Spatial ecology of a top-order marine predator, the tiger shark (*Galeocerdo cuvier*)

by

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School of Animal Biology

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Declaration of authorship

I declare that this thesis is my own composition, all sources have been acknowledged and my contribution is clearly identified in the thesis. This thesis has been substantially completed during the course of enrolment at the University of Western Australia and has not previously been accepted for a degree at any tertiary education institution. I confirm that for any work in this thesis that has been co-published with other authors, I have the permission of all co-authors to include this work in my thesis, and include a signed declaration.

Luciana Cerqueira Ferreira

Date: 12/05/2017
Abstract

Top-order predators are large consumers that occupy the highest trophic level of food-webs. Through both consumptive and behavioural impacts on prey, these animals play important roles in the structure, stability and resilience of communities and ecosystems. In marine environments, top-order predators are often highly mobile and can display large-scale (1000s km) seasonal migrations. This poses a major challenge for conservation of these animals, because common approaches, such as the establishment of marine protected areas, rarely encompass the scale and extent of their movement patterns. Furthermore, broad-scale migrations make it likely that top-order predators will encounter multiple human threats across their range and as a consequence, populations of many species have undergone rapid declines. Identification of the key environmental drivers of movement patterns and habitat use by top-order predators is thus urgently required in order to understand the scale and consequences of anthropogenic threats that these sharks now face. Here, I address these issues for the tiger shark (*Galeocerdo cuvier*), a keystone top-order consumer in tropical and warm-temperate marine ecosystems.

In Chapter 2, I reviewed the conservation status of tiger shark according to the guidelines for the International Union for the Conservation of Nature (IUCN) Red List. I summarised information available on its biology, ecology and threats to populations, and indicated gaps in the ecological knowledge of the species. This assessment formally updated the status of the species for this species as “Near Threatened” IUCN Red List. In Chapter 3, I described and analyse spatial patterns in movement of tiger sharks along the coastline of Western Australia as derived from satellite telemetry. Using a Brownian Bridge movement kernel method to analyse tracks, I showed that the extensive movements of tiger sharks (thousands of km) can encompass tropical and cool-temperate environments across international maritime boundaries that offer varying levels of fisheries protection for the species. Individual variability was high with respect to levels of residency, space use and environmental preferences in each climate zone.

In order to describe spatial variability in diet and trophic ecology of tiger sharks, I used the analysis of stable isotopes from multiple tissues (dermis, muscle, blood) of sharks collected from both the western and eastern coasts of Australia (Chapter 4). This continental-scale analysis of isotopic signatures demonstrated that the species resides
near the top of the food chain, but is a generalist with a very broad diet. I showed that tiger sharks explored multiple resources throughout their distribution that led to changes in the position of the species within the food chain in different regions. Finally, in Chapter 5, I compiled and analysed a global dataset of tiger shark tracks across multiple ocean basins to identify the key environmental drivers of movement and habitat use at the scale of the range of the entire species. I applied Biased Random Bridge methods to generate monthly utilization distributions for all individual sharks and overcome issues of data quality and sparseness, and then applied generalised additive mixed-models to identify the key drivers of migratory movements and large-scale patterns of space utilisation. Sea surface temperature and water depth were important predictors of space utilization for all sizes and sexes of sharks and at all locations, but patterns varied greatly at both temporal and spatial scales. Furthermore, these environmental predictors explained only small amounts of variance in habitat utilisation. Geographically weighted regression was used to identify areas within the species range where environmental variables failed to explain space utilisation, allowing the generation of alternative hypotheses to explain patterns of habitat use and the spatial targeting of future research.

Combined, these findings demonstrated the value of using large datasets pooled across studies and locations to provide insights into the spatial ecology of wide-ranging marine predators. My analyses showed that tiger sharks are cosmopolitan and generalist predators that demonstrate high levels of intra-specific variation in their use of space, movement and trophic ecology. This plasticity in spatial and trophic ecology is possibly a key element of their success as a top-order marine predator and might provide some resilience to human threats. However, it also highlights the difficulties involved in establishing effective conservation strategies in order to manage and protect the species.
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Publication from this thesis

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Chapter 3

Chapter 4

Chapter 5
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Statement of candidate contributions

This thesis is presented as a series of four manuscripts in journal formats, as well as the general introduction and general discussion sections. These papers were developed by my own ideas and hypotheses with inputs from my supervisors.

Fieldwork for Chapter 4 and 5 was supported by the Paddy Pallin Science Grant (Royal Zoological Society of NSW), The University of Western Australia, the Australian Institute of Marine Science and OCEARCH. Tuition stipend was provided by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Brazil) and a RCA Top-up scholarship by The UWA Oceans Institute and Australian Institute of Marine Science (AIMS).

Chapter 2 was facilitated by Dr Colin Simpfendorfer (James Cook University) and the IUCN Shark Specialist Group (SSG) that supported travel to attend the SSG Australian Regional Workshop. Existing tracking data for Chapter 3 was provided by Dr Mark Meekan (Australian Institute of Marine Science), Dr Rory McAuley (Department of Fisheries, Government of Western Australia) and Dr John Stevens (CSIRO, Commonwealth Scientific and Industrial Research Organisation).

I collected samples at Ningaloo Reef for Chapter 4. Samples from other locations were obtained from Dr Adam Barnett (James Cook University), Dr Bonnie Holmes (University of Queensland), Dr Julian Pepperell (Pepperell Research) and the Queensland Shark Control Program. Dr Michael Heithaus (Florida International University) provided existing isotope data for Shark Bay. I deployed tags at Ningaloo Reef for Chapter 5 and existing tag data was provided by the by Dr Mark Meekan, Dr Rory McAuley, Dr John Stevens, Dr Neil Hammerschlag (University of Miami), Dr Fabio Hazin (Universidade Federal Rural de Pernambuco), Dr Richard Fitzpatrick (Biopixel) and Dr Michael Heithaus.

The analyses described in all data chapters were carried by myself and all chapters were written by me with feedback from Prof Jessica Meeuwig (University of Western Australia, Chapters 1-3, 6), Dr Mark Meekan (all chapters), Dr Michele Thums (all chapters), Dr Colin Simpfendorfer (Chapter 2), Dr Gabriel Vianna (Rare Brasil, Chapter 3), Dr Rory McAuley (Chapter 3), Dr John Stevens (Chapter 3), and Dr Ben Radford (AIMS, Chapter 5)
Co-author authorisation

By signing below, co-authors agree to the listed publication being included in the candidate’s thesis and acknowledge that the candidate is the primary author, i.e. contributed greater than 50% of the content and was primarily responsible for the planning, execution and preparation of the work for publication.

**Publication title:** Crossing latitudes—long-distance tracking of an apex predator.

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Chapter 1  General Introduction

Top-order predators play keystone roles in the structure, stability and resilience of communities and ecosystems (Mills et al. 1993) by both consuming prey (Tegner & Levin 1983; Werner et al. 1983; Estes & Duggins 1995; Creel & Christianson 2008) and influencing their behaviour (Lima & Dill 1990; Schmitz et al. 1997; Lima 1998; Kie 1999; Estes et al. 2001; Wirsing & Ripple 2011). Such predators are often capable of moving long distances (100-1000s km; Harestad & Bunnel 1979; Hays & Scott 2013), creating linkages between multiple ecosystems (McCauley et al. 2012). This movement also brings them into contact with multiple human threats such as habitat loss and fragmentation, pollution and overexploitation (Ritchie & Johnson 2009; Heupel et al. 2014). As a result, top-order predators have been disproportionately and negatively affected by anthropogenic impacts in both terrestrial and marine environments. The removal of top-order predators can result in major shifts in the structure and function of communities, reducing the resilience of ecosystems to human impacts and climate change (Heithaus et al. 2008a, 2014; Beschta & Ripple 2009; Estes et al. 2011; Ruppert et al. 2013; Atwood et al. 2015).

In this chapter, I examine the role of top-order predators in the trophic ecology of ecosystems and show why the study of movement ecology is essential for the development of an understanding of the ecology of these species. I describe the current research challenges for these highly mobile predators and outline the rationale for my choice of study species for this thesis.

1.1 Top-order predators

The terms “apex” and “top-order predator” encompass carnivores that occupy the highest level of the trophic ladder (Estes et al. 2001; Wallach et al. 2015). These animals are often large-bodied and specialized hunters (Ritchie & Johnson 2009), invest in K-selected reproductive strategies and parental care, have large territories and display complex social behaviours (Wallach et al. 2015). In terrestrial systems, carnivorous mammals typically occupy these roles. Tigers (Panthera tigris), for example, are large, solitary, territorial carnivores that are specialized forest-edge hunters of large ungulates and preferentially predate on wild boar (Sus scrofa) and sambar deer (Rusa unicolor) (Smith et al. 1989; Hayward et al. 2012). The species displays high investment in a low
numbers of offspring, with litters of females averaging only 1 - 5 cubs that are dependent on their mother for up to two years (Sankhala 1967; Singh et al. 2013). Carnivorous mammals can also act as top-order predators in some marine ecosystems. In the Antarctic, leopard seals (Hydrurga leptonyx) are strongly territorial, solitary predators whose predation on Adelie penguins (Pygoscelis adeliae) is a significant structuring force of penguin colonies (Ainley et al. 2005). However, in marine environments, top-order roles are more often occupied by fishes, notably sharks, billfishes and tunas. These taxa differ from their mammalian counterparts by having greater reproductive output (for example, the broadcast spawning of many hundreds of thousands of tiny, pelagic eggs in tunas) and having little or no investment in parental care. They also exhibit ontogenetic shifts in diet, habitat use and behaviour that complicate their classification as top-order predators throughout their life cycle. For example, white sharks (Carcharodon carcharias) use coastal habitats and have a diet of fish as juveniles and are susceptible to predation by other species (e.g. orca, Orcinus orca; Pyle et al. 1999). As adults, they target marine mammals and use offshore habitats (Bruce et al. 2006; Estrada et al. 2006; Weng et al. 2007b; a; Bruce & Bradford 2008; Carlisle et al. 2012; Hoyos-Padilla et al. 2016). Thus, the size of predatory fishes has a strong influence both on their prey and on whether they have a role as a top-order carnivore or lower, secondary-order consumer within a food chain. For many large (>3 m length) sharks such as the white (Carcharodon carcharias), tiger (Galeocerdo cuvier) and hammerhead (Sphyrna sp.), only the adult life history stages can be classified as truly top-order predators (Heupel et al. 2014).

Many top-order predators preferentially target specific types of prey (Hayward et al. 2011, 2012; Lyngdoh et al. 2014), although feeding strategies vary both among and within species and can range from specialist to generalist. Dietary specialization is often strongly associated with the availability of resources (Cherel et al. 2007; Woo et al. 2008). Populations of a species that have a generalist diet may be composed of multiple, generalist individuals or of sub-groups or even individuals, each of which is specialized on different types of prey (or some combination of the two options) (Van Valen 1965; Bolnick et al. 2002; Bearhop et al. 2004; Urton & Hobson 2005). For example, orcas are described as a generalist predator, hunting a diverse range of marine prey including fishes, marine mammals and even large sharks, however, different populations exhibit high levels of specialization on particular types of prey that reflect their availability in
Irrespective of their degree of specialisation, predators regulate the structure, composition and diversity of prey communities directly by consumption and indirectly through evoking predator risk effects in prey. Risk effects include shifts in the types of habitat used by prey to reduce the likelihood of predation, altering the location of foraging to reduce detection and/or facilitate evasion of predators and increased investment in vigilance. These behaviours are costly to prey, since time spent avoiding predators will result in a reduction in activities that enhance fitness such as foraging, territory defence or reproduction (Brown et al. 1999; Ripple & Beschta 2004; Wirsing & Ripple 2011). Behavioural responses to risk effects have been recorded and described in a variety of terrestrial systems (Holmes 1991; Schmitz et al. 1997; Lima 1998; Brown et al. 1999; Kie 1999; Sinclair et al. 2003; Creel & Christianson 2008; Thaker et al. 2011), such as the effects of grey wolves (Canis lupus) on the grazing rate, habitat selection and group dynamics of elk (Cervus elaphus) (Ripple & Beschta 2004; Creel et al. 2005; Fortin et al. 2005) and the behavioural responses of ungulates under the threat of lions (Panthera leo) in the African savanna (Sinclair & Arcese 1995; Valeix et al. 2009a,b; Thaker et al. 2010; Creel et al. 2014). Risk effects have been the subject of a number of studies in aquatic communities (Tegner & Levin 1983; Werner et al. 1983; Lima & Dill 1990; Lima 1998). However, there is relatively little information available about the role of large top-order teleosts and sharks in creating risk effects in marine environments, with the exception of the well-documented behavioural responses of large herbivores such as turtles and dugongs to the threat of predation by tiger sharks in seagrass habitats (Wirsing et al. 2007a,b, Heithaus et al. 2007b, 2009).

Although predator risk effects are exhibited by prey in both terrestrial and marine ecosystems (Wirsing & Ripple 2011), the physical properties of marine environments have some unique elements that can structure these interactions, such as three-dimensional distributions of species, greater spatial structure of populations and “openness” of the environment, stronger and more complex trophic relationships, and the presence of pronounced ontogenetic shifts in trophic relationships (Carr et al. 2003). Additionally, top-order predators in nearly all terrestrial ecosystems (with perhaps the exception of the Arctic) are now constrained to only a fraction of their historical range due to habitat loss and indiscriminate hunting as a result of the encroachment of humans and livestock (see review by Ripple et al. 2014). Despite markedly reduced abundances,
in marine systems many top-order predators still occupy much of their original ranges, although the extent and impacts of anthropogenic threats in these ecosystems are growing rapidly (McCauley et al. 2015). Conservation and management strategies for these wide-ranging and highly mobile species in marine ecosystems need to accommodate their complex life-histories, the dynamics of oceanic habitats and their spatio-temporal overlap with various human threats (Hooker et al. 2011).

1.2 Movement ecology

Movement is a change in the location of an individual in space over time (Nathan et al. 2008) and is a major component of some part of the life history of almost every organism (Holyoak et al. 2008). Movement has implications for the individual, populations, communities, ecosystems and, ultimately, evolution (Turchin 1991; Webster et al. 2002; Dingle & Drake 2007). The decision to move is related to the organism’s internal state (physiology, locomotory and navigation capabilities; Nathan et al. 2008), but is influenced by external environmental factors such as the landscape, weather, physical processes, resource availability, and other organisms that can act as competitors, predators or mates. Movement can thus be considered as the result of an interaction between environmental and internal factors and is driven by ecological processes at various spatial and temporal scales (Crist et al. 1992; Nathan et al. 2008). Animal movement can be classified into a wide range of modes depending on the definition of the goals, motivation or temporal dynamics of the processes (e.g. foraging, dispersion, nomadic, migration), but most frequently is connected to the search for and use of resources (Dingle & Drake 2007; Nathan et al. 2008; Sims et al. 2008).

Resources in environments are spatially heterogeneous, resulting in unequal or patchy distributions that drive the dispersion and foraging behaviours of organisms (Turchin 1991; Johnson et al. 1992). Moreover, this patchiness is argued to have a hierarchical spatial structure, where a patch at a larger spatial scale has nested, internal structures of heterogeneity at increasingly finer scales (Kotliar & Wiens 1990). For example, small pelagic fishes, the prey of many larger marine predators, occur in high density schools at small scales (m - km) that are aggregated into patches associated with mesoscale oceanographic features at intermediate scales (10 - 100s km), which occur on migration, feeding or spawning grounds at large (100 - 1000s km) spatial scales (Fauchald 1999; Fauchald & Tveraa 2006). As a result of these patchy distributions of prey, in the absence of knowledge of the distribution of resources, predators must optimize their
movement in order to maximize the probability of encountering food (Fauchald 1999; Fauchald & Tveraa 2003; Bartumeus et al. 2005). According to theories of optimal search strategies, animals will display more directed, straight-line movements in areas with a low density of resources, whereas in areas of high density of prey they will slow down and increase the frequency of turning angles to maximize the probability of prey encounter (Kareiva & Odell 1987). Without previous knowledge of the distribution of resources, predators may adapt their search and movement patterns to optimise prey encounter (Sims et al. 2008). A specialised type of random walk known as Lévy walks (Viswanathan et al. 2000; Bartumeus et al. 2005; Sims et al. 2008) appears to describe probabilistic search patterns of some species consisting of numerous discrete steps that are linked by rarer longer steps, which are repeated across multiple scales. However, much controversy exists around the validity of Lévy foraging hypothesis to describe optimal search in comparison with cue-driven Brownian-type motion (Benhamou & Collet 2015), where animals would move in a straight-line random direction until prey is found, and then switching to a smaller steps described by a Brownian walk (Benhamou 2007).

Environmental conditions and habitat characteristics create much of the patchiness within the marine environment. This occurs through the influence on movement of currents and wind (Weimerskirch et al. 2000; Fritz et al. 2003; Chapman et al. 2011); variation in optimal ranges of salinity, temperature and dissolved oxygen (Jonsen et al. 2007; Heupel & Simpfendorfer 2008; Espinoza et al. 2011; Bestley et al. 2013) and/or by physical features that may have an aggregating function such as thermal fronts, upwelling, eddies, canyons and shelf breaks (Klimley & Butler 1988; Royer et al. 2004; Croll et al. 2005; Cotte et al. 2007; Doniol-Valcroze et al. 2007; Scales et al. 2014; Bouchet 2015; Bouchet et al. 2015; Queiroz et al. 2016). In turn, this patchiness also affects the movements of predators (Humphries et al. 2010). For example, the thermal structure of the water column shapes the vertical distribution of the sardine (Sardinops sagax) and as a result it influences the vertical movements of their predators, the Pacific bluefin tuna (Thunnus orientalis) (Kitagawa et al. 2004, 2007). Relationships between such environmental drivers and movement of animals is largely scale dependent, both spatial and temporally (Guinet et al. 2001; Pinaud & Weimerskirch 2005; Fryxell et al. 2008; Avgar et al. 2013). For instance, at a large scale (1000s km) the habitat use of yellow-nose albatrosses (Thalassarche carteri) is related to bathymetry (a proxy for ocean and shelf habitats) and sea surface temperatures (SST) associated with subtropical
waters, but at mesoscales (10 – 100s km) habitat use is associated with chlorophyll-a and sea-surface height anomalies that are indicative of mesoscale oceanic features such as eddies (Pinaud & Weimerskirch 2005).

The patchy nature of marine environments constrains the movements of animals. The area within which animals move continuously for feeding, resting and reproduction is termed the home range (Burt 1943). As an statistical concept, home range is define as a fixed percentage (commonly 95%, 50%, 25%) of the confidence region obtained from the relative frequency distribution of an animal’s location, usually two dimensional, over time (Worton 1987). However, as noted above, how much an individual utilises specific areas within its home range will vary temporally, and according to resources available and habitat quality (Benhamou 2011; Benhamou & Riotte-Lambert 2012). Areas of high use will be related to accessibility of food, but must also offer environmental conditions that are within an optimal range. For example, dusky sharks (*Carcharhinus obscurus*) in the Gulf of Mexico, although highly mobile, spend the majority of their time within waters off the continental shelf where water temperatures are between 24-28°C (Hoffmayer *et al.* 2014).

Seasonal events such as migration may break the stability of an animal’s use of space (Bunnefeld *et al.* 2011). Similar to ‘animal movement’, the term “migration” is used to describe a large array of movement types, from vertical movements in the water column to seasonal largescale movements of several species, and to describe movements from individual to population levels (Dingle & Drake 2007; Nathan *et al.* 2008). However, it generally refers to largescale movements occurring as a result of seasonal variability in the distribution of resources (Alerstam *et al.* 2003; Dingle & Drake 2007) or spatial segregation between breeding and non-breeding areas (Webster et al 2002). More than 12% of vertebrates make long-distance (100-1000s km) migrations throughout the continents and oceans, however, in general these are more common in swimming and flying vertebrates as a result of the lower cost of locomotion (Robinson *et al.* 2009). In marine systems environmental conditions have been identified as major element of migratory movements. For instance, migration of juvenile bluefin tuna (*Thunnus thynnus*) to the waters of the northern California coast during spring is associated with warmer ocean temperatures and reduced wind stress, which also results in higher prey availability (Kitagawa *et al.* 2007).
Large marine predators, such as epipelagic sharks and tunas, are found throughout the world’s oceans and considerable information is available on the horizontal movements of some of the most wide-ranging species (Table 1.1). These top-order predators display a mix of resident behaviours interspersed with extensive pelagic movements. Environmental variables, such as sea surface temperature (SST) and chlorophyll-a, have been identified as some of the major drivers of movement patterns for these large predators (Block et al. 2005, 2011; Queiroz et al. 2016). However, for some of these species, drivers have only been defined for a limited region within their distribution range, and the motivation behind large scale movements (foraging, breeding) has yet to be determined. Defining environmental and habitat preferences of mobile predators during residency and along migration pathways allows key habitats within their distribution to be identified (Cooke 2008; Block et al. 2011). This information is also a key step for ecosystem-based fisheries management (Pikitch et al. 2004) such as dynamic ocean management (Hobday et al. 2014; Maxwell et al. 2015), where management adapts to the spatial and temporal dynamics of the ocean based on the integration of real-time biological, oceanographic and socio-economic data (Maxwell et al. 2015). The identification of preferred environmental conditions and association with oceanographic features (i.e. mesoscale features such as upwelling areas, fronts and eddies) could be used to inform fisheries and enhance dynamic management actions for highly mobile species (Hobday & Hartog 2014; Lewison et al. 2015).
Table 1.1 Range and drivers of movement patterns displayed by large epipelagic top-order sharks and teleosts.

<table>
<thead>
<tr>
<th>Species</th>
<th>Common name</th>
<th>Maximum size (cm)</th>
<th>Range of movements</th>
<th>Drivers of movements</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thunnus thynnus</td>
<td>bluefin tuna</td>
<td>&gt; 450</td>
<td>Seasonal residency, migration to breeding grounds, longitudinal and transatlantic movement to foraging grounds</td>
<td>SST**, chlorophyll-a, body size, population</td>
<td>(Lutcavage et al. 2000; Block et al. 2005, 2011; Walli et al. 2009; Galuardi et al. 2010; Galuardi &amp; Lutcavage 2012)</td>
</tr>
<tr>
<td>Carcharodon carcharias</td>
<td>white shark</td>
<td>&gt; 600</td>
<td>Residency and site fidelity to coastal areas, philopatry, long-distance pelagic movements, trans-oceanic migration</td>
<td>foraging, mating and breeding (hypothesised), SST**</td>
<td>(Boustany et al. 2002; Bruce et al. 2006; Weng et al. 2007b,a, Domeier &amp; Nasby-Lucas 2008, 2013; Bonfil et al. 2010; Jorgensen et al. 2010; Block et al. 2011)</td>
</tr>
<tr>
<td>Isurus oxyrinchus</td>
<td>mako shark</td>
<td>400</td>
<td>Extensive offshore movements and site fidelity to slope and shelf edge, seasonal latitudinal movements,</td>
<td>SST, SST gradients, chlorophyll-a</td>
<td>(Musyl et al. 2011; Block et al. 2011; Rogers et al. 2015; Queiroz et al. 2016; Vaudo et al. 2016)</td>
</tr>
<tr>
<td>Carcharhinus longimanus</td>
<td>oceanic whitetip</td>
<td>350</td>
<td>Long-distance pelagic movements, some indication of philopatry, trans-equatorial migration*</td>
<td>SST**</td>
<td>(Kohler et al. 1998; Musyl et al. 2011; Carlson &amp; Gulak 2012; Howey-Jordan et al. 2013)</td>
</tr>
<tr>
<td>Sphyrna lewini</td>
<td>great hammerhead</td>
<td>&lt; 350</td>
<td>Residency and site fidelity in continental shelves and islands, occasional offshore movements</td>
<td>SST gradients, water temperature, currents</td>
<td>(Klimley 1993; Bessudo et al. 2011; Hammerschlag et al. 2011b; Ketchum et al. 2014a,b; Queiroz et al. 2016)</td>
</tr>
<tr>
<td>Prionace glauca</td>
<td>blue shark</td>
<td>320</td>
<td>Overwintering around Gulf Stream and Sargasso Sea (central North Atlantic), long-distance pelagic movements, trans-oceanic migrations*</td>
<td>SST, foraging</td>
<td>(Kohler et al. 2002; Queiroz et al. 2005, 2016; da Silva et al. 2010; Campana et al. 2011; Block et al. 2011; Vandeperre et al. 2014)</td>
</tr>
</tbody>
</table>

* Information obtained from tag-recapture data.

** Driver only identify for the North Pacific by Block et al. 2011a

SST = sea surface temperature
1.3 Challenges for the conservation of large marine predators

Recent analyses show that body size is one of the strongest predictors of the risk of human-driven extinction in the modern oceans, with large-bodied animals suffering the most elevated levels of threat (Payne et al. 2016) because they are preferentially targeted by human hunting (Pauly et al. 1998a; Pauly & Palomares 2005). Top-order marine predators are typically large animals and this trait, combined with their life history strategies and wide-ranging movements has led to declines in many species so that they are now classified as Vulnerable, Threatened or Endangered by the International Union for the Conservation of Nature (IUCN) Red list guidelines (IUCN 2012).

The mobility of marine predators such as large sharks presents one of the greatest challenges for conservation, as is the case for many other species (Shuter et al. 2011; Runge et al. 2014; Campana 2016). For some species, nomadic movement behaviours might be predominant, in which home ranges, and breeding timing and areas are not predictable (Dingle & Drake 2007). Nomadic or migratory behaviour brings these animals into contact with multiple threats and at the same time, it hinders our ability to assess impacts on their populations (Shuter et al. 2011; Runge et al. 2014; McCauley et al. 2015). Mobile species are extremely vulnerable when large portions of a population migrate to restricted breeding or wintering locations, as is the case for many taxa including fishes, reptiles and pelagic birds (Webster et al. 2002) or when migrations traverse socio-political boundaries that have varying levels of protection as occurs for many sharks and fishes (Martin et al. 2007; Berger et al. 2008; Hooker et al. 2011; Dallimer & Strange 2015). For terrestrial species, a common response to ensure the conservation of mobile species has been a focus on the protection of migration corridors (Berger 2004; Berger et al. 2008), but for marine predators, particularly in the open ocean, such essential habitats are much harder to identify and delineate.

Significant efforts have been directed towards the protection of “hotspots” of biodiversity through the designation of Marine Protected Areas (MPAs) (Mittermeier et al. 1998; Médail & Quézel 1999; Myers et al. 2000; Hughes et al. 2002; Roberts et al. 2002) and these have become a key strategy for ecosystem-based conservation and management (Hooker et al. 2011; Abecasis et al. 2014; Lascelles et al. 2014; O’Leary et al. 2016). In recent years, the mean size of MPAs has increased greatly, however most are still too small relative to the scale of movements and home ranges of many
top-order predators such as sharks to ensure the protection of all life history stages (Heupel et al. 2015; McCauley et al. 2015). In such species, individuals can be spread over many thousands of kilometres, which prevents protection of the entire population (Hooker et al. 1999; Chapman et al. 2005; Game et al. 2009; Hays & Scott 2013). If MPAs are to be an effective strategy for the conservation of large predators, they must target areas of higher vulnerability such as mating and foraging grounds, migration corridors, or nursery areas (Heupel et al. 2007; Lascelles et al. 2014; Pendoley et al. 2014; Hays et al. 2014). Dynamic ocean management has also indicated great potential benefits to managing highly mobile species or processes (Lewison et al. 2015; Maxwell et al. 2015; Dunn et al. 2016). Real-time tracking has been suggested as a useful tool for several migratory species (Hobday & Hartmann 2006; Hobday & Hartog 2014; Hazen et al. 2016). For example, a management tool “WhaleWatch” has been developed for blue whales (Balaenoptera musculus) in the California Current by combining tracking data with distribution models and the collection of environmental data to develop near-real-time habitat prediction tool (Hazen et al. 2016). Optimisation of these strategy requires a clear understanding of the relationships between movement patterns, environmental drivers and habitat preferences of these animals (Bailey & Thompson 2009; Game et al. 2009; Hooker et al. 2011; Abecasis et al. 2014). For many species, particularly large sharks, we still lack much of this data.

One of the key issues hampering our understanding of the relationship between movement patterns and environmental drivers of marine predators has been limitations on the numbers and components of populations animals tracked in tagging programs. Over the last three decades, satellite tags have provided unprecedented insights into the movement behaviours of marine predators and their relationships to environmental cues (Biuw et al. 2007; Block et al. 2011; Schlaff et al. 2014; Hussey et al. 2015a). However, due to the expense of this technology and the logistics involved in capturing animals for tagging (Hussey et al. 2015a) most studies of large marine predators rarely tag more than a few dozen individuals, unless the species is targeted by fisheries, as is the case for tunas (Block et al. 2005). Moreover, the ontogenetic stage and sex of animals tagged is rarely representative of the entire population due to differential accessibility of different demographic components during sampling. This has limited our understanding of patterns across species and populations. However, the combination of information from multiple studies of the same species, or from studies of multiple species within a single region, has begun to overcome this issue, allowing
generalisations of spatial patterns of habitat use and drivers of movement on a population level and even for entire communities. For example, in the Pacific Ocean, the Tagging of Pacific Predators (TOPP) program compiled tracking data for 23 species and was able to describe how various taxa including tunas, sharks, cetaceans, seabirds and marine turtles were associated with the California Current Large Marine Ecosystem, where seasonal movements were associated with changes in ocean temperature and measures of productivity (Block et al. 2011). Similar studies in other marine ecosystems are urgently required, given that many of the threats facing marine systems such as climate change and ocean acidification are global in scope (Hoegh-Guldberg & Bruno 2010; Hazen et al. 2013; Jones & Cheung 2015). Due to the importance of environmental cues for migratory patterns, climate change is predicted to affect the distribution and abundance of marine fishes worldwide (Perry et al. 2005; Jones & Cheung 2015). However, most of our knowledge about the effects of climate change on migratory patterns of animals is related to birds, with large gaps in our knowledge of long distance movement and potential human impact in other groups (Robinson et al. 2009). Detailed information about the environmental drivers of movement is necessary to understand the impacts of projected climate changes, predict what areas and which species are at greater risk, and to plan conservation strategies.

1.4 The tiger shark

Tiger sharks (Galeocerdo cuvier) (Figure 1.1) are distributed worldwide in most of the tropical, subtropical and temperate habitats of oceanic and coastal ecosystems (Randall 1992). They are categorised as a top-order predator in tropical marine ecosystems and can exert strong structuring forces in prey communities through predator risk effects. For example, in the shallow seagrass habitats of Western Australia, green turtles (Chelonia mydas), dugongs (Dugong dugon) and cormorants (Phalacrocorax varius) often select habitats that are less profitable for foraging, but reduce the chance of interactions with tiger sharks at times when these predators are abundant (Heithaus 2005; Wirsing et al. 2007a,b, Heithaus et al. 2007b, 2008b). The impact of tiger sharks on the behaviour of prey species in these seagrass communities is well established and is frequently cited as an example of risk effects in marine predator-prey interactions (Heithaus et al. 2008b; Wirsing & Ripple 2011). However, tiger sharks exhibit a generalist diet (Stevens & McLoughlin 1991; Simpfendorfer 1992; Lowe et al. 1996; Simpfendorfer et al. 2001) and also often feed at lower trophic levels in food chains or
scavenge on dead prey. Despite their importance as top-order predators in some habitats, such as the seagrass system described above, this role may not be duplicated across all the marine environments they traverse. For example, analyses of specialization of diet and trophic niche using stable isotopes have shown that tiger sharks are indeed true generalists (Matich et al. 2011; Trystram et al. 2016) and although they occupy apex levels of seagrass and reef-associated food webs (Heithaus et al. 2013; Frisch et al. 2016), the species feeds at the lowest trophic level within the assemblage of large sharks off coastal reefs in South Africa (Hussey et al. 2015b). Such conflicting results imply that the movement patterns, habitat use, diet and trophic role of tiger sharks are intertwined and not necessarily consistent throughout the species range. To disentangle these factors, and others such as sex and ontogenetic stage that might also influence the role of these sharks (MacNeil et al. 2005; Borrell et al. 2011; Carlisle et al. 2014; Munroe et al. 2015), comprehensive data sets are required that document patterns of movement, habitat use and diet across multiple spatial and temporal scales.

