Conservation ecology of coastal sharks and rays with a focus on the location and function of juvenile habitats

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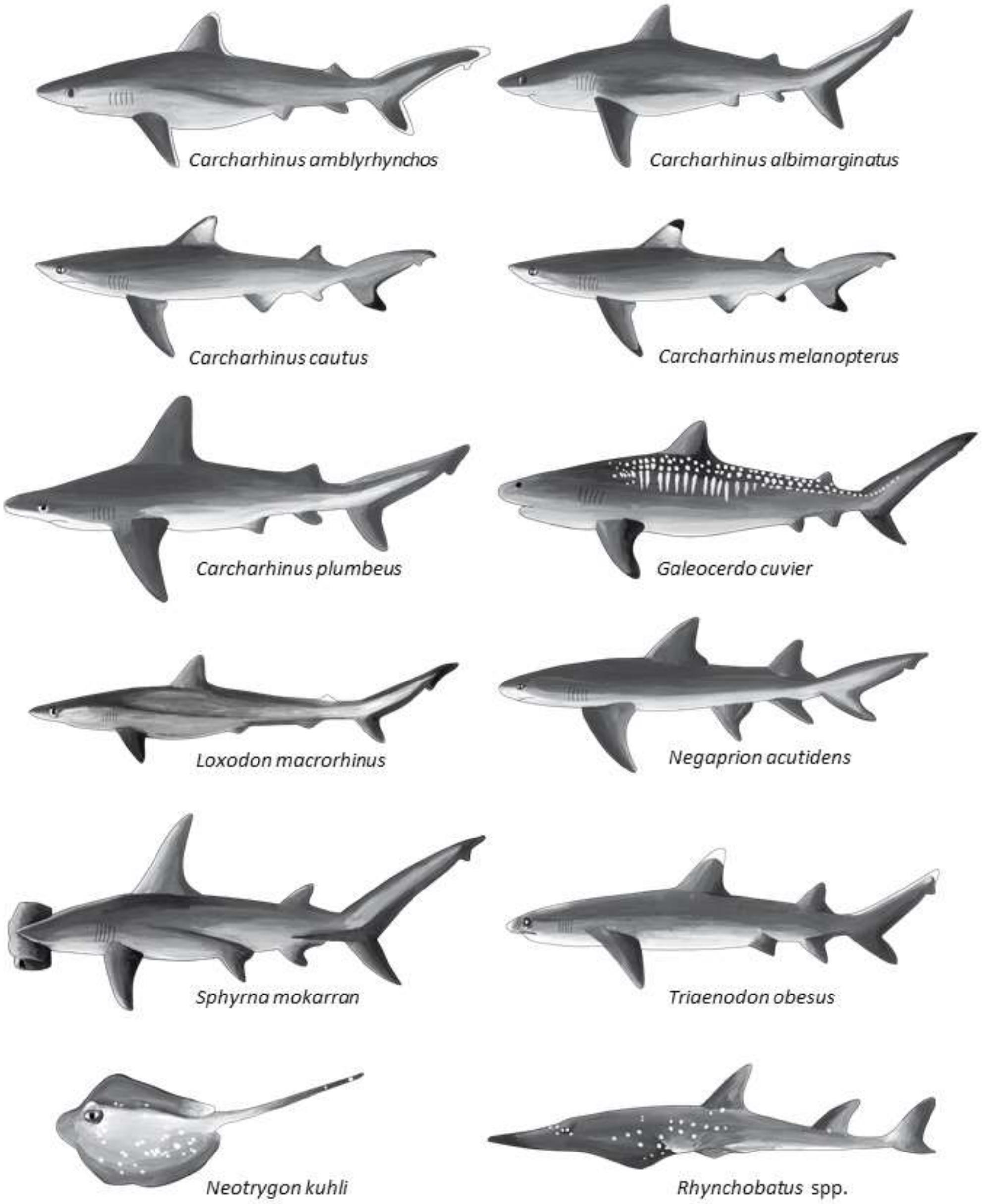

Illustration of the shark and ray species examined in this thesis.

(Credit: Natalie Oh)

Declaration of authorship

I declare that this thesis is my own composition, all sources have been acknowledged and my contribution is clearly identified in this 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.

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Date: 13 December 2016

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“Look deep into nature, and then you will understand everything better”

– Albert Einstein

Abstract

Marine protected areas (MPAs) are a key strategy for supporting the recovery of marine populations, in addition to the more general conservation of marine biodiversity. The effectiveness of this approach relies on the identification and protection of essential habitats and the processes that support habitat quality. The challenge here is to evaluate the importance of habitats in relation to their influence on population persistence, such as their role in promoting survival. For relatively mobile species such as coastal sharks, small-scale MPAs can be effective where key life stages are linked to predictable habitat features that are protected. Many sharks undergo changes in habitat requirements with increasing size that have implications for their vulnerability to anthropogenic impacts and the effectiveness of MPAs. In this thesis, I combine conservation biogeography and ecological approaches to assess the habitat requirements of coastal shark populations. In doing so, I quantified the habitat and foraging requirements of juvenile sharks at local scales, nested within a broader investigation of the habitat determinants of shark and ray distribution at regional (200–2,000 km) and continental (>2,000 km) spatial scales. My principal tools were baited remote underwater video stations (BRUVS), acoustic telemetry and stable isotope analysis. I found that latitude and depth can serve as surrogates of representative shark and ray assemblages for continental-scale conservation planning. Assessment of conservation planning at the regional-scale showed that high quality habitats for juvenile sharks were poorly represented in MPAs with the highest restrictions on fishing. I also found that salinity, temperature, turbidity, depth and distance to shore were important predictors of habitat suitability for juvenile sharks, but that preferences were species-specific. Movement models revealed that the youngest juveniles had high spatial and temporal overlap of distributions within inshore sandflat and fringing mangrove habitats in their natal environment. Small-scale MPAs (<20 km^2) can therefore provide effective protection of these natal environments but the degree of protection will be size- and species-specific. Finally, isotopic signatures of juvenile sharks indicate a dependency on coastal food webs and that diet overlap was likely mediated by intra-specific partitioning in δ^{15}N niche space by specialist species and in δ^{13}C space by generalist species. Vulnerability to resource fluctuations may be greater for specialist sharks rather than generalists. Establishing shark and habitat linkages enabled the evaluation of the effectiveness of MPAs for coastal shark populations at

multiple scales and jurisdictions. Large-scale (>2,000 km) conservation planning to protect representative assemblages of coastal sharks and rays can benefit from bioregional habitat surrogates. However, strategic placement of large MPAs (200–2,000 km) to encompass the most suitable habitats for juvenile sharks will be enhanced by mapped predictions at the species-level rather than aggregate-level. Where species-specific information is missing or inadequate, no-take MPAs will likely need to be large to apply the precautionary principle and provide protection for mobile sharks. Small-scale MPAs (<20 km^2) can be highly effective for species or life-stages with restricted movements and dependency on coastal food webs. Together, this multi-scale approach validates the importance of species-focused knowledge acquisition and management within this diverse predatory guild. In this context, the identification of key habitats and the processes that support habitat quality for sharks can inform spatial planning and complementary management efforts beyond MPA boundaries that are needed to fully protect exploited species.

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Publications from this thesis

This thesis is submitted as a series of papers, which have been submitted to international peer-reviewed journals. The data chapters presented (Chapters 2 to 5) are formatted in accordance with the requirements of each journal.

Chapter 2

Oh BZL, Meekan MG, Meeuwig JJ. (In preparation) Quantifying shark and ray biogeography in the Austral tropics. *Biological Conservation.*

Chapter 3

Oh BZL, Sequeira AMM, Meekan MG, Ruppert JLW, Meeuwig JJ. (In press) Predicting habitat suitability for juvenile sharks to improve conservation planning. *Conservation Biology*. DOI: 10.1111/cobi.12868

Chapter 4

Oh BZL, Thums M, Babcock RC, Meeuwig JM, Pillans RD, Speed C, Meekan MG. (Minor revisions) Contrasting patterns of residency and space use of coastal sharks within a communal shark nursery. *Marine and Freshwater Research*

Chapter 5

Oh BZL, Meekan MG, Meeuwig JJ. (In preparation) Overlap and ontogenetic shifts in the diet of sympatric sharks in a coastal nursery ecosystem. *Coral Reefs*

Statement of contributions to thesis

This thesis contains a General Introduction (Chapter 1), four manuscripts (Chapters 2-5) arranged in journal format and a General Discussion (Chapter 6).

Supervision

These manuscripts were primarily developed from my own concepts and hypotheses with input from my supervisors, Professor Jessica Meeuwig, Dr Mark Meekan and Dr Michele Thums.

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Contribution to data chapters

I collected the acoustic telemetry data and isotope samples used in Chapters 4 and 5. I processed all datasets and performed all the data analyses featured in this thesis. I performed analysis on archived datasets that had been processed and collected using baited remote underwater video systems (BRUVS) for Chapters 2 and 3. The elasmobranch sightings data from BRUVS were made available through the financial commitment and foresight of local government, community and industry partners. Data was collected through various research programs: the 'Great Barrier Reef Seabed Biodiversity Project' collaboration between Australian Institute of Marine Science (AIMS), CSIRO, Queensland Department of Primary Industries and Fisheries, currently the Department of Agriculture Fisheries and Forestry and Queensland Museum and the 'Western Australian Marine Science Institute' collaboration between AIMS, CSIRO, PTTEP Australasia Ltd, Chevron, Woodside and the University of Western Australia. Access to environmental data collated by Geoscience Australia was made available through Dr Roland Pitcher. Other environmental variables were sourced and compiled from open-access repositories and published literature, as detailed in each chapter.

Dr Ana Sequeira at the Indian Ocean Marine Research Centre (UWA) provided expert guidance on the habitat suitability modelling component of Chapter 3 and Dr Douglas Ford at the Western Australian Biogeochemistry Centre (UWA) processed the stable isotope samples for Chapter 5.

I wrote all the chapters with feedback from Professor Jessica Meeuwig (all chapters), Dr Mark Meekan (Chapters 2-5), Dr Michele Thums (Chapters 2-5), Dr Ana Sequeira (Chapter 3), Dr Jonathan Ruppert (Chapter 3), Dr Russ Babcock (Chapter 4), Dr Richard Pillans (Chapter 4) and Dr Conrad Speed (Chapter 4).

Fieldwork approvals

All field procedures were approved under the University of Western Australia's Animal Ethics Committee (RA/3/100/1168), Department of Parks and Wildlife licences (SF009588, 163165, CE004244) and Western Australian Department of Fisheries exemptions (2150, 2355) and carried out in accordance with the approved permits.

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 60% of the content and was primarily responsible for the planning, execution and preparation of the work for publication, unless indicated otherwise.

Publication title: Quantifying shark and ray biogeography in the Austral tropics.

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Chapter 1 General Introduction

The coastal ocean approximates 4% of the areal extent of the Earth’s surface but supports an unprecedented one-third of the world’s human population (Barbier *et al.*, 2008). As a carbon sink, storm buffer, seafood provider, water purifier and reservoir of life, coastal ecosystems sustain globally important resources and ecosystem services essential to the well-being of humankind (Barbier & Hacker, 2011). From an economic perspective, the fisheries and aquaculture sectors generate 260 million jobs and over USD 100 billion in global seafood production every year (Mcclanahan *et al.*, 2015), marine-derived oncology drugs pending discovery have been valued at upwards of USD 560 billion (Erwin *et al.*, 2010) and annual revenues from marine megafauna tourism were estimated at USD 2 billion for whale-watching (O’Connor *et al.*, 2009) and USD 314 million for shark-diving activities (Cisneros-Montemayor *et al.*, 2013). Thus, coastal oceans have been pervasively burdened by expanding human populations through impacts ranging from overfishing, incidental mortality, pollution to habitat degradation and climate change (Worm *et al.*, 2006; Halpern *et al.*, 2008, 2015; Cheung *et al.*, 2009; Lewison *et al.*, 2014; Pauly & Zeller, 2016). Human activities have resulted in the loss or degradation of 50% of salt marshes (MEA, 2005), 35% of mangroves (Valiela *et al.*, 2001), 30% of coral reefs (Pandolfi *et al.*, 2003) and 29% of seagrasses (Waycott *et al.*, 2009). The loss of these coastal ecosystems has led in part to consequent reductions in fisheries production (33%), vital nursery habitats (69%) and water purification by suspension feeders, submerged vegetation or wetlands (63%) (Worm *et al.*, 2006). The rapid erosion of global marine biodiversity has impaired the oceans’ capacity to maintain water quality, provide food, store carbon, recover from perturbations, and ultimately affects the welfare of all humankind (Worm *et al.*, 2006). We are now firmly rooted in the Anthropocene (Crutzen, 2002), the Earth’s sixth recognized mass extinction event (Barnosky *et al.*, 2011). Recent extinction rates across both marine and non-marine taxa are unprecedented in human history and if allowed to continue unabated, can deprive humanity of a multitude of biodiversity benefits in as little as three human lifetimes (Ceballos *et al.*, 2015). Human dependency on marine resources, coupled with the pace of marine biodiversity loss and a changing climate, necessitates that we improve our management of ocean resources so that species loss of the magnitude observed on land can be averted in the oceans (McCauley *et al.*, 2015).

At present, less than 4% of the 73,600 species assessed by the International Union for the Conservation of Nature (IUCN) are from marine taxa and rates of classification of data-deficient species are double those for non-marine taxa (Webb & Mindel, 2015). Finite resources and time mean that data paucity, limited description of patterns and processes, and gaps in theory persist in all domains of ecology (Hortal *et al.*, 2015). However, data scarceness is especially acute in the marine realm where organisms are out of sight, insufficiently mapped and often poorly understood (Edgar *et al.*, 2016). This lack of information stems in part from the logistical and financial challenges associated with data collection in marine environments and constraints imposed by scientific capacity and accessibility between countries and regions (Richardson & Poloczanska, 2008). For instance, inventories of marine biodiversity tend to be more comprehensive near locations that offer convenient access, research infrastructure and logistical support, and hence are often restricted to regions such as North America and Europe (Costello *et al.*, 2010; Hortal *et al.*, 2015; Edgar *et al.*, 2016). The uneven spatial distribution of survey effort affects knowledge about intrinsic traits and species interactions (Hortal *et al.*, 2015). In addition, multiple drivers of change in marine systems complicate interpretations of biogeographic patterns, particularly in coastal ecosystems where threats are most prevalent (Crain *et al.*, 2008; Halpern *et al.*, 2015). For instance, differences in assemblage composition among coral reef systems have been concomitantly attributed to bottom-up impacts from cyclones and bleaching as well as top-down trophic cascades driven by predator removal (Ruppert *et al.*, 2013). Improvements in remote sensing technologies, statistical techniques and logistical costs have transformed our ability to map habitats and organisms at increasing spatial scales (Kerr *et al.*, 2007; Leaper *et al.*, 2012; Edgar *et al.*, 2016), yet much of our knowledge of marine biodiversity remains confined to surface layers, leaving pervasive gaps within the water column (Webb *et al.*, 2010). These gaps have contributed to two major shortfalls in human knowledge of biodiversity: (1) most of the extant species on Earth remain undescribed or uncatalogued (the Linnean shortfall) and (2) knowledge of the geographic distribution of most species is acutely inadequate (the Wallacean shortfall) (Lomolino, 2004; Caley *et al.*, 2014; Hortal *et al.*, 2015).

1.1 The challenge of conservation under the Wallacean shortfall

In light of the Anthropocene's accelerating extinction rates (McCauley *et al.*, 2015), quantifying the spatial distribution of taxa is a prerequisite for the preservation of biodiversity (Riddle *et al.*, 2011). Common to all sampling techniques in the marine realm is the trade-off between spatiotemporal coverage and data resolution, with high-resolution datasets frequently restricted in spatial and temporal extent. For instance, fishery-dependent catch records have provided the most spatially and temporally extensive means of characterizing biogeographic patterns at large-scales (>100 km), identifying hotspots and mapping species distributions (Morato *et al.*, 2010; Bouchet *et al.*, 2015), but are often spatially inconsistent, low in taxonomic resolution and requires extensive standardization processes. As an alternative, well-designed scientific fishery-independent surveys can reduce spatial biases in sampling (Conners *et al.*, 2002), but commonly have a restricted spatial extent and ethical constraints in their utility for surveying protected areas or threatened species (Heupel & Simpfendorfer, 2010; Murphy & Jenkins, 2010). Acoustic or satellite tracking is dependent on the scale of movement of tagged animals, cost and transmission constraints, but can be mitigated by intense efforts to tag individuals and species (Block *et al.*, 2011). Hydro-acoustic surveys are constrained by the speed at which vessels can collect high-resolution information, but can be scaled up through increased vessel hours (Kloser *et al.*, 2009; Irigoien *et al.*, 2014). Remote underwater videography yields rich-information typically at restricted spatial scales, but their cost-effective and standardized nature facilitates broad scale application (Espinoza *et al.*, 2014a; Mallet & Pellerier, 2014). The historical and on-going trend of increased protection of ocean space (Gaines *et al.*, 2010a) will likely limit the use of fisheries catch data and the spatial extent of extractive monitoring. Non-extractive methods will become increasingly important in filling this gap (Letessier et al. 2015) but will likely under-sample the ocean in space and time unless extensive effort is invested.

Due to difficulties in surveying marine biodiversity over broad spatial scales, aggregate assemblage and habitat attributes have had wide attention as surrogates for species-level patterns, derived from space-borne instruments, acoustic surveys and image analysis (Pressey & Bottrill, 2009; Mellin *et al.*, 2011; Roland Pitcher *et al.*, 2012; Edgar *et al.*, 2016; Hunter *et al.*, 2016). Ecological surrogacy is the representation of an ecological system using components such as species, ecosystems or habitats (Hunter *et al.*, 2016). A clear distinction between “indicator surrogates” that inform on ecological systems and “management surrogates” (e.g. umbrella species) that facilitate biodiversity or ecosystem resilience goals is crucial to evaluating the effectiveness of surrogates (Hunter *et al.*, 2016). For instance, whales are an ineffective indicator surrogate as they are difficult to count and select habitats on coarser scales than most species (Braithwaite *et al.*, 2012), yet organizing biodiversity management around whales as a management surrogate is valuable as they occupy large habitats, sustain profitable eco-tourism activities (O’Connor *et al.*, 2009) and serve as iconic species that can garner strong public support (Sergio *et al.*, 2008; Kyne & Adams, 2016). Management surrogacy based on abiotic habitats has gained traction as the foundation of proposals to adapt to climate change by designing conservation plans around static abiotic factors such as distance to domain, bathymetry, topography, geology and hydrology (Pressey *et al.*, 2007; Mellin *et al.*, 2010; Beier & de Albuquerque, 2015; Sutcliffe *et al.*, 2015). However, indicator surrogates often show little congruency across different biodiversity metrics (Rodrigues & Brooks, 2007; Mellin *et al.*, 2011), and much ecological variation remains veiled within mapped abiotic habitats (Mumby *et al.*, 2008; Sutcliffe *et al.*, 2012; Tornroos *et al.*, 2013). For instance, the effectiveness of biological surrogates is especially low in complex ecosystems such as coral reefs, where high functional diversity likely weakens the predictive and surrogacy relationships among taxa (Mellin *et al.*, 2011). Moreover, evidence from terrestrial and marine environments show that hotspots of total species richness are not always concordant with hotspots of endemism or threat and that concentrations of local endemics or threatened species may occur in areas of low richness (Bellwood & Hughes, 2001; Grenyer *et al.*, 2006; Lucifora *et al.*, 2011; Stuart-Smith *et al.*, 2013). Therefore a conservation strategy cannot be based solely on a hotspot approach, but needs to consider unique biogeographic units to protect the full range of biodiversity (Kareiva & Marvier, 2003).

1.2 The challenge of marine protection

A key strategy for marine ecosystem-based management is the establishment of marine protected areas (MPAs), defined as “areas of the ocean designated to enhance conservation of natural resources” (Lubchenco *et al.*, 2003). MPAs vary widely in size, name (i.e. marine park, highly protected marine reserve, marine conservation zone, green zone), objectives and the subset of human activities restricted (Lubchenco *et al.*, 2003; Day *et al.*, 2012). No-take MPAs refer specifically to MPAs that are fully protected from all extractive activities. MPAs can be used to protect species and habitats from exploitation and hence support biodiversity conservation (Wood *et al.*, 2008; Sciberras *et al.*, 2013), maintain key ecological processes (Roberts *et al.*, 2005) and contribute to fisheries management (Roberts *et al.*, 2005; McCook *et al.*, 2010; Vandeperre *et al.*, 2011; Harrison *et al.*, 2012; Spalding *et al.*, 2013) although there remains some dissenting views on the latter (Fletcher et al. 2015). However, variation in their objectives, and level of protection and enforcement make it difficult to generalize the benefits of MPAs in achieving conservation outcomes (Lester *et al.*, 2009).

