of juvenile scalloped hammerheads sharks (CHAPTER 3). The research also characterised the thermal niche of hammerhead and co-existing large shark species to identify the likelihood of occurrence related to sea surface temperature (CHAPTER 4). In addition to these data, seasonal dietary shifts were identified for great and scalloped hammerheads and were found to have high resource overlap. Also identified was temporal overlap of resources with tiger (Galeocerdo cuvier), bull (Carcharhinus leucas) and white (Carcharodon carcharias) sharks along the south east coast of Queensland. Overall, mt results identified new habitat locations and resource overlap amount hammerhead shark species and co-existing large sharks in coast waters of Queensland, Australia (CHAPTER 5).

These predictive features could be used to model likelihood of interaction between sharks and human activities and provide valuable data in the development of non-lethal methods of shark protection to
humans. This General Discussion Chapter and Conclusion chapter acts as a summary of individual data chapters within this thesis and recommends future research to further understand the ecology of hammerhead sharks in the southern hemisphere. Although hammerhead species are considered critically endangered by the IUCN, they are still open to commercial fisheries as adults, and are not assigned a threatened status under Australian or Queensland legislation (Environmental Protection and Biodiversity Conservation Act or Nature Conservation Act). It is hoped that this work will contribute to the data required to increase protective measures over juvenile habitat, and adult populations.

6.2. Distribution of suitable juvenile scalloped hammerhead shark habitats

This study was the first to use MaxEnt modelling to determine suitable habitats for the scalloped hammerhead shark. Our results determined that highly suitable environmental parameters occurred in several places along the coast within shallow estuarine areas as well as nearshore coastal habitats. Our results further extend findings from previous studies on juvenile scalloped hammerheads movement, where sharks occurred in shallow coastal and estuarine habitats (Holland et al. 1992, Holland et al. 1993, Simpfendorfer and Milward 1993, Adams and Paperno 2007, Rosende-Pereiro and Corgos 2018, Zanella et al. 2019). These studies showed juvenile scalloped hammerheads utilised shallow, turbid areas of bays and coastlines that were connected by river openings. Similarly, juvenile white sharks were found to visit and reside within similar bay/estuarine systems in south east Australia, though reasons for their occurrence with the system is also still not well understood, but foraging has been hypothesised (Harasti et al. 2017, Sievers et al. 2019). Juvenile white sharks are larger than juvenile scalloped hammerheads therefore use of these sheltered areas are more likely to act as shelter from predation and water currents, as well as foraging grounds during developments. In addition, high turbidity within these estuarine areas may aid in predatory avoidance but allow the shark to predate more effectively on prey sources (Blaber and Blaber 1980, Sievers et al. 2019). The state-switching model (CHAPTER 3) showed foraging behaviours were more likely to occur near seagrass habitats, which are also prime habitats for a majority of small crustacea and fish species juvenile sharks have been found to predate on (Torres-Rojas et al. 2010, Torres Rojas et al. 2015, Zarco-Perello and Enríquez 2019). If these estuarine/bay environments are used by threatened juvenile shark species; conservation of these areas would contribute to species recovery by supporting juvenile recruits to make adulthood. Only 11% of highly suitable hammerhead shark habitat occurred within no-take MPAs; and although recreational fishing licences do not allow for the take of hammerhead species,
juveniles are at high risk of accidental and bycatch mortality in inshore net and line fishing. The intense effort and cost of conducting research on large mobile marine species results in a paucity of ecological data; which gives conservation managers little information to work with (Oh et al. 2017, Dwyer et al. 2020).

6.3. Fine-scale movements and state-switching

In chapter 3, I described the diving behaviours of juvenile scalloped hammerhead sharks using fine-scale acoustic tracking. Most sharks undertake vertical diving behaviours, exhibiting diel patterns and preference for certain depths (Queiroz et al. 2012, Andrzejaczek et al. 2018, Andrzejaczek et al. 2019, Coffey et al. 2020). My research found that juvenile scalloped hammerheads constantly performed multiple dives throughout the track, over deep and shallow waters. I described two dive patterns: A-type dives were characterised as a single long dive with multiple small vertical movements occurred on the bay floor; B-type dives were also characterised as a single long dive without the extra movements described in A-type dives. A-type dive has longer bottom times than B-type which generally lasted one-minute in SHH1. A-type diving occurred more frequently at the refuge point for SHH1 than B-type when compared to other areas of the track. SHH2 was found in a high tidal current area, and appeared to follow the tidal current, rather than swim against it. During the lower current speeds at the start of the track, the juvenile remained closer east and only started swimming west as the flood tide begun to flow. SHH2 also showed both dive patterns, but with longer bottom time and remained near the channel slope rather than in the middle. U-shaped dives in sandbar tiger sharks were related to foraging behaviours occurring over deep and shallow waters near dusk (Andrzejaczek et al. 2018), it is possible that juvenile scalloped hammerheads were foraging during these dives types due to bottom times. Though longer tracks would be needed to validate patterns. Temporal state modelling shed further light on habitat use where low activity behaviours (forage) occurred mostly in the refuge point for SHH1 and at the dredged channel slope. SHH2 also showed an affinity for channel slopes, rarely venturing into the deeper channel centre, and these sloped areas were also observed to have the majority of recreational fishers casting lines towards. State modelling also showed forage behavioural states were more likely to occur at shallow depths changing into directional behaviours as depth increased for both SHH1 and SHH2, but as habitat depth increased foraging behaviours had a higher probability to transition into directional movements. Seagrass habitats occurred at shallower sites and juvenile sharks showed a higher probability to forage at these areas. These results reiterate the
importance of shallow estuarine areas with fringing wetlands as important habitats for juvenile foraging.