Figure 1.1 The tiger shark.

Tiger sharks have a global distribution and display high utilisation of coastal systems (Heithaus et al. 2002). As a result, a number of research programs have investigated movement patterns and habitat use of tiger sharks throughout most of the species range (Table 1.2). These sharks have been tagged with a wide range of tags (acoustic, PAT, SPOT, accelerometers) and both vertical and horizontal movements have been described. Typically, tagging studies of tiger sharks show great individual variability in the use of space (Holland et al. 1999; Heithaus et al. 2007c; Fitzpatrick et al. 2012; Hammerschlag et al. 2012; Hazin et al. 2013; Papastamatiou et al. 2013; Holmes et al. 2014; Lea et al. 2015). Sharks tagged in seagrass habitats off Shark Bay, Western Australia, exhibited either restricted movements near the area where they were tagged, remaining within the coastal embayment and surrounds, or moved to oceanic waters.
The same pattern of individual variation in residency and migration has been recorded for tiger sharks in waters off Hawaii and the eastern coast of the United States (Hammerschlag et al. 2012; Papastamatiou et al. 2013). Some individuals also displayed large seasonal migrations (1000s km) in the North Atlantic and off both the east (Holmes et al. 2014; Lea et al. 2015) and west coasts (Ferreira et al. 2015) of Australia. However, these studies tagged mostly female sharks and many satellite tag deployments were short, typically in the order of only a few weeks or months. Longer durations of tagging have been achieved using acoustic tags, however detection rates are typically low (Meyer et al. 2009, 2016; Papastamatiou et al. 2010; Werry et al. 2014). Furthermore, only two studies have modelled tracking information in order to define the drivers of movement and residency for tiger sharks (Fitzpatrick et al. 2012; Papastamatiou et al. 2013). Although tiger sharks have been tagged in many sites across their distribution range and in different habitats, the explanation for the female bias in most datasets is still unresolved. This bias can be a result of the habitats being sampled (warm, coastal habitats); however, Lea et al. (2015) described the seasonal use of coral reef systems in the Caribbean by male tiger sharks.

Since most studies have tagged females, little is also known about critical habitats and movement patterns of the other components of the population, particularly males, juveniles and neonates (Driggers et al. 2008). Moreover, contrasting evidence of ontogenetic habitat shifts have been reported, with sub-adult sharks believed to forage over large areas in some regions (Meyer et al. 2009) but showing limited movement in others (Werry et al. 2014; Afonso & Hazin 2015). Although most sharks have a K-selected life history (Stevens et al. 2000; Frisk et al. 2001; Dulvy et al. 2014a), tiger sharks produce litters of up to 80 pups (Stevens & McLoughlin 1991; Simpfendorfer 1992; Whitney & Crow 2007). In contrast, other large predatory sharks often produce a limited number of embryos, usually less than 10 (Gilmore 1993), such as white sharks (litter sizes of only 2-10 pups; Francis 1996) and the grey nurse or sand tiger shark (Carcharias taurus), which produces only two embryos (Pollard et al. 1996). Tiger sharks also display extreme rapid growth in their early life history stages (Branstetter et al. 1987; Natanson et al. 1999; Wintner & Dudley 2000; Afonso et al. 2012), doubling their size at birth in the first year of life. These biological traits suggest that tiger sharks might have higher population growth rates and be more resilient to fishing pressure than most sharks that are top-order predators (Simpfendorfer 2009). However, they are a key target in coastal shark control programs (Dudley & Simpfendorfer 2006; Green et al.
2009; Simpfendorfer et al. 2010; Reid et al. 2011) and components of catches in many artisanal and unregulated fisheries (Field et al. 2009; Moir Clark et al. 2015). At present the limited information available on trends in population sizes suggests that abundances are declining, leading to tiger sharks being classified as “Near Threatened” by the IUCN (Chapter 2).

The progress made by tracking studies that have pooled information from different sampling sites across an ecosystem (Costa et al. 2010a; Block et al. 2011; Raymond et al. 2015) or species range (Biuw et al. 2007; Hindell et al. 2016) demonstrate a means to move towards a better understanding of key aspects of the ecology of marine predators. These studies show the value of large datasets in defining environmental preferences and critical habitats for populations and communities in areas such as the California Current Large Marine Ecosystem in the North Pacific Ocean (Block et al. 2011) and the Antarctic continental shelf, an important foraging ground for southern elephant seals (Mirounga leonina) (Hindell et al. 2016). For tiger sharks, the pooling of key data sets could advance our understanding of the movement and feeding ecology of the species: firstly, tracking studies over locations distributed across the species range and composed of different parts of the populations (males and females sub-adults etc.); and secondly, dietary information across a range of habitats and environments. The latter will allow a better understanding of the role of food availability as one of the major biological drivers of movement patterns.
Table 1.2 Tiger shark tagging programs with the number of tags deployed, sex ratio of animals tagged, size range of sharks tagged and information provided by telemetry devices.

<table>
<thead>
<tr>
<th>Tagging program</th>
<th>Ocean basin</th>
<th>N Tags</th>
<th>Tag type</th>
<th>Sex ratio (F:M)</th>
<th>Total length (cm)</th>
<th>Track duration (days)</th>
<th>Distance (km)</th>
<th>Temperature range (°C)</th>
<th>Data collected</th>
<th>Aims</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hawaii</td>
<td>Pacific</td>
<td>140</td>
<td>Acoustic, PSAT, SPOT, accelerometers</td>
<td>2.1:1&lt;sup&gt;a&lt;/sup&gt;</td>
<td>99 - 464</td>
<td>&lt;1&lt;sup&gt;b&lt;/sup&gt;-464&lt;sup&gt;b&lt;/sup&gt;, 161&lt;sup&gt;c&lt;/sup&gt;</td>
<td>1000s</td>
<td>5 - 30</td>
<td>Presence, location, depth, temperature, swimming direction, stroke frequency, video, acceleration, speed</td>
<td>Diel movements, horizontal and vertical movement, depth-temperature profile, yo-yo diving, foraging behaviour, residency, utilization distribution and migration (and drivers), site fidelity</td>
<td>(Tricas et al. 1981; Holland et al. 1999; Meyer et al. 2009, 2010, Papastamatiou et al. 2010, 2013; Nakamura et al. 2011)</td>
</tr>
<tr>
<td>East Australia</td>
<td>Pacific</td>
<td>17</td>
<td>PSAT, SPOT</td>
<td>5.7:1</td>
<td>150 - 350</td>
<td>6 - 408</td>
<td>15791&lt;sup&gt;d&lt;/sup&gt;</td>
<td>6-29.5</td>
<td>Location, depth, temperature, light-level (geolocation)</td>
<td>Depth - temperature profile, horizontal movements, habitat use, residency</td>
<td>Holmes et al. 2014</td>
</tr>
<tr>
<td>Coral Sea</td>
<td>Pacific</td>
<td>34</td>
<td>PSAT, SPOT, Acoustic</td>
<td>3.4:1</td>
<td>154 - 390</td>
<td>1 - 255&lt;sup&gt;b&lt;/sup&gt;, 210&lt;sup&gt;c&lt;/sup&gt;</td>
<td>1141</td>
<td>5.6 - 32.2</td>
<td>Presence, depth, temperature, location</td>
<td>Site fidelity, migration, diving, habitat use, depth- temperature profile</td>
<td>Werry et al. 2014</td>
</tr>
<tr>
<td>Florida and Bahamas</td>
<td>North Atlantic</td>
<td>25</td>
<td>SPOT</td>
<td>11.5:1</td>
<td>184 - 403</td>
<td>26 - 297</td>
<td>3500</td>
<td>-</td>
<td>location</td>
<td>Horizontal movements, residency, activity space, impacts of provisioning ecotourism</td>
<td>Hammerschlag et al. 2012</td>
</tr>
<tr>
<td>Challenger Bank</td>
<td>North Atlantic</td>
<td>24</td>
<td>SPOT</td>
<td>0.2:1</td>
<td>173 - 369</td>
<td>&lt; 45 - &gt;1000</td>
<td>42996</td>
<td>18 -26&lt;sup&gt;e&lt;/sup&gt;</td>
<td>location</td>
<td>Migration, seasonal horizontal movements,</td>
<td>Lea et al. 2015</td>
</tr>
<tr>
<td>Location</td>
<td>Sea</td>
<td>N</td>
<td>Method(s)</td>
<td>Ratio</td>
<td>Min - Max</td>
<td>Min - Max</td>
<td>Depth, temperature, light-level (geolocation)</td>
<td>Notes</td>
<td></td>
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</tr>
<tr>
<td>U.S. Virgin Islands, Bermuda</td>
<td>North Atlantic</td>
<td>14</td>
<td>PSAT</td>
<td>0.5:1</td>
<td>210 - 305</td>
<td>9 - 184</td>
<td>1354</td>
<td>6.3 - 29.1</td>
<td>philopatry, straightness of movement</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bermuda Recife</td>
<td>South Atlantic</td>
<td>21</td>
<td>PSAT, miniPAT,</td>
<td>1.6:1</td>
<td>120 - 295</td>
<td>6 - 159</td>
<td>1156</td>
<td>4 - 25</td>
<td>Depth, temperature, light-level (geolocation)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ningaloo Reef</td>
<td>Indian</td>
<td>8</td>
<td>Acoustic SPOT, SPLASH</td>
<td>4.5:1</td>
<td>145 - 333</td>
<td>7 - 517</td>
<td>&gt; 4000</td>
<td>6-33</td>
<td>Depth, temperature, light-level (geolocation)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shark Bay</td>
<td>Indian</td>
<td>57</td>
<td>SPOT, acoustic, crittercam</td>
<td>1.7:1</td>
<td>230 - 401</td>
<td>&lt;1 - 99</td>
<td>505</td>
<td>-</td>
<td>Location, depth, temperature</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Presence, video, depth, location, site fidelity, horizontal and vertical movements, habitat use, foraging behaviour</td>
<td></td>
<td></td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Notes</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td>Sex ratio of reported numbers, sex ratio of acoustic tagged sharks was up to 6.3:1 (Papastamatiou et al. 2013)</td>
</tr>
<tr>
<td>b</td>
<td>Acoustic tag</td>
</tr>
<tr>
<td>c</td>
<td>Satellite tag</td>
</tr>
<tr>
<td>d</td>
<td>track length (km)</td>
</tr>
<tr>
<td>e</td>
<td>Remote sensed sea surface temperature</td>
</tr>
<tr>
<td>f</td>
<td>Minimum distance travelled</td>
</tr>
<tr>
<td>g</td>
<td>Fork length (cm)</td>
</tr>
<tr>
<td>h</td>
<td>A movement of 8000 km was registered by a single location</td>
</tr>
</tbody>
</table>

Ningaloo Reef: Hazin et al. 2013a; Afonso & Hazin 2014, 2015
1.5 Aims

The overall goal of my thesis is to describe the movement ecology of tiger sharks (*Galeocerdo cuvier*) and identify the drivers of movement patterns and habitat use across a range of spatial and temporal scales. My research aims to:

1) Outline the current understanding of the biology and population trends, and assess the conservation status of the species.

2) Describe large-scale movements, residency and environmental preferences of tiger sharks along the coastline of Western Australia.

3) Identify spatial patterns of diet and trophic ecology of different sexes and sizes of tiger sharks in Australia. Describe the variability and stability in diets in relation to local food-webs at different temporal scales.

4) Describe the movement patterns and habitat use of tiger sharks at a global scale and use novel statistical approaches to identify the potential physical and biological factors that drive these patterns.

In line with these aims, my thesis is organised into an introductory literature review, four research chapters, and the findings are drawn together in a final discussion chapter.

1.6 Thesis outline

In Chapter 2 I review the global literature on the distribution, population, ecology and threats to tiger shark populations. I then use this information to re-assess the conservation status of the species. This review followed the category guidelines of the International Union for Conservation of Nature (IUCN) and will update the IUCN Red List assessment for tiger sharks.

Chapter 3 describes depth and temperature preferences associated with movements and residency of tiger sharks along the coastline of Western Australia. Movement-based home range analyses were applied to satellite tracking data to define areas of residency and space used by individual sharks. Mixed models were then fitted to the relationship between residency and environmental variables (depth and sea surface temperature). In this chapter, I show that, as top-order predators, tiger sharks are able to move extensive
distances, linking tropical and temperate ecosystems and that their environmental preferences vary among different regions (north/south) of the coast of Western Australia.

An important motivation behind predator movement is the distribution of prey. Knowledge of spatial changes in diet is likely to be key in understanding the function of habitats used by marine predators. In Chapter 4, I use stable isotope analysis to characterise diet and trophic ecology of tiger sharks throughout Australia and identify factors driving spatial and temporal variation in isotopic signatures of tissues. I discuss diet in the context of the differential use of multiple habitats and food webs by tiger sharks across their range in northern Australia.

In Chapter 5, I compile and analyse a global dataset of tiger shark tracks across the Atlantic, Indian and Pacific oceans to search for and identify environmental drivers of movement and habitat use for tiger sharks at the scale of the entire range of the species. Using a novel analytical approach, I examine how the influence of environmental factors varies across different ocean basins and between sexes, and identify areas where environmental variables did not explain habitat use. These areas can then be targeted for future study.

I integrate and synthesise the findings of my thesis in Chapter 6. I discuss how insights into the movement, habitat use and diet of tiger sharks across multiple spatial and temporal scales can fill some of the gaps in our knowledge on the ecology of the species. Using this information, I examine the role of the species as a top-order predator, how the behaviours and traits of the species compare to other top-order predators and the implications for the resilience of tiger sharks in marine environments. Finally, I evaluate the benefit of better understanding of the drivers of movement ecology of marine predators for conservation planning.
Chapter 2   Review of tiger shark ecology and conservation status

2.1   Introduction

Globally, shark populations have shown accelerated declines due to overfishing and habitat degradation (Dulvy et al. 2008; Ward-Paige et al. 2010; McCauley et al. 2015; Campana 2016), with one quarter of shark and ray species now classified as “Threatened” by the International Union for Conservation of Nature (IUCN) Red List (Dulvy et al. 2014a). The IUCN Red List assessments are regarded as reliable tools to determine the conservation status of species because they use a comprehensive and scientifically rigorous approach to estimate extinction risk (Rodrigues et al. 2006). The goal of the assessment is to provide information and analyses on the status, trends and threats to species in order to inform conservation actions. Current assessments of sharks have been undertaken during regional Red List workshops coordinated by the IUCN Shark Specialist Group (SSG) in the past 5 - 10 years (Dulvy et al. 2014a), with the last assessment for tiger sharks occurring in 2009 (Simpfendorfer 2009). In this chapter, I update the IUCN assessment for tiger sharks, reviewing their current conservation status and indicating the research needs for the future using the guidelines of the IUCN Red List (IUCN 2012), with some adaptations appropriate for a thesis chapter.

2.2   Distribution

Tiger sharks (*Galeocerdo cuvier*) have a worldwide distribution in tropical and warm temperate oceans, ranging between the latitudes of approximately 40°N - 36°S (Figure 2.1). Compagno (1984) and Randall (1992) describe the distribution across ocean basins as follows:

- In the western Atlantic, they range from the USA (from Cape Cod, Massachusetts) to Uruguay, including the Gulf of Mexico, Bermuda and islands of the Caribbean. In the eastern Atlantic, they are found along the West African coast, from Morocco to Angola, including the Canary Islands and at isolated islands such as Fernando de Noronha in the South Atlantic.

- Tiger sharks are also reported from locations throughout the Pacific Ocean. In the eastern Pacific they range from southern California to Peru, including the Galapagos
and Revillagigedo Islands. In the western Pacific they occur off the coasts of Japan, east China, Australia and northern New Zealand; as well as in the western, central Pacific in Palau, east to Solomon, Marshall and Hawaiian Islands, French Polynesia and other isolated atolls.

- In the Indian Ocean, tiger sharks are found all along the east coast of Africa, including remote localities such as Réunion Island and the British Indian Ocean Territory, north to the Red Sea, and throughout the tropical Indian Ocean off the coasts of Pakistan, India, Sri Lanka, Thailand, Vietnam, Southern China, the Indo-Pacific region and most of western Australia.

Tiger sharks also appear seasonally in cool temperate waters, most likely following warmer currents with reports from the United Kingdom (Compagno 1984) and Iceland (Matsumoto et al. 2005), the southern coasts of New South Wales and Western Australia (Pepperell 1992; Holmes et al. 2014; Ferreira et al. 2015) and South Africa (Dicken & Hosking 2009).

Figure 2.1 Distribution range of tiger sharks (blue).

2.3 Population trends

Long-term trends of catch rates of tiger sharks are only available from limited sources including regional shark control programs and fisheries observer and fisheries-independent longline survey datasets for the US east coast and Gulf of Mexico (Table 2.1). Tiger sharks are not usually targeted by large commercial fisheries, but occur as by-catch in low numbers. As a result, captures are often not recorded and there is a lack
of adequate data for stock assessment, definition of population structure and documentation of trends in demography of the species.

Table 2.1 Summary of long-term trends of catch rates of tiger sharks based on regional datasets.

<table>
<thead>
<tr>
<th>Region</th>
<th>Pop trend</th>
<th>Period</th>
<th>Source</th>
<th>Metric used</th>
</tr>
</thead>
<tbody>
<tr>
<td>NW Atlantic</td>
<td>Increasing</td>
<td>1994-2013</td>
<td>Northeast Fisheries Science Centre</td>
<td>Relative abundance</td>
</tr>
<tr>
<td>Queensland</td>
<td>Declining</td>
<td>1993-2010</td>
<td>Queensland Shark Control Program</td>
<td>CPUE (projection)</td>
</tr>
<tr>
<td>New South Wales</td>
<td>Declining</td>
<td>1998-2007</td>
<td>NSW Shark Meshing Program</td>
<td>CPUE</td>
</tr>
<tr>
<td>South Africa</td>
<td>Increasing</td>
<td>1978-2003</td>
<td>KwaZulu-Natal Beach Protection Program</td>
<td>CPUE</td>
</tr>
</tbody>
</table>

In the northwest Atlantic, the bottom longline fishery for sharks is active along the east coast of the US and Gulf of Mexico (Gulak et al. 2013), and the Northeast Fisheries Science Centre (NEFSC) conducts fisheries-independent surveys of large and small coastal sharks in waters off Florida to the Mid-Atlantic (http://nefsc.noaa.gov/nefsc/Narragansett/sharks/survey.html). Data from NEFSC surveys conducted from 1960-2000 showed an upward trend in the relative abundance of tiger sharks, with an increase of 6.7% per year since the 1980s. Because relative abundance is calculated as an index of actual or absolute abundance based on standardised catches (Blackhart et al. 2006), these trends reflect changes in CPUE (catch per unit effort) rather than being a consequence of an increase in effort. Similarly, the Shark Bottom Longline Observer Program (SBLOP) also showed an increase in relative abundance of the species of 8% per year between 1994 and 2013. However, the Pelagic Observer Program from the Southeast Fisheries Science Centre (SEFSC) showed no change in abundance for the same period (Figure 2.2) (J. Carlson, pers. comm.) and previous estimates based on the standardised CPUE time series of logbook data for the U.S. pelagic longline fleets in the northwest Atlantic suggested a decline of 61 - 65% in abundance of tiger sharks (Baum et al. 2003). These estimates of declines might be biased due to analytical issues (Burgess et al. 2005)
In Australia, the Queensland Shark Control Program (QSCP) has used a combination of nets and drumlines adjacent to popular swimming beaches to target large sharks since 1962 (Paterson 1990). Catch per unit effort (defined as sharks net$^{-1}$ day$^{-1}$ or sharks drumline$^{-1}$ day$^{-1}$) of tiger sharks showed an overall declining trend for the QSCP between 1993 and 2010 (Figure 2.3), with the most significant decline in the southern region (Holmes et al. 2012). A separate analysis for nine beaches in Cairns and Townsville, northern Queensland (Figure 2.4), showed that annual, standardised catch rates (annual catch was modelled including effort by beach in all models to account for changes in effort over time and generate an index equivalent to CPUE) increased up until the 1980s and then decreased to approximately 66% of their original level in the 2000s (Simpfendorfer et al. 2010). Based on the CPUE for 1993 and 2010 from Holmes et al. (2012), and a generation length of 17.5 to 22.5 years for tiger sharks (Natanson et al. 1999; Holmes et al. 2015), a prediction of population change within three generations was calculated according to the rules for estimating reductions by the Red List guidelines (IUCN 2012). Generation length was calculated according to the formula: Age at first maturity + (Maximum age - Age at first maturity/2). The prediction considered CPUE values from 1993 and 2010 as “Past” population sizes assuming a regression with an exponential rate of decline. The prediction showed that

**Figure 2.2** Relative abundance (calculated as an index of standardised catch) for the Shark Bottom Longline Observer Program (SBLOP, blue diamonds) and longline survey of the Northeast Fisheries Science Centre (NEFSC, green triangles) and SEFSC Longline (MS longline, red squares). Figure produced by J. Carlson (pers. comm.).
tiger shark CPUE will undergo a decline of 90 - 96% for drumlines and of 94-99% for nets over the next 30-45 years in relation to the CPUE for the QSCP in 1993 (Figure 2.3). These predictions should nevertheless be treated with caution, as they do not account for fluctuations in CPUE or demographic characteristics of the tiger shark population.

**Figure 2.3** CPUE (number of sharks gear\(^{-1}\) day\(^{-1}\)) by year and size (small < 3 m and large > 3 m) of sharks for drumlines (A) and nets (B) by the QSCP between 1993 and 2010. Figure extracted from Holmes *et al.* (2012).

**Table 2.2** Average CPUE(number of sharks gear\(^{-1}\) day\(^{-1}\) x1000) for drumlines from the QSCP for 1993 and 2010 from Holmes *et al.* (2012) and projected CPUE for three generation lengths (Projection 1 = generation length of 17.5 years, Projection 2 = generation length of 22.5 years).

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</thead>
<tbody>
<tr>
<td>QSCP Drumlimes</td>
<td>0.631</td>
<td>0.430</td>
<td>0.044</td>
<td>0.015</td>
</tr>
<tr>
<td>QSCP Nets</td>
<td>0.244</td>
<td>0.187</td>
<td>0.010</td>
<td>0.003</td>
</tr>
</tbody>
</table>
In southeast Australia, the New South Wales Shark Meshing Program (SMP) has operated since 1937 (Reid et al. 2011), with marked fluctuations in tiger shark CPUE seen in the first four decades of the program (Figure 2.5). The overall CPUE has not changed significantly between 1950 and 2010 ($R^2 = 0.048$, $p = 0.0937$, Reid et al. 2011), although a downward trend in CPUE was observed in the last two decades (Figure 2.5). The size-frequency distribution of tiger sharks caught by the program has changed over 60 years (1998 - 2007) with a significant reduction in the modal size of tiger sharks from 3.5 to 3.0 m. The apparent decline in CPUE over the last 20 years combined with the decrease in the proportion of large individuals suggests changes in the population structure, and raises concern on impacts the program is having on the tiger shark population off New South Wales (Reid et al. 2011).

In contrast, the KwaZulu-Natal beach protection program in South Africa has deployed large-mesh gillnets off popular swimming beaches since 1952, and has found an annual increase of 3% in the CPUE of tiger sharks between 1978 - 2003 (Dudley & Simpfendorfer 2006) (Figure 2.6).
2.4 Life-history and ecology

Tiger sharks occur throughout tropical and subtropical waters on continental shelves, coral reefs, offshore islands and atolls. Tiger sharks are encountered from very shallow waters (Heithaus et al. 2002) to open ocean areas (Polovina & Lau 1993; Meyer et al. 2009; Hammerschlag et al. 2012; Werry et al. 2014; Holmes et al. 2014; Ferreira et al. 2015; Lea et al. 2015; Domingo et al. 2016; Queiroz et al. 2016). Vertical movements have been recorded to depths of up to 1,136 m (Werry et al. 2014); however they
typically spend approximately 90% of time within the first 50 - 100 m of the water column (Meyer et al. 2010; Fitzpatrick et al. 2012; Vaudo et al. 2014; Afonso & Hazin 2015).

Relative to other requiem sharks, family Carcharhinidae, tiger sharks show higher intrinsic rates of population increase based on life history parameters (Dudley & Simpfendorfer 2006). Size at birth has been estimated to be 50 - 90 cm (Stevens & McLoughlin 1991; Simpfendorfer 1992; Winter & Dudley 2000; Whitney & Crow 2007) and growth rates during early life stages are thought to be high (36 - 118.4 cm yr\(^{-1}\)) (Branstetter et al. 1987; Natanson et al. 1999; Kneebone et al. 2008; Afonso et al. 2012). In comparison, the grey nurse shark (Carcharias taurus) is estimated to grow between 14.5 - 18.5 cm per year in early life stages (Goldman et al. 2006). Maximum total length attained by tiger sharks is estimated to be 6 m but individuals larger than 5 m are rarely seen (Compagno 1984; Randall 1992). The maximum age and generation length are estimated to be 27 - 33 years and 17 - 22.5 years respectively. Tiger sharks reach maturity between 5 - 13 years (Branstetter et al. 1987; Smith et al. 1998; Natanson et al. 1999; Wintner & Dudley 2000; Meyer et al. 2014; Holmes et al. 2014), with females maturing at sizes (total lengths) between 274 - 345 cm and males around 250 - 305 cm (Compagno 1984; Stevens 1984; Stevens & McLoughlin 1991; Randall 1992; Simpfendorfer 1992; Wintner & Dudley 2000; Whitney & Crow 2007; B. Holmes, in press) although estimates of size and age at maturity vary greatly among locations. The high level of separation between tiger shark in the Indo-Pacific and western Atlantic (Bernard et al. 2016) suggests that hat these dissimilarities in estimates of size and age at maturity may be due to differential population parameters among ocean basins.

Several studies have reported aspects of tiger shark reproduction, but the complete reproductive cycle has only been described for Hawaii (Whitney & Crow 2007). In this location, the cycle occurs triennially, with mating thought to occur in the boreal winter between January and February and females storing sperm in the oviducal gland while oocytes develop. Ovulation occurs in June to July with pupping during the boreal autumn between late September and early October of the following year after a 15 - 16 month gestation (Whitney & Crow 2007). Conflicting information on the seasonality of reproduction is available for other parts of the world. For example, in Australia, a female was sighted bearing fresh mating wounds during the austral autumn in early May (LC. Ferreira, pers. obs.) and pupping is reported to occur during the austral summer
The number of embryos in a litter ranges from 3 - 82 and litters have on average 26 - 33 embryos (Stevens & McLoughlin 1991; Simpfendorfer 1992; Whitney & Crow 2007). Little is also known about pupping areas for the species. In the North Atlantic tiger sharks do not appear to use specific areas for pupping that can be defined as nurseries, because parturition takes place over an extensive area of shelf waters <100 m deep between the Gulf of Mexico and the northwest Atlantic, with higher abundances of neonates recorded between the longitudes of 30° - 33°N (Driggers et al. 2008). No information on pupping areas exists for the Indian or Pacific Oceans and rates of juvenile mortality remain unknown.

Telemetry data show that tiger shark movements vary greatly among individuals, with some individuals displaying elevated levels of residency in discrete areas and others displaying extensive movements of thousands of kilometres between tropical and temperate ecosystems, as well as seasonal migrations to open oceanic waters (Kohler et al. 1998; Hammerschlag et al. 2012; Papastamatiou et al. 2013; Werry et al. 2014; Holmes et al. 2014; Ferreira et al. 2015; Lea et al. 2015). Although many tracking programs exist globally, the likely drivers of movements (e.g. prey abundance, temperature, bathymetry, productivity, ocean currents, etc.) remain mostly unknown. In Western Australia, residency of tiger sharks is associated with shallow depths and water temperatures above 23°C (Ferreira et al. 2015), and in Hawaii inter-island movements are associated with season (late summer/early spring), sea surface temperatures of 23° - 26°C and chlorophyll-a concentrations above 0.12 mg m⁻³ (Papastamatiou et al. 2013). Variability in movement behaviour may be due to partial migrations, where only part of the population performs large-scale movements while the remainder shows more resident behaviour (Papastamatiou et al. 2013). Tiger sharks also seem to show ontogenetic changes in habitat use and range of movement, with smaller individuals restricting their movements to coastal areas (Werry et al. 2014; Afonso & Hazin 2015).

2.5 Threats

Tiger sharks are caught as secondary target species in multi-species shark fisheries and are also retained as bycatch in commercial, small-scale and artisanal fisheries where they are valued for their high quality flesh, fins, skin, liver oil and cartilage. The fins of tiger sharks are a common component of the Hong Kong fin trade (Clarke et al. 2006). The species has been increasingly exploited by fisheries since the 1950s largely due to the increasing demand for shark fins (Ward-Paige et al. 2010). Tiger sharks are also
subject to illegal, unreported and unregulated (IUU) fishing operations and are regularly caught in recreational fisheries and targeted by shark control programs in Australia (Paterson 1990; Reid et al. 2011), South Africa (Dudley & Simpfendorfer 2006; Cliff & Dudley 2011), and since 2014 at Réunion Island.

2.5.1 Shark Fisheries

Catches of tiger sharks in multi-species shark fisheries have been documented in a number of regions including the western Atlantic (Hoey & Casey 1986; Berkeley & Campos 1988; Bonfil 1994; Morgan et al. 2009; Carlson et al. 2012), Brazil (Bonfil 1994), Australia (Stevens et al. 1982; Lyle et al. 1984; Macbeth et al. 2009; Tillett et al. 2012), Papua New Guinea (Kumoru 2003), Peru (Gonzalez-Pestana et al. 2014), Taiwan (Bonfil 1994), India (Bineesh et al. 2014) and Saudi Arabia (Spaet & Berumen 2015). Tiger sharks are also a common, non-target component of the US east coast/Gulf of Mexico commercial shark bottom longline fishery that targets large coastal species (*Carcharhinus plumbeus* and *Carcharhinus limbus*), where the species accounts for 8-36% of the catch (Morgan et al. 2009; Carlson et al. 2012). Tiger shark mortality rate is estimated at 30.9% with only 14% of the catch being landed and the remaining used as bait or discarded. Of sharks caught alive (69%) almost half are released upon capture (Morgan et al. 2009). Most of the captured individuals are juveniles and sub-adults as the average size of individuals caught by this fishery is 113.9 cm for females and 112.1 cm for males, with sizes ranging from 40 - 336 cm (J. Carlson pers. comm.).