When designed and implemented effectively, MPAs can increase the density, biomass, body size and reproductive potential of species within their boundaries and maintain keystone species, connectivity processes and habitat diversity, (Lester *et al.*, 2009; Babcock *et al.*, 2010; Russ & Alcala, 2011; Sciberras *et al.*, 2013; Green *et al.*, 2015). Diverse and complex habitats support species diversity (Komyakova *et al.*, 2013; Graham, 2014; Rogers *et al.*, 2014) that in turn promotes productivity (Worm *et al.*, 2006), resilience to perturbations (Palumbi *et al.*, 2008; Bates *et al.*, 2013; Ruppert *et al.*, 2013; Graham, 2014; Olds *et al.*, 2014; Mellin *et al.*, 2016), stable food web dynamics (Wing & Jack, 2013) and functional capacity to maintain ecosystem balance when individual species disappear (Palumbi *et al.*, 2009). At present, no-take MPAs encompass less than two percent of the world's oceans (Lubchenco & Grorud-Colvert, 2015; O'Leary *et al.*, 2016), well below the proportion needed to adequately represent all biogeographic zones (Spalding *et al.*, 2013). Policy instruments such as the Convention on Biological Diversity (CBD) have set national targets of 10% of coastal and marine areas to be protected by 2020 (Secretariat of the CBD, 2010; Harrop & Pritchard, 2011), in part driving a surge in the number and extent of networks of MPAs over the past decade (Edgar *et al.*, 2014). Given the compelling evidence for the benefits of MPAs in enhancing species diversity and abundance (Lester *et al.*, 2009; Babcock *et al.*, 2010; Edgar *et al.*, 2014; Mellin *et al.*, 2016), a primary imperative is to establish non-extractive baselines from which to gauge the effectiveness of different management regimes and for the informed expansion and implementation of MPA networks. The expansion of the world's MPA coverage is a phenomenon with complex ecological, scientific and socioeconomic aspects (Metcalfe *et al.*, 2015). While the establishment of shark sanctuaries and mega MPAs (>100,000 km^2) such as those in the British Indian Ocean Territory (BIOT), Cook Islands and the Coral Sea and have vastly increased the global coverage of MPAs, they vary greatly in the types of fishing activities prohibited within their boundaries (Vianna *et al.*, 2012, 2016; Devillers *et al.*, 2015; Lubchenco & Grorud-Colvert, 2015; Jaiteh *et al.*, 2016). This raised debate about the value of extensive, remote MPAs in achieving conservation outcomes (Graham *et al.*, 2010; Koldewey *et al.*, 2010; Davidson *et al.*, 2012; Chapman *et al.*, 2013; Dulvy, 2013; Kaplan *et al.*, 2013; Toonen *et al.*, 2013). Present trends in systematic conservation planning have focussed on protecting biodiversity hotspots and ecologically representative areas to benefit the most species at the least cost (Gaston *et al.*, 2008). However, the potential benefits of MPAs to threatened species are compromised without explicit conservation targets and spatial data on their distribution (Pressey *et al.*, 2007). Indeed, mounting evidence suggests that the bias towards protecting biodiversity hotspots and representative habitats can compromise the conservation of threatened and rare species (Dulvy, 2013), as in the case of dugongs (Cleguer *et al.*, 2015), turtles (Dryden *et al.*, 2008) and whales (de Castro *et al.*, 2014). Effective design and implementation of MPA networks is necessary to maximise their conservation value (Gaines *et al.*, 2010a). A landmark study revealed that MPAs that were no-take, well-enforced, old (>10 years since establishment), large (>100 km^2) and isolated (by sand or deep water), encompassed five times more large fish and fourteen times more shark biomass than MPAs with less than three of these features (Edgar *et al.*, 2014), yet only 4.6% of the 87 MPAs examined globally possessed all five criteria. Even within "successful" MPAs with all five essential criteria (Edgar *et al.*, 2014), declines in marine megafauna still occur unless there is adequate enforcement to control fishing (White *et al.*, 2015). As networks of MPAs expand worldwide, there is a need to ensure that protection of large, remote ocean spaces does not obscure continuing biodiversity declines and be used to misrepresent ineffective protection as conservation success (Devillers *et al.*, 2015), as has been the case on land (Venter *et al.*, 2014).

1.3 The emergence of conservation biogeography

Conservation biogeography is an emerging field that applies biogeographical principles, theories and analyses to problems regarding biodiversity conservation (Whittaker *et al.*, 2005). Species distribution models (SDMs) have proven to be fundamental tools for conservation biogeography and are used to support spatial planning at large scales, mitigating the frequent paucity of on-the-ground data (Guisan & Thuiller, 2005). The term "species distribution model" refers to any model that provides understanding or predicts the distribution of species or communities in relation to abiotic or biotic attributes (Guisan & Harrell, 2000; Elith & Leathwick, 2009). Ascertained species-habitat relationships have increasingly allowed high-resolution mapping of species and communities in un-sampled locations or times from mapped habitat or environmental surfaces (Leaper *et al.*, 2012). They provide a strong foundation for integrated spatial planning, such as to assess the impacts of climate change (Cheung *et al.*, 2010; Tittensor *et al.*, 2010; Sequeira *et al.*, 2014; Jones & Cheung, 2015), identify biodiversity hotspots (Mellin *et al.*, 2010; Lucifora *et al.*, 2011; Parravicini *et al.*, 2013), locate priority areas for monitoring (Halpern *et al.*, 2008), evaluate areas of human-wildlife conflicts (Davidson *et al.*, 2012; Maxwell *et al.*, 2013; Lewison *et al.*, 2014; Selig *et al.*, 2014; Winiarski *et al.*, 2014), aid reserve mapping (Guisan *et al.*, 2013; Barker *et al.*, 2014; Mazor *et al.*, 2016) and assess reserve efficacy (Scott *et al.*, 2012; Bridge *et al.*, 2016; Mellin *et al.*, 2016).

While the overarching goal of conservation biogeography is to support effective conservation decision-making, there will ultimately be debate concerning which socioeconomic, ecological or cultural properties are given precedence in spatial planning (Richardson *et al.*, 2006; Mazor *et al.*, 2014; Fletcher *et al.*, 2015). For example, decision makers may place emphasis on socio-economic values of minimizing fisheries displacement and implementation costs, while considering the protection of threatened species, intact assemblages of marine wildlife, unique seascapes, culturally significant ecosystems, ecosystem services or biotic integrity (Richardson & Whittaker, 2010). As maintaining ecosystem function encompasses all the goals of MPA networks, information on biogeographic units, representative habitats, connectivity, vulnerable life stages, species of special concern (i.e. rare or threatened species) or exploitable species form part of a set of universally applicable criteria for the attainment of biologically adequate networks (Roberts *et al.*, 2003). Conservation biogeography is well poised to make significant contributions to the process of providing conservation planners with alternative scenarios addressing differing end goals.

1.4 The challenge of spatial protection for mobile species

Management and conservation issues are especially pertinent for highly mobile species that move long distances and hence play key ecological roles as mobile link species (Lundberg & Moberg, 2003) in energy transfer and trophic dynamics across different habitats and ecosystems (McCauley *et al.*, 2012; Rosenblatt *et al.*, 2013). For instance, seasonal variation in the abundance of tiger sharks (*Galeocerdo cuvier*) induced shifts in the foraging strategies and habitat use of dugongs (*Dugong dugon*) and green turtles (*Chelonia mydas*) in a seagrass ecosystem (Heithaus *et al.*, 2008, 2014; Wirsing & Heithaus, 2008), which ultimately had cascading effects on seagrass community composition (Burkholder *et al.*, 2013). American alligators (*Alligator mississipienis*) are thought to regulate blue carbon storage in coastal marshes and mangroves through the consumption of predatory blue crabs (Nifong & Silliman, 2013). Mobile link species such as humpback whales (*Megaptera novaeangliae*) travel over 16,000 km between low-latitude waters for reproduction and high-latitude feeding sites (Rasmussen *et al.*, 2007), while leatherback turtles (*Dermochelys coriacea*) undertake excursions of up to 12 months to distant foraging grounds (Benson *et al.*, 2011). These migratory behaviours may have evolved in response to patchy, seasonally-available prey fields (Austin *et al.*, 2004; Fauchald & Tveraa, 2006), hence marine conservation biogeography has focused on quantifying the linkages between wildlife and dynamic attributes such as food availability, thermal gradients, current eddies and chlorophyll fronts (Tew Kai *et al.*, 2009; Tittensor *et al.*, 2010; Sequeira *et al.*, 2012; Miller & Christodoulou, 2014; Miller *et al.*, 2015; Morato *et al.*, 2015; Scales *et al.*, 2015). Less empirical attention has been paid to the influence of static habitat features on coastal species, even if environmental gradients are known to correlate strongly with spatial or bathymetric gradients (Roy *et al.*, 1998) and reef geomorphology provides suitable habitats that attract a broad array of predator guilds (Mumby *et al.*, 2008; Mellin *et al.*, 2010; Espinoza *et al.*, 2014b). Understanding how static habitat features affects wildlife may thus be valuable for capturing discrete regions with unique attributes (Lucifora *et al.*, 2011).

Progress in conservation planning worldwide facilitates the implementation of adaptive management. However, a clear definition of appropriate conservation goals and spatial data to assess these goals are still lacking for mobile species, many of which play high-level roles in the trophic pyramid. Connectivity or the linking of populations through the movement of animals between habitats has implications for population persistence and configuration of MPAs (Sale *et al.*, 2005; Gaines *et al.*, 2010b; Grüss *et al.*, 2011; Olds *et al.*, 2013; Grüss, 2014; Green *et al.*, 2015). Species that move at distances exceeding MPA size will only be afforded partial protection (Green *et al.*, 2015), however, MPAs can provide benefits for these species if they protect specific locations where individuals aggregate for an extended period during key life stages (Heupel *et al.*, 2007; Meyer *et al.*, 2007; Knip *et al*., 2012) or when they are especially vulnerable to fishing mortality (Woodson *et al.*, 2013). For mobile species, protecting even part of their range of life cycles, especially critical habitats such as important foraging or nursery grounds, reduces overall population mortality (Claudet *et al.*, 2008; Knip *et al.*, 2011; Scott *et al.*, 2012; Lascelles *et al.*, 2014). Finite resources and time mean that small MPAs may be the only feasible management tool in many locations (Alcala & Russ, 2006) and can potentially be effective for species that have restricted ranges or key life stages linked to predictable or fixed habitat features (Garla *et al.*, 2006; Schofield *et al.*, 2013). However, research to this effect is limited (but see Meyer et al. 2007; Knip et al. 2012b; Escalle et al. 2015).

Distinct management agendas often drive conservation efforts at different scales (Redford *et al.*, 2003) and various currencies of conservation priority (i.e. abundance, richness, endemism, declines) are sensitive to variations in the spatial grain and extent of measurement (Wiens 1989; Hurlbert and Jetz 2007; Pittman and Brown 2011; Sandman et al. 2013; Grubbs et al. 2016). These issues of scale-dependency are likely exacerbated when defining the environments used by mobile species, as they intermittently use resources that are patchily distributed across a seascape in space and time (reviewed in Gaillard et al. 2010). Fluctuation in biodiversity with changes in analytical resolution have been shown for birds (Böhning-Gaese, 1997), plants (Nogués-Bravo *et al.*, 2008), mammals (Andelman & Willig, 2002), amphibians (Belmaker & Jetz, 2011) and fish (Pittman & Brown, 2011). The organisation of species or communities in both terrestrial and marine systems likely reflects a combination of local, regional and continental-scale processes whose perceived importance is in part dictated by the choice of spatial grain size (Rahbek & Graves, 2001; Rahbek, 2005). While remotely-sensed information allows the investigation of macro-ecological processes over the geographic range of species that is useful for large-scale planning (MacNeil *et al.*, 2009; Mellin *et al.*, 2010), such coarse-resolution data may fail to detect important habitat features relevant for management at local and regional scales. Conversely, local-scale investigations indicate that particular abiotic and biotic factors (such as tidal height, competition and predation), drive species and community responses at the scale at which species interact (Wetherbee *et al.*, 2007; Bolnick *et al.*, 2010; Guttridge *et al.*, 2012). The importance of identified local drivers often breaks down when re-evaluated over large scales (Webb *et al.*, 2009; Mora *et al.*, 2011). If unaccounted for, scale-dependencies can lead to incongruence in the number, size and configuration of MPAs within networks (Warman *et al.*, 2004; Shriner *et al.*, 2006; Huber *et al.*, 2010). Collectively, these studies suggest that any hypothesis about the utility of MPAs for mobile species must be investigated at a variety of spatial scales using scale-appropriate techniques to elucidate robust surrogates of distribution and movement.

In this thesis, I apply a hierarchical (multi-scale) conservation biogeography and ecology approach to evaluate the relevance of various abiotic and biotic metrics as a surrogate of coastal wildlife distribution. I use sharks and rays as primary model taxa, as these are economically and ecologically important populations that have been exploited by overfishing, yet closing the coastal ocean to human activities to aid their recovery remains a socio-politically unfeasible option. The identification of robust abiotic and biotic surrogates of their distribution and movement may facilitate strategic placement of MPAs to prevent further degradation and enhance the rebuilding of populations.

1.5 Elasmobranchs as model species

The chondrichthyan fishes (sharks, rays, skates and chimaeras) are a group of over 1,200 species that are among the oldest of extant vertebrates, having inhabited the Earth for over 400 million years (Compagno, 1990; Kriwet *et al.*, 2008). Sharks and rays (including skates) are ubiquitous carnivores in tropical, subtropical and temperate waters. Members of the *Elasmobranchii* subclass are prized for their meat, fins and gill rakers (Fowler *et al.*, 2005; Clarke *et al.*, 2006) and sustain some of the most diverse and profitable fishing activity. Landings of elasmobranchs have undergone a continuous rise in the last 50 years, due to declining teleost fish catches and the rising value of shark fins (both from sharks and shark-like rays) that are worth an estimated USD 300–450 million every year since 2000 (Dent & Clarke, 2015). Although global catch statistics have stabilised at 520,000 tonnes of sharks per annum since 2005 (FAO, 2014), most catches are aggregated with animals misidentified, unrecorded or discarded at sea, suggesting that true mortality rates are likely three- to four-fold greater, particularly as the demand for shark meat remains on the rise (Clarke *et al.*, 2006; Dhaneesh & Zacharia, 2013; Worm *et al.*, 2013; Bornatowski *et al.*, 2014a; Jabado *et al.*, 2015).

Notwithstanding some variation among species, most elasmobranchs possess conservative *k*-selected life history characteristics involving slow growth, late sexual maturity, long gestation periods and low litter sizes (Frisk *et al.*, 2005; García *et al.*, 2008; Dulvy & Forrest, 2012), rendering them ill-equipped to withstand exploitation (Cortés, 2002; Ferretti *et al.*, 2010). As such, cumulative impacts from overfishing, incidental bycatch, including entanglement in drifting fishing gear (Molina & Cooke, 2012; Filmalter *et al.*, 2013a; Oliver *et al.*, 2015), habitat degradation and pollution have reduced populations of sharks globally, with sharp declines in abundance observed in the Northwest Atlantic (Baum *et al.*, 2003; Baum & Worm, 2009), the Mediterranean (Ferretti *et al.*, 2008), the Greater Caribbean (Ward-Paige *et al.*, 2010), the western and central Pacific (Clarke *et al.*, 2013) and the Indian (John & Varghese, 2009; Graham *et al.*, 2010) oceans. Declines in abundance of over 50% relative to their pre-industrial fishing levels have been estimated (Lotze & Worm, 2009; Ferretti *et al.*, 2010). The relatively high declines in the Indian Ocean (Worm *et al.*, 2013), likely reflect the rampant and poorly regulated nature of offshore fisheries in the region (Graham *et al.*, 2010). Among the Pacific Island nations (defined as Micronesia, Polynesia, New Caledonia, Vanuatu, Norfolk Island and Fiji), six percent of elasmobranchs are considered threatened (Polidoro *et al.*, 2011). Altogether, some 25% of sharks and rays assessed by the IUCN are considered threatened globally, and are comparatively more threatened than insects, mammals and amphibians (Bradley & Gaines, 2014). In particular, larger-bodied species found in shallower waters exhibited the highest extinction risk, although considerable variation in the status of elasmobranchs between regions indicate that more information on regional populations is needed to clarify global trends (Dulvy *et al.*, 2014).

Trajectories in shark and ray populations under present levels of global fishing effort have garnered widespread concern, and research interest in their management and conservation. Their conservative life-history strategies mean that conventional fisheries management based on input and output controls will have limited success in reversing shark population declines even under low mortality scenarios (García *et al.*, 2008; Ward-Paige *et al.*, 2012). The trend of increasing MPA coverage presents opportunities to maximise benefits especially for highly mobile shark species (Lascelles *et al.*, 2014; Green *et al.*, 2015), in jurisdictions with adequate enforcement resources. As many sharks traverse large distances (>20–110 km across), MPAs are often too small to provide adequate protection at a population level unless the MPAs are 1000s of km across (Claudet *et al.*, 2008; Lascelles *et al.*, 2014; Green *et al.*, 2015). Despite limited behavioural data on individual species, numerous studies have demonstrated that coastal shark abundances are generally greater inside than outside no-take MPAs (Robbins *et al.*, 2006; McCook *et al.*, 2010; Bond *et al.*, 2012; Ruppert *et al.*, 2013; Edgar *et al.*, 2014; Espinoza *et al.*, 2014b), with exponential increases in biomass when MPAs are large (>100 km^2) and isolated (Edgar *et al.*, 2014). Tracking studies have shown that the extent of mobility within coastal species appears to depend on habitat connectivity (Papastamatiou *et al.*, 2009; Speed *et al.*, 2011; Barnett *et al.*, 2012; Espinoza *et al.*, 2015), resource dependency (Papastamatiou *et al.*, 2010; Speed *et al.*, 2012a), life stage (Speed *et al.*, 2011; Chin *et al.*, 2016) and sex (Whitney *et al.*, 2012a; Brooks *et al.*, 2013; Vianna *et al.*, 2013), with males dispersing more widely than females (Chin *et al.*, 2016). Ontogenetic shifts in habitat use have been hypothesized as a trade-off between predation risk and foraging rate or may reflect a change in diet preferences with age, mechanisms to reduce intraspecific predation or competition or changes in reproductive status (Werner & Gilliam, 1984; Lucifora *et al.*, 2009; Grubbs, 2010; Speed *et al.*, 2010). The identification of patterns of habitat use by specific life history stages such as pupping or nursery areas that are linked to predictable habitat features can provide significant benefits to conservation planning at local scales (Heupel & Simpfendorfer, 2005a). Information on species movement patterns from tracking studies have gained momentum to guide MPA design and enhance effectiveness for a coastal sharks, including juvenile blacktip (*Carcharhinus limbatus*), blacktip reef (*C. melanopterus*), Caribbean reef (*C. perezi*), grey reef (*C. amblyrhynchos*), nervous (*C. cautus*), nurse (*Ginglymostoma cirratum*), pigeye (*C. ambonensis*), spottail (*C.sorrah*), sicklefin lemon (*Negaprion acutidens*) sharks (Chapman *et al.*, 2005; Garla *et al.*, 2006; Knip *et al.*, 2011, 2012a; Filmalter *et al.*, 2013b; Escalle *et al.*, 2015; Speed *et al.*, 2016). While theory predicts that predation risk and food resources determine the quality and use of nursery areas (Simpfendorfer & Milward, 1993; Heithaus, 2007; Heupel *et al.*, 2007), information on movement and diet that are needed for assessing human-wildlife conflicts and the efficacy of MPAs is restricted to few species and regions.

Many elasmobranchs are inherently elusive, highly mobile and undergo ontogenetic changes in movement. Hence, progress in the conservation of coastal sharks and rays can be greatly guided by scale-appropriate, multi-disciplinary techniques to understand abiotic and biotic processes at continental, regional and local scales.

1.6 Aims of research

The overall objective of this thesis is to determine the abiotic and biotic drivers of the biodiversity, movement and diet of coastal sharks using a multi-scale (hierarchical) approach. This will be achieved using the following specific aims:

1) Establish foundational knowledge of continental-scale variability in assemblage composition, species richness and abundance of sharks and rays.
2) Predict the occurrence of juvenile sharks by identifying key abiotic and biotic drivers and determine how this relates to MPA placement at the regional-scale.
3) Investigate abiotic and biotic influences on residency and space use of juvenile sharks in relation to local-scale MPAs.
4) Identify the biological traits that influence resource use, trophic niche and diet composition of juvenile sharks within a shared natal environment.

Northern Australia constitutes an ideal natural setting to conduct this research. The region harbours two UNESCO World Heritage areas encompassing the world's largest barrier (i.e. Great Barrier Reef) and fringing (i.e. Ningaloo Reef) reef ecosystems (Abdulla *et al.*, 2013). Both coasts contain high concentrations of elasmobranchs (Lucifora *et al.*, 2011), including close to half of the shark species known globally (White & Kyne, 2010), and have been designated as a region of high scientific and conservation priority (Dulvy *et al.*, 2014). It is also an area with an extensive continental shelf subject to increasing industrial activity and human population growth (Devillers *et al.*, 2015) and where governing bodies have displayed commitment to marine spatial planning using benthic habitats and fishes as surrogates for biodiversity (Heap & Harris, 2008; Last *et al.*, 2010).