6.4. Thermal niche influencing shark catches in the QSCP

The objective of this chapter was to investigate the thermal conditions that drive hammerhead shark catch abundance. The Queensland coastline showed defined temperature differences between the southern areas (Gold and Sunshine Coasts), mid (Mackay) and the northern areas (Townsville and Cairns) in mean monthly SST, where sea surface temperatures were always warmer than southern areas. Occurrences of both hammerhead species showed change to SST in northern areas as a response to the warmer annual waters. In south and mid areas, catches were more likely with an optimal thermal range between 20 -25°C and 23 -28°C respectively, similarly great hammerheads were likely to occur when temperatures were higher than 20°C. Further evidence to support this range was reported by Hammerschlag et al. (2011) suggested that a tagged great hammerhead off the northwest Atlantic followed the northeast pathway of the Gulf Stream where SST average 21.9 °C and nearshore waters were < 18 °C during the same tracking period. It could be hypothesised that during the winter periods, hammerhead species may move further offshore in the warmer East Australian Current (EAC) which can reach up to 5 °C warmer than surrounding waters during cooler months. Monthly variations in EAC could drive warmer waters towards the coast and also upwelling can push cold water along the coast (Cresswell et al. 2016, Azis Ismail et al. 2017), effectively changing water temperatures and presence of hammerhead species. More information through tagging studies would be needed to further these investigations. The thermal range of hammerheads were smaller than those determined for tiger and bull sharks, which showed likely occurrences between 20 – 30 °C and 18 – 27 °C respectively. Furthermore, our results determine an optimal range for species rather than an optimal temperature for mean occurrence. This information could be used to select times and locations where nets and drumlines should be removed to decrease the mortality of threatened hammerhead shark species.
6.5. Resource competition between hammerhead species and co-existing large sharks

This chapter details the first comparison of the two largest hammerhead species which coexist in SEQ sharing dietary resources. Both species exhibited seasonal dietary shifts between nearshore and oceanic carbon sources. This seasonal shift could also be related to the seasonal temperature changes in temperate areas determined in chapter 4, and has been described for shortfin mako sharks in the north west Atlantic (MacNeil et al. 2005). During winter, hammerheads could be pushed into oceanic feeding grounds closer to the warmer EAC waters and return nearshore during summer when pupping in estuarine areas (CHAPTER 1 and CHAPTER 2). The research also showed a specialised dietary range for great hammerheads and a wider range for scalloped hammerheads yet exhibited 69% overlap in dietary resource on pelagic fish and ray. Great hammerhead specialisation was also reported in a recent study where great hammerheads specialised in feeding on small shark species (Raoult et al. 2019). Seasonally, hammerheads also shared resources with bull and tiger sharks during warmer months and only overlapped with white sharks during early spring. Overlap with tiger sharks generally occurred at lower trophic levels as this species is generalist bottom feeder and we identified hammerhead species to feed through a range of prey from bottom dwellers (rays and eel) to pelagic fish (tuna, snapper). This data is important to understand food web dynamics in the conservation of the species.

6.6. Future directions

Further work is required to enhance the protection of hammerhead shark species in Australia. Satellite tagging studies would greatly benefit our understanding of shark movement patterns, and the influence of climate change including changing sea surface temperatures and the shifts of meanders in the major current system, the East Australian Current. A single great hammerhead was tracked on the warm Gulf Stream during the winter migration (Hammerschlag et al. 2011); and so further tracking studies would provide the southern context to drivers of migration in the southern hemisphere. The technology is available for fine scale tracking; satellite and acoustic tagging can identify critical habitats for hammerheads; and there is a need to identify movements related to life history patterns, for example from juvenile nursery grounds to adult habitats. Continuing acoustic tracking of juvenile and adult hammerheads with passive and continuous tags, will identify more detailed habitat use and residency
times within high use areas. Tracking data would also give some temporal and spatial context to juvenile habitat use, providing us with more information to refine protective measures in essential marine protected areas.

6.7. References