Tiger sharks are relatively common in the Indonesian shark fishery and contributed 5.2% of the total biomass of sharks in catches between 2001 and 2006 (White 2007). In Australia, tiger sharks are also targeted by commercial shark fisheries in northern New South Wales and in Western Australia. Tiger sharks compose 3.12 t and 5.9% of total catch of the Ocean Trap and Line (OTL) Fishery in northern New South Wales. However, catches by this fishery are probably smaller than landings from recreational fisheries in that same area (Park 2007; Macbeth et al. 2009). In the Western Australia Tropical Shark Fishery, tiger sharks were caught as a secondary target species and annual catches averaged approximately 41 t between 2000 and 2004. However, this fishery was closed in late 2005 due to indication of overfishing the target species, sandbar sharks (*Carcharhinus plumbeus*) (Department of Fisheries 2005; Department of Fisheries Western Australia 2006). Tiger sharks are also caught in the seamount gillnet
and longline fishery off the west coast of India but species-specific catches are not recorded (Bineesh et al. 2014).

2.5.2 Non-shark commercial fisheries

Tiger sharks (along with many other sharks) are taken as bycatch in a variety of commercial fisheries that target large teleosts such as tuna and swordfish (ICCAT 2014). They are typically caught in small numbers compared to pelagic sharks that are considered to be of high value, and, as a result, catch is often not reported or only recorded in very coarse resolution. Catch of tiger sharks is reported for datasets that encompass complete ocean basins (International Commission for the Conservation of Atlantic Tunas, ICCAT) or for national longline pelagic fisheries (US longline) and for fisheries that act within the exclusive economic zone of a country (Panama, Australia). Tiger sharks are occasionally caught in the international tuna longline fishery in the Atlantic Ocean regulated by ICCAT, where an average of 16 t was landed per year between 1982 and 2013 (ICCAT database). Although the overall catch (in tons as effort data is not available for the computation of CPUE) of tiger sharks is low, it has shown an upward trend in the last decade, driven mostly by increased catch from US, Brazil and Netherlands (ICCAT database). Between 2007 and 2013, annual landings by tuna longline boats regulated by the ICCAT averaged 54 t (ICCAT database, P. de Bruyn, pers. comm.). Tiger sharks also represented less than 10% of the total bycatch of all shark species in each of the management zones of the U.S. pelagic longline fishery (Mandelman et al. 2008). In the Panama longline fishery, tiger sharks represented 1.6% of the estimated catch of 109,500 t of various sharks since the mid-1980s (Harper et al. 2014). In the central and western Pacific, tiger sharks are caught in low numbers (0.025 sharks per set of longline; P. Williams, pers. comm.) by tuna longline boats from most countries fishing in that region (PNG, Australia, Kiribati, New Caledonia, Hawaii, Solomon Islands, Fiji, Vanuatu, Federated States of Micronesia, Tonga, French Polynesia, Palau). Tiger sharks are bycatch (27 t in 2012) in the Offshore Net and Line Fishery of northern Australia (Lyle et al. 1984; Northern Territory Department of Primary Industry and Fisheries 2012) and the species is also taken in the Southern and Western Demersal Gillnet and Demersal Longline Fishery in Western Australia, with a catch of 112 t reported in 2005/2006 (McAuley & Leary 2008). Tiger sharks also constitute bycatch in squid, fish and crustacean trawl fisheries, although normally in small numbers and there are few records of landings for these fisheries. The Australian Commonwealth Trawl Sector reported a total catch of tiger sharks of 4.7 t from 2004 -
2011. Tiger sharks are caught occasionally in the longline fisheries of Costa Rica (CPUE = 0.006 shark hook\(^{-1}\) × 1000, Dapp et al. 2013), Mozambique (Sousa 2012) and Saudi Arabia (<1% of all sharks, Spaet & Berumen 2015) and by purse seiners in the Indian Ocean (Chassot et al. 2014) with no data available on catches of tiger sharks for most regions.

### 2.5.3 Recreational fisheries

Tiger sharks are a common target of recreational fisheries in the United States (east coast), Australia, South Africa and in the Gulf of Mexico. Approximately 96% of the catch in US waters are released alive and many shark fishing tournaments have become catch and release. Survival rates of tiger sharks are assumed to be high in catch-and-release activities based on blood chemistry analyses (Gallagher et al. 2014). In the game fishery off the southeast coast of Australia (New South Wales Gamefish Tournament), tiger sharks comprised 10% of catches from 1961 to 1990 with captured individuals ranging in mass from 21 to 560 kg (Pepperell 1992). Between 1993 - 2005, tiger shark catches in that game fishery were approximately 8 t year\(^{-1}\), comprising approximately 1-5% of the total catch for all species and 10-30% of all sharks in that period (Park 2007). The largest shark caught in this tournament weighed 626 kg in 1939. A decline in CPUE from approximately 1.2 to 0.5 shark vessel-day\(^{-1}\) has been recorded in New South Wales game fishing tournaments between 1993/94 and 2004/05, even though fishers still target tiger sharks during the tournaments; thus suggesting a decline in the population (Park 2007). Tiger sharks are probably caught by recreational fishermen in many countries, and the tournaments documented above and recreational fishing is likely to account for significant mortality of populations in coastal waters of other countries, although catches and potential impacts remain unmonitored.

### 2.5.4 Artisanal and IUU Fisheries

Artisanal fisheries and IUU fisheries are also likely to be catching tiger sharks, however information about landings from these fisheries is scarce as they remain mostly unmonitored, not allowing further analysis of catch rates and trends. Tiger sharks are commonly caught in artisanal fisheries in the tropics and subtropics, including in Mexico (Cartamil et al. 2011), Panama (Harper et al. 2014), Brazil (Bornatowski et al. 2014; Pimenta et al. 2014) and African countries (Food and Agriculture Organization of the United Nations 2014) but information on catch rates is extremely limited. In
Bangladesh, landings of tiger sharks of 4.48 t represent an average 1.36% of the total shark catch (Jit et al. 2014). Although gear limitations probably preclude the capture of large individuals in artisanal fisheries, catches are often not reported and it is not possible to fully quantify the impact that these fisheries may have on the population status of tiger sharks.

Tiger sharks compose 19% of the total shark biomass and 7.4% of total catch in numbers from Indonesian and Taiwanese IUU fishing vessels (Marshall 2011). There is also evidence that tiger sharks have been overfished by illegal Indonesian fishing boats at Ashmore, Cartier and Scott Reefs in northern Australian waters. This area had been targeted by Indonesian fishermen since the 1800s but fishing was banned in 1988 at Ashmore Reef and 2000 at Cartier Reef (Meekan et al. 2006). A study using baited remote cameras showed an absence of tiger sharks at reefs historically fished despite the 18 and 6 years of protection, respectively, whereas they were recorded as present at nearby atolls that had been always protected from fishing (Meekan et al. 2006).

2.5.5 Shark Control Programs

Shark control programs are established on the basis that by reducing the abundance of large shark species, human safety will be increased. The evidence as to whether such programs reduce the probability of shark/human interactions is inconclusive. In Australia, the Queensland Shark Control Program (QSCP) captured 4,757 tiger sharks between 1993 and 2010 (Holmes et al. 2012) and the species represented approximately 10 to 30% of total catch in the northern locations of the QSCP between 1964 - 2007 (Simpfendorfer et al. 2010). This pattern is most likely due to the replacement of nets with drumlines, which are particularly effective in catching tiger sharks (Simpfendorfer et al. 2010). In southeast Australia, tiger sharks were commonly captured in low numbers by the New South Wales (NSW) Shark Meshing Program with a total of 352 sharks caught between 1950 and 2008, representing approximately 10% of the common shark species caught by the program in each of its locations (Reid et al. 2011). The NSW program also showed marked fluctuations in CPUE of tiger sharks, with peaks occurring approximately every 10 years (Green et al. 2009; Reid et al. 2011). In South Africa, the KwaZulu-Natal beach protection program has caught an average of 48.7 (± 13.3 SD) tiger sharks annually from 1978 and 2003, which represents a catch rate much lower when compared to dusky sharks Carcharhinus obscurus (232.7 ± 113.3) and sand tiger sharks Carcharhinus taurus (194.4 ± 101.8) (Dudley & Simpfendorfer 2006).
Since 1989, all sharks caught alive by the KwaZulu-Natal program are released; however, mortality of tiger sharks in nets is 27% of captures (Dudley & Simpfendorfer 2006).

2.6 Assessment Rationale

In summary, tiger sharks are a large, highly mobile top order predator with a worldwide distribution throughout the world’s tropical and warm temperate oceans. Growth and reproductive rates are known for some areas within the species distribution range and are comparatively higher than rates for other large sharks. These biological characteristics suggest that tiger sharks can support some levels of exploitation. However, the triennial reproductive cycle suggested for the species could greatly reduce its ability to recover from fishing pressure. Moreover, we still lack information on natural mortality for the species, especially in terms of juvenile survivorship. Tiger sharks are caught by several commercial, recreational and artisanal fisheries as a target species or as bycatch. However, records on the actual catch of tiger sharks by many fisheries globally are still mostly under-reported or unknown. The species is also one of the major components in catches from shark control programs that target large shark species in Australia, South Africa and Reunion Island.

My assessment of the tiger shark remains as “Near Threatened”. The species is close to being classified as Threatened under criterion A3bd (Figure 2.6, IUCN 2012). The basis for this assessment is: projected declines in CPUE for eastern Australia that indicated potential significant reduction in the population in that region. However, tiger sharks have a wide-ranging distribution, and although they are caught in a variety of fisheries that represent a major threat for the species, population estimates for the species are scarce. Biological traits of tiger sharks such as rapid growth rates, relatively high reproductive output, moderate rates of intrinsic population increase and low estimated fishing mortality indicates resilience to fishing but also creates vulnerabilities, particularly regarding the three year reproductive cycle and the lack of information on juvenile mortality. Information on stock assessment, population structure and overall population trends for the tiger sharks are still lacking for much of the species distribution and available trends in CPUE that could be used for this assessment were based on three long-term datasets (north-eastern Australia, South Africa and the Northwest Atlantic). The dataset from the Queensland Shark Control Program in Australia is the longest available for the species and allowed projections of trends in
CPUE to be calculated, which suggested a marked decrease of around 95% in CPUE over the length of three generations. However, these projections should be interpreted with caution, as they are based on regression relationships that do not account for demographic metrics or the fluctuation in the catch rate and considering that the time series used in the predictions is relatively short.

Evidence of regional declines is compounded by the continuing exploitation of tiger sharks by commercial, recreational and unregulated fisheries. Catches of the species remain unrecorded by many fisheries and the low numbers of sharks caught by regulated, commercial fisheries do not allow for population trends to be calculated at this time, despite raising concern over population trajectories. Projections from the KwaZulu-Natal beach protection program in South Africa suggest an increase in populations over a period of 25 years. The program releases sharks that are caught alive, which might have contributed to the recorded increase in CPUE. Although the rate of increase in South Africa is lower than the projected decline seen in Queensland, it provides estimates of population trends from standardised catches and suggests that the meshing program is not impacting the tiger shark population of southern Africa. In the northwest Atlantic, increases of 6 - 8% per year in relative abundance (index of absolute abundance based on standardised catch) were also recorded by the Southeast Fisheries Science Centre and the Northeast Fisheries Science Centre (NOAA) for the bottom longline shark fishery and fisheries independent longline surveys that are active throughout the Gulf of Mexico and US eastern coastline. However, this rate of increase should be treated with caution, since the time series of data has a much shorter temporal range than data from Queensland.

It is recommended that further research is required to accurately assess exploitation rates by fisheries and to define population size, structure and trends throughout the species range. It is also recommended that the trends from shark control programs in Australia should continue to be monitored in relation to the Red List criteria (A3bd) and the projections made by this assessment. Continuing declines in Queensland and New South Wales may possibly determine if these populations have attained a level of threat that would recommend the update of the status assessment to “Vulnerable”. Recent evidence based on global genetics of tiger sharks indicated separation between the populations in the western Atlantic and Indo-Pacific (Bernard et al. 2016). Based on these results, it is also recommended that tiger shark populations from different ocean basins and regions should be assessed separately by the IUCN. Regional assessments
could consider CPUE trends reported from the northwest Atlantic and South Africa separately from the trend in Australia and will potentially better reflect the threat level, population trends and conservation status for each population of tiger sharks.

**SUMMARY OF THE FIVE CRITERIA (A - E) USED TO EVALUATE IF A TAXON BELONGS IN AN IUCN RED LIST THREATENED CATEGORY (CRITICALLY ENDANGERED, ENDANGERED OR VULNERABLE).**

<table>
<thead>
<tr>
<th>A. Population size reduction. Population reduction (measured over the longer of 10 years or 3 generations) based on any of A1 to A4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Critically Endangered</td>
</tr>
<tr>
<td>A1</td>
</tr>
<tr>
<td>A2, A3 &amp; A4</td>
</tr>
</tbody>
</table>

- Population reduction observed, estimated, inferred, or suspected in the past where the causes of the reduction are clearly reversible AND understood AND have ceased.
- Population reduction observed, estimated, inferred, or suspected in the past where the causes of reduction may not have ceased OR may not be understood OR may not be reversible.
- Population reduction projected, inferred or suspected to be met in the future (up to a maximum of 100 years) [to be used for A3].
- An observed, estimated, inferred, projected or suspected population reduction where the time period must include both the past and the future (up to a max. of 100 years in future), and where the causes of reduction may not have ceased OR may not be understood OR may not be reversible.

- (a) direct observation (except A2)
- (b) an index of abundance appropriate to the taxon
- (c) a decline in area of occupancy (AOO), extent of occurrence (EOO) and/or habitat quality
- (d) actual or potential levels of exploitation
- (e) effects of introduced taxa, hybridization, pathogens, pollutants, competitors or parasites.

<table>
<thead>
<tr>
<th>B. Geographic range in the form of either B1 (extent of occurrence) AND/OR B2 (area of occupancy)</th>
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</thead>
<tbody>
<tr>
<td>Critically Endangered</td>
</tr>
<tr>
<td>B1. Extent of occurrence (EOO)</td>
</tr>
<tr>
<td>B2. Area of occupancy (AOO)</td>
</tr>
</tbody>
</table>

AND at least 2 of the following 3 conditions:

- (a) Severely fragmented OR Number of locations = 1
- (b) Continuing decline observed, estimated, inferred or projected in any of: (i) extent of occurrence; (ii) area of occupancy; (iii) area, extent and/or quality of habitat; (iv) number of locations; (v) subpopulations; (vi) number of mature individuals
- (c) Extreme fluctuations in any of: (i) extent of occurrence; (ii) area of occupancy; (iii) number of locations or subpopulations; (iv) number of mature individuals

<table>
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<tr>
<th>C. Small population size and decline</th>
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<tbody>
<tr>
<td>Critically Endangered</td>
</tr>
<tr>
<td>Number of mature individuals</td>
</tr>
</tbody>
</table>

AND at least one of C1 or C2

- C1. An observed, estimated or projected continuing decline of at least (up to a max. of 100 years in future):
  - 25% in 3 years or 1 generation (whichever is longer)
  - 20% in 5 years or 2 generations (whichever is longer)
  - 10% in 10 years or 3 generations (whichever is longer)

- C2. An observed, estimated, projected or inferred continuing decline AND at least 1 of the following 3 conditions:
  - (a) Number of mature individuals in each subpopulation ≤ 50
  - (b) % of mature individuals in one subpopulation ≤ 90-100%
  - (c) Number of mature individuals in one subpopulation ≤ 95-100%
  - (d) Number of mature individuals in one subpopulation ≤ 100%

<table>
<thead>
<tr>
<th>D. Very small or restricted population</th>
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<tr>
<td>Critically Endangered</td>
</tr>
<tr>
<td>Number of mature individuals</td>
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</tbody>
</table>

- D2. Only applies to the VU category
- Restricted area of occupancy or number of locations with a plausible future threat that could drive the taxon to CR or EX in a very short time.

- D2. typically:
- AOO < 20 km² or number of locations ≤ 5

<table>
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<tr>
<th>E. Quantitative Analysis</th>
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<tr>
<td>Critically Endangered</td>
</tr>
<tr>
<td>Indicating the probability of extinction in the wild to be:</td>
</tr>
</tbody>
</table>

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1 Use of this summary sheet requires full understanding of the IUCN Red List Categories and Criteria and Guidelines for Using the IUCN Red List Categories and Criteria. Please refer to both documents for explanations of terms and concepts used here.

**Figure 2.7** Summary table of the criteria (A - E) used to evaluate Red List status (IUCN 2012).
Chapter 3  
Crossing latitudes - long-distance tracking of an apex predator

3.1  Abstract

Tiger sharks (*Galeocerdo cuvier*) are apex predators occurring in most tropical and warm temperate marine ecosystems, but we know relatively little of their patterns of residency and movement over large spatial and temporal scales. We deployed satellite tags on eleven tiger sharks off the north-western coast of Western Australia and used the Brownian Bridge kernel method to calculate home ranges and analyse movement behaviour. One individual recorded one of the largest geographical ranges of movement ever reported for the species, travelling over 4000 km during 517 days of monitoring. Tags on the remainder of the sharks reported for shorter periods (7 - 191 days). Most of these sharks had restricted movements and long-term (30 - 188 days) residency in coastal waters in the vicinity of the area where they were tagged. Core home range areas of sharks varied greatly from 1166.9 to 634,944 km$^2$. Tiger sharks spent most of their time in water temperatures between 23$^\circ$ - 26$^\circ$C but experienced temperatures ranging from 6$^\circ$C to 33$^\circ$C. One shark displayed seasonal movements among three distinct home range cores spread along most of the coast of Western Australia and generalized linear models showed that this individual had different patterns of temperature and depth occupancy in each region of the coast, with the highest probability of residency occurring in the shallowest areas of the coast with water temperatures above 23$^\circ$C. These results suggest that tiger sharks can migrate over very large distances and across latitudes ranging from tropical to the cool temperate waters. Such extensive long-term movements may be a key element influencing the connectivity of populations within and among ocean basins.

3.2  Introduction

Throughout human history, top-order predators have been disproportionately and negatively affected by anthropogenic activities, both directly through human behaviour such as hunting and indirectly by alteration of habitat and depletion of their food resources (Jackson *et al.* 2001; Sydeman *et al.* 2006; Beschta & Ripple 2009; Estes *et al.* 2011). We now know that the ecological impacts of our elimination of top-order predators can be severe, leading to shifts in the composition and resilience of
ecosystems through processes such as mesopredator release and trophic cascades (Pace et al. 1999; Heithaus et al. 2008a; Estes et al. 2011). Globally, the removal of sharks due to fishing has accelerated rapidly in recent decades, with the result that many species are now threatened with or vulnerable to extinction in many regions (Baum et al. 2003; Dulvy et al. 2008, 2014a; Field et al. 2009; Ward-Paige et al. 2010; Ruppert et al. 2013). There is a growing recognition of the importance of sharks as keystone species in the structuring of marine ecosystems through their influence on species composition, biomass and the trophic roles of prey assemblages (Estes et al. 2001; Johnson et al. 2007; Heithaus et al. 2010; Ruppert et al. 2013). However, we remain largely unaware of some of the most basic aspects of the ecology of many species, including movement patterns and habitat requirements. As top-order predators, sharks tend to have large body sizes (Heupel et al. 2014) and thus generally require large areas in which to forage. For this reason, they are likely to undergo long distance (10 - 1000s km) movements that could bring them into contact with multiple habitats, ecosystems and anthropogenic threats (Harestad & Bunnel 1979; McCauley et al. 2012; Heupel et al. 2014).

Tiger sharks (Galeocerdo cuvier) are one of the largest sharks, growing to over 5 m (Compagnio 1984; Randall 1992; Holmes et al. 2012) and the species is both an apex predator and scavenger that occurs in most tropical and warm-temperate marine ecosystems. They feed on a wide array of prey (Grudger 1949; Clark & von Schmidt 1965; Stevens 1984; Stevens & McLoughlin 1991; Randall 1992; Simpfendorfer 1992; Lowe et al. 1996; Heithaus 2001; Simpfendorfer et al. 2001), on which they exert both lethal and behavioural risk effects (Heithaus et al. 2007b). Globally, anthropogenic threats to populations of tiger sharks include commercial fisheries (Polovina & Lau 1993; Bonfil 1997; Castillo-Geniz et al. 1998; Baum et al. 2003; Handley 2010) and illegal, unreported and unregulated (IUU) fishing (Field et al. 2009). Moreover, they have been targeted by shark control programs as a species potentially dangerous to humans (Paterson 1990; Wetherbee et al. 1994; Dudley 1997; Dudley & Simpfendorfer 2006; Hazin et al. 2008; Green et al. 2009) and evidence of declines in populations of tiger sharks have been reported by beach meshing programs in some areas of Australia (Reid et al. 2011; Holmes et al. 2012). However, while the species is classified as “Near Threatened” by the International Union for the Conservation of Nature (IUCN) due to evidence of declines in some populations (Simpfendorfer 2009), broad-scale trends in abundances are still unknown.
Given the anthropogenic threats to these apex predators, information on their movement behaviour, particularly over large spatial and temporal scales (100s - 1000s of km, months to years) is essential for the development of appropriate management and conservation strategies (Sims 2010; Block et al. 2011; Papastamatiou & Lowe 2012; Drymon et al. 2013). To date, most information on the horizontal movements of tiger sharks is available from SPOT and PAT satellite tracking studies conducted at relatively small temporal scales (<1 year; e.g. (Heithaus et al. 2007c; Meyer et al. 2010; Fitzpatrick et al. 2012; Hazin et al. 2013; Werry et al. 2014)). The information provided by SPOT transmitters is usually limited by the relatively short intervals that sharks spend on the surface, which results in low numbers of location estimates, obtained at irregular intervals and typically with low spatial resolution (Heithaus et al. 2007c; Fitzpatrick et al. 2012). Additionally, physical damage, biofouling and premature shedding of tracking devices are also widely reported (Kerstetter et al. 2004; Heithaus et al. 2007c; Hays et al. 2007; Meyer et al. 2010), resulting in short and sparse location data sets. For PAT tags in particular, deployment periods are commonly much shorter than programmed due to tag damage and biofouling that may cause premature release of the tag. Longer-term tracking studies have used passive acoustic telemetry to monitor movements of tiger sharks (e.g. (Holland et al. 1999; Meyer et al. 2009; Papastamatiou et al. 2013; Werry et al. 2014)), but these are limited by the detection range of receivers and the number and scale of receiver arrays (Heupel et al. 2006). Overall, these studies have shown high individual variability in movement patterns of tiger sharks, with some degree of residency in particular habitats interspersed with occasional forays into the open ocean (Heithaus et al. 2007c; Meyer et al. 2010; Werry et al. 2014).

Due to the short duration of most tracking datasets it is unclear whether the wider movements across scales of 1000s of km, typical of other large sharks such as basking (Cetorhinus maximus), white (Carcharodon carcharias) and whale sharks (Rhincodon typus) (Boustany et al. 2002; Bonfil et al. 2005; Bruce et al. 2006; Wilson et al. 2007; Skomal et al. 2009; Farmer & Wilson 2011; Domeier & Nasby-Lucas 2013) might also exist for tiger sharks. Our study reports on the results of the deployment of eleven satellite transmitters on tiger sharks, one of which produced one of the longest duration tracks ever recorded for the species (517 days). In combination with the results from the other deployments, we examined horizontal and vertical movements of tiger sharks and quantified habitats of high and low use. We hypothesise that tiger sharks display a mix
of both restricted and transient movement, and that residency patterns will be driven by water temperature and bathymetry.

3.3 Material and Methods

Ethics statement

This project was conducted under permit number SF6104, WA Fisheries permit 2007–30–32, and ethics approvals A07035 (Charles Darwin University Ethics Committee) and DPIW 7/2007–08.

Tiger sharks were caught using longlines off Ningaloo Reef, Western Australia, in June 2007, August 2008 and May-June 2010. Between 118 and 350 hooks were set at approximately 10 m intervals along one to five demersal longlines deployed on the seaward side of the reef each day. Longlines were usually deployed at dawn, with a few deployments at dusk. Short soak times of between 2.2 h to 5.2 h were used to maximise the survival rates of captured sharks. One shark (Shark 7) was caught by rod and reel between longline sets. Hooked sharks were brought on deck or restrained in a stretcher at the stern of the vessel, measured and sexed. Eleven tiger sharks were instrumented with fin-mounted satellite-linked transmitters (SPOT4, SPOT5 or SPLASH tags, Wildlife Computers, Redmond, Washington, USA); however, three did not report any data after they were deployed (Table 3.1). All reporting transmitters relayed satellite positions via the ARGOS satellite network and time-at-temperature histograms in 14 user-defined temperature ranges from 0°C to 60° (± 0.2°C). Two SPLASH tags (Table 3.1) also relayed summaries of time-at-depth with user-defined depth ranges of 0-600 m and 0-800 m (± 0.5 m).

Position estimates were provided by ARGOS with an associated error (Location Class (LC) of 3 (<250 m), 2 (250–500 m), 1 (500–1500 m), 0 (>1500 m), A and B (not specified), www.argos-system.org). A small amount (0.5%) of location points were excluded or substituted by the secondary location estimate reported by ARGOS because they were obviously erroneous, i.e. they were well beyond the bounds of possible distances the shark could have travelled based on both earlier and later location estimates for the track. An analysis of the travel speed found that these erroneous locations required a travel speed of >1000 km per day. More advanced filtering methods were attempted, such as a Bayesian state-space model; however, the models did not converge, probably due to the sparseness of the data.
We calculated the home range of tiger sharks using the Brownian Bridge kernel method using the adehabitatHR package in R software V2.15.3 (Calenge 2011; R Core Team 2013). This method takes into account not only the shark locations, but also the path travelled by the animal between successive locations (Bullard 1991; Horne et al. 2007) by applying a conditional random walk to model the expected path between locations. Two smoothing parameters were set: sig1, which controlled the width of the “bridge" connecting successive positions (this is the Brownian Bridge motion variance parameter - BMV); and sig2, which was related to the imprecision of the positions. Values of sig1 were chosen using the function liker that implemented the maximum likelihood approach developed by Horne (Horne et al. 2007) and sig2 was set at 1.9 km, the median ARGOS location error across pooled position classes (Costa et al. 2010b). Tracks from Sharks 1 and 2 were removed from the analysis due to their very short length (7 and 14 days respectively). Because of the possibility of effects of tagging on behaviour, we assumed that the first two weeks might not be representative of the shark’s natural behaviour (Afonso & Hazin 2014). Location estimates from Sharks 3 and 8 were particularly sparse (0.18 and 0.04 locations per day respectively), and Shark 3 had a very high Brownian Bridge motion variance parameter compared to the scale of the shark’s movements (sig1 = 822.5). Consequently, these tracks were not included in further analyses of home range.

The proportion of observations in each temperature and depth bin was calculated from time-at-temperature and time-at-depth histograms provided by the tag to determine thermal and depth range of all sharks. For one shark (Shark 5), time-at-temperature histograms associated with latitude/longitude information were used to assess variation in the proportion of time at temperature. Water temperature profiles were constructed from data downloaded from IMOS floats (IMOS, http://imos.aodn.org.au/imos/) located in the vicinity of position uplinks within a week of the time the uplinks were recorded (South coast of WA: 35.378°S, 119.531°E; North coast of WA: 17.604°S, 117.657°E). Maximum possible diving depth of Shark 5 was estimated by comparing the minimum temperature registered by the shark’s tag with profiles of water temperature from IMOS floats in the same region where the shark was resident. The maximum depth of descent was assumed to be the greatest depth in the water temperature profile where the minimum temperatures reported by the tag and those of the water temperature profile were the same. For the track with multiple home range cores (Shark 5), movement patterns were categorised as within and outside the 25% utilisation distribution. We then
used generalised linear models with a binomial distribution and a logit link function to assess the relationship between the probability of the shark being in a home range core and water temperature, bathymetry and region of the WA coast (north - latitude < 24°S and south - latitude >24°S). We were not able to fit all three explanatory variables in one model as there was no overlap of the temperature ranges between the two regions. Consequently, we fitted a model to examine the probability of being in a home range core in relation to bathymetry and region and two separate models (using the data from north and south coasts, respectively) to examine the probability of the shark being in a home range core in relation to sea surface temperature. To address the autocorrelation present in the data we used a matched-block bootstrap sampling for all models with replacement procedure (Carlstein et al. 1998; Politis & White 2004) that resampled blocks of data randomly and then recombined them in a random order, creating a bootstrapped dataset that minimized the effect of autocorrelation (Carlstein et al. 1998; Politis & White 2004; Patton et al. 2009). Model fitting was applied to 100 bootstrapped samples and model selection used the sample-corrected Akaike’s information criterion (AICc), AICc weight (wAICc), and percent deviance explained (%DE) (Burnham & Anderson 2004; Vianna et al. 2013). Bathymetry data with a grid resolution of 2° from ETOPO1 database hosted by the NOAA was obtained by the R software package marmap (Pante & Simon-Bouhet 2013). Daily Sea Surface Temperature was obtained through the daily Optimum Interpolation Sea Surface Temperature (OISST) analysis (Reynolds et al. 2007) on a 0.25 degree latitude/longitude grid from NOAA’s National Climatic Data Centre (ftp://eclipse.ncdc.noaa.gov/pub/OI-daily-v2/NetCDF).

Table 3.1. Details of satellite transmitter deployments on tiger sharks.

<table>
<thead>
<tr>
<th>ID</th>
<th>Fork length (cm)</th>
<th>Sex</th>
<th>Date deployed</th>
<th>Location</th>
<th>Type</th>
<th>Duration of transmission (days)</th>
<th>Locations day⁻¹ (mean ± SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>145</td>
<td>F</td>
<td>19/06/2007</td>
<td>23.32°S 113.71°E</td>
<td>SPOT</td>
<td>7</td>
<td>0.75 (±1.16)</td>
</tr>
<tr>
<td>2</td>
<td>276</td>
<td>F</td>
<td>21/06/2007</td>
<td>22.97°S 113.76°E</td>
<td>SPLASH</td>
<td>14</td>
<td>0.92 (±1.50)</td>
</tr>
<tr>
<td>3</td>
<td>179</td>
<td>F</td>
<td>17/08/2008</td>
<td>21.86°S 113.96°E</td>
<td>SPOT</td>
<td>105</td>
<td>0.18 (±0.43)</td>
</tr>
<tr>
<td>4</td>
<td>214</td>
<td>F</td>
<td>19/08/2008</td>
<td>22.38°S 113.73°E</td>
<td>SPOT</td>
<td>70</td>
<td>0.54 (±0.83)</td>
</tr>
<tr>
<td>5</td>
<td>222</td>
<td>F</td>
<td>19/08/2008</td>
<td>22.42°S 113.71°E</td>
<td>SPOT</td>
<td>517</td>
<td>0.43 (±0.95)</td>
</tr>
<tr>
<td>6</td>
<td>333</td>
<td>M</td>
<td>27/05/2010</td>
<td>23.07°S 113.70°E</td>
<td>SPOT</td>
<td>191</td>
<td>1.86 (±1.66)</td>
</tr>
<tr>
<td>7</td>
<td>224</td>
<td>M</td>
<td>2/06/2010</td>
<td>21.58°S 114.52°E</td>
<td>SPOT</td>
<td>38</td>
<td>0.60 (±0.72)</td>
</tr>
<tr>
<td>8</td>
<td>240</td>
<td>F</td>
<td>30/05/2010</td>
<td>22.27°S 113.72°E</td>
<td>SPLASH</td>
<td>154</td>
<td>0.04 (±0.19)</td>
</tr>
<tr>
<td>9</td>
<td>155</td>
<td>F</td>
<td>19/06/2007</td>
<td>23.35°S 113.72°E</td>
<td>SPOT</td>
<td>Did not report</td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>252</td>
<td>F</td>
<td>21/06/2007</td>
<td>22.97°S 113.76°E</td>
<td>SPLASH</td>
<td>Did not report</td>
<td></td>
</tr>
<tr>
<td>11</td>
<td>254</td>
<td>F</td>
<td>20/08/2008</td>
<td>22.66°S 113.60°E</td>
<td>SPLASH</td>
<td>Did not report</td>
<td></td>
</tr>
</tbody>
</table>
3.4 Results

The time that data was received from the tagged sharks varied greatly among individuals (7 to 517 days; Table 3.1). 49% of locations were from ARGOS Location Class B, 20% were from Location Class A and only 31% of locations were within Location Classes 3-0. Four satellite transmitters provided data for less than 100 days but even the longest deployments had long periods of no transmission. For example, Shark 5 had a period of 118 days between May and September 2009 when no location data were transmitted, while Shark 8 did not transmit data between July and October 2010.