1.7 Thesis outline

Success in filling in continental-scale knowledge gaps is contingent on the ability to synthesize fishery-independent data at large scales. Chapter 2 utilises historical shark sightings encountered on baited remote underwater video surveys (BRUVS) to offer a continent-wide view of shark assemblages, abundance and richness in relation to spatial habitat features.

Chapter 3 harnesses a subset of data collected using stereo-BRUVS (i.e. paired cameras) that allow the quantification of shark length and consequently the designation of age classes. These were combined with newly-refined maps of abiotic and biotic features around the Australian continental margin that provide the data resolution needed to characterize important drivers of the distribution of juvenile sharks using habitat suitability modelling. Assessing the degree of overlap between predicted habitat suitability for juvenile sharks and the country's network of MPAs permits me to highlight current gaps in spatial protection.

Figure 1.1 Schematic illustration of the nested hierarchy of thesis chapters

Characterising nursery habitats and assessing the effectiveness of small-scale MPAs for juvenile sharks requires fine-scale information on residency and space use within these areas. In Chapter 4, I focus on the youngest juveniles to identify abiotic and biotic factors that regulate movement and the effectiveness of small-scale MPAs (<20 km^2) for juvenile sharks that utilise nursery habitats.

Nursery areas presumably offer refuge from predation however sharks sharing these habitats must partition resources to co-exist. In Chapter 5, I utilise stable isotope analysis to characterise the trophic niche, size-related diet shifts and diet composition of sharks sharing a communal shark nursery. I discuss trophic niche in the context of varying dietary strategies.

Finally I synthesise the main findings of my thesis in Chapter 6. I discuss how insights on shark-habitat associations gained here can be applied to inform conservation planning at multiple scales and jurisdictions. I finally evaluate the merits of habitat features as inputs to MPA placement.

1

Chapter 2 Quantifying shark and ray biogeography in the Austral tropics

Abstract: Knowledge of the spatial correlates of shark and ray distributions is critical for the assessment of population status and understanding of the role of these predators within ecosystems. We tested the hypothesis that location, depth, habitat cover and distance from shore, reef and mangrove features drive the distribution of shark and ray assemblages at large spatial scales (>1000s km). Datasets collected by 3277 deployments of baited remote underwater video systems (BRUVS) across the tropical coastline of northern Australia were analysed using multivariate and boosted regression tree models to predict assemblage structure, species richness, total abundance and the species-specific abundance of sharks and rays. Bathymetry and proximity to land were the primary predictors of assemblage structure, followed by longitude and habitat type. Boundaries were characterised by gradual change in assemblage structure rather than abrupt transitions. Representative demersal assemblages of elasmobranchs with subtle differences in structure, were found in coastal (<48 m), mid-shelf (48–135 m) and outer-shelf (>135 m) habitats and on insular, high-profile reefs. The assemblage structure of the elasmobranch community broadly aligned with the bioregions identified by changes in fish distribution and oceanography, which have been used to delimit representative biodiversity for management strategies. Latitude had the greatest influence on the relative abundance and species richness of sharks and rays, which increased at northern and southern ends of the study range relative to intermediate latitudes. Predictive models of multivariate and univariate indices of elasmobranch biodiversity offer an efficient and comprehensive tool for understanding species responses to multiple pressures by providing quantitative baseline information against which change can be assessed.

2.1 Introduction

Elasmobranchs face the highest risk of extinction among vertebrates, with at least one quarter of all known species considered to be threatened due to the multiple pressures of targeted fisheries, bycatch, habitat loss and climate change (Stevens *et al.*, 2000; Ferretti *et al.*, 2010; Dulvy *et al.*, 2014). These pressures threaten the important functional roles that many elasmobranchs, particularly sharks, exert in the top-down control of coastal and oceanic ecosystem structure and function (Heithaus *et al.*, 2008; Ferretti *et al.*, 2010). Despite the pace and scale of the global decline in the abundance of sharks and rays (Worm et al. 2013), for many species we lack even basic knowledge of their broad-scale distributions. The development of predictive models of habitat associations of elasmobranchs in response to physical and biological features of the environment is thus a key goal for research, principally because this information is central to achieving effective marine spatial planning (Pittman & Brown, 2011).

Earlier studies have shown that the patterns of biodiversity of sharks and rays are associated with latitudinal and bathymetric gradients, with increasing species richness towards the equator and in shallow, continental shelf waters (<200 m), where approximately 41% of all species are found (Lucifora et al. 2011, Guisande et al. 2013). While some species exhibit strong associations with defined habitats, such as coral reefs (Papastamatiou et al. 2010, Bond et al. 2012), many sharks and rays are generalists that use a range of habitats along the continental shelf, potentially acting as trophic links in the transfer of energy and nutrients from one system to another (McCauley *et al.*, 2012). The drivers responsible for assemblage structure and species-habitat associations can vary considerably among regions, but are typically poorly quantified. Hence, ascertained species-habitat associations over large scales can reveal complex ecological processes such as connectivity within and across ecosystems, aid in measuring the likely resilience of these taxa to changing environments and identify important areas for conservation.

The tropical continental margin of Australia lies at the confluence of the Eastern Indian and Western Central Pacific oceans and is recognised as a globally important hot spot of elasmobranch diversity, endemicity, threat and data deficiency (White & Kyne, 2010; Lucifora *et al.*, 2011; Dulvy *et al.*, 2014). It deserves high priority for study and conservation, particularly because it abuts the coasts of Indonesia and Papua New Guinea, which are global hotspots of illegal, unregulated and unreported (IUU) shark fisheries (Field *et al.*, 2009a; Dulvy *et al.*, 2014) and because it provides an important opportunity to study elasmobranchs in a region that likely constitutes one of the last strongholds for these animals within the Indo-Pacific Biodiversity Triangle.

Prediction of the distribution of elasmobranchs within the marine environment is challenging due to the limited availability of comprehensive survey data on continental scales (Simpfendorfer et al., 2011). Fisheries records provide the most accessible data sets, but most of this is available only as species occurrence or presence/absence with generally poor levels of taxonomic resolution and data standardisation, a problem further exacerbated by the broad geographic ranges and naturally low abundances of most species. Additionally, because sampling by fisheries is often confined to areas where target species are likely to be encountered (White et al., 2013), these datasets lack the ability to adequately quantify species richness, abundance hotspots and conspecific assemblages that are required for an understanding of functional diversity in elasmobranch assemblages (Stuart-Smith *et al.*, 2013).

Baited remote underwater video systems (BRUVS) offer an alternative means to quantify the relative abundance and composition of elasmobranch communities. The technique is non-extractive and fisheries-independent, with the added advantages that BRUVS are easily deployed across most of the continental shelf (at least to depths of 150 m) and generate a permanent video record of both abundance and size of elasmobranchs and the habitats they occupy (Cappo *et al.*, 2004, 2007). BRUVS have been used to survey fish assemblages along geographic gradients (Cappo *et al.*, 2007; Fitzpatrick *et al.*, 2012; Langlois *et al.*, 2012a; Harvey *et al.*, 2013), understand sampling gear bias (Brooks *et al.*, 2011; Langlois *et al.*, 2012b), document distribution patterns of elasmobranchs (White *et al.*, 2013a; Espinoza *et al.*, 2014a) and quantify fish densities inside and outside of MPAs (Mclean *et al.*, 2011; Bond *et al.*, 2012). The technique provides an ideal means to sample elasmobranch assemblages at broad spatial scales, particularly where sampling must include localities such as MPAs that prohibit extractive methods.

Here, we use a very large dataset of elasmobranch communities generated by BRUVS sampling across the entire tropical margin of northern Australia to identify the principal physical and biological factors driving assemblage structure in this fauna at continental scales. Specifically, we identify the geographic, habitat and bathymetric variables that best predict the (i) assemblage structure, (ii) species richness, (iii) total abundance and, (iv) species-specific abundance of coastal sharks along the tropical continental margin. These predictive models of the abundance and composition of elasmobranch communities will aid in the understanding of the role of these animals in marine ecosystems, spatial planning for conservation and management, and prediction of the likely resilience of these taxa under changing environments.

2.2 Methods

2.2.1 Study area and data collection

An archive of data from BRUVS surveys conducted between June 2003 and March 2011 was analysed (Table 2.1). Sampling was stratified on biological criteria over a wide range of habitat types such as reef, inter-reef, shoals and lagoons. BRUVS were deployed in Australian tropical waters, between Ningaloo Reef Marine Park (hereafter 'Ningaloo') in the west and the Great Barrier Reef Marine Park (hereafter 'the GBR') in the east (Figure 2.1). This region features over 5000 reefs distributed over ~8600 km, with some located offshore on the mid- and outer-continental shelf while the remainder are located inshore either as fringing reefs around continental islands and coastline or as shoals, patches or atoll-like platform reefs. The study region is influenced by oceanographic features such as the Indonesian Throughflow, Leeuwin, Holloway, East Australian and South Equatorial Currents (D'Adamo et al., 2009; Waite et al., 2007; Woo and Pattiaratchi, 2008). Bioregional planning is often used to support conservation planning (*cf*. Commonwealth of Australia 2006, Barr & Possingham 2013); however, the challenge is to determine the degree to which chosen bioregions reflect the biogeography of multiple taxa of concern. The spread of sampling locations offered the opportunity to investigate patterns across seven provincial bioregions based on the Integrated Marine and Coastal Regionalisation of Australia (IMCRA; Commonwealth of Australia 2006), which was used to delineate bioregions of representative biodiversity for conservation planning (Supporting Information, Table 2.1). Detailed information on the design of single- and stereo-video systems and the analysis of video footage can be found in the Supporting Information (Section 2.6.1).

2.2.2 Explanatory variables

The date, time, location (latitude and longitude), depth (m) and nearest reef feature were recorded for each BRUVS deployment. We included spatial variables such as distance from each deployment to shore, reef and mangrove (Supporting Information, Table S2.2) that are known drivers of shark distribution (Espinoza *et al.* 2014; Yates *et al.* 2015). We used spatial data layers from the United Nations Environment Programme – World Conservation Monitoring Centre website: <http://data.unep-wcmc.org/> and world equidistant cylindrical projections to calculate great circle distances with the *Near* tool in ArcMap version 10.0 (ESRI, 2012). A qualitative index (1-5; low to high) was used to assess the degree of topographic complexity of the seafloor in each image; low values typically correspond to flat ocean bottom (or areas of sediment deposition) while high values correspond to steep coral reefs (or rocky ledges). To standardize habitat characterization across the BRUVS dataset, bottom type was allocated to one of nine categories (bare rock, coral, encrusting algae/rubble, dense macroalgae, medium macroalgae, sand/mud, dense seagrass, medium seagrass, other sessile invertebrates, or mixed biota where multiple substrate types were present) based on highest percent cover recorded by trained observers. When habitat characterization was not possible due to visual occlusion or poor visibility, bottom type was determined based on the three nearest deployments.

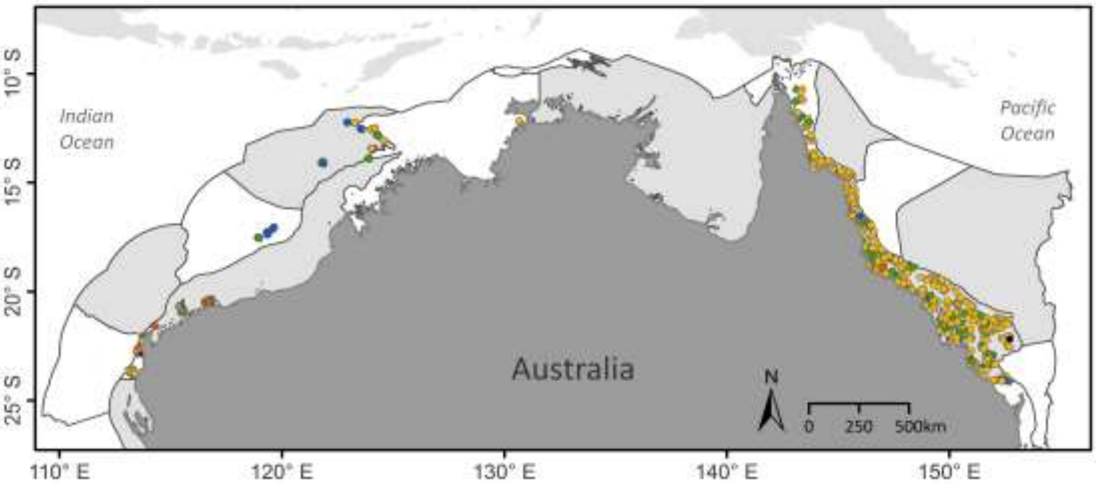

Figure 2.1 Map of northern Australia showing locations of all BRUVS sampling sites. Sites are shaded by a summarisation of the five bottom types into: sediment-associated (orange circles), vegetation-associated (green circles), coral-associated (blue circles), sessile invertebrates (red circles) and bare rock (black circles). IMCRA bioregions are outlined in black and transition zones defined by IMCRA are filled in grey areas.

2.2.3 Data preparation and analyses

As the data presented here represent the amalgamation of multiple individual research programs with a variety of goals, some locations were sampled more intensively than others. In particular, some of the southern sites in the GBR were sampled more intensively (> 300%) in later years and were removed from the analysis to control for sampling bias across the continent. To further minimise potential sampling bias and spatial autocorrelation, the dataset was analysed at the level of sites, defined as BRUVS that were deployed on the same date and less than 1 km apart. For each species, relative abundance was estimated as the maximum number of individuals observed in a frame (MaxN), a measure that avoids repeated counts of the same individual (Cappo *et al.*, 2004). To standardize sampling effort, the relative abundance of each species per site was defined as the total sum of MaxN across the within site replicates, divided by the total length of video imagery for those replicates (MaxN/hr). Only BRUVS with soak times between 50 and 70 min were included in the analyses to minimise bias in species richness estimates with differential soak times (Watson *et al.*, 2010). Unidentified species (<5% of records) were pooled at the genus or family level and hereafter referred to as 'species'. The Rhynchobatinae consisted of three species (*Rhynchobatus australiae*, *Rhynchobatus laevis* and *Rhynchobatus palpebratus*) that were pooled as a single species (*Rhynchobatus* spp.) because of problems with misidentification (Last & Stevens, 2009). We generated accumulation curves of observed and estimated asymptotic species richness at the level of sites, separately for sharks and rays, using five common species estimators (i.e. Chao1, Chao2, Jacknife1, Jacknife2, Bootstrap) (Gotelli & Colwell, 2011) available in the vegan package in R (R Core Team, 2015). The order in which shark and ray species were analysed was randomized 999 times and the cumulative number of observed and estimated new species per site was determined for each randomization. Subsequently, the number of sites was plotted against the mean and standard deviation of observed species richness.

Shark and ray assemblage structure was analysed using multivariate regression trees (MRT) performed on Hellinger-transformed estimates of relative abundance at the site level. MRTs were preferred over linear or additive models as they have the ability to fit complex functions for large numbers of sparsely distributed species including interactions between predictor variables and nonlinear distributions, while producing models that are easy to interpret (De'ath, 2002). As our focus was on characterizing broad spatial patterns rather than potential statistical noise or local features that may be associated with rare species (Poos & Jackson, 2012), only species that were sighted in at least 5% of the sites were included in these analyses (McGarigal *et al.*, 2000). These species were: silvertip (*Carcharhinus albimarginatus*), grey reef (*Carcharhinus amblyrhynchos*), sandbar (*Carcharhinus plumbeus*), tiger (*Galeocerdo cuvier*), sliteye (*Loxodon macrorhinus*), great hammerhead (*Sphyrna mokarran*) and whitetip reef

(*Triaenodon obesus*) sharks, and blue-spotted stingray (*Neotrygon kuhlii*) and wedgefishes (*Rhynchobatus* spp.). As BRUVS deployments were pooled at the level of sites, the mean of continuous explanatory variables used in the MRT analysis were calculated for each site and used as predictors in the models. The nodes of the MRT define a hierarchy of maximal dissimilarity assemblages characterized by distinct spatial-habitat associations. Cross validation was used to identify the size of the tree that minimised prediction error. To determine indicator species of assemblages, Dufrêne-Legendre index (DLI) values were estimated for each species at each node of the tree (Dufrêne & Legendre, 1997). For each species and group of sites, DLI is defined as the product of the mean species abundance occurring in the group divided by the sum of the mean abundances in all other groups (specificity), multiplied by the proportion of sites within the group where the species occurs (fidelity), multiplied by 100. Each species was associated with the node of the tree where it had the maximum DLI value. High (>20) DLI values were used to define indicators of species assemblages and the relative importance of predictors that explained their abundances.

Shark and ray species richness, total abundance and species-specific abundances of indicator species identified by MRT (species with DLI values >20: *C. amblyrhynchos, C. plumbeus, T. obesus* and the *Rhynchobatus* spp. complex) were also analysed independently using aggregated boosted regression trees (ABT) at the site level. ABTs are a regression and classification technique based on adaptive learning that can be used to examine detailed species-habitat relationships. ABTs are an extension of boosted trees that use cross-validation to improve the predictive performance of boosted regression trees (Elith *et al.*, 2008). ABT models included all predictors (Table S2.2) and up to third-order interactions and monotonic constraints were applied to the functional form of selected predictors. Models were evaluated using: 1) mean square predictive error for each model expressed as a percentage of the variance of the response variable (% PE); 2) the importance of each predictor estimated as the percentage of the variance explained; and 3) partial dependency plots to illustrate the relationship between responses and predictors. All analyses were conducted in R statistical package (R Core Team, 2015) using the libraries *vegan* for accumulation curves, *mvpart* for multivariate trees and *gbm* for boosted trees.

2.3 Results

Assemblage structure, abundance and species richness were examined using 3372 BRUVS deployments at 1169 sites (Figure 2.2). Overall, sharks and rays were uncommon with a total of 2115 individuals from 63 species sighted on 38% of the BRUVS deployed (Table S2.3). Thirteen percent of species (8) were sampled at depths beyond their maximum records and sixteen percent (10) had new depth records as no maximum depths were reported previously (Last & Stevens, 2009; Froese & Pauly, 2014) (Supporting Information, Table S2.3).

2.3.1 Abundance and species richness

Sharks were observed on 1077 (32%) of the 3372 BRUVS deployments, and MaxN per deployment ranged between 1 and 9 individuals (mean ± SD; 0.51 ± 0.98; Table S2.3). Rays were sighted at 346 deployments and MaxN varied between 1 and 9 rays (mean ± SD; 0.12 ± 0.43). Species richness of sharks varied between 1 and 4 (mean ± SD; 0.40 ± 0.65), with most deployments where sharks were sighted (77%) recording only one species (Table S2.3). Species richness of rays ranged between 1 and 3 (mean ± SD; 0.11 ± 0.34), with 93% of the BRUVS at which rays were sighted recording only 1 species. Cumulative species richness curves showed strong curvature towards an asymptote. Mean observed species richness for sharks and rays (42 and 22 respectively) was consistent with extrapolated species richness (41 and 21 respectively), indicating that sampling effort was sufficient to accurately describe shark and ray assemblages in the study area (Figure 2.2). In order of decreasing abundance, *C. amblyrhynchos*, *L. macrorhinus*, *T. obesus*, *Rhynchobatus* spp., *C. albimarginatus, C. plumbeus, N. kuhlii, S. mokarran* and *G. cuvier* were the nine most common species, with each recording a total MaxN greater than 70 and together accounting for over 71% of the total abundance of elasmobranchs.