Transmitters deployed on three sharks (1, 2 and 7) provided data for only 7, 14 and 38 days respectively. During this time they occupied waters with average depths of 42.2 m (± 26.8 m SD) and their movements were restricted to the vicinity of where they were initially tagged (Figure 3.1a) on the shelf. Three sharks (3, 4 and 6; Figure 3.1b-c) stayed within shelf waters that averaged 117.5 m deep (± 113.0 m SD). Shark 6’s movements were restricted to a relatively small area (1166.9 km²) off the Ningaloo Reef for six months (Figure 3.1c). Shark 8 moved 303.4 km from the point of first capture and tagging into waters over 5000 m deep, where the last data transmission was received (Figure 3.1b). There were six position estimates in this area and the data were very limited for the duration of tracking (154 days between tagging and the last uplink). One shark (Shark 5) ranged over 4000 km and apart from one period of approximately three and a half months, provided relatively frequent transmissions over 517 days of monitoring (Figure 3.1d).
Figure 3.1 Movement patterns of tiger sharks in Western Australia. Maps show location uplinks of 8 tiger sharks. Triangles indicate tagging location and grey polygons indicate Commonwealth Marine Reserves.

The kernel utilisation distributions of all sharks indicated movement between coastal regions and islands or atolls off the north coast of Western Australia, with predominant use of coastal waters (Figure 3.2). The 50% kernel utilisation distributions varied greatly in area from 1166.9 km$^2$ to 634,944 km$^2$ among sharks (Figure 3.2). Overall, a total of 56.7% of all locations received from the satellite transmitters were within the Commonwealth Marine Reserve network. All sharks had some locations inside marine reserves and six of the sharks had 50% or more locations inside reserves (Figure 3.1).
Figure 3.2 Home range of tiger sharks. The utilisation distribution calculated using the Brownian Bridge kernel method. Black line represents the 50% Brownian Bridge home range distribution.

Shark 5, a 222 cm female, was monitored for 517 days and ranged from 10.4°S to 35.8°S of latitude and from 113.0°E to 124.1°E of longitude (Figure 3.1d). The transmitter was deployed on this shark at Ningaloo Reef and the shark then moved along the 500 m bathymetric contour to the Rowley Shoals and Kimberley region. It then made a path to Sumba Island, Indonesia, and returned, crossing ocean depths of 5 km and covering a distance of more than 1000 km in 2 weeks. In December 2008 the shark moved south, traveling to waters off Jurien Bay and Perth between January-February 2009. Between April and May 2009 the shark rounded Cape Leeuwin with transmissions clustering off Albany. After a period of no transmissions (118 days), the tag then started to transmit again in September when the shark moved towards the north, returning again to Perth/Jurien Bay in January 2010. The shark had three distinct areas of 50% Brownian Bridge kernel utilisation that included a large area off the north coast of Western Australia, another off Jurien Bay and Perth and a smaller one off the coast of Albany (Figure 3.2).
Table 3.2 Ranked Generalised Linear Models with bootstrap sampling of the probability of a shark being in a 25% utilisation distribution explained by bathymetry (Depth) and region of the coast (Region).

<table>
<thead>
<tr>
<th>Model</th>
<th>LL</th>
<th>df</th>
<th>AICc</th>
<th>wAICc</th>
<th>%DE</th>
<th>LL.25</th>
<th>LL.75</th>
<th>wAICc.25</th>
<th>wAICc.75</th>
<th>AICc.25</th>
<th>AICc.75</th>
<th>%DE.25</th>
<th>%DE.75</th>
</tr>
</thead>
<tbody>
<tr>
<td>Home · Depth</td>
<td>-82.456</td>
<td>2</td>
<td>168.967</td>
<td>0.508</td>
<td>34.49</td>
<td>-124.637</td>
<td>-101.77</td>
<td>0.001</td>
<td>207.595</td>
<td>253.328</td>
<td>5.75E+00</td>
<td>20.347</td>
<td></td>
</tr>
<tr>
<td>Home · Depth + Region</td>
<td>-82.010</td>
<td>3</td>
<td>170.131</td>
<td>0.284</td>
<td>34.84</td>
<td>-122.153</td>
<td>-97.006</td>
<td>0.167</td>
<td>200.125</td>
<td>250.417</td>
<td>6.85E+00</td>
<td>23.756</td>
<td></td>
</tr>
<tr>
<td>Home · Depth*Region</td>
<td>-81.283</td>
<td>4</td>
<td>170.751</td>
<td>0.208</td>
<td>35.42</td>
<td>-117.994</td>
<td>-95.781</td>
<td>0.221</td>
<td>199.749</td>
<td>244.173</td>
<td>9.53E+00</td>
<td>25.453</td>
<td></td>
</tr>
<tr>
<td>Home · Region</td>
<td>-125.803</td>
<td>2</td>
<td>255.661</td>
<td>0.000</td>
<td>0.05</td>
<td>-134.792</td>
<td>-118.812</td>
<td>0.001</td>
<td>241.678</td>
<td>273.639</td>
<td>2.98E-01</td>
<td>4.687</td>
<td></td>
</tr>
<tr>
<td>Home · 1 (Null)</td>
<td>-125.863</td>
<td>1</td>
<td>253.744</td>
<td>0.000</td>
<td>0.00</td>
<td>-137.028</td>
<td>-124.8</td>
<td>0.000</td>
<td>251.678</td>
<td>276.075</td>
<td>1.91E-14</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

Maximum log-likelihood (LL), degrees of freedom (df), Akaike’s information criterion corrected for small samples (AICc), AICc weight (wAICc), the % deviation explained (%DE), lower quantile LCI (25th quantile) (25%) for LL, wAICc.25, AICc.25 and %DE.25 and upper quantile (75th quantile) for LL, wAICc.75, AICc.75 and %DE.75.

Table 3.3 Ranked Generalised Linear Models with bootstrap sampling of the probability of a shark being in a 25% utilisation distribution explained by sea surface temperature (Temperature) at the north and south coast separately.

<table>
<thead>
<tr>
<th>Model</th>
<th>LL</th>
<th>df</th>
<th>AICc</th>
<th>wAICc</th>
<th>%DE</th>
<th>LL.25</th>
<th>LL.75</th>
<th>wAICc.25</th>
<th>wAICc.75</th>
<th>AICc.25</th>
<th>AICc.75</th>
<th>%DE.25</th>
<th>%DE.75</th>
</tr>
</thead>
<tbody>
<tr>
<td>North</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Home · Temperature</td>
<td>-94.845</td>
<td>2</td>
<td>193.756</td>
<td>0.999</td>
<td>9.67</td>
<td>-101.645</td>
<td>-80.5813</td>
<td>0.748725</td>
<td>1</td>
<td>165.2297</td>
<td>207.3572</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Home · 1 (Null)</td>
<td>-111.514</td>
<td>1</td>
<td>212.024</td>
<td>0.000</td>
<td>0.00</td>
<td>-111.514</td>
<td>-91.553</td>
<td>0.251</td>
<td>185.128</td>
<td>225.05</td>
<td>2.184</td>
<td>25.802</td>
<td></td>
</tr>
<tr>
<td>South</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Home · Temperature</td>
<td>-16.535</td>
<td>2</td>
<td>37.337</td>
<td>1</td>
<td>44.54</td>
<td>13.75475</td>
<td>0</td>
<td>1</td>
<td>4.267</td>
<td>31.7765</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Home · 1 (Null)</td>
<td>-29.812</td>
<td>1</td>
<td>61.711</td>
<td>0.000</td>
<td>0.00</td>
<td>-32.895</td>
<td>-29.812</td>
<td>0</td>
<td>61.711</td>
<td>67.877</td>
<td>30.254</td>
<td>57.026</td>
<td></td>
</tr>
</tbody>
</table>

Maximum log-likelihood (LL), degrees of freedom (df), Akaike’s information criterion corrected for small samples (AICc), AICc weight (wAICc), and the % deviation explained (%DE), lower quantile LCI (25th quantile) (25%) for LL, wAICc.25, AICc.25 and %DE.25 and upper quantile (75th quantile) for LL, wAICc.75, AICc.75 and %DE.75.
Temperatures experienced by sharks ranged from 6°C to 33°C. Overall, tiger sharks spent most of their time in temperatures between 23°-26°C (Figure 3.3). The shark with the widest latitudinal range of movements (Shark 5) also experienced the greatest range of temperatures (from 10°-33°C), but spent approximately 78% of time in temperatures between 23°-29°C. It also experienced different ranges of temperature in each home range (Figure 3.4). Off the Kimberley and Pilbara coasts (10°-24°S of latitude) the
temperature range experienced by the shark was much greater (10°-33°C) than when the shark visited the south coast off Albany (35°S of latitude; 18°-23°C).

**Figure 3.4** Latitudinal variation of temperature profiles for Shark 5. Percentage of time spent in each temperature bin at each region of Western Australia for Shark 5.

**Figure 3.5** Time spent in each depth bin. Percentage of time spent in each depth bin for two tiger sharks tagged with SPLASH tags.

**Figure 3.6** Vertical profiles of water temperature. Plots show temperature profiles recorded by Argo floats of the north (17.6°S 117.6°E) and south (35.78°S 119.5°E) sections of the WA coast. Vertical lines represent the minimum temperature reported by the shark’s satellite transmitter and horizontal lines represent the estimated diving depth.
Time-at-depth histograms of the two sharks with SPLASH tags showed that these individuals differed greatly in depth range (Figure 3.5). The first (Shark 2) did not dive deeper than 150 m, with 27% of observations between the surface and 5 m and 97% in water depths up to 75 m. Locations for this shark were all close to the coast in areas around the 100 m isobath. The second (Shark 8), which moved to pelagic waters experienced a greater range of depths. Though this shark spent 57% of time between the surface and 10 m, it had a maximum recorded depth of 400 m, with approximately 20% of time spent at 150 m.

Water temperatures reported by Shark 5, which was tracked for 517 days, were used to estimate diving depths. Analyses of the vertical profiles of water temperature in each region where location data were recorded indicated that the shark was diving up to 380 m in tropical latitudes, but not descending below 100 m in temperate latitudes (Figure 3.6). Sea surface temperatures were consistent with a strong Leeuwin Current that supplied a warm mass of water around the Cape Leeuwin and Albany coasts with temperatures of 19°-23°C during the time locations were registered in this region (Figure S 3.1). Here, the shark spent 82% of time in waters between 21-23°C (Figure 3.4), indicating that it remained relatively close to the surface.

Figure 3.7 Generalised linear model for Shark 5. Generalised linear model (GLM) predicted probabilities (solid line) of a shark being in a 25% utilisation distribution in relation to (a) water depth, (b) water temperature in the north and (c) in the south. Dotted lines show the standard error.
The highest ranking model describing whether the shark remained in a 25% home range core (i.e. remained resident and did not switch to transit behaviour), included water depth only, and explained 34.5% of the deviance in the data set (Table 3.2). There was a negative relationship between the probability of the shark being in a 25% home range core and water depth, meaning the shark was more likely to be resident (in a home range core) in the shallower areas and less likely to remain resident in deeper waters (Figure 3.7). Even though the tiger shark crossed areas over 5000 m deep while migrating, it had low probability of being in a home range core in deeper water (> 1000 m). Temperature explained 9.7% of the deviance in the probability of Shark 5 being in a home range core on the north coast and 44.5% in the south (Table 3.3). In both regions, the shark had a greater than 80% chance of being in a home range core in temperatures of 23-24 °C, suggesting that this was a preferred temperature in both regions (Figure 3.7).

3.5 Discussion

Tiger sharks are typically considered to be residents of tropical and warm temperate habitats (Randall 1992), but individuals appear on a seasonal basis in temperate or cool temperate waters (Last & Stevens 1994). The most extreme examples of this pattern are the occasional records of tiger shark catches in the waters of countries such as Iceland (Matsumoto et al. 2005) and far off the south coast of New South Wales in Australia (Pepperell 1992). Such occurrences seem to be related to the influx of warm waters brought by western boundary currents such as the Gulf Stream and the East Australian Current (Schmitz & McCartney 1993; Reid 1994; Cresswell 2000). Similarly, in Western Australia the Leeuwin Current flows southward bringing warm, low salinity water along the shelf into the cool temperate environments off Albany (35°S) (Smith et al. 1991). In our study, one shark moved into temperate waters twice, both times during the summer months of January-February. This implies that such behaviour is most likely to be the result of directed and seasonal migrations, rather than simply a haphazard event. Other evidence to support this idea of regular southward movements of tiger sharks during the austral summer comes from data from beach protection programs, which show that tiger sharks are more common off the coast of New South Wales, a temperate region in the southeast of Australia, during summer (Krogh 1994; Reid et al. 2011), when the warm East Australian Current flows southward. A recent tagging study found that a tiger shark moved to warmer waters off Queensland during winter and went south to 37°S latitude during the austral summer (Holmes et al. 2014).
Similarly, the abundance of tiger sharks in the Aliwal Shoals off South Africa increases during summer months (Dicken & Hosking 2009).

The shark we tracked for 517 days had home range core areas in both the tropics (15°-20°S) and the cool-temperate coast off Albany (35°S). The movement of this shark to temperate waters off Perth occurred twice in consecutive years, both times during January. Overall, this track was the longest and covered one of the greatest range of latitudes recorded by satellite telemetry for the species. However, such movements are not entirely without precedent. For example, a fisheries tagging study recorded tiger sharks travelling more than 3,400 km in the Atlantic (Kohler et al. 1998) and recent satellite tagging studies have shown tiger sharks swimming distances of over 1000 km in the South Pacific (Werry et al. 2014; Holmes et al. 2014), and as far as 3500 km from the tagging site in the North Atlantic (Hammerschlag et al. 2012). A study by Heithaus et al. (2007b) recorded a potential movement of a tiger shark of 8000 km from the point where it was tagged in Shark Bay, WA to the coast of South Africa. However, this result was inferred from a single low-quality position fix that could not confirm if the tag was still attached to the shark or determine if the position estimate was simply an artefact of the position estimation algorithm. In our study, associated water temperature data reported by the tag and multiple position fixes showed that the track of the shark was both reliable and that the tag remained deployed on the shark. In terms of geographic scale, the movements of this tiger shark were comparable to those of white sharks (Carcharodon carcharias), which in certain regions appear to display seasonal residency at cool temperate coastal locations, mostly in areas with high abundances of pinnipeds (Bruce 1992; Klimley et al. 2001a; Domeier & Nasby-Lucas 2007; Johnson et al. 2009), interspersed with long oceanic migrations into the tropics (Boustany et al. 2002; Bonfil et al. 2005; Bruce et al. 2006; Domeier & Nasby-Lucas 2008).

The durations of residency and distances of migration of tiger sharks recorded by our study appear to be at least partly related to the length of tag deployment. When tags reported for a short time, movements of sharks tended to be restricted to one home range core within a relatively small area. However, longer-term tag deployments revealed a very different pattern, where periods of residency were interspersed with long distance (100 -1000s km) movements that appeared both directed and predictable. However, some individuals appeared highly resident despite relatively long tagging records (up to 6 months) suggesting that two forms of movement may be present. In our study, home range cores (averaging 4,474.1 km², excluding Shark 5) were consistent
with earlier work that has shown movement patterns of tiger sharks off the east coast of Australia (Holmes et al. 2014) and the Florida coast (Hammerschlag et al. 2012).

Similar to our results, most other studies of tiger sharks have also shown that the degree of residency varies greatly among individuals. Fitzpatrick et al. (2012) found that some sharks remained in the area of Raine Island on the Great Barrier Reef throughout the year, while others ventured into the Coral Sea and to the Torres Strait and northern Great Barrier Reef. Werry et al (Werry et al. 2014) found that tiger sharks could reside year-round at the atolls of the Chesterfield Reefs, with other sharks venturing over 1000 km into the open ocean. Meyer et al. (2010) found that some tiger sharks were resident on the French Frigate Shoals of Hawaii throughout the year, while others were recorded at this locality only when fledging seabirds were available as a food source during summer. It has been suggested that variations in movement behaviour of tiger sharks might be due to partial migrations, where only a part of the population would be transient and perform large scale movements while the other part would show resident behaviour (Papastamatiou et al. 2013; Werry et al. 2014). Although our study was comprised of a small sample size, recent tagging studies in Florida, Bahamas, Australia and New Caledonia have consistently demonstrated that a few individuals can move over large distances while most of the remainder sharks show more restricted residency patterns (Hammerschlag et al. 2012; Werry et al. 2014; Holmes et al. 2014). Analyses involving larger datasets are needed to understand the characteristics of individuals that show these partial and/or complete migrations, to determine their prevalence and to identify the drivers that lead to differential patterns of movement.

Despite the number of satellite and acoustic telemetry studies now describing the horizontal movements of tiger sharks (approximately 10 to date) it is difficult to determine if there are consistent patterns in the life stage or sex of individuals that are likely to remain resident or migrate. Meyer et al. (2009) suggested that juveniles were more likely to display broad-scale patterns of movement than other components of the population, a pattern also recorded in Northeast Brazil (Hazin et al. 2013). The individual that we recorded moving the greatest distance on the WA coast was also a sub-adult (female). In contrast, Papastamatiou et al. (2013) found that adult females were the most likely to migrate among the islands of Hawaiian Archipelago, a pattern they attributed to the movement of females to pupping sites. However, these researchers mostly relied on records generated from acoustic tracking and a receiver array in coastal waters, limiting the possibility of recording movements of sharks into the open ocean.
The tagged tiger sharks showed preferences for temperatures between 23° and 26°C, consistent with surface waters off Ningaloo Reef (Taylor & Pearce 1999), although the sharks experienced temperatures as low as 6°C. These lower temperatures suggest that sharks were descending below the thermocline (± 100-200 m depths at Ningaloo Reef; Rousseaux et al. 2012). Data from a SPLASH tag deployed on Shark 8 recorded occasional transits to depths of 400 m, although time-at-depth histograms showed a preference by this shark for shallow waters (65% of time in depths < 50 m) within the mixed layer of the water column, similar to patterns reported by other studies (Holland et al. 1999; Meyer et al. 2010; Nakamura et al. 2011; Fitzpatrick et al. 2012; Hazin et al. 2013; Werry et al. 2014; Vaudo et al. 2014). For five sharks, location estimates at Ningaloo Reef with depths <15 m suggested that some sharks spent time in the shallow lagoon.

Shark 5 experienced a wide range of temperatures within a home range in the tropics, suggesting that it used the water column to depths of 380 m, well below the thermocline in this region (Rousseaux et al. 2012). When the shark moved to the south coast off Albany, it remained in waters above 100 m deep, implying that its vertical movements may have been constrained by water temperatures when in the cooler waters at more southern latitudes.

The long-term residency of tiger sharks in limited areas implies that they may have strong structuring effects on those ecosystems. A study conducted for 15 years (Heithaus et al. 2012) found that the presence of tiger sharks at Shark Bay had major influences on the behaviour, movement and feeding of prey such as dolphins, turtles and dugongs, but beyond this largely seagrass habitat, we have little idea of the role of these predators in environments such as coral or temperate reef systems. In addition to quantifying the residency patterns of tiger sharks, our study showed large-scale movements that have implications for conservation, since this behaviour may take them across management and national boundaries. In our study, more than half of the locations provided by satellite transmitters were within the Commonwealth Marine Reserves network, although our results also support the suggestion that such regional scale management zones are likely to only provide temporary protection for some parts of the population or life history stages (Hooker et al. 1999; Chapman et al. 2005; Heupel et al. 2014; Werry et al. 2014). The movement of sharks from Australia to Indonesian waters also shows that conservation of these animals will also depend on international cooperation to mitigate anthropogenic threats to the resilience of the
species, such as the large IUU shark fishery in Australia’s northern waters and small-scale shark fishing industry in Indonesia to the north (Field et al. 2009).

Future research efforts will be aided by technological developments of satellite transmitters and attachment methods. One such development, the Fastloc™ GPS, already exists, however is unavailable on fin-mounted devices. Fastloc tags are capable of acquiring the data required for a location fix in a much shorter period of time and with greater location accuracy than other types of satellite tags, improving both the frequency of location estimates and the accuracy of position fixes. Ultimately, there are two key goals that must be achieved in order to obtain a better understanding of the movement ecology of tiger sharks: firstly, improved attachment techniques for tags that allow both frequent uploads of position data and long deployments (> 1 year) and secondly, tagging of a larger number of animals and a wider range of life history stages of both sexes. Our study shows that these advances will be necessary to gain a better appreciation of the role of these animals in the ecology of marine ecosystems.

3.6 Acknowledgments

We acknowledge the Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil.
3.7 Supporting information

**Figure S 3.1.** Sea Surface Temperature map (smoothed OISST data) for 16th May 2009 with location uplinks for Shark 5.
Chapter 4  Diet and trophic role of a large marine predator, the tiger shark *Galeocerdo cuvier*

4.1  Abstract

Stable isotope analysis of tissues reveals diet, trophic niche and food-web interactions of animals over a range of temporal scales. Multiple tissues (muscle, fin, dermis, blood) of tiger sharks were sampled at Ningaloo Reef and Shark Bay in Western Australia and from the Great Barrier Reef (GBR), southern Queensland and the central New South Wales (NSW) coasts in eastern Australia. Stable isotope analysis was used to investigate the effects of location, size and sex of sharks on diet, trophic ecology and role among these locations. Sharks sampled in Shark Bay and on the GBR had a diet that was based on seagrass food chains, whereas sharks at Ningaloo Reef had diet that was transitional between pelagic and seagrass chains. Sharks collected in NSW had a diet based on pelagic food chains with an isotopic signature consistent with earlier studies of the species at Réunion Island and in South Africa. Tiger sharks were located at the top of the food-chain at Shark Bay and on the Great Barrier Reef (GBR); however, these predators did not occupy apex roles at Ningaloo Reef or in New South Wales. Bayesian standard ellipses were used to assess niche occupancy and generalised linear models were used to test the effect of shark size, location and sex on $\delta^{13}C$ and $\delta^{15}N$ values derived from the results of isotope analyses of each tissue. Analysis of muscle samples suggested that niche width of female sharks in Queensland was broader than that of males in the same locality and the niche widths of both sexes in NSW. The diet of tiger sharks became more enriched in $^{13}C$ with increasing body size and towards tropical latitudes consistent with a diet shifted towards large marine herbivores. Analysis of other tissues (dermis, red blood cells and plasma) also showed a distinct trophic niche of sharks at Ningaloo Reef, where they exhibited lower levels of $\delta^{13}C$ values than at Shark Bay or on the GBR. Diets of sharks at Ningaloo were more stable in the short term (weeks) than at Shark Bay or on the GBR. The large amount of spatial variation in $\delta^{13}C$ values indicated that diet and trophic role seems to be context and habitat dependent, and reflects variations in food-web complexity, the availability of resources and body size of tiger sharks.
4.2 Introduction

Marine megafauna such as large sharks, cetaceans, billfishes and tunas typically occupy upper trophic levels in marine food webs. Although their direct predation on - and induced anti-predator behaviours (risk effects) in - their potential prey can structure marine ecosystems (Heithaus et al. 2010; Wirsing & Ripple 2011; Heupel et al. 2014), it is often difficult to quantify their trophic interactions. First, top-order predators are a relatively rare component of food-webs and documenting their feeding behaviours within a three-dimensional environment presents some unique logistic obstacles that still challenge available technology (Hays et al. 2016). Second, the prey targeted by many top-order species may not be consistent in space and time. Most predators can switch among potential prey taxa depending on context and availability in order to optimise energy gain from foraging behaviour (Beck et al. 2007; Thums et al. 2011).

Difficulties involved in the direct observation of feeding behaviour of marine megafauna have led to the use of alternative techniques to provide insights into the process of foraging. One of the most common of these is the analysis of stable isotopes of carbon and nitrogen of consumers’ tissues, which can provide information on diet (Hobson & Clark 1992; Hussey et al. 2011), trophic niche (Bearhop et al. 2004; Newsome et al. 2007), trophic interactions among different species (Churchill 2015; Kiszka et al. 2015), and migratory movements (Hobson 1999; Phillips et al. 2009). Ratios of nitrogen isotopes ($^{15}$N/$^{14}$N = δ$^{15}$N) indicate the trophic position of a predator in the food web and the δ$^{15}$N composition of its prey, whereas ratios of carbon ($^{13}$C/$^{12}$C = δ$^{13}$C) indicate the basal source of carbon in the food chain (Post 2002). Together, δ$^{15}$N and δ$^{13}$C can provide a general understanding of the structure of a food web (Vander Zanden & Rasmussen 2001).

In marine ecosystems, values of δ$^{13}$C in primary producers are indicative of environmental (inshore to offshore) and carbon source (benthic to pelagic) gradients (Hobson et al. 1994; Clementz & Koch 2001). However, for highly mobile and slow-growing predators such as some large sharks, the interpretation of stable isotopic values must consider the time taken to incorporate isotopes into different tissues (Hobson & Clark 1992; Malpica-Cruz et al. 2012). Blood plasma and liver have rapid turnover rates due to their high catabolic rate and represent a short-term (days to weeks) integration of a predator’s diet (Meyer et al. 2010). In contrast, muscle, red blood cells, cartilage and fin have slower turnover rates and provide long-term (months to years) integration of...
dietary information (Matich et al. 2010; Malpica-Cruz et al. 2012). This means that the isotopic composition measured from different tissues within the same individual can resolve dietary information at different time scales (MacNeil et al. 2005; Madigan et al. 2015) and thus assess individual strategies of dietary specialisation (Matich et al. 2011).

Because isotopic signatures integrate diet over time and space (Carlisle et al. 2012), changes in composition in different tissues of mobile marine predators can “track” their use of isotopically distinct environments at different time scales (Hobson 1999). This attribute has been used successfully to define shifts in diets of marine megafauna that relate to changes in use of habitats (Hatase et al. 2002; Cherel et al. 2007).

Here, stable isotope analyses were used to examine the trophic role of tiger sharks (*Galeocerdo cuvier*). These apex predators are highly mobile, large-bodied sharks distributed globally in tropical, sub-tropical and temperate regions (Randall 1992; Domingo et al. 2016). Based on their diet, size and lack of predators, adult tiger sharks (>3 m) are classified as apex predators (Heupel et al. 2014). In at least some contexts, they play an important role in structuring the environments they inhabit (Heithaus et al. 2002; Burkholder et al. 2013). Tiger sharks have a diverse diet, feeding on prey from many trophic levels including invertebrates, teleosts, sea snakes, large marine herbivores such as sea turtles and sirenians, seabirds and other (Stevens & McLoughlin 1991; Simpfendorfer 1992; Lowe et al. 1996; Heithaus 2001; Simpfendorfer et al. 2001; Trystram et al. 2016). The species also exhibits high individual variability in movement patterns with some evidence of ontogenetic expansion in habitat utilisation (Werry et al. 2014; Holmes et al. 2014; Afonso & Hazin 2015; Ferreira et al. 2015; Lea et al. 2015). It is likely, therefore, that their role in structuring marine ecosystems will vary both in space and with ontogenetic stage. Sampling over broad spatial and temporal scales and multiple habitats could allow incorporation of stable isotope data into studies of the spatial ecology (movement patterns, space use and habitat preferences) of these predators, and provide novel insights into both the motivations behind patterns (prey preference and foraging locations) and the role of these sharks within the various marine habitats that their movements encompass.

In this study, we compare the stable isotope composition of multiple tissues of tiger sharks collected at locations spread across their range in Australian waters. Sampling encompassed tropical and warm-temperate environments to provide insights into the trophic ecology and niche of the species across multiple habitats. This study also sought
evidence for the influence of biological (size, sex) and spatial (latitude, location) factors that could influence the stable isotopic composition of tiger sharks and how that relationship changed at both short (days to weeks) and long (months to years) time scales by analysing tissues with different turnover rates.

4.3 Methods

4.3.1 Sample collection

Samples were collected under permit numbers: 2563 (WA Department of Fisheries), SF010311 (WA Department of Parks and Wildlife); G14/36467.1 and G14/37133.1 (Great Barrier Reef Marine Park Authority); 100541, 165491 and 56095 (NSW Department of Primary Industries and Fisheries); QS2009/GS001, QS2010/MAN26 and QS2010/GS059 (QLD Department of Environment and Resource Management). All methods and experimental protocols were performed in accordance with approved guidelines by Animal Ethics Committees from the University of Western Australia (RA/3/100/1209), James Cook University (A1974) and University of Queensland (CMS/300/08/DPI/SEAWORLD and CMS/326/11/DPI).

Tiger sharks were sampled from Ningaloo Reef and Shark Bay in Western Australia, the Great Barrier Reef (GBR), and the coast of Queensland and deeper continental shelf waters (> 100 m) of New South Wales (NSW) (Figure 4.1). Two different data sets were available from Queensland, one composed of muscle samples collected between 2005 and 2014 from sharks captured by the Queensland Shark Control Program (QSCP) between latitudes of 28°S and 10°S (hereafter the QSCP dataset), and another of multiple tissues (muscle, dermis, blood) from individual sharks collected at different locations throughout the Great Barrier Reef (hereafter the GBR dataset). The majority of the individuals sampled in the QSCP were captured in coastal waters of southern Queensland, below the latitude of the southern extremity of the GBR. QSCP and GBR data sets were not pooled due to the different analytical methods applied to each (see below).

Sample collection was a collaborative effort across multiple research programs in Australia and as a consequence, the number of samples for each location, sex, types of tissues collected and sampling methods varied among locations. For the sampling at Ningaloo Reef and the GBR, tiger sharks were caught using drumerlines inside the reef lagoon and led onto a submerged platform. The platform was raised clear of the water
and the shark was restrained by a tail rope. A hose with a continuous flow of oxygenated seawater was inserted in the mouth of the animal. The shark was then measured and sexed and fitted with electronic tags prior to release (described below). A small sample (3 g) of white dorsal muscle and dermis were collected with a scalpel or an 8-mm diameter tissue punch, about 5 cm lateral to the first dorsal fin. Blood samples of 5 ml were collected with an 18-gauge needle from the caudal vein. The blood was separated into plasma and red blood cells with a portable centrifuge (6500 rpm) and all samples were immediately frozen in either liquid nitrogen (-80°C) or -20°C freezers after collection. Dermal denticles were removed from dermal samples prior to analysis. Stable isotope data from sharks captured in Shark Bay were collected by a multi-year program (Heithaus et al. 2012, 2013) and added to the dataset. For field and sampling procedures for sharks captured in Shark Bay see Heithaus (2001) and Wirsing et al. (2006). For sharks caught by the QSCP, muscle samples were collected from the musculature adjacent to frozen vertebrae. In NSW, shark muscle was collected from the dorsal region next to the first dorsal fin at recreational game-fishing competitions and frozen immediately for storage. Sampling procedures for Queensland and NSW are described by Holmes et al. (2015).

![Figure 4.1 Map showing the study locations across Australia and sampling sites within each region in colour coded triangles. Circles represent relative and total sample size for each dataset. GBR = Great Barrier Reef, QSCP = Queensland Shark Control Program, NSW = New South Wales. Map was created with ArcGis 10.3 (http://www.esri.com/).](image-url)
Table 4.1. Mean and standard deviation (SD) stable isotopic composition of tiger sharks sampled in Queensland (QSCP), New South Wales (NSW) the Great Barrier Reef (GBR) and Ningaloo and Shark Bay for each sex (F = female, M= male). $\delta^{15}$N and $\delta^{13}$C given in parts per mill (‰). N= number of samples, TL = mean total length (cm) ± SD.

<table>
<thead>
<tr>
<th>Location</th>
<th>Sex</th>
<th>N</th>
<th>TL</th>
<th>Muscle</th>
<th>Dermis</th>
<th>Fin</th>
<th>Red Blood Cells</th>
<th>Plasma</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$\delta^{15}$N</td>
<td>$\delta^{13}$C</td>
<td>$\delta^{15}$N</td>
<td>$\delta^{13}$C</td>
<td>$\delta^{15}$N</td>
</tr>
<tr>
<td>QSCP</td>
<td>F</td>
<td>36</td>
<td>207 ± 84.8</td>
<td>12.4 ± 1.0</td>
<td>-16.8 ± 0.7</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>12</td>
<td>161 ± 37.3</td>
<td>12.2 ± 1.1</td>
<td>-17.4 ± 0.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NSW</td>
<td>F</td>
<td>17</td>
<td>322 ± 50.9</td>
<td>12.6 ± 0.8</td>
<td>-18.2 ± 0.6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>25</td>
<td>345 ± 39.5</td>
<td>12.3 ± 0.8</td>
<td>-18.3 ± 0.8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GBR</td>
<td>F</td>
<td>14</td>
<td>296 ± 48.3</td>
<td>11.6 ± 0.9</td>
<td>-14.2 ± 1.6</td>
<td>11.3 ± 0.5</td>
<td>-12.0 ± 1.3</td>
<td>11.0 ± 0.3</td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>2</td>
<td>232 ± 235</td>
<td>12.8 ± 0.7</td>
<td>-16.2 ± 0.1</td>
<td>11.9 ± 0.2</td>
<td>-13.8 ± 0.1</td>
<td>11.9 ± 0.5</td>
</tr>
<tr>
<td>Ningaloo</td>
<td>F</td>
<td>20</td>
<td>348 ± 46.3</td>
<td>12.0 ± 0.4</td>
<td>-13.9 ± 1.4</td>
<td></td>
<td></td>
<td>11.6 ± 0.3</td>
</tr>
<tr>
<td>Shark Bay</td>
<td>F</td>
<td>124</td>
<td>280 ± 59.2</td>
<td></td>
<td></td>
<td>11.8 ± 0.7</td>
<td>-16.6 ± 1.3</td>
<td>11.4 ± 0.5</td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>23</td>
<td>268 ± 52.6</td>
<td></td>
<td></td>
<td>12.0 ± 0.6</td>
<td>-11.9 ± 1.4</td>
<td>11.0*</td>
</tr>
</tbody>
</table>

* n=1
Samples from Ningaloo Reef, the GBR, the QSCP and NSW were analysed by the Western Australian Biogeochemistry Centre at the University of Western Australia. Samples were freeze dried for 48 h and homogenised using a Mixer Mill MM 200 with 6.4-mm ball bearings. Samples were analysed using a continuous flow system in a Delta V Plus mass spectrometer coupled to a Thermo Flush 1112 via Conflo IV (Thermo-Finnigan/Germany). Stable isotope ratios were expressed as δ^{13}C and δ^{15}N and reported in parts per mil (‰) relative to the standard reference Vienna Pee Dee Belemnite (VPDB) for δ^{13}C and atmospheric N\_2 for δ^{15}N. Samples were standardised against primary analytical standards from the International Atomic Energy Agency, Vienna (δ^{13}C: NBS22, USGS24, NBS19, LSVEC; δ^{15}N: N1, N2, USGS32 and laboratory standards). The analytical precision (standard deviation of mean values) of both carbon and nitrogen isotopes was 0.1‰. Samples had mean C:N ratios of 2.5 ± 0.5 (mean ± SD) for samples analysed at the Western Australian Biogeochemistry Centre, and because elasmobranchs are reported to have low lipid content with relatively small changes to δ^{13}C values after lipid extraction, we did not correct δ^{13}C values for the effects of lipids (Post et al. 2007; Hussey et al. 2010; Vaudo & Heithaus 2011; Speed et al. 2012; Heithaus et al. 2013). Samples from Shark Bay were analysed at Yale University and Florida International University (Matich et al. 2011; Heithaus et al. 2013) with analytical precision of 0.10 - 0.19‰ for δ^{13}C and 0.02 - 0.08‰ for δ^{15}N (Heithaus et al. 2013) and showed low C:N ratios (2.45 ± 0.39).

### 4.3.2 Data analysis

**Stable isotopic composition**

In order to assess variations in the isotopic signature of tiger sharks among widely distributed locations, isotopic signatures of muscle samples previously described by studies in South Africa (Hussey et al. 2015), the Great Barrier Reef (Frisch et al. 2016) and Reunion Island (Trystram et al. 2016) were plotted against the average values of δ^{15}N and δ^{13}C of slow and intermediate tissues (dermis, muscle, and fin) from this study. Dermis is likely to have faster turnover rates than muscle (Carlisle et al. 2012; Li et al. 2016a), however, in the absence of muscle samples at Ningaloo, dermis was considered as the longer-term representation of diet. Dermis is a poorly vascularised structural tissue that may reflect longer-term (months) signals in diet (Zamora et al. 2016) when compared to tissues that are metabolically active such as blood (Kim et al. 2012). To assess the trophic position of tiger sharks in each ecosystem, the stable
isotope composition of each tissue (muscle, dermis, red blood cells and plasma) for all sharks at each location was also plotted against that of taxa from different trophic positions from each location (Ningaloo Reef, Shark Bay, GBR and NSW), with values extracted from published literature. Additional isotope data from muscle tissue of four tiger sharks sampled on the GBR (Lizard Island and southern GBR) between 2013 and 2014, and analysed at James Cook University, were combined with isotopic values from the literature for the comparison with the values obtained in the present study. As earlier studies were analysed in different laboratories with varying sample handling and processing protocols (Bessey & Vanderklift 2014), these comparisons were made visually and no statistical analysis was attempted.

Isotopic niche

Isotopic niche space occupied by tiger sharks in each location in Australia was measured by calculating standard ellipse areas corrected for sample size (SEAc), the SEAc parameters of eccentricity (E) and theta (θ), the Bayesian estimation of SEA (SEAb) and the overlap between paired groups as a probability index with values between 1 and 0 (Jackson et al. 2011). The Bayesian approach used vague and non-informative priors and was built with 2 Markov chains with 20,000 steps per chain, a discarded burn-in of 1,000 iterations and a thinning interval of 10. This produced a range of SEAb with 95% credible intervals that allowed for direct probabilistic interpretation of pairwise comparisons between groups that could be interpreted as the probability of the Bayesian ellipse area of one group being larger than another (Jackson et al. 2011; Reid et al. 2016). The total area (TA) occupied was calculated as the areas of the convex hull that incorporated all individuals and represents a measure of niche width and reflects the isotopic diversity of a group (Layman et al. 2007; Vaudo & Heithaus 2011). The mean distance to centroid (CD) was calculated as the distance in isotopic space of each individual to the mean of all individuals and represented a measure of the average trophic diversity within a group (Vaudo & Heithaus 2011). As eccentricity (E) was related to the variance on the x ($\delta^{13}\text{C}$) and y ($\delta^{15}\text{N}$) axes and to the circularity of the SEAc, high values of E were representative of ellipses that were stretched either in the x or y-axes. Theta was a measure of the inclination of the ellipse and is reported here in radians but was converted to the angular range between -90 to 90, with positive and negative values indicating the direction of inclination of standard ellipses (Jackson et al. 2011; Reid et al. 2016). Values for each tissue were analysed separately using the R packages siar (Parnell & Jackson 2013) and SIBER (Jackson et
Sexes were considered as separate groups within a region for datasets that contained a representative number of samples (n > 10) for both male and female sharks.

**Spatial patterns of isotopic composition of multiple tissues**

Generalised linear models (GLMs) with a Gaussian distribution were used to assess if δ^{13}C and δ^{15}N varied spatially (by location or latitude), and in relation to sex and size of sharks and at different temporal scales by using tissues with different turnover rates. Data from each tissue (muscle, dermis, red blood cells and plasma) was modelled separately using both δ^{13}C and δ^{15}N as response variables and a set of explanatory variables that were dependent on the data available for each tissue. The set of predictors varied among tissues and was selected based on datasets available (e.g. sex was only used as predictor if the number of males was sufficient, whereas season was only included in the analysis of datasets of muscle). For muscle, the stable isotope composition was analysed with regard to the latitude, season (austral summer, autumn, winter and spring), sex, total length (TL, in cm) and interaction terms between sex and latitude, and sex and TL. For dermis, stable isotopes were assessed against the categorical variable (location) rather than the continuous variable (latitude), due to sampling locations on the west and east coast of Australia having similar latitudes. Total length and an interaction term between location and TL were also included. For red blood cells and plasma, variables analysed included location, TL, and the interaction terms between TL and location. Fin samples were only available from Shark Bay and, therefore, these were not included in this analysis. All potential combinations of these predictor variables were fit with the package **MUMIn** (Barton 2013). Model selection was done by ranking the models by Akaike’s Information Criterion corrected for sample size (AICc) and the AICc weight (wAICc) which varies from 0 (no support) to 1 (complete support). When multiple models were ranked equally (models within 2 AICc units), the most parsimonious model was selected (the model containing the lowest number of explanatory variables). Goodness of fit was assessed by the percentage deviance explained (%DE). Conditional plots for each variable in the top-ranked model were plotted using the R package **ggplot2** and **visreg** (Breheny & Burchett 2016).

**Diet Stability**

Tiger sharks at Ningaloo Reef were also tagged internally with a V16TP or V16 acoustic transmitters (Vemco Ltd., Canada) (Table S 4.1). Upon capture, sharks were restrained and rolled to expose their ventral side. A 4 cm incision was made along the
centre line of the abdomen, an acoustic tag was inserted and the incision was closed with three stiches in the muscle and skin using surgical sutures. Sharks tagged with an acoustic transmitter were monitored by receiver arrays around Ningaloo Reef (Figure S 4.1) deployed by the Australian Animal Tracking and Monitoring System. This tracking allowed sharks that were resident at Ningaloo Reef to be identified so that their isotopic composition could be used as a baseline value for analyses. An earlier study at Ningaloo Reef demonstrated that tiger sharks either resided in the areas where they were tagged for up to 6 months or departed and ranged 1000s of km along the coast of Western Australia (Ferreira et al. 2015). Consequently, we assumed that individuals that remained resident after tagging and tissue sampling were likely to have been resident at Ningaloo Reef prior to capture. As receiver downloads were sporadic during the duration of the study, sharks were defined as residents if they were detected by the receiver arrays for at least five successive months after tagging and prior to the last download of receivers (Table S 4.1), again consistent with residency times recorded by earlier studies (Ferreira et al. 2015). As blood has an isotopic turnover rate of months (Logan & Lutcavage 2010), the signature of this tissue was used as a baseline for resident sharks.

Stability of diet was assessed based on differences in δ^{13}C between paired tissues (red blood cells and plasma) for the locations where multiple tissues were collected from the same sharks (Ningaloo Reef, Shark Bay and GBR). Plasma has a faster isotopic turnover rate than red blood cells (a half-life of 32 vs. 60 days, Kim et al. 2012) than red blood cells (~60 days, Kim et al. 2012). The contrasting turnover rates of these tissues allowed for comparison of isotopic values within an individual, giving an insight into the temporal stability of diet (Matich et al. 2011; Malpica-Cruz et al. 2013). Preliminary analysis of this dataset and previous studies of tiger sharks in Shark Bay showed greater inter-tissue differences in δ^{13}C than in δ^{15}N (Matich et al. 2010, 2011), therefore, this analysis only considered δ^{13}C values. Linear regression was fitted to the paired values of δ^{13}C for sharks from Ningaloo Reef, Shark Bay and the GBR in order to describe the consistency of differences in δ^{13}C between tissues and to quantify the inter-tissue relationship, as a measure of tissue discrimination differences (Matich et al. 2010; Matich & Heithaus 2014; Davis et al. 2015). As paired tissue discrimination shows stable relationships in other species including seabirds, mako (Isurus oxyrinchus) and white sharks (Carcharodon carcharias) (Quillfeldt et al. 2008; Malpica-Cruz et al. 2013), it can be used to compare stability of diet in samples from various locations by
identifying individuals that are not in a steady state. AIC values were compared for the regression of $\delta^{13}C$ between red blood cells and plasma against a null model. If there was strong support for the regression model and the $R^2$ value was high (>0.8), the relationship was considered significant and stable. Stable relationships between $\Delta\delta^{13}C$ values of paired tissues suggest a stable discrimination of differences among locations and validate use of the fitted line of the regression and $\delta^{13}C$ differences to investigate dietary stability in individual sharks. Since only a relationship with strong support was used among different locations, mean values of the paired tissue differences of resident sharks at Ningaloo Reef were used as a proxy for the $\delta^{13}C$ for discrimination between red blood cells and plasma ($\Delta\delta^{13}C$). Paired tissue differences for each individual ($\Delta\delta^{13}C$) were then plotted over the fitted line and interval ($\pm$ mean $\Delta\delta^{13}C$) around it. Data points that plotted more than $\Delta\delta^{13}C$ above the fitted line indicated plasma values with higher $\delta^{13}C$ values than predicted by the model and data points that plotted less than $\Delta\delta^{13}C$ below the fitted line indicated plasma values with lower $\delta^{13}C$ than predicted by the model (Matich & Heithaus 2014; Davis et al. 2015). Values of plasma outside the $\pm$ mean $\Delta\delta^{13}C$ interval area around the fitted line, therefore, indicated a recent shift in diet. Values within the $\pm$ mean $\Delta\delta^{13}C$ interval around the fitted line were considered “stable” and were assigned a value of 1. Values that were either higher or lower than the $\pm$ mean $\Delta\delta^{13}C$ interval were considered “non-stable” and assigned a value of 0. Generalised linear models with a binomial distribution were used to test the probability of sharks having a stable diet in relation to total length and location. All potential combinations of the predictor variables (location, total length and an interaction term with total length and location) were used and model selection was as described previously.

4.4 Results

4.4.1 Comparisons of stable isotopic signatures among locations

A comparison of slow-turnover tissues (dermis, fin and muscle) shows a spread of mean isotopic signatures that indicated variation in the diet of tiger sharks across both latitudes and shelf positions (inshore/offshore habitats) (Figure 4.2a). Most of the variation occurred along the $\delta^{13}C$ axis. Individuals from Shark Bay had higher $\delta^{13}C$, whereas sharks from the QSCP, NSW and Reunion Island had lower $\delta^{13}C$. Sharks sampled on the GBR had intermediate $\delta^{13}C$ values and were very similar to those of
muscle tissue collected and analysed by other studies in the same locality (Frisch et al. 2016; Figure 4.2a). However, δ^{13}C values of dermis from GBR sharks were high and overlapped with those of Shark Bay individuals. There was limited variation in mean δ^{15}N values of sharks among localities, with the exception of tiger sharks in South Africa, which had higher δ^{15}N values (Figure 4.2a).

The collection of multiple tissues from the same animals in some localities allowed the isotopic composition of both fast (blood, plasma) and slow (muscle, dermis and fin) turnover tissues to be compared (Figure 4.2b). Once again, there was greater variation in δ^{13}C than δ^{15}N values. Fast tissues tended to have lower δ^{13}C compared to slow turnover tissues collected at the same locality. At Ningaloo, red blood cells and plasma had lower δ^{13}C compared to dermis (Figure 4.2b), whereas at Shark Bay, plasma had a lower δ^{13}C compared to red blood cells and blood cells had lower δ^{13}C compared to fin (Figure 4.2b). Analyses of the GBR samples revealed a somewhat different pattern, with blood and plasma having lower δ^{13}C compared to dermis, but muscle samples having similar δ^{13}C values to these fast turnover tissues (Figure 4.2b).
4.4.2 Comparisons of isotopic signatures within locations

Stable isotopic composition of tiger sharks was plotted with those of other fishes, sharks and taxa from differing trophic levels at each location (Figure 4.3). Only values for slow turnover tissues of sharks were included in these plots since signatures for other vertebrates were largely derived from the analysis of muscle (Figure 4.3). Only values for slow turnover tissues (muscle and dermis) of sharks were included in these plots since stable isotopic compositions for other vertebrates were largely derived from the analysis of muscle. At Ningaloo, tiger sharks were identified as upper-order predators, but did not display the highest average δ¹⁵N values in the shark community. Two species of reef sharks (grey reef, *Carcharhinus amblyrhynchos* and blacktip reef, *Carcharhinus melanopterus*) had higher δ¹⁵N (Speed et al. 2012) in comparison to tiger sharks, implying a higher trophic position and had higher δ¹³C (Figure 4.3a). In Shark Bay, tiger shark muscle had higher δ¹⁵N than all other sharks at this location (Vaudo & Heithaus 2011; Heithaus et al. 2013) (Figure 4.3b). On the GBR, tiger sharks had higher δ¹⁵N compared to other sharks at this location, with the exception of *C. obscurus*, the dusky shark. This pattern was consistent across tissue types (dermis and muscle) of sharks sampled on the GBR (Figure 4.3c). Muscle tissue from sharks collected by the QSCP displayed similar δ¹⁵N values as dermis and muscle tissue from animals collected on the GBR, but had lower δ¹³C, suggesting a diet based on a more pelagic food chain for sharks sampled in the QSCP than on the GBR (Figure 4.3c). The isotopic composition of muscle from tiger sharks collected on the NSW coast was also consistent with a diet based on pelagic food chains or different basal sources of carbon. In contrast to both the GBR and Shark Bay, the stable isotopic composition of Australian fur-seals (*Arctocephalus pusillus doriferus*) (Davenport & Bax 2002) and a number of large pelagic fishes including tunas and mako sharks (*Isurus oxyrinchus*) (Revill et al. 2009) had higher δ¹⁵N than those of tiger sharks, suggesting that these species feed at higher trophic levels. The isotopic composition of tiger shark tissues in this location was similar to those of billfishes (Figure 4.3d).
Table 4.2. Isotopic niche area described by Standard Ellipse Area SEAc (‰), Bayesian SEAb and parameters; N= number of samples, TA = total area of the convex hull, CD = mean centroid distance and standard deviation, E = eccentricity, θ = angle of ellipse and CI = confidence interval. F = Females, M = Males, QLD = Queensland Shark Control Program and GBR, GBR = Great Barrier Reef and NSW = New South Wales.

<table>
<thead>
<tr>
<th>Location</th>
<th>N</th>
<th>SEAc</th>
<th>SEAb</th>
<th>TA</th>
<th>CD ± SD</th>
<th>E</th>
<th>θ</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Muscle</strong></td>
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</tr>
<tr>
<td>F NSW</td>
<td>18</td>
<td>1.16</td>
<td>1.36</td>
<td>4.52</td>
<td>0.55 ± 0.23</td>
<td>0.74</td>
<td>60.6</td>
<td>0.85 - 2.26</td>
</tr>
<tr>
<td>M NSW</td>
<td>25</td>
<td>2.06</td>
<td>1.83</td>
<td>7.26</td>
<td>0.74 ± 0.27</td>
<td>0.68</td>
<td>51.5</td>
<td>1.17 - 2.71</td>
</tr>
<tr>
<td>F QLD</td>
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<td>3.79</td>
<td>4.23</td>
<td>15.32</td>
<td>1.34 ± 0.17</td>
<td>0.88</td>
<td>-28.9</td>
<td>3.14 - 6.68</td>
</tr>
<tr>
<td>M QLD</td>
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<td>2.38</td>
<td>1.01</td>
<td>5.25</td>
<td>0.84 ± 0.25</td>
<td>0.77</td>
<td>-72.8</td>
<td>0.57 - 1.82</td>
</tr>
<tr>
<td><strong>Dermis</strong></td>
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</tr>
<tr>
<td>Ningaloo</td>
<td>20</td>
<td>1.61</td>
<td>1.7</td>
<td>5.04</td>
<td>0.22 ± 0.09</td>
<td>0.97</td>
<td>-6.4</td>
<td>1.00 - 2.51</td>
</tr>
<tr>
<td>GBR</td>
<td>1.42</td>
<td>1.54</td>
<td>23.33</td>
<td>1.21 ± 0.73</td>
<td>0.98</td>
<td>-18.9</td>
<td>0.89 - 2.70</td>
<td></td>
</tr>
<tr>
<td><strong>Red Blood Cells</strong></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ningaloo</td>
<td>17</td>
<td>1.78</td>
<td>1.57</td>
<td>5.05</td>
<td>0.80 ± 0.69</td>
<td>0.98</td>
<td>2.7</td>
<td>0.99 - 2.69</td>
</tr>
<tr>
<td>Shark Bay</td>
<td>25</td>
<td>2.48</td>
<td>2.33</td>
<td>7.01</td>
<td>1.02 ± 0.93</td>
<td>0.95</td>
<td>-9.2</td>
<td>1.55 - 3.47</td>
</tr>
<tr>
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<td>14</td>
<td>2.58</td>
<td>2.33</td>
<td>5.61</td>
<td>0.89 ± 0.46</td>
<td>0.98</td>
<td>-7.4</td>
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</tr>
<tr>
<td><strong>Plasma</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ningaloo</td>
<td>19</td>
<td>1.85</td>
<td>1.66</td>
<td>5.04</td>
<td>1.39 ± 0.69</td>
<td>0.93</td>
<td>-6.6</td>
<td>1.06 - 2.70</td>
</tr>
<tr>
<td>Shark Bay</td>
<td>45</td>
<td>5.65</td>
<td>5.48</td>
<td>23.33</td>
<td>0.93 ± 0.43</td>
<td>0.79</td>
<td>-3.6</td>
<td>3.97 - 7.38</td>
</tr>
<tr>
<td>GBR</td>
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<td>6.72</td>
<td>5.93</td>
<td>15.07</td>
<td>1.09 ± 0.24</td>
<td>0.86</td>
<td>-12.9</td>
<td>3.30 - 10.40</td>
</tr>
</tbody>
</table>
4.4.3 Comparison of tissues among locations

Muscle

Differences in isotopic niches were assessed separately for each sex. For this analysis, muscle samples from the QSCP and the GBR were pooled (QLD; Figure 4.4 Female tiger sharks in QLD had a larger niche and higher trophic diversity than all other combinations of sex and location, based on the distribution of SEAb and TA (Table 4.2; Figure 4.4a-b). The SEAc parameter for females from QLD showed that the ellipse for this group was stretched with dispersion both on the $\delta^{13}$C axis and the $\delta^{15}$N axis ($E=0.88, \theta=-28.87^\circ$; Figure 3a, Table 1). In contrast, male sharks in QLD waters had a greater dispersion over the $\delta^{15}$N axis ($E=0.77, \theta=-72.85^\circ$) than the $\delta^{13}$C axis as did both males and females from NSW ($E=0.68$ and $0.74, \theta=51.5$ and $60.6$, respectively). Sharks in NSW waters had a large overlap between sexes (0.68) and little difference in niche area (probability = 0.29). Females and males in QLD displayed high niche overlap (0.60), but little overlap with tiger sharks from NSW waters. Females in NSW showed the lowest trophic diversity and total area, despite having a larger SEAb than males in QLD (Table 4.2).

The generalised linear model that included latitude, sex, total length and the interaction between latitude and sex had the highest support (wAICc = 0.76) and explained 65.3% of the deviance in the response (Table 4.3). This model indicated a shift to higher $\delta^{13}$C from smaller to larger sharks and towards lower latitudes for both sexes, trends that were more pronounced for females than males (Figure 4.4c-d). In the analysis of the $\delta^{15}$N data set, the four top-ranked models were all within two AICc points of the most parsimonious model (i.e. with the least number of parameters) including latitude only. The model indicated lower $\delta^{15}$N values towards lower latitudes, but explained only 7.6% of the deviance in the response.
**Figure 4.4. Muscle.** Standard ellipse areas for analysis of muscle tissue corrected for sample size (SEAc) (A) and Bayesian Standard ellipse areas (SEAb) (B), representing the 50, 75 and 95% credible intervals in decreasing order of box size, with SEAb mode indicated by a black circle and SEAc by a triangle. Partial dependence plots of the relationship between δ^{13}C and the explanatory variables in the top-ranked model, total length (C) latitude and sex and their interaction (D). Points represent residuals and shaded areas show the 95% confidence intervals.

**Dermis**

Dermis was only collected from sharks captured at Ningaloo Reef and the GBR and data from both sexes were pooled for analysis due to low numbers of males in samples (n=2). Samples from sharks on the GBR had greater dispersion over the δ^{15}N axis (θ Ningaloo Reef = -6.4, θ GBR=-18.90) than those at Ningaloo (Figure 4.5a-b). Although the size of the SEAb area was similar in both locations, niches were mostly distinct with sharks in GBR showing a larger TA and trophic diversity (Figure 4.5a, Table 4.2) with only 0.2 probability of overlap. Of the three models selected to describe variation in δ^{13}C values, the most parsimonious included only total length (wAICc = 0.28) and explained 28% of the deviance (Table 4.3). Model predictions indicated a shift to lower δ^{13}C with increasing total length (TL) of sharks (Figure 4.5c). For δ^{15}N data sets, the three top-ranked models were within two AICc points, with the most parsimonious model including location only and explaining 32% of the deviance.
Dermis tissue of sharks at Ningaloo Reef had higher $\delta^{15}$N than those of sharks from the GBR (Figure 4.5d).

**Figure 4.5. Dermis.** Standard ellipse areas for analysis of dermal tissue corrected for sample size (SEAc) (A) and Bayesian Standard ellipse areas (SEAb) (B), representing the 50, 75 and 95% credible intervals in decreasing order of box size, with SEAb mode indicated by a black circle and SEAc by a triangle. Partial dependence plots of the relationship between $\delta^{13}$C (C) and $\delta^{15}$N (D), and the explanatory variables in the top-ranked models; total length (C) and location (D). Points represent residuals and shaded areas show the 95% confidence intervals.
Table 4.3. Ranked generalised linear models of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for each tissue. The top six models for each response are shown; values in bold indicate the top ranked model (or the most parsimonious model). Degrees of freedom (df), Sample corrected Akaike’s Information Criterion (AICc), change in AICc relative to the model with the lowest AICc value (ΔAICc), relative AICc weight (wAICc) and percent deviance explained (DE%). Lat = latitude, TL = total length (cm).

<table>
<thead>
<tr>
<th>Response</th>
<th>Model</th>
<th>df</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>wAICc</th>
<th>%DE</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Muscle</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\delta^{13}\text{C}$</td>
<td>lat + sex + TL + lat × sex</td>
<td>6</td>
<td><strong>237.9</strong></td>
<td>0.00</td>
<td>0.76</td>
<td>6.29</td>
</tr>
<tr>
<td>$\delta^{13}\text{C}$</td>
<td>lat + sex + TL</td>
<td>5</td>
<td>241.4</td>
<td>3.57</td>
<td>0.13</td>
<td>63.01</td>
</tr>
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<td>$\delta^{13}\text{C}$</td>
<td>lat + sex + lat × sex</td>
<td>5</td>
<td>243.5</td>
<td>5.61</td>
<td>0.05</td>
<td>62.18</td>
</tr>
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<td>63.03</td>
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<td>$\delta^{13}\text{C}$</td>
<td>lat + season + sex + TL</td>
<td>8</td>
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<td>8.69</td>
<td>0.01</td>
<td>63.77</td>
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<td>lat + TL</td>
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<td>247</td>
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<td>0.00</td>
<td>59.74</td>
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<td>lat</td>
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<td>0.34</td>
<td>7.65</td>
</tr>
<tr>
<td>$\delta^{15}\text{N}$</td>
<td>lat + sex + lat × sex</td>
<td>5</td>
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<td><strong>Dermis</strong></td>
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<tr>
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<td>TL</td>
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<td><strong>Red blood cells</strong></td>
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<td></td>
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<tr>
<td>$\delta^{13}\text{C}$</td>
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<td>300.8</td>
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<tr>
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<td>224.3</td>
<td>6.04</td>
<td>0.03</td>
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</table>
Red Blood Cells

Red blood cells were obtained from female sharks at Ningaloo and from both males and females at Shark Bay and on the GBR. Samples from different sexes were pooled within locations due to the very low numbers of males (3 in total). Plots of isotopic niches of sharks from all locations had ellipses stretched across the x-axis with high variation in δ¹³C values (Figure 4.6a, Table 4.2). Sharks at Ningaloo Reef had a more distinct, smaller and less diverse niche than in Shark Bay and on the GBR based on SEAb, TA and CD (probability=0.86 and 0.85, respectively), who were more similar to each other (Figure 4.6a-b). In the analysis of the δ¹³C data set there was one top-ranked model, which included total length and location and explained 56% of the deviance (Table 4.3 Red blood cells had lower δ¹³C with increasing size and higher δ¹³C at Shark Bay and on the GBR than at Ningaloo (Figure 4.6c-d). The top-ranked model for the δ¹⁵N dataset only included location and explained 16% of the deviance, indicating marginally higher δ¹⁵N at Ningaloo (δ¹⁵N = 11.6 ±0.1‰) in comparison to individuals from Shark Bay (δ¹⁵N = 11.4 ±0.1‰) and the GBR (δ¹⁵N = 11.11 ±0.12‰).

![Figure 4.6. Red Blood Cells. Standard ellipse areas for analysis of red blood cells corrected for sample size (SEAc) (A) and Bayesian Standard ellipse areas (SEAb) (B), representing the 50, 75 and 95% credible intervals in decreasing order of box size, with SEAb mode indicated by a black circle and SEAc by a triangle. Partial dependence plots of the relationship between δ¹³C and the explanatory variables in the top-ranked model: total length (C) and location (D). Points represent residuals and shaded areas show the 95% confidence intervals.](image)
Plasma

Samples used for determination of niche area were collected from female sharks at Ningaloo Reef and from both sexes at Shark Bay and the GBR. Again, data were pooled for analysis between sexes within locations due to limited sample sizes. Sharks from the GBR and Shark Bay had significantly greater SEAb and TA areas than those at Ningaloo Reef (probability=1 for both). However, sharks at Ningaloo Reef showed higher trophic diversity than in Shark Bay and on the GBR based on CD (Table 4.2). At all locations the dispersion of stable isotopic composition occurred on both axes (θ= -6.6 Ningaloo, θ= -3.6 Shark Bay, θ= -13.9 GBR, Table 4.2, Figure 4.7a-b) and no niche overlap was evident in samples from Ningaloo Reef and the GBR, but there was an overlap of niche area with individuals from Shark Bay (0.30). The model including location and total length had majority support (wAICc = 0.83) and explained 33% of the deviance in the response (Table 4.3). The model predictions showed lower δ¹³C with increasing body length, with the lowest δ¹³C value recorded for sharks at Ningaloo Reef (Figure 4.7c-d). For δ¹⁵N values, the top-ranked model only included location and had the majority of support (wAICc = 0.66), but explained only 9% of the deviance in the data set.
Figure 4.7. Plasma. Standard ellipse areas for analysis of plasma corrected for sample size (SEAc) (A) and Bayesian Standard ellipse areas (SEAb)(B), representing the 50, 75 and 95% credible intervals in decreasing order of box size, with SEAb mode indicated by a black circle and SEAc by a triangle. Partial dependence plots of the relationship between δ\(^{13}\)C and the explanatory variables in the top-ranked model; total length and location. Points represent and shaded areas show the 95% confidence intervals respectively.