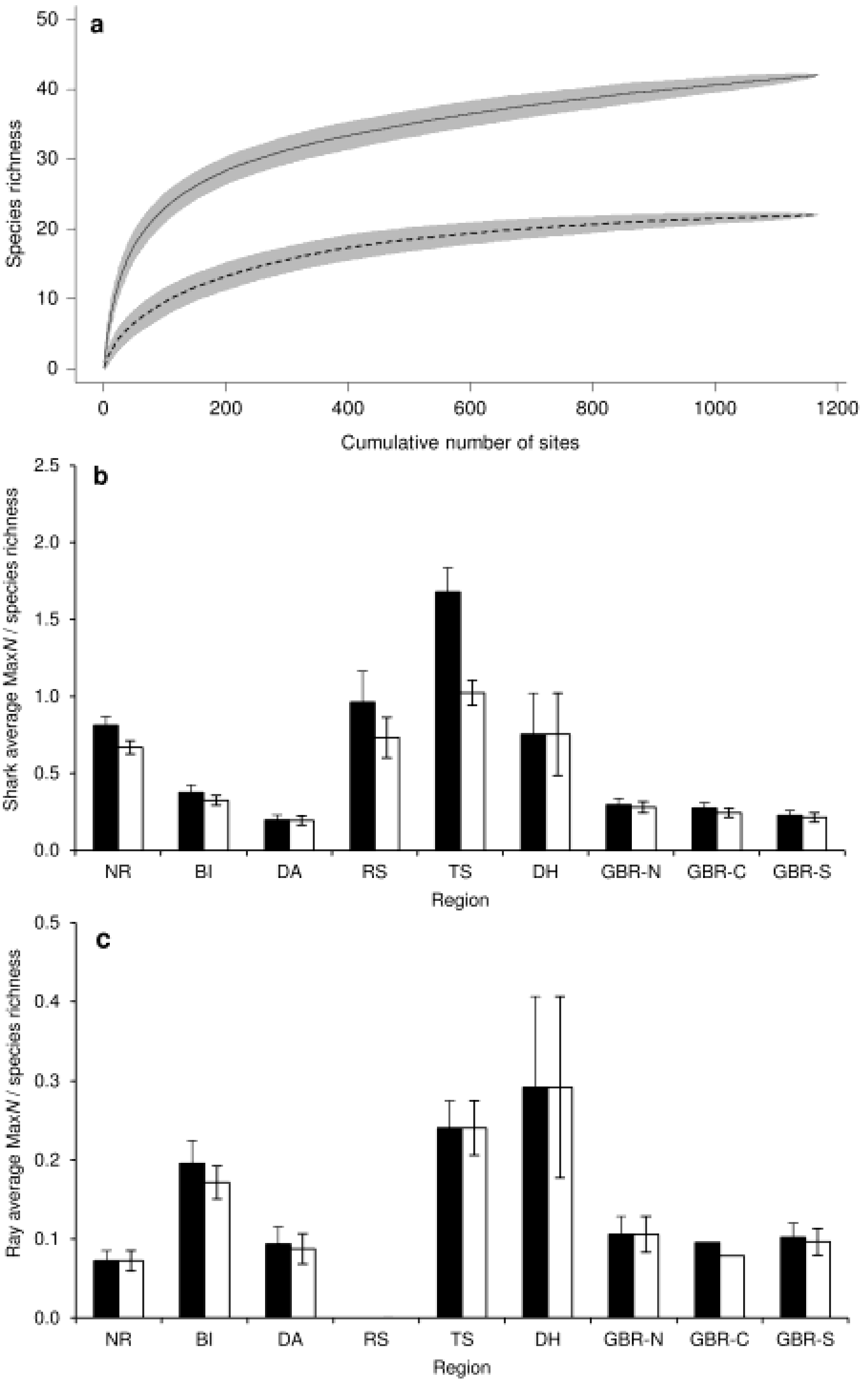

Figure 2.2 Plots of (a) shark (solid lines) and ray (dashed lines) species richness (mean ± SD) by the cumulative number of sites surveyed, and the relative MaxN (black bars) and species richness (white bars) of (b) sharks and (c) rays grouped by region. Regions include NR (Ningaloo Reef), BI (Barrow Island), DA (Dampier Archipelago), RS (Rowley Shoals), TS (Timor Sea), DH (Darwin Harbour), GBR-N (Great Barrier Reef – North), GBR –C (GBR – Central) and GBR-S (GBR – South).

2.3.2 Predictors of assemblage structure

The MRT analyses showed that the most parsimonious tree consisted of 10 terminal nodes (hereafter nodes) representing distinct assemblages (hereafter terminal assemblage) (Figure 2.3). Combined the tree explained 14% of the variation in transformed species abundance data. Depth was the primary predictor of assemblage structure, with *C. plumbeus* emerging as an indicator species that dominated the assemblages at deep sites (≥135 m; node 3). Proximity to mainland was the second split of the tree that separated inshore and offshore sites at ~120 km from the mainland. Offshore assemblages were further separated based on depth into shallow (<48 m) and mid-depth sites (≥48 m), with *C. amblyrhynchos* identified as an indicator species for shallow, offshore sites (node 10). The fourth split in the tree was longitude, which separated Ningaloo sites (>114 °S) from all other sites. Depth further separated Ningaloo sites into shallow (0–52 m) and mid-depth (52–135 m), with *L. macrorhinus* identified as an indicator species for mid-depths (node 19). Shallow sites at Ningaloo were further split by zone into open-access (open) and no-take (closed) sites (nodes 36 and 37). Open-access sites had relative higher abundances of the blue-spotted stingray *N. kuhlii*, while *C. amblyrhynchos* dominated the assemblage at no-take sites. However, no indicator species had moderate DLI values at open-access or no-take sites. Bottom type was the eighth split which separated non-Ningaloo sites dominated by coral or encrusting-algae-rubble from sites dominated by other habitat types, with the whitetip reef shark *T. obesus* identified as an indicator species for high coral sites. Longitude separated Barrow Island sites (<116 °S) from the other remaining sites (≥116 °S). The final split was between high vegetation sites (i.e. macroalgae; medium macroalgae, seagrass and sessile invertebrates) and low vegetation sites (i.e. sand/mud or mixed biota) at Barrow Island. Overall, latitudinal variation in assemblage structure was more pronounced on the west coast than the east, where sites across the GBR shared similar assemblage structure (node 32). Most species that occurred in each terminal assemblage were rare, but four species (*C. amblyrhynchos, C. plumbeus, T. obesus* and *Rhynchobatus* spp.) had consistently higher abundances and DLI values ≥20 and contributed to most of the variation in assemblage structure (Figure 2.3).

2.3.3 Predictors of abundance and species richness

The ABT models showed that latitude had the greatest influence on univariate descriptors of shark and ray distribution (relative influence ranged from 17.3 – 28 %; Figure 2.4; Figure 2.5a). Species richness and abundance of sharks and rays were highest at northern sites between latitudes 12° – 14°S, lowest at intermediate latitudes and had a smaller, secondary peak at southern sites between latitudes 23.5° – 24° S (Figure 2.4). Sites located between 110–180 km from mangroves had more species and higher abundances of sharks than sites closer (<110 km) or further from mangroves (≥180 km). Longitude and depth were also important in predicting species richness and abundance of sharks (combined relative influence: >33%), which increased longitudinally from east to west and with depth. In contrast, species richness and abundance of rays increased with distance to the nearest reef and decreased with depth (combined relative influence: >30%). Additionally, species richness of rays was higher at sites >100 km from mangroves and abundance increased with proximity to the mainland (relative influence: >11%).

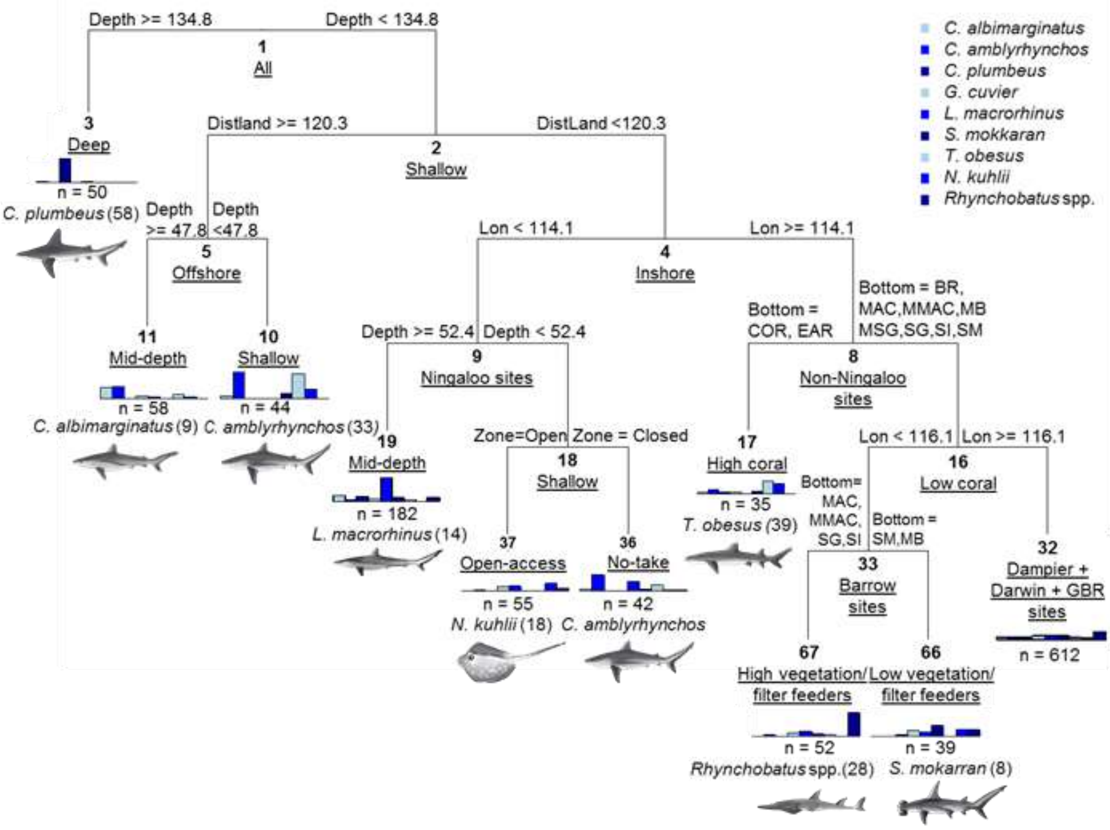

Figure 2.3 Multivariate regression tree analysis of the relative abundance (MaxN) of elasmobranch species explained by nine habitat predictors (cross-validated error: 0.86 ± 0.03 SE). The bold numbers at each leaf (i.e. node) show covariates that were most influential in predicting different shark and ray assemblages. Histograms on each node show the relative abundance of each species and number of sites (n). The Dufrêne-Legendre species indicators (DLI) characterising each branch and terminal node of the tree were included next to the species name in parentheses. Bottom type; BR – bare rock, COR – hard and soft corals; EAR – encrusting algae/rubble; MAC – dense macroalgae; MMAC – medium macroalgae; MB – mixed biota; SG – dense seagrass; MSG – medium seagrass; SM – sand/mud; SI – filter-feeding sessile invertebrates.

Table 2.1 Summary of BRUVS sampling in northern Australia including region, survey period, type of BRUVS used, mean depth, number of BRUVS and sites within closed or open fishing zones, and shelf features as specified by bioregion descriptions. Only bioregions in which BRUVS were deployed have been included.

Region	Region name	Survey period (year)	BRUVS type	Mean depth (m)	BRUVS per Zone		Sites per Zone		Shelf description	Bioregion
					Closed	Open	Closed	Open		
Ningaloo Reef	NR	2006, 2009	stereo	92.9 ± 63.4	205	508	81	249	reefs, banks, pinnacles	Central Western IMCRA Transition
Barrow Island	BI	2008 - 2010	stereo	11.2 ± 5.3	*na*	530	*na*	111	reefs, banks, pinnacles	Northwest IMCRA Province
Dampier Archipelago	DA	2008	stereo	16.0 ± 6.9	*na*	396	*na*	163	reefs, banks, pinnacles	Northwest IMCRA Province
Rowley Shoals	RS	2003-2004	stereo	42.4 ± 19.2	63	*na*	25	*na*	banks and sandwaves	Northwest Transition
Timor Sea	TS	2003-2004, 2011	stereo	34.8 ± 11.3	*na*	283	*na*	71	reefs, banks, pinnacles	Timor Province
Darwin Harbour	DH	2003	single	17.8 ± 0.0	*na*	29	*na*	11	plateau	Northwest IMCRA Transition
Great Barrier Reef - North	GBR-N	2003-2007	single & stereo	32.9 ± 13.7	94	304	29	114	sandwaves/sandbanks	Northeast IMCRA Transition
Great Barrier Reef - Central	GBR-C	2003-2007	single & stereo	38.9 ± 18.2	126	289	37	107	coral reefs, banks	Northeast IMCRA Province
Great Barrier Reef - South	GBR-S	2003-2005, 2007	single & stereo	43.6 ± 18.5	191	354	51	120	coral reefs, banks	Northeast IMCRA Province

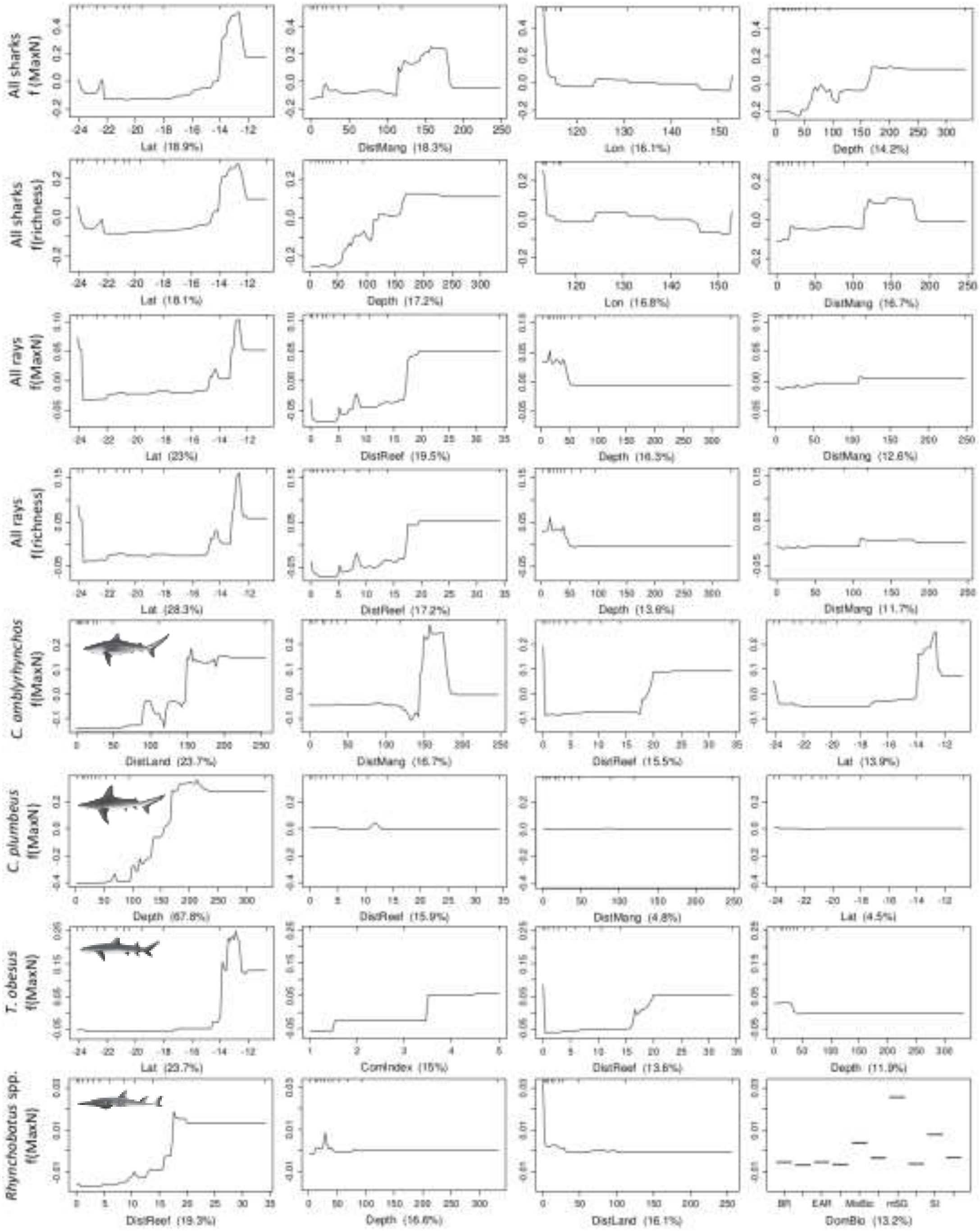

Figure 2.4 Partial dependency plots from ABT models showing the effects of the four most influential habitat predictors on species richness and total abundance (MaxN) of all sharks and rays, and the relative abundance of candidate indicator species: *C. amblyrhynchos, C. plumbeus, T. obesus* and *Rhynchobatus* spp. identified from the MRT model (see Figure 2.3). Y-axes represent mean responses centered at zero across all sites and x-axes represent continuous variables: latitude ('Lat'), longitude ('Lon'), depth ('Depth'), distance to the nearest mangrove edge ('DistMang'), distance to the nearest reef edge ('DistReef'), distance to the mainland ('Distland'), complexity index of the seafloor ('ComIndex) and bottom type of the seafloor in the BRUVS field of view ('DomBio').

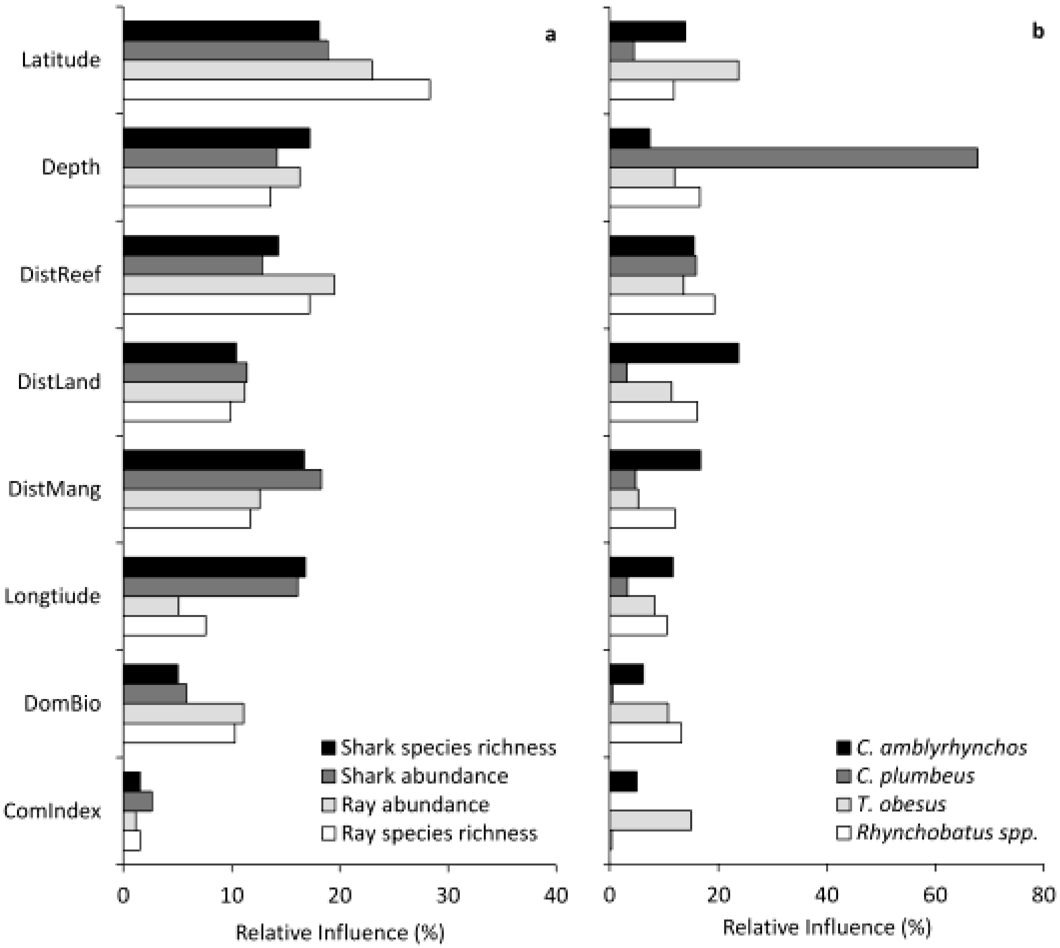

Figure 2.5 Summary of the relative influence of eight habitat predictors assessed by aggregated boosted regression tree models on (a) species richness and total abundance of all sharks and rays and (b) abundance of indicator species of shark assemblages (see Figure 2.2). Models were developed with cross-validation on data from 1169 sites using tree complexity of 5 and learning rate of 0.0025.

Indicator species (DLI value ≥20) identified from MRT analysis were influenced in different ways by habitat predictors used in the ABT models (Figure 2.4). However, distance to the nearest reef, depth and latitude were consistently identified as the best predictors of their abundance (Figure 2.4; Figure 2.5b). Distance to mainland was an important predictor of abundance of *C. amblyrhynchos*, with higher numbers offshore (≥100 km), at sites ~160 km from the mangrove edge and close to reefs (<1 km) (combined relative influence of over 67%). Depth was the best predictor of the abundance of *C. plumbeus*, with higher numbers recorded in depths >150 m (relative influence: 68%). Northern sites between latitudes 12.5°–14°S, with greater structural complexity (i.e. coral reef and rocky shoals environments) had higher abundances of *T. obesus* than soft-sediment habitats (i.e. mixed biota, sand/mud environments) with lower structural complexity (combined relative influence: 54.4%). *Triaenodon obesus* were also more abundant on the reef edge (<0.5 km) and at shallower sites (<40 m). Finally, *Rhynchobatus* spp. occurred in higher abundances with decreasing proximity to reefs, increasing proximity to the mainland, in depths of 40 m and habitats with moderate cover by seagrass (combined relative influence: 63.3%).

2.4 Discussion

Strong patterns in the bathymetric zoning of elasmobranch assemblages in this study confirm the primary role of bathymetry in structuring elasmobranch assemblage composition (Menni *et al.*, 2010; Guisande *et al.*, 2013). At broad scales, assemblage structure was mediated by the interaction between bathymetry and proximity from the mainland. Elasmobranch assemblages in deeper (>135 m) habitats differed from those at offshore shoals in shallow (<48 m) or mid-depth (48 – 135 m) waters and also from those inshore. Assemblage transitions at the 135 m isobath coincided with the interface between the mid- and outer-continental shelf (Last *et al.*, 2011), which may constitute a natural break between species that rely on benthic habitats such as coral reefs or seagrass patches in contrast to those that are bentho-pelagic and able to exploit resources in the open ocean. Breaks or transitions in assemblage composition have previously been documented for demersal fish and invertebrate distributions in Australia although this break was more pronounced between the outer shelf and slope (Last *et al.,* 2011, Woolley *et al.,* 2013).