4.4.4 Diet stability

Six of the 18 tiger sharks tagged at Ningaloo Reef were considered to be residents as they were detected by receiver arrays at Ningaloo Reef (Table S 4.1 for five or more months after tagging and tissue sampling. A mean \(\Delta\delta^{13}\)C value of -1.26 ‰ for the difference between red blood cell and plasma of resident sharks was considered as a threshold for the comparison of paired tissues that defined sharks as having stable diets. Due to a lack of tagging data from Shark Bay and the GBR in this study, the threshold calculated for Ningaloo was used in analyses for three locations. Linear regressions between \(\delta^{13}\)C values from red blood cells and plasma from the same individuals had strong support when compared to a null model (wAICc =1, 0.82 %DE) and the fitted line was then used for the identification of stability of diet (Figure 4.8a). The most parsimonious binomial generalised linear model (wAICc =0.33, Table 4.4) to explain the probability of diet stability over one or two months only included location and explained 16% of the deviance. The predictions from this model showed that sharks
at Ningaloo had a higher probability of having a stable diet than those sampled on the GBR and at Shark Bay (Figure 4.8b).

Table 4.4. Ranked binomial generalised linear models of stability of diet for sharks (stable with the local food web), using paired tissue values of δ\(^{13}\)C from red blood cells (RBC)-plasma comparisons. All models are shown, values in bold indicate the most parsimonious model. Sample corrected Akaike’s Information Criterion (AICc), change in AICc relative to the model with the lowest AICc value (ΔAICc), relative AICc weight (wAICc) and percent deviance explained (DE%). TL= total length (cm).

<table>
<thead>
<tr>
<th>Response</th>
<th>Model</th>
<th>df</th>
<th>AICc</th>
<th>Δ AICc</th>
<th>wAICc</th>
<th>%DE</th>
</tr>
</thead>
<tbody>
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<td>0.30</td>
<td>11.10</td>
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<tr>
<td>Stability</td>
<td>TL</td>
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<td>79.9</td>
<td>5.11</td>
<td>0.05</td>
<td>0.17</td>
</tr>
<tr>
<td>Stability</td>
<td>Location + TL × location</td>
<td>6</td>
<td>80.1</td>
<td>5.28</td>
<td>0.04</td>
<td>12.51</td>
</tr>
</tbody>
</table>

Figure 4.8. Relationship between δ\(^{13}\)C values of paired tissues of fast (plasma) and intermediate (red blood cells) turnover rates (A). Individuals with a difference between tissues (calculated from resident sharks) larger than mean differences Δ\(^{13}\)C are highlighted in filled symbols. Open symbols represent individuals in steady state (stable). Solid line represents the relationship between paired tissues and hashed lines enclose the area within ± mean Δ\(^{13}\)C. Partial dependence plots for the relationship between the stability of diet (probability of steady state) and the explanatory variable in the top-ranked model; location (B). Numbers indicate sample sizes.

4.5 Discussion

Our analysis of stable isotopes suggested that the functional role of tiger sharks varied among different marine habitats within the range of the species distribution along the tropical and temperate coasts of Australia. Typically, there was less variation in δ\(^{15}\)N than δ\(^{13}\)C values in slow turnover tissues (muscle, dermis and fin), indicating that the species remains close to the top of food webs at the body sizes we sampled, but that the
ultimate sources of nutrition varied among localities and were dependent on body size, habitat and food-web composition.

Sharks sampled in the enclosed seagrass habitats of Shark Bay on the west coast and the large, shallow lagoon of the GBR showed the strongest evidence of long-term diets based in coastal-associated food-webs originating with seagrass. Dugong and turtles are likely prey in these localities (Heithaus 2001; Heithaus et al. 2013). At higher latitudes, such as the coast of NSW, mean stable isotopic composition indicated a diet more closely linked to pelagic food chains. However, isotopic composition also appeared to be affected by an interaction between latitude and oceanographic setting. Most of the samples collected by QSCP were obtained from beaches south of the GBR, which are exposed to prevailing oceanic swells, upwelling and open waters across the shelf (Oke & Middleton 2000). Stable isotopic compositions in this locality were similar to NSW, where equivalent oceanographic conditions prevail (Tranter et al. 1986; Suthers et al. 2011), but were also similar to samples from Reunion Island, an exposed and isolated island in the Indian Ocean that does not feature an extensive shelf or abundant seagrass (Trystram et al. 2016). In NSW, sharks were collected in deeper, pelagic waters at the edge of continental shelf during game-fishing competitions. These results suggest that lower δ¹³C was not just a function of latitude but also the oceanographic setting and proximity of pelagic food chains. When plotted in the isotopic space, values of δ¹³C of sharks sampled at Ningaloo Reef were between pelagic and seagrass food chains, as might be expected given that this location occurs at the narrowest point of the continental shelf along the Australian coast and so is strongly influenced by the Leeuwin Current, seasonal upwelling and the oceanographic conditions of the open ocean (Taylor & Pearce 1999; Harris et al. 2005; Rousseaux et al. 2012). Although seagrass beds exist at Ningaloo Reef in the shallow lagoon that extends one to two kilometres behind the reef crest to the shore (Cassata & Collins 2008), these are relatively small in area compared to those in the inter-reefal lagoon of the GBR or at Shark Bay, where they are a dominant type of benthic habitat (Walker et al. 1988; Wachenfeld et al. 1998; Carruthers et al. 2002).

The average δ¹⁵N for tiger sharks in the present study differed greatly from those calculated by Hussey et al. (2015b), who obtained samples from sharks caught in bather protection programs along beaches off the Natal coast of South Africa. Hussey et al. (2015b) reported δ¹³C values for tiger sharks that were consistent with samples from the exposed sub-tropical coastlines of the present study (the QSCP and NSW datasets), but
$\delta^{15}N$ values were higher relative to all sampling locations in Australia. It is possible that the difference seen in South Africa may have been a reflection of differences in isotopic baselines and composition of the food-web, nutrient inputs or and/or sample treatment between these locations (Spies et al. 1989; Graham et al. 2010; Li et al. 2016b).

Tiger sharks are a wide-ranging species and tracking studies show that these animals move between tropical and temperate environments and between coastal habitats and the open ocean off the continental shelf. Our results suggest that the role of tiger sharks within food webs and their classification as an apex predator varies as they move across these environmental gradients. Tiger sharks occupied the apex position of the foodwebs in seagrass habitats and shallow lagoons of Shark Bay and the GBR, where nearly all other shark species for which isotopic data were available had lower $\delta^{15}N$ values. In contrast, at Ningaloo Reef, other, smaller sharks such as grey reef (Carcharhinus amblyrynchus; adult size 1.9 m total length, Wetherbee et al. 1997) and blacktip reef (C. melanopterus; adult size 1.8 m total length, Compagno 1984; Last & Stevens 1994), had higher $\delta^{15}N$ (Speed et al. 2012) than tiger sharks. These differences may reflect the feeding by reef sharks on mesopredator teleosts whose productivity is driven by complex coral reef food chains, whereas the diet of tiger sharks can also include species such as herbivorous teleosts, turtles and sirenians, which feed at a more basal level of the food web. As a result of the large home range areas of tiger sharks off the northwest coast of Australia (Ferreira et al. 2015), it is also possible that sharks were feeding in different habitats or offshore areas (i.e. pelagic food-webs) with a lower stable isotopic baseline (Sherwood & Rose 2005) which could explain the differences between the stable isotopic composition of tiger sharks and the more resident reef shark community at Ningaloo Reef (Speed et al. 2016).

In NSW, large oceanic fishes such as tunas and other sharks including makos (Isurus oxyrinchus and I. paucus) (Revill et al. 2009) had higher $\delta^{15}N$ values than tiger sharks, suggesting that they fed at higher trophic levels, which is supported by the high proportion of other predatory teleosts reported in the stomach contents of these species. This was also the case for Australian fur-seals (Arctocephalus pusillus doriferus), which feeds on the continental shelf (Kirkwood et al. 2006). A lower trophic level for tiger sharks has also been reported in the coastal waters of warm temperate environments in southern Africa, where tiger sharks occupy the lowest trophic position within the community of large sharks (Hussey et al. 2015b). Our results suggest that when tiger sharks move into pelagic and offshore habitats where other large teleost and sharks are
present, these predators will occupy higher trophic levels than tiger sharks by having more specialised diets largely focused on fishes that are tertiary consumers or higher. Because no community isotopic data was available for the southern Queensland coast, it was not possible to determine the extent to which tiger sharks occupied the highest trophic level in these environments. However, the similarity of oceanographic conditions in this locality to the coast of NSW and the migrations of tiger sharks along much of the eastern coast of Australia suggests (Holmes et al. 2014) that they are likely to have similar trophic roles in both locations.

The position of tiger sharks in a food chain may also reflect sampling bias of other predators within these systems. For example, Vaudo & Heithaus 2011 and Heithaus et al. 2013 comprehensively sampled the fauna of elasmobranchs and dolphins in shallow banks and sandflats habitats of Shark Bay and these shallow habitats might not be suitable for many large pelagic fishes such as tunas. The classification of tiger sharks as the highest trophic level predators in these habitats thus seems appropriate because all other species that might act in this role had been sampled. At Ningaloo Reef, sampling of the shark and predatory fish community was limited to reef environments, so that the larger pelagic species that might occupy higher trophic positions such as tunas could not be included in plots. With the exception of Shark Bay, where samples were collected over 6 years, there was also a lack of temporal context for sampling in Ningaloo and GBR localities. It may be possible that the diet and role of tiger sharks could vary across both seasons and years, as is the case with other marine predators (MacNeil et al. 2005; Cherel et al. 2007; Carlisle et al. 2012), although such variation may be limited, given the fact that the composition of samples in terms of δ\textsubscript{15}N values was very similar across all locations and that the mean stable isotopic composition from muscle tissues of tiger sharks analysed by earlier studies on the GBR (Frisch et al. 2016) were nearly identical to those presented here (Figure 4.3c).

There was some evidence that size affected the diets of tiger sharks, although patterns were inconsistent among tissues. Muscle, a slow turnover tissue, provided the largest data set available for analysis and showed higher δ\textsubscript{13}C with increasing size (total length) suggesting a diet increasingly shifted towards prey from seagrass habitats. This is likely due to larger sharks having a greater capability to attack and subdue large marine herbivores such as turtles and dugong than smaller, younger sharks. It is also consistent with the results of studies of the stomach contents of tiger sharks that show a change in diet towards larger prey with increasing size (Simpfendorfer 1992; Lowe et al. 1996;
Heithaus 2001). There was also a shift to higher $\delta^{13}$C at lower latitudes where these large herbivores such as turtles and dugongs are more abundant. In addition, plots of isotopic niches calculated from muscle tissues and generalised linear models suggested that there was some effect of sex on diet. Female sharks had a larger trophic niche (SEAb, TA and CD) and showed greater variability in $\delta^{13}$C values, a pattern that may be due to high physiological and energetic demands associated with reproductive cycles (Sulikowski et al. 2016) which may require a more adaptable and opportunistic diet than male sharks. However, analysis of dermis tissue revealed an opposite pattern to muscle, with decreasing $\delta^{13}$C values with increasing body size. This result must be treated with caution because sample sizes of dermis were low ($n = 34$) and the range in total lengths of the animals from which they were obtained were truncated compared to analyses of muscle. Furthermore, with the exception of a single individual, dermis samples of the largest sharks (>350 cm TL) were only collected from Ningaloo Reef and these clustered at one end of the plot, thus may have strongly weighted the relationship with size. Plots of the niche areas for all tissues did, however, separate samples from Ningaloo Reef from those collected on the GBR, suggesting a diet shifted towards more planktonic food webs at the former locality.

Analysis of fast-turnover tissues (red blood cells and plasma) also displayed a decrease in $\delta^{13}$C values with size, contrasting with results for muscle. In this case the shift in the relationship with size could represent a seasonal or short term (months) component to the diet that differed between smaller and larger sharks. Given that blood samples were only taken within a time window of a few months of the year, even where sampling extended over multiple years (as was the case at Shark Bay), it is difficult to determine how often this trend with size was likely to occur. Notably, the effect of location evident from the analysis of muscle tissue was also present in these tissues, with the trophic niches of sharks from the GBR and Shark Bay largely overlapping and sharks at Ningaloo having a mostly separated trophic niche with lower $\delta^{13}$C values. The analysis of plasma suggested that sharks sampled in Shark Bay and the GBR had much wider trophic niches than those at Ningaloo, consistent with the stability analysis that also suggested that diets of sharks at Ningaloo were more stable in short term (weeks-months) than those of sharks on the GBR and at Shark Bay. The low probability of sharks showing a stable diet in Shark Bay and the GBR suggests high variability in diet across these short temporal scales and supports the idea that tissues with slower rates of turnover (muscle, dermis, and fin) may provide a better picture of the overall diet of
tiger sharks. Nevertheless, results from the analysis of diet stability should be interpreted with caution as residency was defined on the basis tracking data that was only collected from sharks at Ningaloo Reef.

Overall, the local environment appeared to be a better determinant of the diet of tiger sharks than latitude, despite the ability of the species to migrate long distances from the tropics to cool temperate environments (Holmes et al. 2014; Ferreira et al. 2015). Sharks sampled at locations that were separated by <300 km such as Ningaloo and Shark Bay displayed very distinct stable isotopic compositions, which is unexpected considering the movement patterns of these sharks between those locations (Heithaus et al. 2007c; Ferreira et al. 2015). In contrast, stable isotopic composition of sharks sampled from the mid-NSW coast were similar to those collected in central and southern QLD, around 1000 km to the north, which may reflect seasonal movements along that coastline (Holmes et al. 2014). The isotopic composition of sharks in more temperate and pelagic habitats in Australia were also similar to sharks sampled at Reunion Island (Trystram et al. 2016), an isolated atoll in the far western Indian Ocean. Environment also appeared to determine the degree to which the species acted as an apex predator, although in some localities (notably Ningaloo Reef and southern Queensland) more comprehensive sampling of other elements of the fauna of pelagic consumers is required to accurately place tiger sharks within the trophic pyramid.

The description of the species as a generalist predator (Simpfendorfer 1992; Lowe et al. 1996; Simpfendorfer et al. 2001; Matich et al. 2011; Trystram et al. 2016) appears justified with stable isotopic compositions being habitat-dependent and ranging from seagrass (Shark Bay) to planktonic food chains (NSW coast) or a mixture of both (Ningaloo Reef). Given that individuals tagged at Shark Bay and Ningaloo have dispersed across the north-western coast of Australia (Heithaus et al. 2007c; Ferreira et al. 2015) and sharks tagged in NSW have dispersed to the tropical Queensland coast (Holmes et al. 2014), it appears that the degree of specialisation by an individual shark on prey at any one time is likely to be context-dependent and reflect both resource availability and to some extent, body size. Although tiger sharks at Ningaloo Reef showed greater trophic diversity based on tissues with fast turnover (e.g. plasma), they also had a greater stability of diet than sharks in Shark Bay and on the GBR. This might suggest that tiger sharks at Ningaloo Reef have wider diet than those in Shark Bay and on the GBR, but are more likely to remain within the same habitat, at least over short time frames (weeks - months).
Our results emphasise the flexibility of the trophic ecology and role of tiger sharks throughout their distribution range in Australia. Generalist predators such as tiger sharks are able to explore multiple habitats and food-webs, likely adapting foraging strategies to specific prey in different habitats. This generalist behaviour may both drive or be driven by scale- and habitat-dependent space use by the species. However, separating the cause and consequence of the relationship between movement and trophic ecology for large, highly mobile, top-level predators is still challenging (Hays et al. 2016). An important next step to better understand the relation between movement strategies and feeding behaviour of these sharks is offered through the combination of diet analysis and the information collected by high resolution tags (Fastloc GPS, camera tags and accelerometers) that could provide a more comprehensive picture of animal movement behaviours and patterns of prey search, and how they change in different habitats and over time, so that can then be matched against animal trophic ecology.

4.6 Acknowledgements

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4.7 Supporting information

Table S 4.1 Details of tiger sharks tagged at Ningaloo Reef in April-May 2015, their duration of detection (until last receiver download) by receivers stations at Ningaloo and their behavioural classification (resident or non-resident).

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<th>Behaviour</th>
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<td>2</td>
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<td>282</td>
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Figure S 4.1. Location of acoustic receivers (grey and black circles) around Ningaloo Reef, Australia. Black circles represent receivers where tiger sharks were detected. Star indicates tagging location.
Chapter 5  Scale and habitat-dependent movement behaviour of a large marine predator, the tiger shark *Galeocerdo cuvier*

5.1 Abstract

Tiger sharks are top-order marine predators found throughout the world’s tropical and temperate oceans. Although many tracking datasets are available for the species, we still lack information on the major processes that structure movement patterns and habitat use at large spatial scales. This study combined multiple tracking datasets (108 tracks) from locations in the Atlantic, Pacific and Indian oceans in order to define the major environmental predictors of movement and space use of tiger sharks throughout most of the distribution range of the species. Movement-based kernel methods and generalised additive mixed models were applied to define predictors of utilisation distributions (UD), and migratory movements. Geographically weighted regression (GWR) was then used to test for spatial non-stationarity in the relationship between values predicted from the models and those generated by kernel methods. Bathymetry and sea surface temperature (SST) were identified as the major drivers of utilisation distributions and migration patterns of tiger sharks of both sexes in different ocean basins, however, the strength of the relationship with these drivers varied greatly among regions and the explanatory power was relatively low (15% DE). This was due to spatial non-stationarity, showing that the relationships changed across space. Although this may have been due to missing biological covariates in models, notably food availability, spatial resolution of both response and explanatory variables appear to be the main driver. The combined results of additive mixed models and GWR show that the relationships between sharks and the environment occurred at finer scales on the shelf than in the open ocean, suggesting that movement patterns were both scale- and habitat-dependent. This implies that the physical processes that aggregate food occur at different spatial scales in each of these habitats and the analysis indicates the locations where further research might reveal these underlying patterns.
5.2 Introduction

Large fishes and sharks, reptiles, cetaceans and pinnipeds (marine megafauna) tend to act as top-order consumers and commonly occupy keystone roles in the trophic ecology of marine ecosystems (Estes et al. 2016). The relative rarity of these top-order species in food chains and their typically slow life history traits make them vulnerable to growing anthropogenic threats (climate change, over-harvesting, pollution, habitat loss etc.) now present throughout the world’s oceans (Stevens et al. 2000; Schipper et al. 2008; Hazen et al. 2013; Worm et al. 2013; McCauley et al. 2015). As a consequence, the abundance of many species has declined, so that they are now classified as Vulnerable, Threatened or Endangered by the International Union for the Conservation of Nature (IUCN) (Dulvy et al. 2014b).

Despite the importance of marine megafauna, management and conservation strategies for this group are complicated by a lack of understanding of movement patterns (Hooker et al. 2011; Hays et al. 2016). Although we know that most can range over relatively large distances (100–1000s km), many of the key drivers of these behaviours have not yet been quantified. In part, this is due to the difficulty of monitoring movement patterns of such animals in the open ocean. Satellite-linked tags offer an effective means to track marine megafauna (Hussey et al. 2015a; Hays et al. 2016), however this technology is expensive and researchers must usually deal with significant logistic hurdles in order to attach these tags to animals. As a result, most studies tend to deploy relatively few tags, so that low sample sizes preclude the population or species-level analyses of movement patterns necessary for the evaluation and optimisation of conservation strategies and recovery plans (Hays et al. 2016).

Recent collaborative initiatives that have facilitated data sharing (e.g. TOPP, CLIOTOP, Marine Megafauna Movement Synthesis Group, MEOP) have now enabled researchers to overcome some of these issues (Costa et al. 2010a; Block et al. 2011; Hindell et al. 2016). For example, the pooling of the results of tagging of southern elephant seals (*Mirounga leonina*) among studies has provided high-resolution information about the physical environment occupied by the species throughout the entire Southern Ocean (Biuw et al. 2007; Hindell et al. 2016). Nevertheless, such studies remain exceptions and limitations on our ability to collect replicated, multi-year tracking data still impedes a comprehensive understanding of the long-term movement behaviour and migration patterns of many species of megafauna (Lea et al. 2015; Hays et al. 2016).
The tiger shark (*Galeocerdo cuvier*) is a large marine predator that typifies these problems. In addition to the difficulties of deploying satellite tags, these sharks spend limited time at the surface, restricting the opportunities for tags to broadcast location data to satellites. Consequently, location estimates along tracks tend to be both sparse and patchy, even when long (months–years) deployments of tags are achieved (Pinaud 2008; Meyer *et al.* 2009; Hammerschlag *et al.* 2012; Papastamatiou *et al.* 2013; Werry *et al.* 2014; Ferreira *et al.* 2015; Lea *et al.* 2015). This complicates the analysis of movement patterns, information that is urgently required given that there is increasing concern over the conservation status and management of the species due to unsustainable demand for shark products in some markets, compounded by high rates of bycatch of sharks in many fisheries (Pauly *et al.* 2005; Lewison *et al.* 2014; Dulvy *et al.* 2014b). Such threats and uncertainty in population trajectories have led to designation of the species as “Near Threatened” by the IUCN (Ferreira *et al.* in review).

Here, these issues were addressed using two approaches. Firstly, the results of a large number of tracking studies of tiger sharks were pooled to form a large, global data set so that general patterns in movement behaviour could be identified across the entire range of the species. Secondly, a novel combination of statistical approaches was applied to identify the drivers of movement patterns and to disentangle the biological and physical factors likely to structure this process. Although the focus of the work was on tiger sharks, these techniques are applicable to a wide range of marine megafauna, given that sparse data with low sample sizes are common issues for most tracking studies. Firstly, the Biased Random Bridge (BRB) kernel method (Benhamou 2011) was used to estimate monthly utilisation distributions (UD) from the tracks of each shark. This method differs from traditional kernel approaches in that it incorporates movement trajectories between locations and aspects of the landscape, in addition to accounting for the temporally auto-correlated nature of animal trajectories (Benhamou 2011). Utilisation distributions created by BRB analyses were then used as response variables in generalised additive mixed models that examined the influence of a variety of physical variables (sea surface temperature (SST), depth, current direction etc.) in driving migration and high use of particular areas. Finally, geographically weighted regression (GWR) (Fotheringham *et al.* 1998) was used to identify non-stationarity in the relationships between these variables, showing areas where there was higher or lower utilisation than predicted by the model. This approach is a new concept for marine species, but has been used for studies of species distribution and occurrence in
the terrestrial realm (Foody 2004; Osborne et al. 2007; Powney et al. 2010; Eiserhardt et al. 2011).

Tiger sharks are an ideal model species for this work for a number of reasons. They are a large (up to 5 m total length) and mobile (Heithaus et al. 2007c; Meyer et al. 2009; Hammerschlag et al. 2012; Hazin et al. 2013; Werry et al. 2014; Ferreira et al. 2015; Lea et al. 2015) predator present throughout the world’s tropical and warm temperate oceans (Compagno 1984; Randall 1992). As top-order predators, they are iconic and charismatic and have been the subject of a number of tracking studies world-wide, although these tend to have limited sample sizes or have been restricted in spatial and/or temporal scope (Meyer et al. 2009; Hazin et al. 2013; Werry et al. 2014; Holmes et al. 2014; Ferreira et al. 2015). Sampling by these studies also tends to be biased towards female sharks (but see Lea et al. 2015), possibly reflecting easier accessibility of this sex for tagging. However, the number and diversity of localities where tagging has occurred offers the opportunity for pooled data sets to provide a global picture of movement behaviours of these predatory sharks. We combine the results of tracking studies from eight localities across the Indian, Pacific and Atlantic oceans and using this pooled data set, we seek to identify the key physical and biological drivers of movement patterns at global scales. We hypothesise that the drivers of high use of areas and migration will be different, thus we identify these components in the data and analyse them separately as response variables against a range of environmental variables and deployment location. We also hypothesise that the variability of movement patterns reported previously for this species might be related to sex and ontogeny and thus we examine the importance of total length (as a proxy for age) and sex as explanatory variables in the models.

5.3 Methods

5.3.1 Telemetry

Telemetry data from 130 adult and sub-adult tiger sharks of both sexes, tagged at Ningaloo Reef (13 sharks), Shark Bay (9), Great Barrier Reef (12), USA (Florida and the Bahamas - 71), Hawaii (3) and Brazil (Recife - 18; Fernando de Noronha Island - 4) between 2008 and 2015 were combined to create a global database (Figure 5.1). Several types of telemetry tags were used, including ARGOS satellite transmitting tags (SAT; mostly Wildlife Computers SPOT and SPLASH), and Pop-up archival tags (PAT;
mostly Wildlife Computers PSAT Mk10 and miniPAT; see Table S1). Sharks were caught by drumlines, longlines and rod-and-reel and tags were attached to the first dorsal fin using either corrodbile bolts or by a 2.0 mm polyamide monofilament line passed through a hole in the anterior region of the fin. All procedures were approved by the Animal Ethics Committees of the organisations that led the field work. For more details on these methods see Heithaus et al. (2007c), Fitzpatrick et al. (2012), Hammerschlag et al. (2012), Hazin et al. (2013), Ferreira et al. (2015).

Location estimates were obtained from either the Argos satellite network (SPOT and SPLASH) or via light-based geolocation (PAT) (Hill & Braun 2001). For SAT tags, all Argos Location Classes (3, 2, 1, 0, A, B, Z) were included in the analysis. Raw locations from Argos were filtered according to Ferreira et al. (2015), with extreme location estimates (e.g. points requiring movement rate of > 1000 km a day) either removed or replaced by the secondary locations reported by Argos. Tracks shorter than 30 days or with very sparse locations (e.g. 5 location estimates in >100 days) were not included in the analysis. This gave a total sample size of 105 individual tiger shark tracks for analysis. We attempted to use the BSAM package in R (Jonsen et al. 2016) to fit state-space models to account for location error, however these models did not converge due to sparse location data.

Location estimates for tiger sharks tagged with PAT tags were calculated from light level data recorded and stored on board the tag. The data was relayed via the Argos Network after detachment of the tag from the shark or downloaded from the archive when the tag was recovered. Locations were estimated from light data using the software WC-GPE: Global Position Estimator Program (Wildlife Computers Inc.). The most probable track was reconstructed using the TrackIt state-space model with a Kalman filter (Nielsen & Sibert 2007) in R (R Core Team 2013). Sea surface temperature (SST) was applied to the model to improve the accuracy of location estimates and reduce confidence intervals (Lam et al. 2010). However, the majority of tiger sharks tracked with PAT tags remained within the equatorial Atlantic Ocean (Fig 1) where SSTs are relatively uniform and cloud cover is high. This led to model under-performance and convergence (Nielsen & Sibert 2007) so that SST corrections were not incorporated in some tracks.
5.3.2 Environmental data

Data for SST and ocean currents (direction and magnitude) were obtained using the Marine Geospatial Ecology Tools (MGET) for ArcGis10.3 (Roberts et al. 2010). Daily and monthly average SSTs were generated by the Moderate Resolution Imaging Spectroradiometer (MODIS), Aqua satellite Level 3 with a 4 km resolution. Daily data on direction and magnitude of ocean currents was derived from the Hybrid Coordinate Ocean Model with a 1/12 degree resolution. Bathymetry data was obtained from the General Bathymetry Chart of the Oceans Gebco15 database in a 30 arc-second resolution grid (http://www.gebco.net). A suite of bathymetric covariates were calculated from this data that have been previously associated with distributions of marine fauna (Bouchet et al. 2015; Yates et al. 2016) and these were used as a proxy for habitat complexity. Bathymetric predictors were calculated in ArcGis 10.3 using digital terrain analysis with fixed window sizes (Holmes et al. 2008) and a resolution of 1 km to match the bathymetry dataset (Table 5.1).

5.3.3 Identification of areas of high use

In order to identify areas of high use through time, utilisation distributions were calculated monthly across a 4 km square grid for each shark using the Biased Random Bridge (BRB) kernel method (monthly UD values were calculated to account for the dynamic nature of some covariates (e.g. SST). Similar to the Brownian Bridge kernel method (Bullard 1991), the time spent between successive locations and the correlation between locations is taken into account in the calculation of utilisation distributions. However, the BRB approach also includes a component of advection in the trajectory so that movement from one location to the next is considered to be biased towards the next location. This is an important distinction, because successive locations in the track of an animal are typically auto-correlated, where the next is bound both to the previous starting location and the capability of an animal for locomotion within the given time period (Papworth et al. 2012). The advection component of the analysis affects the orientation and shape of the bridge, with stronger advection generating longer and narrower bridges (Benhamou 2011). An upper time limit between successive locations is also used as a threshold value in the kernel bridging computation to ensure that steps longer than this maximum are not included in the analysis. Here, a maximum threshold of 5 days was imposed, based on the average rate of transmission from the tiger shark.
tags, as it was assumed that steps longer than this would result in unrealistic estimations of utilisation distributions.

The BRB method also includes a component related to the uncertainty of locations and the mean values for the track of the error associated with each ARGOS Location Class (LC 3 = 270 m, LC 2 = 540 m, LC 1 = 1330 m, LC 0 = 5179 m, A = 8072 m, B = 11484 m) were used for this analysis (Hays et al. 2001a; Hazel 2009). For geolocations, location uncertainty was estimated from the variance of location estimates provided by the TrackIT model. All analyses for the BRB used the adehabitatHR package (Calenge 2011) in the software R (R Core Team 2013).

The monthly utilisation distributions were then converted into point data, where each point contained the UD value for each 4 km grid cell, and the values were normalised to values between 0 and 1, so that the gridded UD value for each cell became the probability of shark use of a grid cell. Utilisation distribution is a similar concept to that of home range (Powell 2000), where home range cores of an animal typically range from 25% to 95% with the lower values containing the highest density of points. However, as a result of the normalisation, utilisation distribution values here were represented as the inverse of home range (i.e. 0.75 UD represented the 25% HR core, whereas 0.25 UD represented the 75% HR core). This produced distributions of values, more useful as a response variable in subsequent models; for example a 25% HR core corresponds to a distribution of values between 0.75-1 UD. The larger the value of the UD for a cell in the grid, the greater the use of that cell by the shark. Normalised values of monthly utilisation distributions for males were log-transformed to improve distribution of the model residuals.

In order to identify general areas of high use for tiger sharks in each ocean basin, these normalised gridded monthly utilisation distribution of values between 0.75-1 UD for all sharks in each region were also averaged, so that each grid cell represented the average UD of all sharks that utilised that cell.

5.3.4 Identification of migratory behaviour

In order to examine the environmental drivers of shark migratory behaviour, periods of migration within tracks were identified, as long, directional, relatively straight, extensive movement (Dingle & Drake 2007; Lea et al. 2015), as opposed to residency, which was defined as a cluster of locations in a defined area (Figure S 5.1). To
quantitatively identify these behaviours, utilisation distributions were calculated for the entire track of each shark using BRB. Tracks were then interpolated to a single location estimate per day with the R package crawl (Johnson 2014) in order to match the resolution of the environmental data. Gaps in the data longer than 20 days were not interpolated to avoid unrealistic interpolated paths (Block et al. 2011; Queiroz et al. 2016). The interpolated track from each individual shark was then overlaid on the 0.75 utilisation distribution indicating a high degree of residency (Ferreira et al. 2015). All locations inside the 0.75 UD were categorised as resident and assigned a value of 0 and locations outside the 0.75 UD categorised as migratory and assigned a value of 1 (Figure S 5.1). Resident was defined as the behaviour associated with high-use areas, whereas migrant is the straight-line behaviour associated with large-scale movement.

5.3.5 Modelling movement behaviour

*Habitat use*

As tagging was skewed towards females (82% of tagged individuals) UD was analysed separately for each sex to avoid over-estimating parameters for males. Due to the large size of the dataset for females (4,211,047 data points), the normalised UD dataset was filtered by removing values below 0.25 UD. These values represented the grids with very low probability of use that were present in large numbers as a result of the shape of a Brownian Bridge (Bullard 1991), but provided only low explanatory power of the drivers of residency. The dataset for females was also analysed separately for each region: North Atlantic, South Atlantic, Indian and Pacific oceans (Hawaii and Great Barrier Reef were analysed separately) due to differences in the range of some of the environmental variables among regions. Utilisation density (normalised for females, normalised and log-transformed for males) was used as the dependent variable in a suite of generalised additive mixed models with a Gamma distribution with an inverse link function, with individual shark as the random effect using the R function `bam` (gam for large datasets) from the R package `mgcv` (Wood 2016). A set of biological, temporal and environmental variables was assembled to determine the important predictors of high use of habitat by tiger sharks (Table 5.1). Exploratory analyses identified any collinearity within the set of bathymetric covariates and only one was selected for use in the models when they were highly correlated (Pearson’s r > 0.8). Models with all possible combinations of selected predictor variables were fitted then compared and ranked according to Akaike’s Information Criterion (AIC), and by the AIC weight
(wAIC). The wAIC varies from 0 (no support) to 1 (complete support). The amount of variance (percentage deviance) in the response variable explained by each of the candidate models was used as a measure of goodness-of-fit to the data (Anderson & Burnham 2002; Burnham & Anderson 2004). We considered all models within 2 AIC units of the top-ranked model, using the principle of parsimony to select the final model. Conditional plots of UD relative to each explanatory variable in the top-ranked models were generated using the package visreg (Breheny & Burchett 2016).
Figure 5.1 Telemetry data included in the analyses, colour coded by individual shark tag ID, from Hawaii (Pacific Ocean) (top left), North Atlantic (top right), South Atlantic (left), Great Barrier Reef, Australia (Pacific Ocean) (middle) and Indian Ocean, Australia (bottom right).
Migration

The drivers of migration were also examined using generalised additive mixed models with a binomial distribution, using the package \textit{gamm4} (Wood 2016). The probability of migration (migrant = 1, resident = 0) was the dependent term in the models with a set of environmental predictors (Table 5.2) and a random effect of individual shark. Because direction of ocean current was a circular variable, it was modelled with a cyclic cubic regression spline, whereas a regular cubic regression spline with shrinkage was applied to the other (non-circular) covariates. The number of predictors in each model was set to two or less and basis dimension “k” to five to avoid over-fitting. Autocorrelation was addressed by using a matched-block bootstrap sampling with replacement procedure (Carlstein \textit{et al.} 1998; Patton \textit{et al.} 2009). Model fitting was applied to 1000 bootstrapped samples and model selection was as described above, but with upper and lower quartiles also presented.

5.3.6 Assessment of spatial variability in model predictions

Geographically Weighted Regression (GWR) is a tool used to explore spatially varying relationships between variables, termed spatial non-stationarity (Fotheringham \textit{et al.} 1998). A global regression model applied to spatial data will estimate a single set of parameters for the relationship between the response and explanatory variables. However, the presence of spatial non-stationarity alters the relationship between variables in space, limiting the descriptive and predictive power of a model (Foody 2004). Non-stationarity might occur due to methodological issues (model misspecification, missing variables and/or their use at inappropriate temporal or spatial scales), spatially auto-correlated data and, in this case, potential differences in movement behaviour of animals among locations. Geographically Weighted Regression accounts for these issues, allowing parameters to be estimated locally by fitting a regression equation to any point in space to explore local spatial relationships. Consequently, it allows relationships to vary over space so that localised model parameters are estimated around each regression point. Geographical weighting is implemented on neighbouring observations according to a spatial kernel function that is then used in the localised model. The weighting of observations decreases as the distance from the centre of the kernel increases and the area or number of neighbouring
observations around the centre of the kernel used in the weighting function is controlled by the bandwidth, which ultimately defines the scale of the analysis (Foody 2004).

Geographically Weighted Regression has been used as a tool to explore localised variation in the relationships of variables used in a global model such as a logistic regression, generalised linear models or generalised additive models (Foody 2004; Osborne et al. 2007; Windle et al. 2009; Miller & Hanham 2011). However, in contrast to previous studies, GWR was used here to identify the presence of non-stationarity in the relationship between the predicted values of UD (from the top-ranked models) against the observed value of UD. The ‘global model’ was thus a regression between predicted and observed values from each top-ranked model in the analysis of drivers of high habitat use. Effectively, the analysis determined if the environmental drivers identified in top-ranked models adequately explained areas of high use and if this relationship varied spatially. A Gaussian kernel was used in the geographical weighting so that all data points contributed to the regression, but points spatially distant from the centre of the kernel were inversely weighted according to a Gaussian curve. An adaptive bandwidth was also used in the weighting function (e.g. an adaptive distance of the kernel bandwidth) that ensured that sufficient local information was used for each local model in an irregular sampling configuration. Automated optimal bandwidth selection was determined by minimising AIC. The presence of spatial non-stationarity was evaluated by the range in the local parameters of GWR coefficients where large variations of values and the presence of highly positive or negative clusters suggested non-stationarity. All GWR analyses were done in ArcGIS 10.3 software.

5.4 Results

The telemetry dataset provided a total of 14,357 tracking days of tiger sharks with average track duration of 136 ± 141 days for females and 85 ± 76 days for males (Figure 5.1, Table 5.3). Females were the dominant sex tagged in all regions (82.3% of all tracks) and the majority of male tiger sharks in the sample (82%) were tagged in the Atlantic Ocean. Female sharks ranged in total length from 120 - 407 cm (average 289 ± 68 cm) whereas males ranged from 130 - 395 cm (average 231 ± 72 cm). Sharks tagged in the South Atlantic appeared to be smaller (average TL of 186 ± 54 cm) than in the Indian (mean 314 ± 55 cm), North Atlantic (mean 288 ± 68 cm) and Pacific (319 ± 52 cm) oceans (Table 5.3).
Figure 5.2 Utilisation densities combined and averaged for each month for each grid cell for all individuals in each regional dataset and filtered to the 0.75UD. Colour scale represents the average utilisation of each cell and grey contours indicate the 500 m isobath.
**Table 5.1** Description of all environmental, temporal and biological predictors for the analysis of monthly utilisation distribution.

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Resolution</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth</td>
<td>30-arc second</td>
<td>Water depth (m) in relation to bathymetry extracted from Gebco15</td>
</tr>
<tr>
<td>Aspect</td>
<td>1 km</td>
<td>Direction of the steepest slope in degrees (0-360°) on a 3 x 3 cell area</td>
</tr>
<tr>
<td>Slope</td>
<td>1 km</td>
<td>First derivative of elevation: Average change in elevation calculated on a 3 x 3 cell area. Calculated in degrees (0-360)</td>
</tr>
<tr>
<td>Curvature</td>
<td>1 km</td>
<td>Combined index of profile (hill cross-section) and plan (contour lines) curvatures</td>
</tr>
<tr>
<td>Standard Deviation</td>
<td>1 km</td>
<td>Standard deviation of elevation on a 3 x 3 cell area</td>
</tr>
<tr>
<td>Plan curvature</td>
<td>1 km</td>
<td>Second derivative of elevation: concavity/convexity perpendicular to the slope, calculated on a 3 x 3 cell area</td>
</tr>
<tr>
<td>Profile curvature</td>
<td>1 km</td>
<td>Second derivative of elevation: concavity/convexity parallel to the slope, calculated on a 3 x 3 cell area</td>
</tr>
<tr>
<td>Hypsometric index</td>
<td>1 km</td>
<td>Indicator of whether a cell is a high or low point within the local neighbourhood</td>
</tr>
<tr>
<td>Local relief (Range)</td>
<td>1 km</td>
<td>Maximum minus the minimum elevation in a local neighbourhood</td>
</tr>
<tr>
<td>Sea Surface Temperature</td>
<td>4 km</td>
<td>Monthly SST(°C) generated from the Moderate Resolution Imaging Spectroradiometer (MODIS), Aqua satellite Level 3</td>
</tr>
<tr>
<td>Month</td>
<td>1 - 12</td>
<td>Month the utilisation distribution was calculated</td>
</tr>
<tr>
<td>Total length</td>
<td>-</td>
<td>Total length of the shark (cm)</td>
</tr>
</tbody>
</table>

**Table 5.2** Predictors used to model migratory movements of tiger sharks.

<table>
<thead>
<tr>
<th>Predictor</th>
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</tr>
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<tr>
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<td>Water depth (m) in relation to bathymetry extracted from Gebco15</td>
</tr>
<tr>
<td>Sea Surface Temperature</td>
<td>4 km</td>
<td>Daily SST (°C) extracted from the Moderate Resolution Imaging Spectroradiometer (MODIS), Aqua satellite Level 3</td>
</tr>
<tr>
<td>Ocean current direction</td>
<td>1/12 degree</td>
<td>Daily direction in degrees (0-360°) derived from the Hybrid Coordinate Ocean Model - HYCOM</td>
</tr>
<tr>
<td>Ocean current speed</td>
<td>1/12 degree</td>
<td>Daily absolute magnitude of water velocity (m/s) derived from the Hybrid Coordinate Ocean Model - HYCOM</td>
</tr>
</tbody>
</table>
Table 5.3 Summary tracking datasets including information of tagging location, number of tags deployed, track duration and size range of sharks tagged. Mean values and SD are presented for total length (TL) and track duration.

<table>
<thead>
<tr>
<th>Ocean</th>
<th>Tagging locations</th>
<th>Tag Types</th>
<th>Deployment years</th>
<th>Sex</th>
<th>N tags</th>
<th>TL range</th>
<th>Duration</th>
</tr>
</thead>
<tbody>
<tr>
<td>Indian</td>
<td>Ningaloo, Shark Bay</td>
<td>SPOT, SPLASH</td>
<td>2007-2015</td>
<td>F</td>
<td>20</td>
<td>312.3 ±53.5</td>
<td>177.95 ±143.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>M</td>
<td>2</td>
<td>395, 271</td>
<td>38, 191</td>
</tr>
<tr>
<td>Pacific</td>
<td>Hawaii, Great Barrier Reef</td>
<td>SPOT, SPLASH, Telonics ST18</td>
<td>2003-2013</td>
<td>F</td>
<td>13</td>
<td>306.3 ±59.8</td>
<td>129.5 ±116.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>M</td>
<td>2</td>
<td>288,292</td>
<td>63, 231</td>
</tr>
<tr>
<td>North Atlantic</td>
<td>Florida, The Bahamas</td>
<td>SPOT, uCricket</td>
<td>2009-2015</td>
<td>F</td>
<td>60</td>
<td>296.1 ±58.3</td>
<td>141.6 ±155.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>M</td>
<td>11</td>
<td>247.8 ±56.5</td>
<td>76.1 ±57.05</td>
</tr>
<tr>
<td>South Atlantic</td>
<td>Recife, Fernando de Noronha Island</td>
<td>PAT-Mk10, MiniPAT</td>
<td>2008-2013</td>
<td>F</td>
<td>15</td>
<td>198.7 ±60.3</td>
<td>58.8 ±38.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>M</td>
<td>7</td>
<td>159.6 ±25.7</td>
<td>45.57 ±2.41</td>
</tr>
</tbody>
</table>
Scale of movement and habitats varied greatly among individual sharks and regions. Wider ranging tracks were recorded in the North Atlantic, the Indian Ocean and off Hawaii, where large-scale (100s - 1000s km) movements along the coast and/or into the open ocean were observed (Figure 5.1). Tracks from the South Atlantic were obtained from PSAT deployments that provided only low resolution estimates of geolocation and tracking durations that were never >120 days. This reduced the likelihood of identifying patterns of high habitat use and migratory behaviour for sharks in this region.

In the North Atlantic, average utilisation distributions for all sharks combined showed areas of high use around the tagging site off the Bahamas, but also in the Gulf of Mexico, in the waters of North Carolina and around the edge of the Gulf Stream (41°N) (Figure 5.2a-c). In Western Australia, high use areas were associated with tagging locations (Ningaloo Reef and Shark Bay, Figure 5.2d), while in Hawaii the sharks mostly used oceanic areas north of the islands (Figure 5.2e). In the South Atlantic, an area of high use was identified in the equatorial region off the coast of northern Brazil (Figure 5.2f), whereas on the Great Barrier Reef, sharks had small areas of high use (Figure 5.2g).

5.4.1 Drivers of high use of habitats

The model including depth, SST, aspect and standard deviation of elevation had 100% support (wAIC = 1) out of the suite of models fitted to explain utilisation distribution of females in the North Atlantic (Table 5.4), whereas for the South Atlantic and Indian Ocean the model with depth and SST only had 100% support (wAIC= 1) (Table 5.4). For Hawaii, the model with SST only had majority support (wAIC = 0.93) and for the Great Barrier Reef, the model with depth only had complete support (wAIC = 1) (Table 5.4). In the North Atlantic, females showed an elevated utilisation of oceanic waters (>3,000 m deep) beyond the continental shelf and in temperatures below 22°C (Figure 5.3a-b). Higher values of UD were also associated with bathymetric aspects in north and northeast directions (350° and 50°), and areas with minor deviations of elevation (Figure 5.3i-j). In the Indian Ocean, residency was greater in water temperature between 22°-24°C and oceanic areas around 3000 m deep (Figure 5.3c,d), with some preference for depths around 250 m. In the Pacific Ocean around the Great Barrier Reef (Pacific Ocean), utilisation increased with increasing depths (>1000 m Figure 5.3e). For sharks in Hawaii, higher values of UD were related to temperatures between 24°-25°C.
(Figure 5.3f). In the South Atlantic, sharks showed both preference for open waters >4000 m and the shallow shelf, and waters around 25°C (Figure 5.3g-h).

Table 5.4 The top ranked generalised additive mixed models from the suite of models used to explain monthly utilisation distributions of female and male tiger sharks. SST = sea surface temperature, Std = standard deviation of elevation. Shown are the percent deviance explained (%DE), Akaike’s information criterion (AIC), and AIC weight (wAIC).

<table>
<thead>
<tr>
<th>Model</th>
<th>% DE</th>
<th>AIC</th>
<th>wAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Females</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>North Atlantic</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Depth + SST + Aspect + Std</td>
<td>11.9</td>
<td>-71047.5</td>
<td>1</td>
</tr>
<tr>
<td>South Atlantic</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Depth + SST</td>
<td>7.94</td>
<td>-69164.7</td>
<td>1</td>
</tr>
<tr>
<td>Indian Ocean</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Depth + SST</td>
<td>14.4</td>
<td>-23959.6</td>
<td>1</td>
</tr>
<tr>
<td>Hawaii</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SST</td>
<td>7.74</td>
<td>-910.2</td>
<td>0.93</td>
</tr>
<tr>
<td>Depth</td>
<td>7.39</td>
<td>-905.2</td>
<td>0.07</td>
</tr>
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<td>Great Barrier Reef</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Depth</td>
<td>12.6</td>
<td>-2636.317</td>
<td>1</td>
</tr>
<tr>
<td><strong>Males</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Depth + SST</td>
<td>14.4</td>
<td>757422.6</td>
<td>1</td>
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</table>

For males, the model including depth and sea surface temperature had complete support (wAIC = 1) and explained 14.4% of the total deviance in the data (Table 5.4). Males exhibited high utilisation of habitats associated with shallow depths, in addition to sea surface temperatures of around 26°C or above 30°C (Figure 5.4), which are representative of coastal and shelf environments.

5.4.2 Drivers of migration

Migration was identified in tracks from female sharks tagged in the North Atlantic, Indian and Pacific oceans. As the tracks from the region of the South Atlantic showed no evidence for this behaviour they were excluded from this analysis. Large-scale movements by sharks to northern areas of the North Atlantic were observed during summer, with sharks reaching the margins of the Gulf Stream, whereas movements south to temperate regions were observed in the Indian Ocean during austral autumn (Figure 5.5). A repeated annual migration to the south was only observed for one shark in the Indian Ocean (T5, Table S 5.1).
The top ranked model to explain the probability of tiger sharks being in migratory mode contained the variables depth and sea surface temperature, with 68% support and accounting for 7% of the total deviance explained (Table 5.5). The model predictions showed a high probability of migration across the full range of environmental variables (>0.5, Figure 5.5). Migration was more likely to occur in oceanic areas over depths >1000 m (Figure 5.5). Increasing probability of migration was also related to water temperatures from both tropical and subtropical-temperate regions with likelihood of migration being highest in water temperatures above 28°C and below 22°C (Figure 5.5).
Table 5.5 The top three ranked generalised additive mixed models with 1000 bootstraps sampling for the suite of models used to explain the probability of migration of tiger sharks. Shown for each model are the median, 25th and 75th quantile Akaike’s information criterion corrected for small samples (AICc), AICc weight (wAICc) and the adjusted R-squared (Adj R²). The top ranked model is in bold.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>wAICc</th>
<th>% DE</th>
<th>AICc.25</th>
<th>AICc.75</th>
<th>wAICc.25</th>
<th>wAICc.75</th>
<th>Adj R².25</th>
<th>Adj R².75</th>
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</thead>
<tbody>
<tr>
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<td>0.07</td>
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<td>2833.11</td>
<td>0.04</td>
<td>1.00</td>
<td>0.04</td>
<td>0.11</td>
</tr>
<tr>
<td>Depth + Current direction</td>
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<td>0.18</td>
<td>0.01</td>
<td>2590.20</td>
<td>2852.38</td>
<td>0</td>
<td>0.10</td>
<td>0.00</td>
<td>0.10</td>
</tr>
<tr>
<td>Depth + Current speed</td>
<td>2718.00</td>
<td>0.14</td>
<td>0.04</td>
<td>2591.91</td>
<td>2856.18</td>
<td>0</td>
<td>0.02</td>
<td>0.03</td>
<td>0.10</td>
</tr>
</tbody>
</table>
Figure 5.3 Conditional plots of female utilisation density relative to the explanatory variables in the top ranked mixed model for each region from the suite of models used to explain the response variable. Solid curves are the model fit and shaded areas indicate the 95% confidence intervals. Tick marks on the x-axis indicate the distribution of observations. Plots a, c, e, g are fits for bathymetry for North Atlantic, Indian Ocean, Pacific (Great Barrier Reef) and South Atlantic, respectively; b, d, f, h are fits for sea surface temperature for North Atlantic, Indian Ocean, Pacific Ocean (Hawaii) and South Atlantic, respectively; i-j are fits for standard deviation of elevation and aspect in the North Atlantic.
5.4.3 Assessment of spatial variability in model predictions

The local coefficient estimates produced by the GWR indicated the presence of spatial non-stationarity in all regions for UD of females (Figure 5.6a-g) but not for males, with the exception of the Great Barrier Reef (Figure 5.7a-d). This was shown by the large variation of GWR estimates for females, indicating the presence of spatial variability in localised relationships, particularly along the east coast of USA (Figure 5.6a,b) and off the coast of Western Australia (Figure 5.6c,d). By mapping the GWR coefficient estimates it was possible to identify areas where the observed values of UD were much higher or lower than the values predicted by the models. For females in the North Atlantic, a core of strongly positive GWR estimates (utilisation higher than predicted by the top-ranked model) were identified along the Florida and North Carolina coasts and in the Bahamas (Figure 5.6a,b). Similarly, localised areas of strongly positive values were also seen on the northwest coasts of Western Australia around the latitudes 19°-20°S and 24°S (Figure 5.6c,d). Small areas of positive values were also found along the Great Barrier Reef (Figure 5.6f). The presence of higher-than-predicted values suggests that other localised factors were accounting for high use in these areas. For females in the South Atlantic, GWR local parameters showed a particularly large variation with a few cores of highly negative and one area with highly positive values (Figure 5.6g).

![Figure 5.4](image)

**Figure 5.4** Conditional plots of male utilisation density relative to the explanatory variables in the top ranked mixed model from the suite of models used to explain the response variable. Solid curves are the model fit and shaded areas indicate the 95% confidence intervals. Tick marks on the x-axis indicate the distribution of observations.
Figure 5.5 Conditional plots of probability of migration relative to the explanatory variables in the top ranked mixed model from the suite of models used to explain the response variable. Solid curves are the model fit and shaded areas indicate the 95% confidence intervals. Tick marks on the x-axis indicate the distribution of observations.
Figure 5.6 GWR-derived local coefficient estimates for the relationship between predicted and observed values from the top ranked mixed model explaining the drivers of habitat use for females. A-B = North Atlantic Ocean and B is zoomed in on the box in A, C-D = Indian Ocean and D is zoomed in on the box in C, E = Pacific Ocean around Hawaii, F = Great Barrier Reef, G = South Atlantic. Grey isolines represent bathymetry. Red and orange show areas where observed UD was higher than predicted (see detail in B and D) and blue and green show areas where observed UD was lower than predicted.
5.5 Discussion

Depth and sea surface temperature were identified as key physical variables structuring patterns of both high habitat use and migration patterns of tiger sharks. However, the relationships between these variables and shark movements were inconsistent among regions. Because tiger sharks mostly occupy the surface layers of the water column (Vaudo et al. 2014), water depth at a location provided an indication of the use of shelf (depth <200 m) and oceanic waters. In the North Atlantic, many of the female sharks tagged off Florida and the Bahamas displayed tracks that followed the Gulf Stream and had excursions into the Atlantic Ocean basin, thousands of kilometres from the coast. This was reflected in the results of the mixed models, which showed preferences for the use of habitats in very deep water (5000-6000 m). In contrast, females tagged in Australia at Ningaloo Reef and Shark Bay tended to reside in waters closer to the coast just beyond the shelf break, so that conditional plots from the mixed models showed preferences of tiger sharks for shallower oceanic habitats (3000 m) than in the North
Atlantic. On the Great Barrier Reef females were tagged at the edge of the shelf and displayed residencies both off the edge of the shelf and in deeper water of the Coral Sea.

Similarly, relationships between utilisation distribution and water temperatures also varied among regions. Females in the North Atlantic and Indian oceans showed a preference for cooler waters of <20°C and 23°C, respectively, whereas females off Hawaii and in the South Atlantic preferred temperatures between 25-26°C. In contrast, males showed greater use of shelf waters and selected temperatures of 25-26°C or above 30°C. Depth and sea surface temperature were also identified as the main drivers of migratory movements of female sharks, with these occurring beyond continental shelves and in water temperatures either below 22°C, or above 26°C. No migratory movements could be identified in the tracks of male tiger sharks. Ocean currents have been previously suggested as a possible driver of shark migration (Hazin et al. 2013; Holmes et al. 2014; Ferreira et al. 2015; Lea et al. 2015). However, our mixed models did not identify current speed or direction as important predictors in the top-ranked model, despite the fact that long-term (several months–years) tracks of sharks in both the North Atlantic and off the coast of Western Australia showed excursions of sharks from tropical waters into temperate regions that followed the path of principal boundary currents (the Gulf Stream in the North Atlantic and the Leeuwin Current in the Indian Ocean). A lack of any easily detectable influence of direction and speed of water flow in these long-distance movements of tiger sharks might be due to animals undertaking vertical movements during migration to take advantage of counter-current flows at depth or for behavioural thermoregulation (Thums et al. 2012), although such behaviour has yet to be fully investigated for the species (Nakamura et al. 2011; Iosilevskii et al. 2012). These phenomena could mask simple relationships between migration patterns and current systems measured by remote sensing at the ocean surface.

Despite amassing the largest tracking data set yet assembled, our models explained relatively little of the variation in patterns of high utilisation and migration of tiger sharks. At best, physical predictors of water depth and SST explained less than 15% of the variance in utilisation distributions for both female and male sharks. The GWR highlighted that spatial non-stationarity existed in the relationship between utilisation distributions and values of UD predicted by top-ranked mixed models for each ocean basin, thereby showing that relationships vary across space, accounting for the low explanatory power of the models (Osborne & Suárez-Seoane 2002). Overall, the GWR showed that the models predictions were consistent with most areas of high utilisation
by tiger sharks, reinforcing that water temperatures and depths were reasonable predictors of spatial patterns of habitat use at least in open ocean environments. The non-stationarity identified for females was most pronounced in the Atlantic and Indian oceans, as evidenced by the large range in GWR coefficient estimates. The GWR highlighted a number of areas where the observed UDs were much higher or lower than those predicted by our models. Two areas at the shelf edge and the mid-shelf off the coast of Western Australia, around latitudes of 19°-21°S (Figure 5.6d), had strongly positive GWR estimates (observed values of utilisation greater than predicted by the models). These matched hotspots of abundances of pelagic fishes documented in earlier studies by Bouchet (2015) (Figure S 5.2). Another zone of strongly positive GWR estimates was present off the coast from 24-25°S, in an area of high occupancy for pygmy blue whales (Balaenoptera musculus brevicauda) (Double et al. 2014) (Figure S 5.2). The coincidence of these distributions suggest that prey availability may indeed account the spatial non-stationarity found in this area. However, many tracks had relatively short duration and, therefore, areas of high use indicated by GWR may also have been a result of local residency demonstrate by sharks tracked for shorter periods.

The GWR also identified areas on the shelf on the eastern coast of the US where the observed UD was higher than model predictions (26°-27°N and 34°-36°N). It is notable that these areas of high use for tiger sharks were also areas of high use for other coastal sharks. For these coastal species, residency and movement patterns were strongly correlated with water temperatures, relationships that were documented using data collected at relatively fine spatial scales by oceanographic buoys and loggers deployed across the study area (Kessel et al. 2014; Kajiura & Tellman 2016). A similar approach may be necessary to fully describe residency and movement patterns of tiger sharks in these habitats. In the South Atlantic, the problem of non-stationarity was probably driven by the low resolution of both tracking and environmental data. This was due to the reconstruction of tracks from geolocations using light data, which have large errors associated with position estimates (Lam et al. 2010). As a consequence, maps of GWR coefficient estimates in the South Atlantic showed a very broad spread of values across the sampling area.

For the North Atlantic and Indian Ocean data sets, it appears that the reasons for spatial non-stationarity are also a result of scale, but in more nuanced way. The results of the GWR suggested that SST and depth could accurately predict the use of oceanic habitats in the North Atlantic and Indian Ocean, probably because tiger sharks in oceanic
Habitats are operating at large and mesoscales (10s -100s km) that can be identified at the scale of resolution of the environmental data sets provided by satellite remote sensing. However, in shelf waters tiger shark movements and the processes driving their utilisation patterns are likely to operate at far smaller spatial scales, where topographic features such as canyons, banks and reefs or habitats such as estuaries and seagrass meadows may locally enhance productivity of food chains that sustain the targets of feeding by tiger sharks (Heithaus et al. 2002, 2007a; Morato et al. 2010; Bouchet 2015). The environmental signals of these habitats may be very difficult to identify in the low-resolution data provided by remote sensing.

It has been suggested that movements of tiger sharks are mainly driven by prey distribution (Heithaus et al. 2002), but to date this variable has not been included in any models that seek to predict movement patterns. This is largely due to the difficulties of collecting data sets of prey availability at scales comparable to the spatial and temporal patterns of movement of these predators and the issue of matching predator and prey fields is recognised as a major problem in the field of ecology of marine megafauna (Hindell 2008; Hays et al. 2016). For tiger sharks, describing the prey field is further complicated by the fact that the species has a very broad diet and is both an top-order predator and scavenger depending on the habitat, prey field and opportunities that are presented within the environment (Lowe et al. 1996; Simpfendorfer et al. 2001; Gallagher et al. 2011; Hammerschlag et al. 2016). This makes identification of potential prey and mapping of their distributions within the environment a very difficult task.

The finding that this scale-dependent behaviour may be causing models to have low predictive power to describe utilisation patterns is perhaps not surprising, given that tiger sharks are recognised as a generalist predator (Lowe et al. 1996; Simpfendorfer et al. 2001; Matich et al. 2011; Trystram et al. 2016). This scale-dependent pattern combined with the high individual variability found in the behaviour of tiger sharks may have been responsible for the low explanatory power of the environmental variables tested to describe their utilisation patterns. In terrestrial systems many predators exhibit preferential patterns of prey choice where they specialise on a specific type of prey that inhabit particular habitats (Hayward et al. 2007, 2012; Lyngdoh et al. 2014). For example, lions (Panthera leo) have been shown to actively and cognitively decide to hunt preferred prey, increasing the chance of encounter by choosing to forage in habitats with higher abundances of those prey (Hayward et al. 2011). In the marine environment, although orcas (Orcinus orca) can be considered as a generalist species,
different populations of killer whales adapt their hunting and behavioural strategies to target preferred prey in the habitat where they are most abundant (Hoelzel 1991, Saulitis et al. 2000, Ford & Ellis 2006, Ford et al. 2010, and references within). In contrast, tiger sharks do not display high levels of specialisation in diet and seem to shift prey preference across their range, seasonally targeting areas with high abundances of prey (Simpfendorfer et al. 2001; Lowe et al. 2006). These generalist predators will thus require multiple foraging strategies to capture prey that will be pursued across multiple habitats, resulting in scale and habitat-dependent space use.

Scale-dependent movements of marine predators are likely to be accompanied by local adaptation of foraging strategies according to prey type and availability. Identifying these behaviours is challenging (Austin et al. 2006), particularly when tracking data is very patchy, as is typically the case for tiger sharks. Location estimates in tracks are often too sparse to extract horizontal displacement metrics that can be used in movement-based models for the identification of foraging behaviour (Fauchald & Tveraa 2003; Jonsen et al. 2013, but see Fitzpatrick et al 2015). The use of GWR provides an understanding of movement patterns from such data sets because it identifies where and how the modelled relationships change across variable space and the potential reason as to why this occurs. Here, it seems likely that tiger sharks respond to environmental signals that occur at smaller spatial scales on the continental shelf than the open ocean, thus indicating where fine-scale studies of the use of habitats should be targeted. Given that sparse tracks and scale-dependent patterns of movement are a frequent outcome of many studies of large marine predators (Bradshaw et al. 2004a; Austin 2007; Bonfil et al. 2009; Hammerschlag et al. 2011a), the combined approach of additive mixed models and GWR has the potential for widespread application to the field of movement ecology.