Bathymetry was also an important driver of the diversity and ecology of assemblages. The increase in shark species richness and abundance with depth could be attributed to: (i) presence of submerged geomorphic features such as submarine canyons or seamounts and (ii) confluence of different water masses driving biological productivity at depth (McCauley *et al.*, 2010; Lucifora *et al.*, 2011; Xu *et al.*, 2015). Many shark species tend to form predictable aggregations in areas of high structural complexity (e.g. seamounts) and strong current flow, which may offer suitable habitat and productive foraging grounds (Barnett et al. 2012). In contrast, lower richness and abundance of rays observed in deeper assemblages was consistent with studies in tropical and temperate locations (Last *et al.*, 2011; Guisande *et al.*, 2013), and may relate to lower habitat complexity at depth with fewer niches to support co-existing species (Schultz *et al.*, 2012). The combination of assemblage level patterns and changes in ecology and diversity with depth suggests that the break between the mid- and outer- continental shelf (~135 – 165 m) forms an important faunal boundary for elasmobranchs.

2.4.1 Latitudinal pattern

Latitudinal gradients in species richness are one of the most widely documented biogeographic phenomena (Tittensor *et al.*, 2010; Last *et al.*, 2011; Guisande *et al.*, 2013), yet latitude has rarely been quantified as a spatial proxy for changes in the abundance and composition of elasmobranchs. The more numerous and diverse assemblage of sharks and rays we observed between latitudes 12°–14°S was consistent both with trends in shark species richness on the GBR (Espinoza *et al.*, 2014a) and global modelling studies (Tittensor *et al.*, 2010). Latitude was likely a proxy for distance to the highly diverse Indo-Pacific Biodiversity Triangle, the centre of global biodiversity (Bellwood & Hughes, 2001). Mid-latitude (22°S - 24°S) peaks in shark species richness are congruent with diversity hotspots off the east and west coasts of Australia, as identified from modelling studies (Tittensor *et al.*, 2010; Lucifora *et al.*, 2011; Guisande *et al.*, 2013; Dulvy *et al.*, 2014) and have been attributed to the mixing of tropical and temperate faunas along the central-east and central-west transition zones (Dunstan *et al.*, 2011; Last *et al.*, 2011; Mccallum *et al.*, 2013; Woolley *et al.*, 2013).

2.4.2 Proximal processes

The distributions of assemblages match geographical regions with unique oceanographic signatures. Offshore assemblages in the north-west shelf are influenced by the Indonesian Throughflow (ITF) that regulates the upwelling of nutrient-rich water from the Indian Ocean resulting in strong vertical temperature gradients (Wijffels & Meyers, 2004). Temperature and light intensity are known to be important drivers of depth segregation between and within reef-associated species such as *C. amblyrhynchos* and *C. melanopterus* (Speed et al. 2012; Vianna et al., 2013). The tree also identified an important faunal break at 114°S in the vicinity of Ningaloo. The oceanography in this region is complex, dominated by the southward penetration of the warm-water Leeuwin Current and the deeper equatorial-bound Leeuwin Undercurrent (LU; Domingues et al. 2007). The LU can extend onto the shelf or form fronts on the shelf break and affects processes such as prey recruitment (Condie et al., 2011) and productivity (Rousseaux *et al.*, 2012), that are likely to influence prey distribution and the composition of elasmobranchs (Lucifora *et al.*, 2011). The tree identified only one widespread assemblage on the north-east shelf that was influenced by the oligotrophic, south-bound East Australian Current that has been suggested to favour the wide dispersion of sharks and rays (Heupel *et al.*, 2010; Jaine *et al.* 2010). In addition, the density of the coral reef matrix and semi-continuous reef environment along the GBR may facilitate long-range dispersal in sharks and rays along the north-east coast. There is increasing evidence that the behaviour and dispersal strategies of sharks may vary across habitats with different degrees of reef-isolation (Werry *et al.*, 2014; Heupel *et al.*, 2015). Movement studies at small spatial scales have proposed that biological factors, such as prey density, competition, reproduction or dispersal, may be more important in driving shark movement rather than environmental or seasonal changes (Heupel & Simpfendorfer, 2014). Regardless of the exact causal processes involved, the strong bathymetric and geographic patterns observed in this study, suggest that a few easily accessible variables can be appropriate for characterizing key components of coastal elasmobranch assemblages at large scales.

2.4.3 Species-specific habitat associations

Multiple predictors interacted to determine habitat suitability of the key indicator species, *C. amblyrhynchos, C. plumbeus, T. obesus* and *Rhynchobatus* spp. The importance of coral reefs for sharks that reside in these habitats, such as *T. obesus* and *C. amblyrhynchos,* has been well-documented (Barnett et al., 2012; Heupel and Simpfendorfer, 2014; Vianna et al., 2013) and *C. amblyrhynchos* have been observed in greater numbers and form predictable aggregations on remote, insular reefs (Papastamatiou et al. 2010, Field et al. 2011, Vianna et al. 2013). The strong influence of coral cover and habitat complexity on the abundance of *T. obesus* may relate to feeding behaviour, as this species specialises in feeding on prey that shelter inside deep holes and crevices (Randall, 1977). Our finding that *Rhynchobatus* spp. preferred habitats with moderate cover of seagrass is consistent with studies showing that they are lower level trophic consumers in seagrass ecosystems (Heithaus *et al.*, 2013) and their prevalence in inshore coastal habitats (White et al., 2013). Use of deep water habitat by *C. plumbeus* in Western Australia has been suggested to correspond with ocean productivity and proximity to highly productive prey patches (McCauley *et al.*, 2010). Deeper continental shelf waters off Western Australia appear to be an important movement corridor for juvenile sandbar sharks to potential mating grounds in the tropical North-west shelf (McCauley *et al.*, 2010). The importance of depth in driving *C. plumbeus* abundances suggest that the delineation of reserves in outer shelf waters (>135 m) could protect *C. plumbeus* from fishing mortality imposed by the Western Australian North Coast Shark Fishery (WANCSF; 22°S 114°E to 22°S 129°E). *C. amblyrhynchos* and *T. obesus* are currently classified as “Near Threatened” globally by the International Union for the Conservation of Nature (Smale, 2005; 2009), while *C. plumbeus* is classified as “Near Threatened” in Australia and “Vulnerable” globally (Musick et al., 2009), and *Rhynchobatus* spp. are “Vulnerable” globally (White et al., 2003; Dudley et al., 2006; Compagno et al. 2016), providing opportunity to protect one of the last strongholds for these species. Important commercial species, such as *C. plumbeus* and *Rhynchobatus* spp. (McCauley *et al.*, 2010; Dulvy *et al.*, 2014), which are likely to respond to management actions that reduce fishing pressure, may be good candidate indicator species and this work provides quantitative information against which future change can be assessed. The strong fidelity of various shark species to isolated offshore seamounts (Field *et al.*, 2011; Barnett *et al.*, 2012) and the wide dispersal of sharks that are commercially important (McCauley *et al.*, 2010), further emphasize the need to couple models of elasmobranch distribution with an understanding of movement and migration corridors to accurately delineate representative, unique and potentially vulnerable habitats for elasmobranch conservation.

2.4.4 Marine protected areas

We observed assemblage transitions from higher abundances of *C. amblyrhynchos* and *T. obesus* at no-take sites to higher abundances of *N. kuhlii* and *G. cuvier* at open-access sites at Ningaloo. Such patterns are consistent with top-down controls such as direct consumption and mesopredator (e.g. *N. kuhlli*) avoidance of no-take sites due to risk effects imposed by larger sharks (Rizarri *et al.* 2014; S. Barley, unpublished data). While bottom-up effects such as differences in habitat quality (Espinoza *et al.*, 2014a) and prey availability among zones may also contribute to the assemblage shifts observed, our findings provide evidence that no-take zones at Ningaloo can support higher shark abundance particularly site-attached species such as *C. amblyrhynchos* and *T. obesus* (Speed *et al.*, 2011). Contrary to the findings of Espinoza et al. (2014b), our analysis was unable to detect differences in shark abundance between open-access and no-take zones on the GBR. This potentially occurred as southern sites in the GBR were sampled more intensively in later years to answer specific questions, and these were removed from our analysis to control for sampling bias across the continent. Nevertheless, this study not only provided an essential framework for evaluating MPA efficacy, but is especially crucial for long-term ecosystem assessments, as many elasmobranch species play a key role in maintaining ecosystem function (Heithaus et al., 2008; 2014; Wirsing & Heithaus, 2008; Ruppert et al., 2013).

2.4.5 Limitations and future directions

Although ideal for sampling at broad scales, the BRUVS deployments in this study were limited to relatively shallow (<350 m) depths along the continental shelf and upper slope, thus precluding sampling of pelagic and bathyal species. Demersal BRUVS were able to document 38% of the total species richness of sharks and rays expected in tropical Australia (Froese and Pauly, 2014). Secondly, many BRUVS were not deployed on shallow coral reefs (<20 m) or inside reef lagoons due to logistic constraints, which could have underestimated the abundance of species that commonly use these habitats such as black-tip reef (*C. melanopterus*) and sicklefin lemon sharks (*N. acutidens*)(Rizzari *et al.*, 2014a). While BRUVS will potentially observe a subset of scavenging and larger species rather than the entire elasmobranch fauna, all fish sampling methods have selectivity biases, and alternatives for sampling continental shelf species (e.g. trawls, mesh-nets and traps) are extractive, lethal and can be destructive to habitats within MPAs. The BRUVS also proved useful in expanding knowledge on depth ranges, which is important for refining models that evaluate extinction risk in elasmobranchs (Dulvy *et al.*, 2014). While integrating different techniques may serve to fully define assemblages, these findings support previous research that endorse BRUVS as a suitable standardised, non-extractive tool for multi-species assessments at broad-scales (Murphy & Jenkins, 2010; Brooks *et al.*, 2011; Langlois *et al.*, 2012b; Mallet & Pellerier, 2014), as elasmobranchs continue to be depleted and economic constraints for comprehensive data collection persist.

The development of continental-scale species distribution models is now warranted by an increasing availability of standardised survey data, but several potentially important aspects require attention. Sampling effort was not equally distributed throughout the continental margin with sites clustered within each zone; as such it is unlikely that all habitat types were sampled equally across the continent. It was logistically impractical to investigate occurrence patterns using a structured survey design over such a large area and time frame. The opportunistic nature of the sampling design thus reflects a trade-off between statistical rigor and biological inference. To maximise spatial coverage in order to detect large-scale patterns, it was necessary to combine data from different years of sampling. While the combination of variable sampling years could have introduced bias, it may also to some extent reduce the potential confounding effects of fishing and protection regimes (implemented at different times) on shark occurrence patterns. Our database revealed low density data and resulting increased uncertainty of model outputs on the north-west and far-north shelf. Increases in relative abundance and species richness of sharks at specific distances to mangroves (i.e. 150 km) rather than a gradual positive trend, could be attributed to lower sample sizes along the far-north shelf or the relatively higher number of sharks sighted in association with remote coral atolls at specific sites such as the Timor Sea. Future directed sampling to increase replication along gradients of varying proximity to mangroves and reefs and in regions of low density data is needed to refine predictive models. An important caveat to our approach was that our multivariate model explained only 14% of the variance for 10 species. However, previous studies using BRUVS and regression tree models showed similar explained variance between 10% and 17% in the abundances of sharks and sea snakes (Udyawer *et al.*, 2014; Espinoza *et al.* 2014). Although bathymetric and geographic predictors can be appropriate for predicting broad-scale patterns of key components of coastal elasmobranch assemblages, more research is required to resolve fine-scale distribution in these habitats. The static nature of the available data also means that this study is a 'snap-shot' of the spatial distribution of elasmobranch assemblages on a large scale and our results should thus be applied cautiously to MPA design. However, a study using BRUVS found that temporal variation within one marine park was relatively minor compared to spatial variation across three marine parks (Malcolm et al. 2007). Dynamic processes such as competition and predation and seasonal or annual fluctuations in climate were not captured in the sampling framework and warrant further studies to validate species-habitat relationships through time. Ideally, future models should incorporate important ecological (e.g. dispersal, connectivity, prey density), environmental or socio-economic variables (e.g. levels of exploitation, proximity to urban areas) that would increase the resolution of management priorities and representative elasmobranch assemblages.

2.4.6 Conservation implications

Notwithstanding the increasing effectiveness of bioregional approaches in conservation planning, establishing management regimes that are robust across taxonomic groups remains a challenge. An important finding was that the biogeographic structure of elasmobranch assemblages in our study area broadly aligns with the bioregions identified by transitions in demersal fish distribution and oceanography, which were originally used to delimit areas of representative biodiversity for conservation planning by the Australian government (IMCRA Technical Group, 1997). However, our results indicate that community boundaries for sharks occurred at different depths to boundaries previously found for fishes and benthic invertebrates along the Australian coastline (Last *et al.*, 2011; Mccallum *et al.*, 2013; Woolley *et al.*, 2013) and supports the concept of using data from as many species and criteria as possible so that the design of conservation strategies can offer the greatest benefit for ecosystems as a whole. Given the wide geographic ranges of many shark and ray species, this study provided a valuable contribution to understanding the habitat characteristics important to coastal elasmobranchs at broad scales.

The global loss of elasmobranch biodiversity requires cost-effective and comprehensive conservation tools for predicting changes in distributions. Such data underpin effective intervention where necessary. Abiotic data are often less spatially restricted than biological data, but proper validation of abiotic surrogates with suitable and available biological data will help to design effective MPAs that incorporate essential criteria and ultimately preserve ecological functionality (Roberts et al. 2003). We demonstrate that latitude and depth can serve as initial surrogates of distributions to predict hotspots and representative assemblages for conservation, attributes that could be particularly useful in data-poor regions adjacent to Australia such as Timor, Eastern Indonesia and Papua New Guinea. However, further research is required to determine the portability and generality of the models through application to different regions. Understanding the drivers of multivariate and univariate indices of biodiversity patterns of elasmobranchs is of paramount importance for understanding species responses to multiple pressures – a crucial step towards the sustainable management of biodiversity. More importantly, we demonstrate the utility of a two-pronged approach where standardized, fishery-independent surveys and abiotic data are combined to delineate assemblages at broad resolutions and serve as a foundation for smaller-scale dedicated studies that can guide the strategic placement of MPAs along a data-limited continental shelf.

2.5 Acknowledgements

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2.6 Supporting Information

2.6.1 BRUV configuration

A galvanised steel frame held either one or two SONY camcorders (models used included Hi-8, Mini-DV, HC 15E, CX7, CX12) within waterproof housings made from PVC pipe with acrylic front and rear ports (Cappo *et al.*, 2004, 2007; Mclean *et al.*, 2011). Single-BRUVS provide a measure of relative abundance but do not allow lengths of objects in the field of view to be calculated. Stereo-BRUVS include paired cameras within housings and a diode attached to a pole in the field of view to enable synchronization of video footage for length measurements (Watson *et al.*, 2010). Wide-angle lens adaptors were fitted to the cameras, with exposure set to 'Auto' and focus set to 'Infinity/Manual' and 'Standard Play' mode selected to provide at least 45 min of filming. Detachable bait arms suspended in the centre of the field of view were made of 20 mm plastic conduit connected to a 350 mm plastic mesh canister and baited with at least 800 g of crushed sardines (*Sardinops or Sardinella* spp.). BRUVS were deployed from a vessel with 8 mm polypropylene ropes, polystyrene surface floats bearing a marker flag and retrieved using a hydraulic winch (Cappo *et al.*, 2004, 2007). BRUVs were set at least 250 m apart to minimise the overlap of bait plumes and likelihood of fish moving between deployments within the sampling period (Watson *et al.*, 2010).

2.6.2 Image analysis

Video analysis commenced at the point each BRUVS stabilised at its sampling depth. Each fish was identified to species or the lowest taxonomic level possible by trained observers, aided by high definition video, relevant literature and a collection of reference images. Correct identification of species that are externally similar using only video footage can be difficult. Therefore, closely related species that could be misidentified were excluded or pooled together for analyses. For each species, relative abundance was estimated as the maximum number of individuals observed in a frame (MaxN), a measure that avoids repeated counts of the same individual (Cappo *et al.*, 2004). In the first four years of the study, the Australian Institute of Marine Science (AIMS) BRUVS Access Database was used to obtain measures of MaxN (BRUVS 1.5 mdb, AIMS, 2006) and more recently, the purpose-built programme EventMeasure (SeaGIS, 2008).

Table S2.2 Predictors used in the multivariate regression tree and aggregated boosted regression tree analyses. The range, mean and standard deviation of predictor variables calculated using all sites were also included. Zone: Closed – closed to fishing; Open – open to fishing. Bottom type: BR – no biota; COR – hard/soft coral; EAR – encrusting rubble/algae; MAC – dense macroalgae; MMAC – medium macroalgae; SM – sand/mud; SG – dense seagrass; MSG – medium seagrass; SI – sessile invertebrates; MB – mixed biota.

Variable	Description	Type	Range	Mean ± SD
Depth	Depth (m)	Continuous	1.1 – 348.1	42.9 ± 42.3
Lat	Latitude (decimal degrees S)	Continuous	24.1 – 10.7	19.9 ± 3.3
Lon	Longitude (decimal degrees E)	Continuous	113.1 – 152.7	129.5 ± 16.1
DistLand	Nearest distance to mainland (km)	Continuous	0 – 255.3	36.8 ± 50.0
DistReef	Nearest distance to reef edge (km)	Continuous	0 – 34.2	6.1 ± 5.7
DistMang	Nearest distance to mangrove edge (km)	Continuous	0.1 – 2470.0	46.0 ± 47.6
Zone	Zone	Categorical	C–O	*na*
ComIndex	Complexity index of seafloor	Categorical	1–5	1.6 ± 1.1
Bottom	Predominant substrate type	Categorical	BR-COR-EAR-MAC-MMAC-MB-SM-SG-MSG-SI	*na*

Table S2.3 Summary of shark and ray abundance (MaxN; % MaxN), sightings and species depth ranges recorded during this study compared to previous records (taken from Froese and Pauly 2014). The distribution, habitat type and IUCN Red List Status for each species are also detailed. MaxN: the sum of the maximum number of individuals from each species observed at any one time on the whole tape; % MaxN: the MaxN of each individual of a species divided by the sum of MaxN for all species. Depth range: *na* – not applicable; *nr* – not reported; * – new depth record for the species; ** – depth range extension. Distribution: AT – Atlantic Ocean; EI – Eastern Indian Ocean; WI – Western Indian Ocean; EP – Eastern Pacific Ocean; WP – Western Pacific Ocean; AE – Australian endemic. Habitat: CR – coral reef; IN – inshore/coastal; SH – shelf. IUCN Red List Status: DD – Data Deficient; LC – Least Concern; NT – Near Threatened; VU – Vulnerable; ED – Endangered; CE – Critically Endangered.