5.6 Acknowledgements

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### 5.7 Supporting information

Table S 5.1 Details of each of the deployments of telemetry devices on tiger sharks.

*TL estimated from fork length using the equation by Stevens & McLoughlin (1991)*

<table>
<thead>
<tr>
<th>ID</th>
<th>Transmitter</th>
<th>Sex</th>
<th>Total length (cm)</th>
<th>Tag Type</th>
<th>Deployment date</th>
<th>Tagging location</th>
<th>Region</th>
<th>Duration (days)</th>
</tr>
</thead>
<tbody>
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</tr>
<tr>
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<td>Indian Ocean</td>
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**Figure S 5.1** Representative example of a tiger shark track (black points) analysed with Biased Random Bridges showing both residency (points within the 0.75 UD (red lines)) and migration (points outside the 0.75 UD).

**Figure S 5.2** Figure extracted from: A) (Bouchet 2015) indicating hotspots in fish abundance off the coast of Western Australia, B) Figure extracted from (Double et al. 2014) showing areas of high occupancy by pygmy blue whales off the coast of Western Australia.
Chapter 6  General Discussion

An understanding of movement ecology is essential for the conservation and management of mobile, top-order predators in marine systems. In this thesis I examined how environment and diet influenced movement patterns and habitat use of tiger sharks at multiple spatial and temporal scales. Firstly, I compiled available information on the biology and ecology of tiger sharks and identified current threats to the species in order to update their conservation status for the International Union for Conservation of Nature (IUCN) Red List (Chapter 2). I then examined patterns of movement of the species along the coast of Western Australia and showed that tiger sharks made extensive movements between tropical and temperate ecosystems and exhibited high individual variability in distances travelled and degree of residency within a habitat (Chapter 3). Isotopic analyses (Chapter 4) showed that these large-scale movements were accompanied by changes in diet, trophic niche and role across multiple habitats at a continental scale. Finally, I analysed a large dataset of satellite tracking from locations in the Indian, Pacific and Atlantic Ocean basins and identified bathymetry and temperature as key drivers of movements and habitat use by tiger sharks at global scales (Chapter 5). The relationship between these physical variables and movement patterns varied among ocean basins and had low predictive power to explain patterns of utilisation of habitats due to their variability in space (spatial non-stationarity). A common thread across all my chapters was the high degree of variation in behaviour that occurred among individual sharks, likely as a consequence of their role as a generalist top-order predator in marine ecosystems.

6.1 Variability in movement behaviour

Why are movement patterns of these large sharks so variable? One key reason might be that such species are not tied to any fixed point in the marine habitat during their ontogeny, such as discrete nursery areas that are commonly used by several sharks (Heupel et al. 2007) or philopatry to specific nesting beaches by sea turtles (Brothers & Lohmann 2015). For example, taxa that have portions of their life cycle associated with land, either for breeding or moulting, such as most pinnipeds, marine reptiles and seabirds, typically show a high degree of predictability in movement patterns and habitat use (Shaffer et al. 2006; Broderick et al. 2007; Egevang et al. 2010; Fitzpatrick et al. 2012; Raymond et al. 2015) because these behaviours are associated with the
regular return to natal beaches, islands and nesting grounds in order to breed. Southern elephant seals (*Mirounga leonina*), for instance, exhibit site fidelity to breeding colonies and foraging grounds, with many individuals returning to the same haul-out site after extended foraging trips (Jonker & Bester 1998; Bradshaw *et al.* 2004b; Fabiani *et al.* 2006; Mulaudzi *et al.* 2008). This highly predictable pattern of movement has allowed key environmental and habitat requirements to be identified throughout the species range (Biuw *et al.* 2007; Hindell *et al.* 2016).

In contrast, tiger sharks and other top-order predatory fishes including mako (*Isurus* sp.), thresher (*Alopias* sp.), billfishes and tunas rarely display such predictable behaviours. This is probably a reflection of the nomadic nature of their ecology with no easily identifiable specific start or end point to their migrations, combined with a lack of association with static points in the environment such as land masses, beaches or ice caps where breeding colonies occur. As a consequence, these animals display a high degree of individual variability in movement patterns and space use (Boustany *et al.* 2002; Walli *et al.* 2009; Carlisle *et al.* 2012) and a plasticity in behaviour and flexibility in habitat associations that hampers our ability to identify the drivers of migration and residency.

### 6.2 Drivers of movement and habitat use

The Biased Random Bridges (BRB) analytical technique provided a means to analyse and visualise tracking data for tiger sharks, while incorporating inherent autocorrelation in the computation of utilisation distributions and addressing gaps in the dataset (Bullard 1991; Benhamou 2011; Benhamou & Riotte-Lambert 2012). The description of utilisation distributions allowed me to assess if residency was potentially associated with foraging (Chapter 3) and to identify the environmental drivers of patterns of high utilisation of some habitats (Chapter 5). In Chapter 3, I found that residency at regional spatial scales was associated with bathymetry and sea surface temperatures (SST), and was more likely to occur in shallow coastal waters with temperatures above 23°C. The same environmental variables drove patterns of residency of tiger sharks in other ocean basins (Chapter 5). Although the distribution and habitat use of a wide range of fauna has been associated with topographic covariates (McConnell *et al.* 1992; Woodley & Gaskin 1996; Sjöberg & Ball 2000; Bouchet *et al.* 2015), tiger sharks are an epipelagic species that spend most of their time in the uppermost surface layer of the water column, above the thermocline (Meyer *et al.* 2010; Fitzpatrick *et al.* 2012; Hazin *et al.*
In my study, bathymetry acted as a surrogate measure of the use of oceanic and shelf habitats for the species (Chapter 3 and 5). As ectotherms, elasmobranchs are strongly influenced by changes in water temperature (Crawshaw 1977; Bernal et al. 2012), implying that these animals are likely to be constantly searching for optimal environmental conditions (Klimley & Butler 1988; Block et al. 1997, 2011; Bestley et al. 2013; Kessel et al. 2014; Schlaff et al. 2014). Despite the fact that water temperatures was a predictor of migration, it seems unlikely that this behaviour was a search for optimal conditions since tiger sharks selected temperatures during migrations to both tropical and temperate regions that were outside the thermal range they preferred while resident (Chapters 3 and 5).

6.3 Low predictability of models

Although SST and bathymetry were selected as major predictors of migration, residency and areas of high use, these explained only a small proportion of the variance in movement behaviour (Chapters 3 and 5). In Chapter 3, this result might have been an outcome of relatively low sample size. However, in Chapter 5, I gathered and analysed the largest global dataset of tiger shark tracks available to date. Despite the large number of tracks, generalised additive mixed models still explained only small amounts of variance in movement and had low power to predict the utilisation distributions (UD) of tiger sharks. To understand why this was the case, I then applied geographically weighted regression (GWR) to determine if patterns of utilisation were changing in space and causing non-stationarity in the relationship between model predictions and observed values. The GWR calculated localised coefficients for a regression by allowing the relationship between variables to vary in space and subsequently mapped the range of coefficients in a spatial context (Brunsdon et al. 1996; Fotheringham et al. 1998). This allowed me to determine the presence of non-stationarity in the relationship and to identify areas where observed values of UD where much higher or lower than predicted by mixed models (Chapter 5). When non-stationarity is detected, there are a number of possible explanations including, model misspecification, missing variables, autocorrelation or inappropriate spatial scales of measurement (resolution) (Brunsdon et al. 1996; Fotheringham et al. 1998; Foody 2004; Osborne et al. 2007). Autocorrelation was incorporated in the computation of utilisation distributions (Benhamou 2011) and so was not an issue here, and the consistent selection of the same predictors (depth and SST) from the suite of fitted models suggested that principal environmental drivers of movement had been identified. There were obvious issues with resolution of data in
tracks from the South Atlantic where geolocations were associated with large errors (Lam et al. 2010) that most likely drove non-stationarity. However, in the Atlantic and Indian oceans, where non-stationarity was also identified, (as evidenced by a large range in estimates of GWR coefficients), location estimates were obtained from satellite telemetry and had less error. For these regions, areas where values of utilisation were higher than predicted by the models seemed to be related to two main issues: missing covariates in the model (such as food availability) and changes in the scale of movement behaviour by tiger sharks between oceanic and coastal habitats.

In the Indian Ocean, off the coast of Western Australia, there were areas that had greater than predicted utilisation giving highly positive values of GWR estimates. These areas overlapped with hotspots for abundances of pelagic fish and occupancy by pygmy blue whales (Balaenoptera musculus brevicauda) (Double et al. 2014; Bouchet 2015), suggesting that prey availability may be accounting for some of the variation not explained by the model and the resulting non-stationarity. In the North Atlantic, patterns of higher than predicted UD values were found in areas with high average utilisation by all sharks off the eastern coast of the USA. This suggests that our models properly explained high use of oceanic areas, but failed to predict use of coastal habitats. In the open ocean, the influence of large and mesoscale scale oceanographic features such as large patterns of SST fields and fronts (Ullman & Cornillon 1999; Fryxell et al. 2008; Belkin et al. 2009) can be identified given the resolution of the environmental data provided by remote sensing. Here, mixed models identified a preference for deeper and colder waters, probably associated with high use of areas around the Gulf Stream as seen in previous studies (Lea et al. 2015; Queiroz et al. 2016). The association of tiger sharks and thermal fronts in the North Atlantic (Queiroz et al. 2016) suggests that mesoscale features such as eddies and coastal frontals may be important habitats for the species, and could explain some of the patterns found here. Whereas, complex shelf habitats influenced by topography and interactions with coastal oceanographic processes would likely have higher explanatory power for areas of high use near the coast if a finer-resolution spatial scale had been used in the analysis. My results suggest that non-stationarity was likely to be a result of scale-dependent patterns in environmental signals and the behaviour of tiger sharks, causing the models to have low predictive power to describe utilisation patterns in shelf environments. The environmental signals created by mesoscale oceanic features and coastal features will be difficult to describe using remotely sensed data ad with a global dataset, however in-situ
environmental data such as provided by CTD-SRL tags combined with high resolution tracking data (such as provided by Fastloc GPS tags and Diary tags) would likely be necessary to define and explain those scale-dependent associations.

Tiger sharks are generalist predators that explore multiple food-webs (Chapter 4), likely with foraging strategies adapted to specific prey in different habitats, a trait that may drive scale- and habitat-dependent space use. Identifying scale-dependent movements of top-predators can be challenging (Austin et al. 2006), especially when tracking data has low resolution (Bradshaw et al. 2007), as is typically the case for tiger sharks. Although my findings show that large scale patterns of SST and bathymetry can explain use of oceanic areas, the application of GWR has allowed me to identify, for the first time that the relationship between space utilisation by tiger sharks and environment operates at finer scale in shelf than in oceanic habitats. The limited predictability of environmental preferences (Chapter 5) and highly generalist behaviour (Chapter 4) currently preclude our understanding of the potential effects of large-scale climate change in the distribution and resiliency of tiger sharks. The prediction of movements and habitat use for the species will likely be only possible in habitat-dependent contexts (e.g. use of specific features or habitats in coastal and oceanic environments), when considering different sections of the populations separately, i.e. movement of females to potential mating and pupping grounds (Papastamatiou et al. 2013) for example. Spatial patterns in trophic ecology

Variability in movement patterns of tiger sharks was paralleled by variability in diet. Comparisons of isotopic signatures of sharks from locations on both the west and east coasts of Australia suggested that tiger sharks have a diet that is size, context and habitat specific. Signatures from muscle tissue showed that larger sharks fed on a diet that had high values of δ¹³C, consistent with these animals targeting large herbivores such as dugong (Dugong dugon) and turtles that are part of a seagrass food chain. Smaller tiger sharks had lower values of δ¹³C, probably reflecting the more limited ability of these size classes to subdue these large herbivores and thus resulting in diets that have a larger component of smaller species such as fishes. These patterns were consistent with previous studies of stomach contents (Simpfendorfer 1992; Lowe et al. 1996; Heithaus 2001).

Diets of tiger sharks also varied by location. The isotopic signatures of sharks sampled on the Great Barrier Reef (GBR) and in Shark Bay were characteristic of a diet based on
a seagrass food chain, whereas sharks sampled on the coast of New South Wales (NSW) had signatures indicative of a plankton-based food chain. Signatures of sharks sampled at Ningaloo Reef were characterised by a diet based both on planktonic and benthic food-webs. Despite the large differences in communities and habitats between Shark Bay (Walker et al. 1988; Heithaus 2004; Vaudo & Heithaus 2011; Heithaus et al. 2013) and on the GBR (Wachenfeld et al. 1998; Carruthers et al. 2002; Espinoza et al. 2014), tiger sharks still remained at the top of the food web in both locations, showing that in these tropical ecosystems, they acted as top-order predators (Heithaus et al. 2008a; Wirsing & Ripple 2011). This did not appear to be the case off the temperate coast of NSW (32° - 35°S) where seals, other oceanic sharks and tunas rather than tiger sharks were located in the top-order positons of the food web (Davenport & Bax 2002; Revill et al. 2009) and may have a larger role in structuring communities in this habitat.

The shift in isotopic signatures of tiger sharks between these tropical and temperate environments was not solely due to latitude, it also appeared to be driven by the oceanographic setting of the environment where these sharks occur. The signatures of sharks sampled in offshore environments of NSW were very similar to those of sharks sampled on the isolated reefs of Reunion Island in the tropical western Indian Ocean (Trystram et al. 2016). Both localities are exposed to the open ocean and these signatures probably reflect the accessibility of planktonic food chains. Similarly, at Ningaloo Reef the continental shelf is very narrow, so that boundary currents occur within 5 - 10 km of the coast accounting for the use of mixed food chains revealed by signatures.

These results emphasise the flexibility of the diet and trophic role of tiger sharks. Whether such traits are a cause or a consequence of their wide-ranging movements is difficult to determine. These sharks are not simply predators, as opportunistic scavenging is also an important feeding behaviour (Gallagher et al. 2011; Bornatowski et al. 2012a,b; Clua et al. 2013; Hammerschlag et al. 2016) and may make an important contribution to energy intake. In some localities, such as at Raine Island, where dead or dying sea turtles make a significant part of seasonal diets (Hammerschlag et al. 2016), it will be very difficult to distinguish between active predation and scavenging, since these will give an equivalent isotopic signal.

Although there is no evidence that tiger sharks display the hunting patterns of other top-order marine predators, such as the stalking strategy of white sharks (Klimley 1994;
Klimley et al. 2001b; Huveneers et al. 2015) or the cooperative group hunting behaviour of killer whales (Orcinus orca) (Hoelzel 1991; Saulitis et al. 2000) and their isotopic signatures place them at the lowest trophic position of assemblages of large sharks in some coastal environments (e.g. Hussey et al. 2015b), few species are likely to represent a predation threat for large tiger sharks (Heupel et al. 2014), with the possible exception of white sharks (Carcharodon carcharias) and killer whales (Pyle et al. 1999).

6.4 Implications for conservation

Biological characteristics such as high growth rates, relatively low fishing mortality (Chapter 2) combined with the high variability in movement and space use (Chapter 3,5) and flexibility in feeding preferences and trophic role (Chapter 4), suggests that tiger sharks could potentially display greater resilience to fishing pressure and human-induced changes in habitats, including climate change (Hazen et al. 2013), compared to other large marine predators. However, a key issue hampering the quantification of resilience to threats and evaluation of the conservation status of tiger sharks is a lack of data on population structure and dynamics, and catch trends of fisheries for the species at both regional and global scales (Chapter 2). This combination of knowledge gaps and somewhat constraining reproductive traits (i.e. producing many pups but having a triennial reproductive cycle) is reflected in the species classification as “Near Threatened” in the IUCN Red List. Recently, a global analysis of tiger shark genetics showed significant genetic separation between sharks from the western Atlantic and Indo-Pacific, with limited gene flow and different population structures among different ocean basins (Bernard et al. 2016). Although insufficient to be designated as subspecies (Bernard et al. 2016), these distinct genetic and population structures suggests that tiger sharks from different ocean basins should be assessed separately by the IUCN. New regional assessments could facilitate the identification of threats and population trends, and possibly result in different, but more appropriate, classifications of conservation status.

Mounting evidence of the key role of top predators in regulating ecosystem health (Heithaus et al. 2008a; Beschta & Ripple 2009; Estes et al. 2011; Ruppert et al. 2013; Atwood et al. 2015), combined with the severe impacts of human activities to their populations (Dulvy et al. 2008, 2014; Schipper et al. 2008; McCauley et al. 2015; Payne et al. 2016) highlight the importance of understanding how predators relate to the
environment if we are to create appropriate conservation measures to remediate and halt the consequences of their removal from ecosystems worldwide. Tiger sharks are top-order predators in tropical and seagrass habitats (Chapter 4) where they have been shown to regulate grazing on seagrass by communities of large herbivores (Burkholder et al. 2013). Their removal could result in a reduction of the control of grazing by herbivores, which in turn could lead to declines in seagrass productivity and eventually result in the collapse of this habitat (Heithaus et al. 2014; Atwood et al. 2015). Marine reserves in the Great Barrier Reef, Ningaloo Reef and Shark Bay in Australia can provide limited spatial protection for mobile species (Preen et al. 1997; McCook et al. 2010; Speed et al. 2010; Heupel et al. 2015). However, due to the very wide-ranging nature of tiger sharks (Chapter 3 and 5) such reserves will not provide protection for individuals throughout their life history. The tracks shown in Chapter 5 show that some sharks routinely moved across 1000s of km of open ocean and coastline and across the territorial waters of different countries, each with different protections, fishery regulations and conservation strategies. Protection for these animals can even differ within the territorial waters of the same country. Thus, it may make sense to aim to identify and focus conservation strategies on those key areas that serve as foraging or breeding habitat and to unify and strengthen management approaches to fisheries that capture these sharks on a regional basis. In the case of tiger sharks in Western Australia, large marine parks such as Ningaloo Reef and Shark Bay seem to offer sufficient protection for the species despite the varied classes of zoning present, and modification of zoning within these reserves would unlikely change the level of protection offered for the species. However, in the North Atlantic areas of high use by large sharks overlap with highly exploited fishing grounds in the North Atlantic Current – Labrador Current convergence zone, and the Mid-Atlantic Ridge, indicating the necessity of ocean-scale management of fisheries (Queiroz et al. 2016). Therefore, the identification of environmental and habitat preferences for tiger sharks, and other large migratory sharks, in areas where no protection currently exists will be a major step for the development of alternative management actions (fisheries regulation, catch quotas, dynamic ocean management) where the development of large-scale marine reserves might not be feasible. Additional tagging effort and larger spread across the population (i.e. also including juveniles and males) that allow the identification of movements related to reproduction and habitats associated with pupping and juvenile grounds, combined with the use of analytical approaches such as geographically weighted regression could aid this goal.
6.5 Future directions

The need for more tracking data to better describe movement patterns derived from all components of the population of sharks was identified as a key goal for conservation strategies. Poor monitoring of catches in commercial and artisanal fisheries that prevent stock assessments and definition of long-term population trends have been identified as one of the major issues regarding management and conservation of tiger sharks (Chapter 2). Management strategies that integrate near-real-time tracking and predictive modelling of habitat and environmental preferences are able to account for the dynamic nature of species and oceanographic features (Hobday & Hartmann 2006; Hobday et al. 2009; Hobday & Hartog 2014; Dunn et al. 2016; Hazen et al. 2016) and offer great potential for management of highly mobile marine predators.

To date, nearly all studies of tiger sharks have focused on horizontal movements and environmental variables obtained by satellite remote sensing techniques from the superficial layers of the water column (Chapter 3 and 5). However, tiger sharks occupy a three dimensional environment where movements also occur in the vertical plane often to depths well beyond the thermocline (Nakamura et al. 2011; Iosilevskii et al. 2012; Chapter 3). I have presented evidence of differential utilisation of the water column between tropical and temperate environments (Chapter 3) and that diet and trophic role of tiger sharks also change between those ecosystems (Chapter 4), which reinforces the need for additional efforts to deploy tags that can be used to link horizontal and vertical movements of individuals across multiple ecosystems. Many predators utilise water column and vertical movements in their hunting strategy (Klimley 1994) or forage while diving (Gallon et al. 2013). Defining the link between horizontal and vertical displacements of tiger sharks, how they relate to and vary according to environmental conditions, could resolve much of the lack of predictability and ‘noise’ associated with ecological models applied to tracking data.

Studies that provide long-term and high-resolution tracking of tiger sharks are rare, likely due to tag failure, shedding, damage and biofouling (Kerstetter et al. 2004; Heithaus et al. 2007c; Hays et al. 2007; Meyer et al. 2010), which results in patchy and sparse position estimates and short track durations. Some of the tracks presented in this thesis were considerably longer than many previously obtained with satellite tags for the species (Heithaus et al. 2007c; Fitzpatrick et al. 2012; Hazin et al. 2013; Papastamatiou et al. 2013) and were able to describe extensive latitudinal movements (Chapter 3) and a
larger utilisation of areas beyond the shelf break than previously recorded for the species (Chapter 5). However, long, high quality tracks represented only a small number of the tracks gathered in this thesis. For non-air-breathing marine taxa the rate of uplink of satellite tags and the use of cutting-edge technology is somewhat limited (Hussey et al. 2015a; Hays et al. 2016). For example, CTD-SRL tags (Boehme et al. 2009) have provided great advances in the understanding of habitat use of marine mammals (Biuw et al. 2007) and could aid in overcoming some of the issues with data resolution and uplink rates of satellite tracking of sharks. However, a towed version that could be deployed on sharks is still not available. Studies using this tag could accelerate our understanding of relationships between locomotion, foraging and the physical environment inhabited by tiger sharks.

My results showed that predicting drivers of movement of tiger sharks is challenging, most likely because sharks are possibly targeting diverse resources and habitats in different ecosystems (Chapter 3 - 4). At fine spatial scales, the deployment of multi-sensor and camera tags such as Customized Animal Tracking devices (CATS-Cam tags) across multiple habitats would allow the identification of inter-specific interactions and feeding events (Heithaus et al. 2002; Nakamura et al. 2011), and illuminate the decision process behind feeding behaviour and prey selection, while linking movement patterns to the role of sharks within specific habitats. At large spatial scales, GWR could be used to test predictions associated with habitat use and to identify areas where general relationships defined by physical parameters fail to explain patterns of use (Chapter 5). The overlap found between patterns of GWR estimates and areas of high utilisation by multiple species aids the targeting of future research efforts in order to identify factors structuring habitat use by tiger sharks. New satellite technologies and the expansion of the tracking data to other sections of the population, such as juveniles and males, would allow the identification ecologically important habitats yet to be defined that warrant special attention for conservation. Tagging programs could also potentially provide the real-time tacking of animals that could feed into dynamic ocean management actions. The analytical methods utilised in this thesis showed great potential applicability to tracking data from a variety of taxa of marine megafauna, particularly when predictive and explanatory power of models are low. Similarly, the technological development of tracking systems and a better understanding of variability in species’ behaviours have also been flagged as a major necessity for directing future research in marine megafauna movement (Hays et al. 2016).
6.6 Concluding remarks

This thesis demonstrated how increasing sample numbers and the use of large datasets can provide new insights into the ecology of a cosmopolitan marine predator. My results revealed that tiger sharks use oceanic habits more often than previously reported for the species, with both movement and residency being influenced by sea surface temperature and bathymetry. Large-scale movements displayed by tiger sharks imply that they act as an important link between different habitats, which is also supported by their context specific trophic ecology. My results also showed how the combination of data obtained from tracking and stable isotopes analysis of multiple tissues can be used for defining large scale habitat use of top-order predators, despite some clear limitations regarding data resolution and temporal scale of sampling. Although ecological modelling of sparse tracking datasets and coarse resolution environmental data are problematic, methods to generate utilisation distributions that can overcome these issues showed great value and possible broad application for tracking of other large marine taxa. Moreover, I provided a novel method to test explanatory power of models, identify when and where model predictions inadequately explain spatial patterns, and guide future efforts in areas where the compilation of high resolution and multispecies datasets should be targeted. This is essential for understanding the spatial ecology and conservation of mobile top-order marine predators such as tiger sharks.


Journal of Fisheries, 61, 29–34.


Department of Fisheries of Western Australia (2005). *Application to the Australian Government Department of Environment and Heritage on the Western Australian Tropical Shark Fisheries (covering the Western Australia North Coast Shark Fishery and the Joint Authority Northern Shark Fishery)*. Department of Fisheries, Western Australia.

Department of Fisheries Western Australia (2006). *Assessment of the Western Australian Tropical Shark Fisheries*. Department of the Natural Environment and Heritage, Western Australia.


Conservation Biology, 13, 592–602.


Johnson, D.S. (2014). Fit continuous-time correlated random walk models to animal movement data. *R* package version 1.4-1


Kerstetter, D.W., Polovina, J.J. & Graves, J.E. (2004). Evidence of shark predation and


Reid, J.L. (1994). On the total geostrophic circulation of the North Atlantic Ocean:


35.


Geophysics, 31, 29–49.


Crossing Latitudes—Long-Distance Tracking of an Apex Predator

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Abstract

Tiger sharks (Galeocerdo cuvier) are apex predators occurring in most tropical and warm temperate marine ecosystems, but we know relatively little of their patterns of residency and movement over large spatial and temporal scales. We deployed satellite tags on eleven tiger sharks off the north-west coast of Western Australia and used the Brownian Bridge kernel method to calculate home ranges and analyse movement behaviour. One individual recorded one of the largest geographical ranges of movement ever reported for the species, travelling over 4000 km during 517 days of monitoring. Tags on the remainder of the sharks reported for shorter periods (7-191 days). Most of these sharks had restricted movements and long-term (30-188 days) residency in coastal waters in the vicinity of the area where they were tagged. Core home range areas of sharks varied greatly from 1166.9 to 834,944 km². Tiger sharks spent most of their time in water temperatures between 23°-26°C but experienced temperatures ranging from 6°C to 33°C. One shark displayed seasonal movements among three distinct home range cores spread along most of the coast of Western Australia and generalized linear models showed that this individual had different patterns of temperature and depth occupancy in each region of the coast, with the highest probability of residency occurring in the shallowest areas of the coast at water temperatures above 23°C. These results suggest that tiger sharks can migrate over very large distances and across latitudes ranging from tropical to the cool temperate waters. Such extensive long-term movements may be a key element influencing the connectivity of populations within and among ocean basins.

Introduction

Throughout human history, top-order predators have been disproportionately and negatively affected by anthropogenic activities, both directly through human behaviour such as hunting and indirectly by alteration of habitat and depletion of their food resources [1–4]. We now know that
Human anxiety about predators is deeply embedded in our evolutionary history and psychology. Sharks, as archetypal predators, attract a disproportionate amount of fear because of our poor ability to assess the real threat associated with ‘fearsome’ risks such as shark bites (Sunstein & Zeckhauser, 2011). This disconnection between reality and human imagination is illustrated by the extreme media attention that surrounds incidents of shark bite (Mauer et al., 2012) and the actual numbers of attacks that occur. Fatalities from shark bites remain much lower than in other recreational activities. For instance, in Western Australia, annual fatality rates from shark bite, at their highest, were 1.3 per year (2008–2013; Australian Shark Attack File, 2013; http://toronga.org.au/animals-conservation/conservation-sciences/australian-shark-attack-file/annual-australian-shark-attack-report-summary-2013.pdf), compared with cycling (average of 5 year⁻¹ (2009–2013); www.bike.gov.au/statistics/safety/total_road_cyclist_database.aspx) and ocean swimming (average of 2.5 year⁻¹ (2008–2013); http://surflifesanl.com.au/documents/coastal-safety-aep.pdf). Analysis also suggests per capita incidents are declining in some locations such that any absolute increase in numbers of fatalities simply reflects growing human populations and coastal environments (Wetherbee, Lowe & Crow, 1994; West, 2011).

Despite the relatively low risk of fatalities, governments have invested significant economic and human resources in mitigating risk associated with shark bites. Historically, such strategies have largely relied on catch-and-kill programs with the goal of driving localized depletions of animals that are considered a threat to humans. Currently, lethal programs, largely based on nets, which started in the 1930s (New South Wales, Australia) and 1960s (Queensland, Australia and KwaZulu-Natal, South Africa), each catch between 600 and 1500 sharks annually. While the frequency of shark bite incidents has also declined over this period, due either to the nets themselves or broader issues relating to general declines in shark populations or environmental change, there is growing recognition of the high ecological costs of lethal programs, particularly in terms of bycatch of other harmless sharks and nontarget species including cetaceans, turtles and rays.

Irrespective of destructive bycatch, some of the most compelling reasons for moving beyond catch-and-kill programs for shark mitigation lie in our understanding of sharks themselves, their place in marine environments, their increasing economic value as a tourism resource and the fact that, as Hazin & Afonso (2014) show here, alternatives are now available. Sharks are highly susceptible to overexploitation with 15% of the world’s species threatened (Dulvy et al., 2014). Species targeted by lethal shark hazard mitigation programs are among some of the most vulnerable. We also know the oceans need sharks: as apex predators, they play critical roles in maintaining ecosystem structure and promoting resilience (Ferretti et al., 2010). Healthy shark populations increasingly generate significant tourism dollars and associated economic benefits for local communities, including species usually considered ‘dangerous’ (Gallagher & Hammerschlag, 2012). Finally, improvements in our understanding of shark biology derived from, for instance, telemetry and neuroscience can underpin nonlethal mitigation strategies such as warning systems predicated on movements and deterrents (Hammerschlag, Gallagher & Lazarre, 2011; Huveneers et al., 2013).

Hazin & Afonso (2014) demonstrate the practical value of nonlethal strategies as an alternative to the traditional policy of catch and kill. Following an upsurge in incidents with sharks and bathers in north-eastern Brazil, the Metropolitan Region of Recife deployed longlines and drumlines to capture and relocate sharks thought to be a threat. This and a companion paper (Hazin et al., 2013) show that over a 4-year period, once potentially dangerous sharks had been captured and relocated, they tended to move away from protected beaches when released. Furthermore, mortality rates of bycatch not considered to be a threat to humans were generally much lower than in nets, as indeed was also the case for the target species. Importantly, when the program was in place, human interactions with sharks were very low, and increased at times when the program was suspended. Overall,
Appendix C

Review
Key Questions in Marine Megafauna Movement Ecology

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It is a golden age for animal movement studies and so an opportune time
to assess priorities for future work. We assembled 40 experts to identify key
questions in this field, focussing on marine megafauna, which include a broad
range of birds, mammals, reptiles, and fish. Research on these taxa has both
underpinned many of the recent technical developments and led to fundamental
discoveries in the field. We show that the questions have broad applicability
to other taxa, including terrestrial animals, flying insects, and swimming inverte-
brates, and, as such, this exercise provides a useful roadmap for targeted
deployments and data syntheses that should advance the field of movement
ecology.

The Breadth of Movement Ecology Studies

The advent of a range of small, reliable data-loggers and transmitters that can record
horizontal and vertical movements, physiology, and reproductive biology has led to many
new, amazing insights into the ecology of taxa ranging from insects to whales [1,2] (Figure 1).
For example, we are now able to track and record the physiological state of animals as they
travel across entire ocean basins or continents, fly over the highest mountains, or dive from
the surface to the ocean depths [3–6]. These types of study have addressed holistic questions
comprising cross-taxon comparisons in both terrestrial and marine systems that have
investigated how animals optimize their locomotion [7]; their search patterns for prey [8]; and
the factors that constrain their migration distances [9], dive performance [10], and swimming
speed [11] (Figure 2).