Family	Species	MaxN (% MaxN)	No. sightings (% BRUVS)	Depth range (m)		Distribution	Habitat	IUCN Red List Status
				Previous	Current study			
Superorder Batoidea		402 (19)	346 (10)					
Dasyatidae	*Dasyatidae spp.*	4 (0.2)	4 (0.1)	*na*	16 – 41	*na*	*na*	*na*
	Dasyatis thetidis	2 (0.1)	2 (0.1)	0 - 440	38 - 348	EI-WI-WP	IN	DD
	Himantura fai	45 (2.1)	19 (0.6)	nr	6 - 56*	EI-WI-WP	CR-IN	LC
	Himantura granulata	2 (0.1)	2 (0.1)	1 - 85	11 – 15	EI-WI-WP	CR-IN	NT
	Himantura jenkinsii	7 (0.3)	6 (0.2)	33 - 50	16 - 36	EI-WI-WP	IN	LC
	Himantura sp.	4 (0.2)	4 (0.1)	*na*	12 - 105	*na*	*na*	*na*
	Himantura toshi	7 (0.3)	7 (0.2)	10 - 140	15 – 65	EI-WI-WP		LC
	Himantura uarnak	4 (0.2)	4 (0.1)	20 - 50	4 - 65**	EI-WI-WP	CR-IN	VU
	Himantura undulata	2 (0.1)	2 (0.1)	nr	16 - 54*	EI-WP	IN	VU
	Neotrygon leylandi	3 (0.1)	3 (0.1)	5 - 80	39 – 44	EI-WP	SH	DD
	Neotrygon kuhlii	96 (4.5)	94 (2.8)	0 - 170	3-76	EI-WI-WP	CR-IN-SH	DD
	Pastinachus sephen	11 (0.5)	11 (0.3)	nr - 60	4 - 156**	EI-WI-WP	CR-IN	DD
	Pastinachus sp.	1 (<0.1)	1 (<0.0)	*na*	13	*na*	*na*	*na*
	Taeniura lymma	26 (1.2)	26 (0.8)	1 - 20	3 - 47**	EI-WI-WP	CR-IN	NT
	Taeniura meyeni	32 (1.5)	32 (0.9)	nr - 500	6 - 136	EI-WI-EP-WP	CR-IN	VU
Mobulidae	*Manta birostris*	6 (0.3)	5 (0.1)	0 - 120	12 – 62	AT-EI-WI-EP-WP	CR-IN-SH	
Myliobatidae	*Aetobatus narinari*	4 (0.2)	4 (0.1)	1 - 80	46 - 283**	AT-EI-WI-EP-WP	CR-IN-SH	NT
Pristidae	*Pristis clavata*	1 (0.0)	1 (<0.0)	nr	15*	EI-WP-AE	IN	CE
Rhinidae	*Rhina ancylostoma*	8 (0.4)	8 (0.2)	3 - 90	13 – 40	EI-WI-EP-WP	CR-IN	VU
Rhinobatidae	*Aptychotrema rostrata*	1 (<0.1)	1 (<0.0)	20 - 60	39	WP-AE	IN	LC
	Glaucostegus typus	9 (0.4)	9 (0.3)	0 - 100	15 – 57	EI-WP	IN-SH	VU
Rhynchobatinae	*Rhynchobatus spp.*	127 (6.0)	126 (3.7)	2 - 61	8 - 178**	EI-WI-WP	IN	VU

Superorder Selachii		1713 (81)	1077 (32)					
Carcharhinidae	*Carcharhinidae spp.*	12 (0.6)	10 (0.3)	*na*	18 - 105	*na*	*na*	*na*
	Carcharhinus albimarginatus	117 (5.5)	102 (3.0)	1 - 800	18 - 239	EI-WI-WP	CR-SH	NT
	Carcharhinus amblyrhynchoides	8 (0.4)	7 (0.2)	nr - 50	20 - 32*	EI-WI-WP	IN-SH	NT
	Carcharhinus amblyrhynchos	392 (19)	239 (7.1)	0 - 1000	5 – 81	EI-WI-WP	CR-IN-SH	NT
	Carcharhinus amboinensis	1 (<0.1)	1 (<0.0)	0 - 150	38	AT-EI-WI-WP	IN-SH	DD
	Carcharhinus brachyurus	3 (0.1)	3 (0.1)	0 - 360	248 - 348	AT-EI-WI-EP-WP	IN-SH	NT
	Carcharhinus dussumieri	17 (0.8)	17 (0.5)	nr - 170	13 - 59*	EI-WI-EP-WP	IN-SH	NT
	Carcharhinus falciformis	1 (<0.1)	1 (<0.1)	0 - 4000	15	EI-WI-EP-WP	IN-SH	NT
	Carcharhinus galapagensis	1 (<0.1)	1 (<0.0)	1 - 286	253	AT-WI-EP-WP	CR-IN-SH	NT
	Carcharhinus leucas	4 (0.2)	4(0.0)	1 - 152	17 - 56	AT-EI-WI-EP-WP	CR-IN-SH	NT
	Carcharhinus limbatus/tilstoni	39 (1.8)	38 (1.1)	0 - 64	5 - 297**	AT-EI-WI-EP-WP-AE*	IN-SH	NT
	Carcharhinus macloti	7 (0.3)	4 (0.1)	nr - 170	89 - 113*	EI-WI-WP	IN-SH	NT
	Carcharhinus melanopterus	27 (1.3)	26 (0.8)	20 - 75	1 – 25	EI-WI-WP	CR-IN	NT
	Carcharhinus plumbeus	115 (5.4)	105 (3.1)	1 - 280	4 - 295**	AT-EI-WI-EP-WP	IN-SH	NT
	Carcharhinus sorrah	5 (0.2)	5 (0.1)	0 - 140	1 - 348	EI-WI-WP	SH	NT
	Carcharhinus spp.	53 (2.5)	45 (1.3)		5 - 222			
	Galeocerdo cuvier	80 (3.8)	79 (2.3)	0 - 371	2 - 194	AT-EI-WI-EP-WP	CR-IN-SH	NT
	Loxodon macrorhinus	239 (11.3)	164 (4.9)	7 - 100	12 - 267**	EI-WI-WP	SH	LC
	Negaprion acutidens	28 (1.3)	27 (0.8)	0 - 92	4 – 60	EI-WI-WP	CR-IN-SH	VU
	Rhizoprionodon acutus	2 (0.1)	2 (0.1)	1 - 200	11 - 256	AT-EI-WI-WP	SH	LC
	Rhizoprionodon sp.	31 (1.5)	25 (0.7)	*na*	32 - 95	*na*	*na*	*na*
	Rhizoprionodon taylori	18 (0.9)	16 (0.5)	nr - 300	18 - 68*	WP	IN-SH	LC
	Triaenodon obesus	238 (11.3)	166 (4.9)	1 - 330	4 - 105	EI-WI-EP-WP	CR	NT
Ginglymostomatidae	*Nebrius ferrugineus*	43 (2.0)	43 (1.3)	1 - 70	2 - 74**	EI-WI-WP	CR-SH	VU
Hemigaleidae	*Hemigaleus australiensis*	7 (0.3)	7 (0.2)	12 - 170	4 – 25	EI-WP-AE	IN-SH	LC
	Hemipristis elongata	13 (0.6)	13 (0.4)	1 - 130	15 – 54	EI-WI-WP	IN-SH	NT
Hemiscylliidae	*Chiloscyllium punctatum*	31 (1.5)	31 (0.9)	0 - 85	3 – 37	EI-WP	CR-IN	NT
	Hemiscyllium trispeculare	1 (<0.0)	1 (<0.1)	0 - 50	6	EI-WP	CR	LC

Orectolobidae	*Eucrossorhinus dasypogon*	1 (<0.0)	1 (<0.1)	2 - 40	6	EI-WI-WP	CR-SH	NT
	Orectolobus maculatus	1 (<0.0)	1 (<0.1)	0 - 110	111*	EI-WP-AE	CR-SH	VU
	Orectolobus ornatus	2 (0.1)	2 (0.1)	0 - 100	8 – 9	EI-WP	CR-IN-SH	VU
	Orectolobus sp.	1 (<0.0)	1 (<0.1)	*na*	164	*na*	*na*	*na*
	Orectolobus wardi	1 (<0.0)	1 (<0.1)	1 - 3	111*	EI-WP-AE	IN-SH	LC
Sphyrnidae	*Sphyrna lewini*	20 (0.9)	20 (0.6)	0 - 512	6 - 270	AT-EI-WI-EP-WP	CR-IN-SH	ED
	Sphyrna mokarran	89 (4.2)	89 (2.6)	1 - 300	1 - 348*	AT-EI-WI-EP-WP	CR-IN-SH	ED
Stegostomatidae	*Stegostoma fasciatum*	3 (0.1)	3 (0.1)	0 - 63	19 - 49.6	EI-WI-WP	CR-IN-SH	VU
Triakidae	*Hemitriakis falcata*	31 (1.5)	23 (0.7)	146 - 197	13 - 193	EI-AE	SH	LC
	Hemitriakis spp.	21 (1.0)	16 (0.5)	*na*	71 - 147	*na*	*na*	*na*
	Iago garricki	2 (0.1)	2 (0.1)	250 - 472	242 - 274	EI-WP	SH	LC
	Mustelus ravidus	5 (0.2)	5 (0.1)	106 - 300	136 - 210	EI-AE	SH	LC
	Mustelus spp.	3 (0.1)	3 (0.1)	*na*	24 - 25	*na*	*na*	*na*

Chapter 3 Predicting habitat suitability for juvenile sharks to improve conservation planning

Abstract: Fishing and habitat degradation have increased the extinction risk of sharks. Despite the rapid expansion of marine protected areas (MPAs) globally, their effectiveness as a means of halting declines in shark numbers remains unclear due to a paucity of monitoring data on large scales (100s–1000s km). In particular, conservation strategies now strive to include the protection of juvenile sharks as juvenile survivorship is recognized as critical for effective management of shark populations. Using data collected by baited remote underwater video systems (BRUVS) in northwest Australia, we developed generalized linear models to elucidate the ecological drivers of habitat suitability for juvenile sharks. We assessed these patterns at two taxonomic levels: order (including all juvenile sharks sampled; *all juveniles*) and species (including the three main species sampled; grey reef *Carcharhinus amblyrhynchos*, sandbar *Carcharhinus plumbeus* and whitetip reef *Triaenodon obesus* sharks). We predicted habitat suitability for juvenile sharks across 490,515 km^2 of coastal waters, and quantified the representation of high suitability habitats within MPAs. Our species-level models had higher accuracy ($\kappa > 0.68$) and deviance explained (DE > 47 %) than our order-level model ($\kappa = 0.36$ and DE = 10 %), as individual species showed distinct areas of high suitability. These differences likely reflect specific physiological or resource requirements and validate concerns over the utility of higher-attribute conservation targets as opposed to species-focused conservation. We found poor representation of high suitability habitats in MPAs providing the highest restrictions on extractive activities. This spatial mismatch likely reflects a lack of explicit conservation targets and omission of information on species distribution in the planning process. Our study demonstrates that non-extractive BRUVS provide a useful platform for building habitat suitability models across large scales to assist conservation planning across multiple maritime jurisdictions, and provide a simple framework to test the effectiveness of MPAs.

3.1 Introduction

Sharks are among the most threatened vertebrates globally (Dulvy *et al.*, 2014) due to exploitation by fisheries and coastal habitat degradation, that have resulted in population declines of some species of at least 50% from their pre-industrial fishing levels (Worm *et al.*, 2013). This high extinction risk reflects a conservative life history that includes *k*-selected life history traits such as slow growth, low fecundity and late maturity. As such, fisheries management frameworks will likely have limited success in reversing population declines even under low mortality scenarios (García *et al.*, 2008). The ecological importance of sharks in maintaining ecosystem structure (Ferretti *et al.*, 2010) and their high economic value in terms of fisheries, aquaculture and eco-tourism (Vianna *et al.*, 2012; Mcclanahan *et al.*, 2015) means conservation of these animals is critical. However, due to the broad geographic distribution and highly mobile nature of sharks, defining an effective conservation strategy is challenging.

No-take marine protected areas (MPAs) that are closed to extractive activities, can support shark recovery by reducing fishing mortality, and can range in scale from coastal no-take zones to national shark sanctuaries (Robbins *et al.*, 2006; Dulvy, 2013). Alternative management strategies include the time-area closure of breeding grounds to shark fishing to allow mature females to breed (Carrier & Pratt, 1998). A corollary of such protection is the need to ensure that juvenile sharks then thrive to breed (Kinney & Simpfendorfer, 2009). Although all life stages should be considered for effective management of sharks (Kinney & Simpfendorfer, 2009) and some fisheries are based on size-selective targeting of juveniles (McAuley *et al.,*2007), the importance of juvenile survival is well recognised, which highlights the importance of identifying essential juvenile fish habitat (Froeschke *et al.*, 2013; Vasconcelos *et al.*, 2014). Juvenile survival is especially important for the persistence of coastal sharks with low reproductive output and significant parental investment in individual young (Smith *et al.*, 1998; Cortés, 2002).

Juvenile sharks typically segregate from adults in nursery areas, which are presumed to enhance survival by providing shelter from predation and abundant prey (Heupel *et al.*, 2007; Schlaff *et al.*, 2014). Fine-scale habitat use within these ecosystems is shaped by the selective balance between biological and environmental influences. For instance, predation risk imposed by the presence of sub-adult sharks can influence habitat use in juvenile lemon sharks *Negaprion brevirostris* (Guttridge *et al.*, 2012), while biological features such as mangroves and seagrass beds are thought to provide shelter and abundant prey resources (Munroe *et al.*, 2014; Yates *et al.*, 2015a). Additionally, aggregation behaviour can potentially dilute predation risk (Heupel & Simpfendorfer, 2005b), but competition for limited resources may result in habitat partitioning within and among species in communal nurseries (Papastamatiou *et al.*, 2006; Kinney *et al.*, 2011). Environmental factors such as salinity (Ward-Paige *et al.*, 2014), temperature (Froeschke *et al.*, 2010), turbidity (Yates *et al.*, 2015a), dissolved oxygen (Drymon *et al.*, 2014), and proximity to tidal inlets (Froeschke *et al.*, 2010) are also important determinants of habitat use, but may be moderated by species-specific physiological requirements (Schlaff *et al.*, 2014). As coastal environments are highly susceptible to a range of anthropogenic pressures (Knip *et al.* 2010), identification of the key ecological drivers of the distribution of juvenile sharks is crucial for effective conservation.

Because sharks can exhibit strong fidelity to particular habitats (Bond *et al.*, 2012) while maintaining wide ecological niches (Munroe *et al.*, 2013), assessing their habitat requirements for conservation planning is challenging (Yates *et al.*, 2012). Moreover, there is evidence of intraspecific variations in habitat use by juvenile sharks among nearby inshore systems (Grubbs & Musick, 2007; Conrath & Musick, 2010; Yates *et al.*, 2015b). Such evidence highlights the need to investigate large-scale patterns (100s-1000s km) to identify the important habitats at relevant scales for conservation and management.

Global targets set through the Convention of Biological Diversity to protect 10% of coastal and marine areas by 2020 (Secretariat of the CBD, 2010), present opportunities to implement adequate spatial protection for highly mobile species such as sharks. Increasing spatial protection warrants new approaches to data collection and analysis that can demonstrate the conservation value of MPAs at progressively larger scales (Pala, 2013). Predicting distribution patterns of juvenile sharks can help overcome the problem of incomplete information and is therefore a powerful approach for conservation planning at large scales where sampling is prohibitively expensive and logistically complex (Richardson & Poloczanska, 2008). Predicting the occurrence of juvenile sharks in un-surveyed locations could inform the design of monitoring surveys and conservation plans (Guisan *et al.*, 2013) given the importance of this life history stage.

Appropriate spatial data and conservation targets are critical to the effective management of threatened marine species (Pressey & Bottrill, 2009)because bias toward protecting representative habitats or a lack of explicit conservation targets can compromise their protection (Dryden *et al.*, 2008; Cleguer *et al.*, 2015). In Australia for example, 14 new MPAs were declared along the northwestern coast as part of a national strategy to establish a comprehensive, representative and adequate network of Commonwealth Marine Reserves (CMRs). However, these large MPAs may be biased towards areas that are remote or unpromising for extractive activities (Devillers *et al.*, 2015). Explicit targets have not been included in the design of the CMR network (Devillers *et al.*, 2015) and the ability of the network to protect specific taxa within these regions remains unclear. We use species distribution modelling to identify the most important drivers of the occurrence of juvenile sharks in northwest Australia to assess the representation of highly suitable habitat for juvenile sharks across MPAs with different levels of protection.

3.2 Methods

3.2.1 Shark data

We analysed shark counts collected from 2,262 stereo-BRUVS deployments between 2003 and 2013 (Supporting Information) and spread across 5key sites in tropical northwestern Australia between 12° to 24°S: Ningaloo Reef, Barrow Island, Dampier Archipelago, Rowley Shoals and Timor Sea (Figure 3.1). The region (490,515 km^2), consists of small coral atolls, and barrier and fringing reefs in shallow water (Lough, 2008), and is characterised by warm, low-salinity waters originating from the Indonesian Throughflow that connect the western Pacific to the Indian Ocean (Wijffels & Meyers, 2004). The stereo-BRUVS were of standard design and dimensions (i.e., paired cameras held within a metal frame), calibrated using standard procedures (Harvey *et al.*, 2002; Watson *et al.*, 2005) (Supporting Information, Section 2.6.1), and deployed across a variety of habitats including reef, inter-reef, shoals and lagoons. Deployments occurred within MPAs (i.e. no-take MPAs (n=403) and multiple-use MPAs (n=658)) as well as areas not included MPAs (i.e. 'no MPAs') (n=1201). No-take MPAs closed to extractive activities covered 2% of study region, whereas multiple-use MPAs, open to varying levels of extractive fishing covered 30% of the region. The remainder of the region (68%) had no-MPAs. We extracted the following information from the BRUVS: shark species, number of sharks and shark fork length (i.e., from tip of the snout to fork of the caudal fin), sampling date, location (longitude and latitude at 0.01° precision), and soak time (number of hours the BRUVS were deployed). We classified sharks as juveniles or adults based on published lengths at which 50% of individuals were mature (i.e., juvenile < L_{50} ≤ adult); Last & Stevens 2009; Harry et al. 2011). Because sex could not be reliably determined from the video imagery, for species with sex-specific L_{50}, we used an average of the lengths at male and female maturity. We included presence-absence records pooled at the taxonomic level of order for 21 species (hereafter all juveniles), and for juveniles of the three most abundant species: grey reef (≤135.0 cm), sandbar (≤131.4 cm) and whitetip reef (≤116.0 cm). Length frequency distributions were determined from presence records of all juveniles, grey reef, sandbar and whitetip reef sharks.

To minimise the potential for spatial autocorrelation between deployments while maintaining adequate numbers of shark presences, we generated a grid of cells with a resolution of 0.01° across the study area. We then pooled shark data obtained from the BRUVS for each grid cell, separately for juveniles (284 presence and 441 absence records) and adults (113 presence and 612 absence records). To account for differences in sampling effort across grid cells, we used the total soak time of all BRUVS within each grid cell (hereafter soak time) as an offset in our models (Supporting Information).

We accounted for potentially unreliable estimates of true absence (i.e., undetected presences that might have been included as absence in the data set (Martin et al. 2005) by randomly iterating through the absences detected on BRUVS in all grid cells 100 times. We selected pseudo-absences in equal number to presences, following Barbet-Massin et al. (2012), by using the *srswor* function (simple random sampling without replacement) from the sampling package in R (R Core Team 2015). , To assess how the choice of absences affected model results, we generated 100 presence-absence data sets (i.e., iterating 100 through the 441 recorded absences).

3.2.2 Ecological predictors

For each 0.01° grid cell there were 15 predictors of juvenile shark occurrence (Supporting Information) including biological (co-occurrence of an adult shark), environmental (oxygen concentration, salinity, turbidity (i.e., the coefficient of light attenuation at 490 nm), midwater temperature, sea-surface temperature, percent gravel and sand, depth, aspect, slope and chlorophyll-a concentration) (derived from Huang *et al.* 2010), and spatial variables, such as distance from the centre of each grid cell to shore, mangrove and reef (Supporting Information, Table S3.3). These spatial variables are important drivers of shark distribution (Espinoza *et al.* 2014; Yates *et al.*

2015). We used world equidistant cylindrical projections to calculate these distances with the *Near* tool in ArcMap version 10.0 (ESRI, 2012). In the context of our study, the co-occurrence of an adult shark provided a proxy for potential underlying biological processes such as predation risk and social facilitation (Gutteridge *et al.* 2011; Jacoby *et al.*, 2012; Mourier *et al.*, 2012). Multi-collinearity between pairs of predictors was assessed using Pearson correlation coefficients and only one predictor from each pair of highly correlated predictors (correlation coefficient > 0.6) was retained to minimize the possibility of model over-fitting (Dormann *et al.*, 2013).

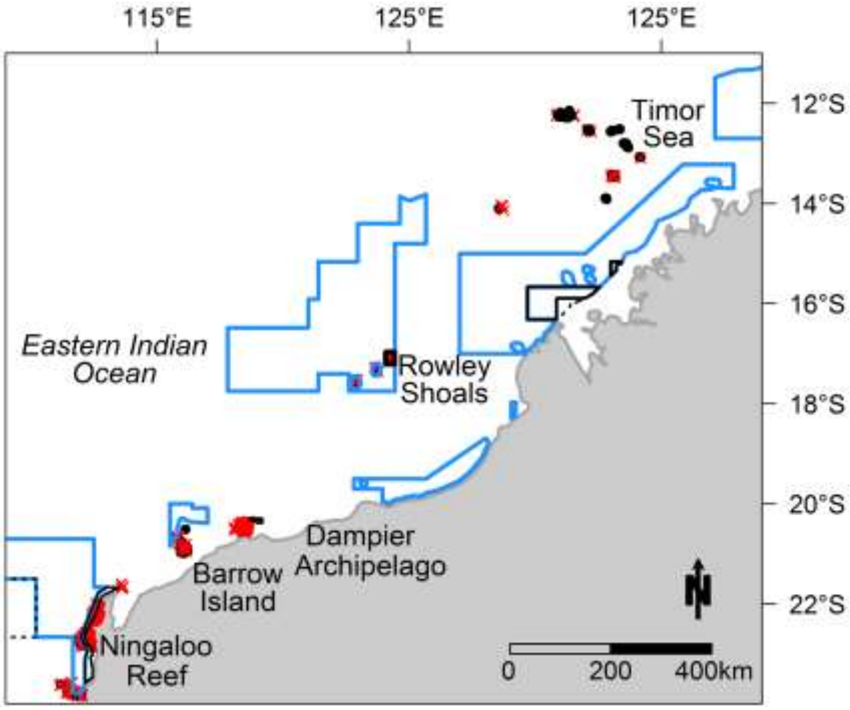

Figure 3.1 Location of 2262 baited remote underwater video stations (BRUVS) deployments along northwest (NW) Australia.

3.2.3 Model development

We developed generalised linear models (GLMs) with binomial error distributions and a logit link function to compare the ability of different combinations of predictors to predict the probability of shark occurrence based on habitat suitability. We repeated this procedure for 4 response variables: all juveniles, grey reef, sandbar and white tip sharks. Prior to model fitting, we standardised all continuous predictors by subtracting the mean and dividing by two standard deviations to allow direct interpretation of model coefficients (Gelman, 2008). To account for model-selection uncertainty, we applied a model averaging approach to a set of 10 candidate models (Table 3.1), including a full model and subsets of ecologically relevant (i.e., spatial, environmental, topographic and sediment) predictors to avoid over-fitting the data (Burnham *et al.* 2011). The strength of evidence of each model was assessed using the relative weight of the sample-corrected Akaike's Information Criterion ($w\mathrm{AIC_c}$). We ran the candidate models for each of the 100 presence -absence iterations to assess how much the location of absences influences model results. We report the median $w\mathrm{AIC_C}$ results across the top-ranked model for all data sets. We averaged each model's contribution based on these $w\mathrm{AIC_C}$ results (Burnham *et al.* 2011) to predict shark occurrence relative to the 4 response variables. Then we inferred the effect sizes of predictors based on the standardised model-averaged coefficients. We quantified the goodness-of-fit of each model using the percentage of deviance explained (DE), and assessed their predictive accuracy using the Cohen's Kappa statistic (κ). Models were considered to be excellent, good or poor if $\kappa > 0.75$, $0.4 < \kappa < 0.75$, or $\kappa < 0.4$, respectively (Woodby *et al.*, 2009). We also used a 5-fold cross validation with 100 iterations to calculate the mean prediction error ($\mathrm{CV_E}$) of the averaged models. We tested for the presence of spatial autocorrelation in model residuals as a function of distance between grid cells using Moran's *I* statistics (Diggle & Ribeiro, 2007).

Using the predictor variables in our models, we predicted shark habitat suitability across northwest Australia. For this, we used the packages *latticeExtra* and *sp* in R (R Core Team, 2015). Predicted values of habitat suitability for each grid cell were then binned in 4 categories: high (>0.8), moderate (0.5 – 0.8), low (0.2 – 0.5) and very low habitat suitability (<0.2). We overlaid our maps of habitat suitability with a composite layer of existing and proposed MPAs in northwest Australia to calculate the frequency of these categories within each protection type (Supporting Information, Table S3.4). We then used chi-square goodness of fit and multiple comparison tests (with Bonferroni correction) to test the null hypothesis of equal representation of suitability categories within each protection type (i.e., 2% in no-take MPA, 30% in multiple use MPA and 68% in no MPA).

3.3 Results

The BRUVS' records included 986 sharks of 21 species; 82.3% of records were carcharhiniform sharks. Of the 986, 807 individuals were juveniles (37% grey reef, 25%

whitetip reef and 7% sandbar sharks). Mean fork lengths of these 3 species were 78.7 (SD 22.6), 94.1 (SD 15.6), and 84.1 (SD 14.2) cm, respectively (Figure 3.2b-d). Juvenile sharks occurred in all 5 sites sampled. Timor and Barrow Island had the highest occurrence rates (i.e., occurrence standardised by number of grid cells sampled), followed by Rowley Shoals and Ningaloo Reef (Figure 3.2, Supporting Information, Table S3.2).

We obtained the highest statistical support for the model that included salinity, temperature and turbidity (model 7 in Table 3.1) for grey reef and whitetip reef sharks ($w\mathrm{AIC_C}$ = 0.95 and 0.88, respectively). The highest ranked models for sandbar sharks and all juveniles were models 3 (aspect, depth, distance to shore and slope) and 2 (adult co-occurrence, distance to reef, oxygen, salinity, temperature and turbidity) ($w\mathrm{AIC_C}$ = 0.75 and 0.74, respectively) (Table 3.1). We found only minor spatial structuring (Moran's *I* <0.3) in the residuals of the models (Supporting Information; Figure S3.6). The iterations of presence-absence data sets led to similar model rankings for all juveniles, grey reef and whitetip reef sharks, which reflects minimal influence on relative model weights, but results varied for sandbar sharks.

Model-averaged coefficients (Figure 3.3) indicated that the occurrence of all juveniles was negatively correlated with salinity and mid-water temperature, and weakly but positively correlated with gravel cover, distance to reef and oxygen concentration (Figure 3.3a). For grey reef sharks, occurrence was higher in waters with relatively low salinity and turbidity (Figure 3.3b). No strong correlation occurred for sandbar sharks; there was only a slight signal for increased occurrences at greater depths and distances from shore (Figure 3.3c). Whitetip reef shark presence increased in waters with relatively high turbidity, low salinity and low temperatures (Figure 3.3d). Deviance explained (DE) was high for models at the species level (≥48%), whereas for all juveniles DE = 10% (Table 3.1). Similarly, model accuracy was higher and mean prediction error was lower for models at the species level ($\kappa \geq 0.69$; $\mathrm{CV_E} \leq 0.20$) than models for all juveniles ($\kappa = 0.36$; $\mathrm{CV_E} = 0.40$) (Table 3.1).

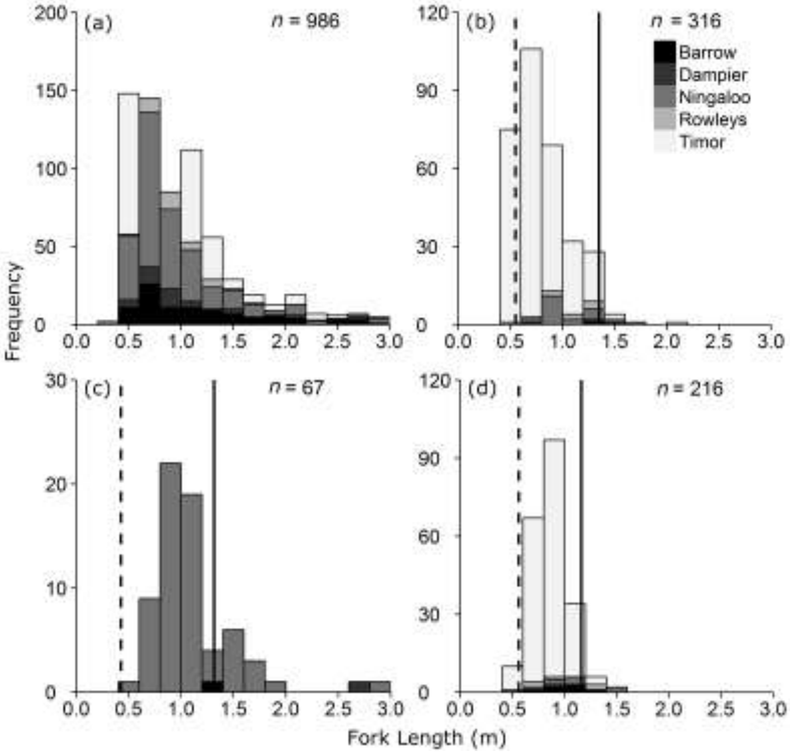

Figure 3.2 Length (fork length, tip of the snout to the fork of the caudal fin) and frequency distributions of (a) all juveniles (pooled for 21 species), (b) grey reef, (c) sandbar, and (d) whitetip reef sharks (n, number of length measurements recorded for each species; solid lines, length at which 50% of individuals are mature (L_{50}); dashed lines, estimated mean length of neonate sharks [Last & Stevens 2009; Harry 2011]; bar shading, location of sampled sharks). The average of lengths at male and female maturity is given for sandbar sharks because known L_{50} differed between sexes.

Table 3.1 Summary of generalized linear models relating the probability of juvenile shark occurrence to ecological predictors. Input predictors include co-occurrence of an adult shark (adult); distance from the centre of grid cell to reef (reef); oxygen concentration (oxygen); physical variables (phy), including salinity, the coefficient of light attenuation at 490 nm (turbidity) and midwater temperature (mid. temp); sediment variables (sed), including percent gravel and sand, depth, distance from the centre of grid cell to shore (shore); topography (topo), including aspect and slope; sea surface temperature (SST), concentration of chlorophyll a (chla); distance from the centre of grid cell to mangrove (mangrove); intercept-only model (null). Shown for each model are weights of the corrected Akaike's information criterion for small sample sizes (wAICc) (only > 0.001 shown) and percent deviance explained (%DE).

[a] Highest ranked model according to wAICC derived from 100 presence-absence iterations.

[b] Mean and standard deviation of Cohen's kappa and CVE (cross validation error) derived from 100 iterations.

Number	Model	All juveniles		Grey reef		Sandbar		Whitetip reef	
		*w*AIC$_C$	%DE	*w*AIC$_C$	%DE	*w*AIC$_C$	%DE	*w*AIC$_C$	%DE
Model evaluation[a]									
1	*adult + reef + oxygen + phy + sed*	0.11	9.44	0.01	48.17	0.02	85.44	0.05	53.29
2	***adult + reef + oxygen + phy***	**0.74**	**9.72**	0.04	48.30	0.15	84.52	0.08	51.95
3	***depth + shore + topo***	0.06	8.51	–	34.53	**0.75**	**79.05**	–	41.12
4	*oxygen + SST*	–	3.89	–	27.33	–	23.35	–	17.93
5	*chla + SST*	–	3.51	–	35.66	–	44.36	0.001	42.58
6	*mangrove + reef*	–	5.39	–	27.74	–	21.23	–	37.65
7	***phy***	0.09	8.50	**0.95**	**47.73**	0.07	72.84	**0.88**	**50.28**
8	*sed*	–	0.96	–	7.87	–	32.89	–	16.50
9	*adult*	–	0.04	–	0.59	–	0.33	–	1.28
10	*null*	–	0.00	–	0.00	–	0.00	–	0.00
Model performance[b]									
	kappa (SD)	0.36 (0.08)		0.69 (0.12)		0.86 (0.14)		0.77 (0.12)	
	CV_E (SD)	0.40 (0.02)		0.20 (0.04)		0.11 (0.05)		0.18 (0.04)	

A majority of the highly suitable habitat predicted for all juveniles (67%) occurred mostly from inshore to offshore waters north of 20°S (Figure 3.4).For whitetip reef sharks, highly suitable habitats occurred across 37% of the region in offshore waters north of 19°S and from inshore to offshore waters between 11–15°S (Figure 3.4). We found a relatively small area of highly suitable habitat for grey reef sharks (15%) from inshore to offshore waters north of 15°S, and for sandbar sharks (3%) in narrow sections of offshore waters from 12.5°S to 17.5°S and south of 19°S (Figure 3.4). Highly suitable habitats were significantly underrepresented in no-take MPAs closed to fishing (i.e., less than the 2% expected; $p < 0.001$) for each of the 4 response variables modelled: 0.2% for all juveniles, 0.5% for grey reef, 0.4% for whitetip reef and 0.1% for sandbar sharks (Figure 3.5). More than expected high-quality habitats were represented in MPAs open to fishing (42% for grey reef; 36% for whitetip reef sharks) and in non-MPA areas (71% for all juveniles; 91% for sandbar sharks) (Figure 3.5).

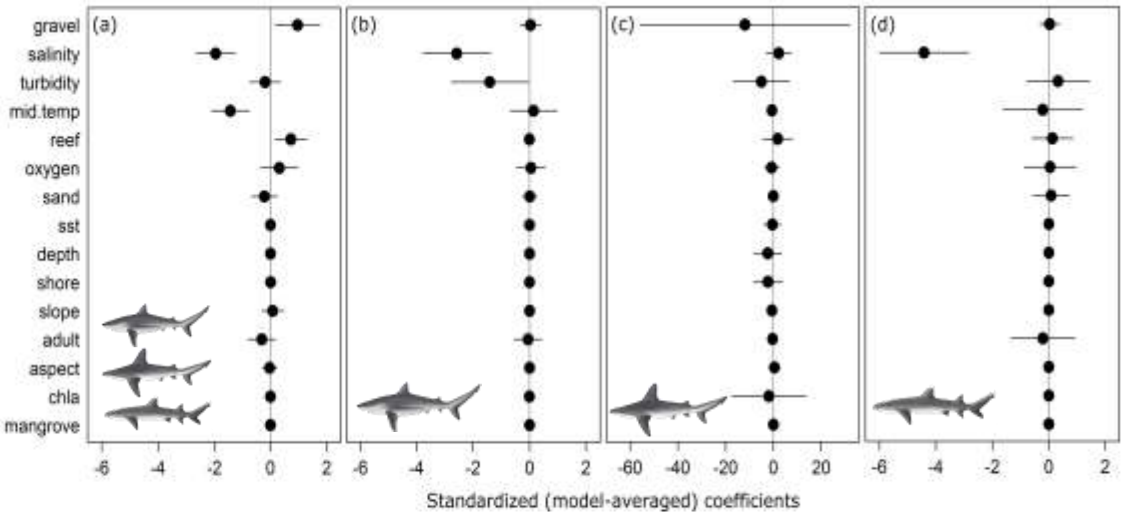

Figure 3.3 Model-averaged effect sizes derived from generalized linear models relating the probability of occurrence of (a) all juveniles, (b) grey reef, (c) sandbar, and (d) whitetip reef sharks to ecological predictors (y-axis) in NW Australia. Results are shown with shrinkage and only for cases where values > 0.001. Ecological predictors are described in Table 1.

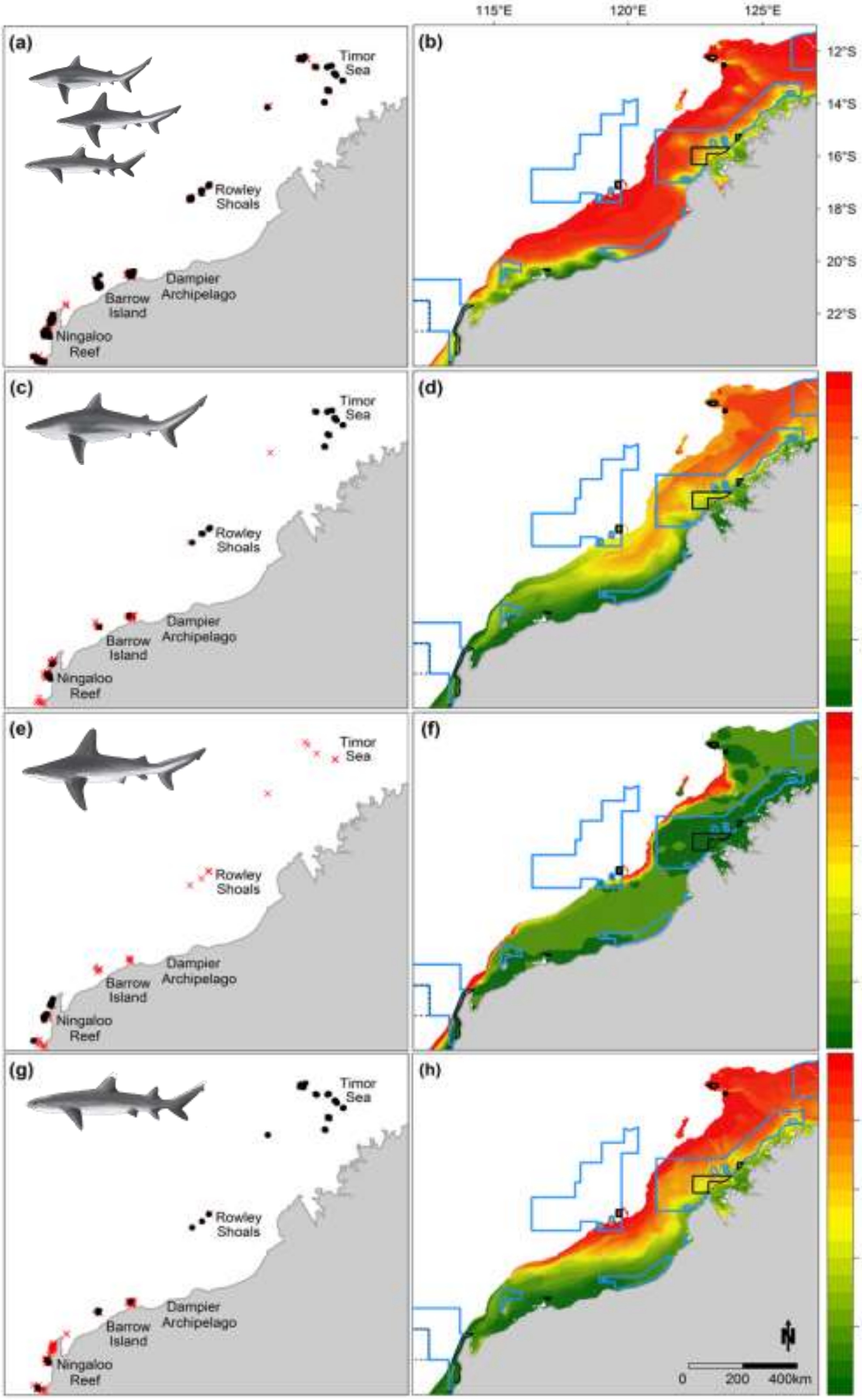

Figure 3.4 Location of presences (black dots) and pseudo absences (red crosses) of sharks used as inputs in generalized linear models (a, c, e, g) and predicted habitat suitability (high >0.8; moderate, 0.5–0.8; low, 0.2–0.5; very low, <0.2) (b, d, f, h) for all juveniles (a, b), grey reef (c, d), sandbar (e, f), and whitetip reef (g, h) sharks in northwest Australia (black polygons, no-take areas closed to fishing, where research, boating, and diving are allowed; blue polygons, multiple use areas open to multiple activities, including fishing). Where environmental inputs fell outside the environmental space used for model fitting, predictions are shaded in grey on the habitat suitability maps.

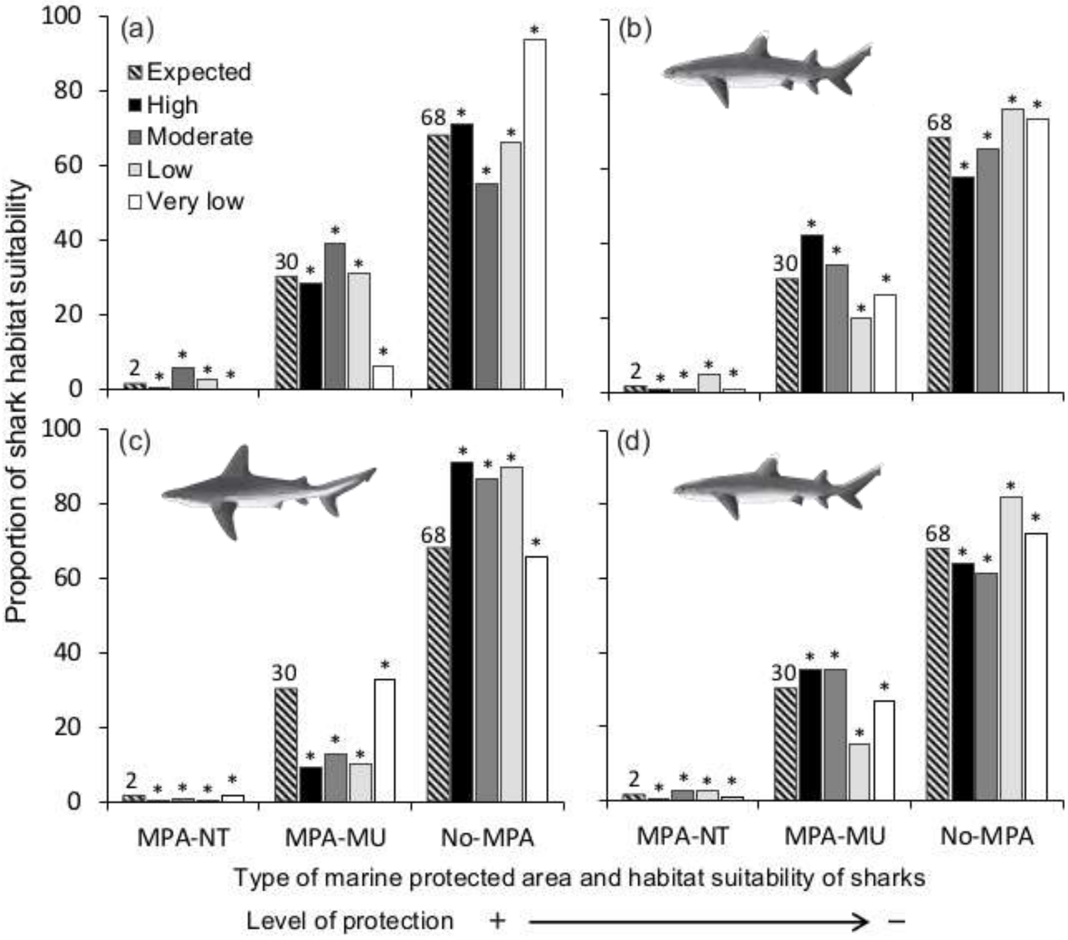

Figure 3.5 Percent of each category of predicted habitat suitability for (a) all juveniles, (b) grey reef, (c) sandbar, and (d) whitetip reef sharks in each type of marine protected area (MPA) in northwest Australia (habitat-suitability categories: high > 0.8; moderate, 0.5 – 0.8; low, 0.2 – 0.5; very low, < 0.2). Each grid cell and associated value of habitat suitability was assigned to 1 of 3 MPA types: MPA-NT, no-take MPA closed to fishing with research, boating, and diving allowed; MPA-MU, multiple-use MPA open to multiple activities including fishing; No-MPA, no MPA in place thus open to fishing, mining, oil and gas exploration, etc.; grey-scale bars, 1 of 3 MPA types; numbers above bars, percent of grid cells of that quality in each MPA type; *, percent of grid cells of that suitability category was significantly different ($p < 0.001$) from the expected percent of grid cells of that suitability category in each MPA type).

3.4 Discussion

Effective conservation requires the identification and protection of their essential habitats and the processes that support them (Ward-Paige *et al.*, 2012). Based on data derived from broad-scale BRUVS sampling, our analyses provided a comprehensive assessment of juvenile shark-habitat linkages, and allowed for the prediction of juvenile shark distributions. Juvenile grey reef, whitetip reef and sandbar sharks are the most abundant species in northwest Australian waters, and although they overlap in distribution, they have different species-specific occurrence patterns characterized by different environmental variables.

Our study corroborates previous findings of the importance of salinity, temperature and turbidity as drivers of juvenile shark distribution (Froeschke *et al.*, 2010; Heupel & Simpfendorfer, 2011; Yates *et al.*, 2015a), established previously for only few species and regions. Selection for relatively low salinities by juvenile sharks may contribute to niche separation from adults, as documented for bull (*Carcharhinus leucas*) (Heupel & Simpfendorfer, 2008) and bonnethead sharks (*Sphyrna tiburo* (Ward-Paige *et al.*, 2014). However, it is unclear whether this selection occurs through tolerances of lower salinities or selection of sub-optimal habitat by juvenile sharks. In addition to temperature (White *et al.*, 2015), our study revealed a preference for higher turbidity by whitetip reef sharks, which may relate to their nocturnal feeding strategy and adaptation to low light conditions (Whitney *et al.*, 2008) or be a mechanism for reducing predation risk. For grey reef sharks, in addition to temperature (Speed *et al.*, 2012b; Vianna *et al.*, 2013), we identified low turbidity as a correlate of higher occurrence. These conditions may improve the ability of sharks to detect prey or predators; however, the nature of this relationship remains poorly understood. We found offshore habitat was important for juvenile sandbar sharks, and in Western Australia the use of such habitat has been proposed as a strategy for maximizing foraging opportunities and reducing intra- and inter-specific predation and competition (McAuley *et al.*, 2006).

Although higher occurrence was observed for grey reef and whitetip reef sharks in northern waters and for sandbar sharks in deeper, offshore waters, it is not clear that these areas constitute 'nurseries' as defined by Heupel et al. (2007). There is limited information on nursery use by grey reef and whitetip reef sharks in the literature, although contrasting movements reported across different habitats (Field et al. 2009, Vianna et al., 2013, Heupel & Simpfendorfer, 2014, Espinoza et al. 2014) suggest the need to investigate site-specific patterns. Juvenile sandbar sharks are known to use discrete nurseries elsewhere (Merson & Pratt 2001), however, this species appears to use diffuse offshore nurseries in Western Australia (McAuley et al. 2007). As sampling for this study took place in in different years for different areas, it was not possible to assess these areas according to the nursery criteria proposed by Heupel *et al*. (2007) of repeated use across month and years, without dedicated future investigation.

Species distribution models integrate biological and environmental influences on species distributions and thus assist in the identification of essential habitats. Our model predicted low suitability off the northwest coast for juvenile sandbar sharks. This finding is consistent with the segregation hypothesis between juveniles and adults of this species because sub-adult and adult sharks are known to be prevalent in this region (McAuley *et al.*, 2006). Our models showed that for all juveniles, grey reef and whitetip reef sharks, the low-salinity waters from the Indonesian Throughflow (Wijffels & Meyers, 2004) and prevalence of reefs along the northern section (13–17°S) of the coast may represent the best integration of environmental conditions contributing to their higher occurrence in these areas. Higher occurrence of these sharks may also be related to mesopredator release of smaller-bodied sharks (Ruppert *et al.*, 2013), due to declines in higher-order predators such as silvertip (*Carcharhinus albimarginatus*) and tiger sharks (*Galeocerdo cuvier*) brought on by illegal fishing in northern Australia (Field *et al.*, 2009a). We found limited evidence for the influence of adult shark co-occurrence; salinity, temperature and turbidity were the most important drivers of juvenile shark occurrence. These results suggest that climate-related changes in ocean temperature may affect the occurrence of juvenile sharks, as has been predicted for many marine species (Cheung *et al.*, 2009, 2010; Jones & Cheung, 2015).

Conservation planning is often based on the distribution of groups of species (Barker *et al.*, 2014). Our order-level predictions for all juveniles provided a basis for maximizing the conservation potential of MPAs by allowing the inclusion of rarer sharks in our analysis (Barker *et al.*, 2014). However, the relatively poor performance of the order-level model relative to the individual species models highlights that generalization may be inappropriate. Conversely, our species-level models allowed for better definition of distributions based on more detailed relationships between species and environmental predictors (Barker et al. 2014). Our results indicate that individual species require distinct habitats to meet specific physiological or resource requirements and validate concerns over the relevance and utility of broad conservation targets as opposed to species-focused conservation (Dulvy, 2013). Although further research is needed to validate and refine model predictions, the accuracy and deviance explained of our species-specific models, suggest that they provide efficient tools for estimating key areas for conservation planning.

Our predictions revealed a clear spatial mismatch between no-take MPAs, which provide the highest levels of protection from anthropogenic activities, and areas of highly suitable habitat for juvenile sharks off northwest Australia. Highly suitable habitat for juvenile sharks occurred in regions that are most affected by anthropogenic activities including illegal fishing (Field *et al.*, 2009a), coastal urbanisation, and oil and gas development (Devillers *et al.*, 2015). Our study and examples of the endangered vaquita (*Phocoena sinus*) and loggerhead sea turtle (*Caretta*; Rojas-Bracho et al. 2006; Schofield et al. 2013) emphasize the value of incorporating the needs of threatened species rather than favouring areas of least value for anthropogenic use when delineating MPAs.

Global research has demonstrated the significant conservation benefits of MPAs for sharks; MPAs that are no-take, well-enforced, old (>10 years), large (>100 km^2) and isolated can support 1,990 % increases in shark biomass relative to fished areas (Edgar *et al.*, 2014). Sharks represent a useful surrogate for multispecies conservation because they often occupy large habitats and are of high economic value (Vianna *et al.*, 2012; Dent & Clarke 2015). More importantly, marine ecosystems with high shark biomass often support high levels of biodiversity and maintain ecosystem function (Ruppert *et al.*, 2013; Edgar *et al.*, 2014) because some shark species are key regulators of ecosystem structure and resilience.

Here, we provide a useful approach for using spatially-constrained data on juvenile sharks to identify habitats of high conservation value on a large regional scale. Although our predictions are not meant to depict absolute distributions, they are the first to provide information on the probability of occurrence of juvenile sharks in the largely data-deficient region of northwest Australia and are a useful foundation for future hypothesis-driven studies. The coarse temporal resolution of the input data and reliance on temporally averaged (i.e., over the same time frame as BRUVS sampling was undertaken) data of ocean properties mean that predictions should only be taken as an index of relative probability of occurrence. Notwithstanding the caveats associated with limitations of BRUVS sampling and modelling assumptions (detailed in Supporting Information), we recommend that no-take MPAs be refined to achieve better representation of areas of high value to juvenile sharks. We anticipate that our approach and resulting predictions will be useful for contemporary management and conservation initiatives because they provide a foundation for integrated spatial planning. The growing availability of high-resolution environmental data from remote sensing platforms together with the prevalence of BRUVS as a standard monitoring tool provide opportunities to develop predictive models and apply them to a range of other taxa and management scenarios or to specific natural or human-mediated disturbances.

3.5 Acknowledgements

We thank all collectors of the BRUVS data (AIMS, UWA); AIMS for access to shark data generated from a study funded by PTTEP Australasia Ltd, and R. Pitcher for access to environmental data collated by Geoscience Australia. B.Z.L.O was supported by a UWA scholarship and Holsworth Wildlife Research Endowment (RA/1/411/59). A.M.M.S was supported by a Collaborative Post-doctoral Fellowship (AIMS, CSIRO and UWA) from the Indian Ocean Marine Research Centre. Finally, we thank two anonymous reviewers for assisting with improving our manuscript.

3.6 Supporting Information

Additional information on BRUVS surveys, caveats on data and models, and a table of sampling effort and shark sightings in the five study sites (Table S3.2), a table of predictors used as model inputs (Table S3.3), Moran's I plots of spatial auto-correlation in the model residuals (Figure S3.6), marine protected areas in northwest Australia (Table S3.4), spatial patterns of key predictors across northwest Australia (Figure S3.7) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of material) should be directed to the corresponding author.

3.6.1 BRUVS surveys

A typical BRUVS consists of a steel frame holding two SONY handycams (models used included HC 15E, CX7, CX12) in waterproof housings. The cameras are mounted 0.7 m apart on a base bar, and converge inwards to provide an overlapping field of view from approximately 0.5 m in front of the cameras. Calibration protocols included the manual synchronization of camera pairs using a clapperboard directly before deployment, and were based on independent calibrations undertaken in an enclosed pool environment prior to the survey using software CAL (SeaGIS Pty Ltd, 2008), as detailed in Harvey & Shortis (1998). Standard procedures for deployment include using 1 kg of crushed sardines (*Sardinop* or *Sardinella* spp.) in a canister suspended 1.2 m in front of the cameras. To minimise the overlap of bait plumes and likelihood of fish moving between deployments over the sampling period (Watson *et al.*, 2010), BRUVS were separated by a distance of 250–400 m. Video analysis commenced at the point when each BRUVS stabilised at its sampling depth, and the total number of hours of footage recorded from this point was defined as the soak time. Trained observers examined each tape using the purpose-built PhotoMeasure programme (SeaGIS Pty Ltd, 2008) to identify each fish species and measure their length. To standardise the sampling unit and ensure accurate and precise measurements, length measurements were restricted to fish observed within 7 m of the cameras (Harvey *et al.*, 2002).

3.6.2 Caveats on data and statistical analyses

Notwithstanding the utility of BRUVS for broad-scale sampling (White *et al.*, 2013a; Espinoza *et al.*, 2014a), there are some limitations such as difficulties in: (a) the visual identification of externally similar species such as carcharhinid sharks (Santana-Garcon *et al.*, 2014), b) sampling in turbid waters (Yates *et al.*, 2015a) and (c) the classification of life-stage for sexually dimorphic species with distinct lengths at maturity due to inability to distinguish sex. Advances in high definition video and the application of low-cost cameras (Letessier *et al.*, 2015) at various angles have the potential to improve the rates of identification of species, sex and individuals. While BRUVS sampling might not yield as precise data as those from fishery-independent longline surveys (Brooks *et al.*, 2011), they are non-extractive, essential sources of information given the logistical, economic and ecological challenges of sampling mobile and rare species.

Our BRUVS datasets were collected opportunistically and therefore their use for a synthesis had inherent assumptions. Sampling effort within the NW coast was clustered around sites prioritised by independent sampling programs and as such it is unlikely that all potential habitats used by juvenile sharks were sampled. However, deployments were made across sites including a variety of habitats such as reef, inter-reef, shoals and lagoons. It was logistically impractical to investigate population-level occurrence patterns using a structured survey design over such a large area and time frame. The opportunistic nature of the sampling design thus reflects a compromise between statistical rigour and biological meaning. It was also necessary to combine data from different years of sampling to maximise spatial coverage and hence to be able to detect large-scale patterns. While the combination of variable sampling years could have introduced bias, it may also to some extent reduce the potential confounding effects of fishing and protection regimes (implemented at different times) on realised shark occurrence patterns. The coarse temporal resolution of the input data and reliance on temporally-averaged (i.e., over the same time frame as BRUVS sampling was undertaken) data of ocean properties mean that predictions should be taken only as an index of relative probability of occurrence. Additionally, models such as those used in this study are correlational and do not elucidate the mechanisms for species-habitat associations. As more data become available, application of similar models would likely improve and assist refining the distinction between locations where sharks are present or absent. Nonetheless, we have provided new insight into the habitat requirements of juvenile sharks and an essential foundation for future hypothesis-driven studies.

Table S3.2 Summary of sampling effort and shark sightings collected in the 5 study sites. Data were pooled across years. Soak is the number of hours BRUVS were deployed (mean ± SD) and letters (a, b and c) indicate soak times that were significantly different from each other (based on a Kruskal-Wallis rank sum test, *df* = 4, *p* <0.05). Under the occurrence categories, occurrence is the total number of grid cells with positive shark sightings and occurrence rate is occurrence standardised by the total number of grid cells sampled. All juveniles included the occurrence of all 21 species of sharks sampled, including grey reef, sandbar and whitetip reef sharks.

Variable	Barrow	Dampier	Ningaloo	Rowley	Timor
Sampling effort					
Year	2008, 2010	2008	2009	2003, 2004	2003,2004, 2011, 2013
Soak (hours)	8.5 ± 4.6^{a}	2.0 ± 2.0^{bc}	1.7 ± 1.2^{b}	1.8 ± 0.9^{b}	3.1 ± 2.7^{c}
No. of grid cells sampled	52	149	387	27	110
Juvenile shark occurrence					
All juveniles	33	20	130	16	85
Grey reef shark	1	1	14	6	64
Sandbar shark	0	0	37	0	0
Whitetip reef shark	4	1	7	3	65
Juvenile shark occurrence rate					
All juveniles	0.635	0.134	0.336	0.593	0.773
Grey reef shark	0.019	0.134	0.036	0.222	0.582
Sandbar shark	0	0	0.096	0	0
Whitetip reef shark	0.077	0.007	0.018	0.111	0.591

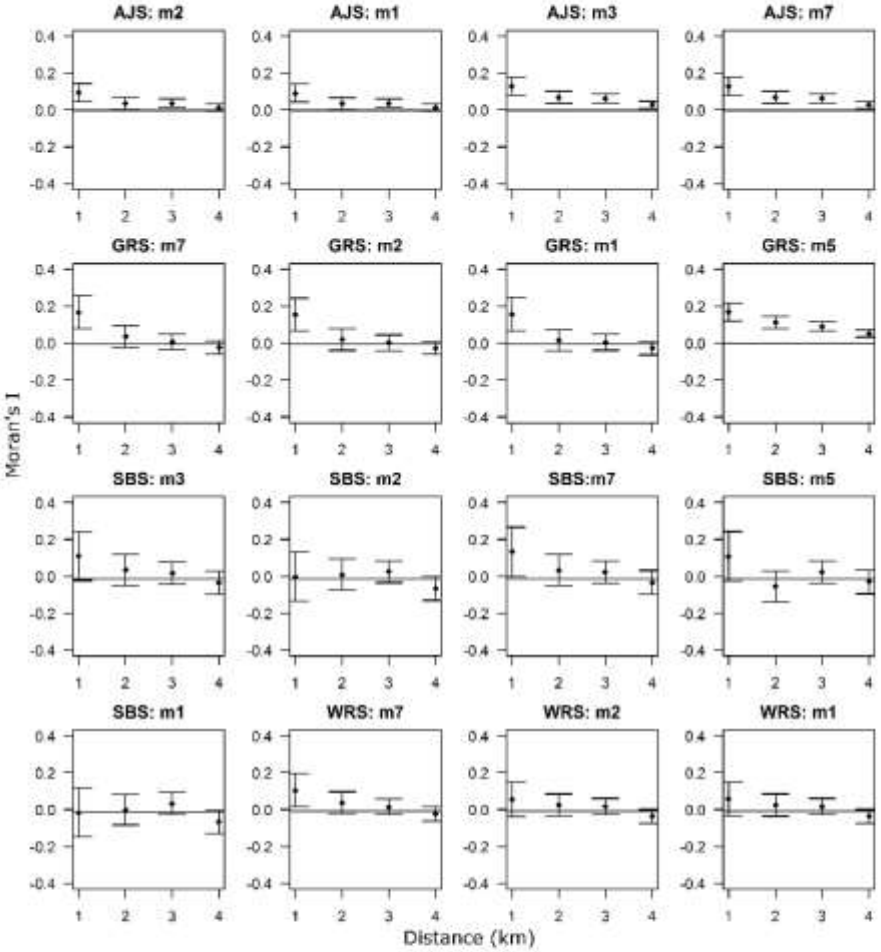

Figure S3.6 Moran's *I* plots showing minor spatial auto-correlation (<0.3) in the residuals of the models where *w*AIC$_C$ >0.001 for all juveniles (AJS), grey reef (GRS), sandbar (SBS) and whitetip reef (WRS) sharks. Plots correspond to the model numbers shown in Table 1 (i.e. m1 represents model 1).

Table S3.3 Summary of ecological predictors used as model inputs with a resolution of 0.01° compiled from: 1) BRUVS datasets supplied by the Australian Institute of Marine Science (AIMS) and The University of Western Australia (UWA); 2) Australian Bathymetry and Topography Grid, June 2009, Geoscience Australia (Whiteway, 2009), available at: www.ga.gov.au/metadata-gateway/metadata/record/gcat_67703; 3) Ocean colour standard annual data products obtained between 2003 to 2009 from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) and Moderate Resolution Imaging Spectroradiometer satellite (MODIS) from the National Aeronautics and Space Administration (NASA), available at: oceancolor.gsfc.nasa.gov/; 4) Marine Sediment Database (MARS; Matthews et al, 2007; Passlow et al, 2005), available at: www.ga.gov.au/oracle/mars; 5) United Nations Environment Programme – World Conservation Monitoring (UNEP – WCMP) Global Distribution of Mangroves and Global Distribution of Coral Reefs, available at data.unep-wcmc.org/datasets, 6) Commonwealth and Scientific Industrial Research Organisation Atlas of Regional Seas (CSIRO – CARS; Ridgway et al, 2002; Dunn et al, 2002), available at: www.marine.csiro.au/~dunn/cars2006/; 7) Outline map of Australia, Geoscience Australia, available at: www.ga.gov.au/metadata-gateway/metadata/record/gcat_61754; 8) Bathymetry derived topographic slope grid, Geoscience Australia (Huang et al., 2010), available at www.ga.gov.au/metadata-gateway/metadata/record/gcat_76992.

Predictor	Description	Units	Source	Mean	Range
Adult	Presence/absence of a shark classified as mature	–	1	–	0:1
Aspect	Aspect of slope derived from bathymetry	degrees	2	217.9	-1 – 357.4
Chl a	Mean chlorophyll	mg m^{-3}	3	0.6	0.13 – 4.29
Depth	Depth from bathymetry DEM	metres	2	-72.5	-350 – 0
Gravel	Percentage of gravel grainsize fraction (Ø >2 mm) in sediment	%	4	7.4	0.06 – 82.5
Mangrove	Distance to mangrove edge	km	5	61.3	0.74 – 248.2
Temperature	Mean temperature (mid-water)	°C	6	24.0	11.0 – 28.5
Oxygen	Mean oxygen concentration	ml L^{-1}	6	4.5	2.47 – 5.12
Reef	Distance to reef edge	km	5	5.9	0 – 30.1
Salinity	Mean salinity (mid-water)	ppt	6	35.1	34.4 – 35.7
Sand	Percentage of sand grainsize fraction (63 µm < Ø < 2 µm) in sediment	%	4	65.6	16.5 – 94.8
Shore	Distance to shore	km	7	29.8	0.3 – 219.9
Slope	Slope derived from bathymetry	degrees	8	1.4	0 – 20.3
Soak	Number of hours BRUVS was deployed	hours	1	2.5	0.47 – 24
SST	Mean sea surface temperature	°C	3	25.9	23.6 – 28.7
Turbidity	k490; Mean diffuse attenuation coefficient at wavelength 490nm	m^{-1}	6	0.07	0.03 – 0.24

Table S3.4 Marine protected areas in Australia and their relevance to juvenile shark protection. Reserves are listed in decreasing order of protection to juvenile sharks. Relevance is the relevance of management to the protection of juvenile sharks: (1) MPA-NT – no-take MPA closed to fishing; research, boating and diving are allowed, (2) MPA-MU – multiple use MPA open to multiple activities, including fishing; IUCN category is the management classification developed by the International Union for the Conservation of Nature (IUCN); Type of MPA is the management classification used by the Australian Government; Authority is the governing body responsible for MPA management: CMR - commonwealth marine reserve, MP – state-managed marine park, MMA – state-managed marine management area.

Relevance	IUCN category	Type of MPA	Name of MPA	Date of creation	Authority	Regulation
MPA-NT	IA	Sanctuary	Ashmore Reef	1983	CMR	Strictly protected areas closed to fishing, where human visitation, use and impacts are strictly controlled.
			Barrow Island	2004	MP	
			Cartier Island	2000	CMR	
			Mermaid Reef	1991	CMR	
			Montebello Islands	2004	MP	
			Muiron Islands	2004	MMA	
			Ningaloo	1987	MP	
			Rowley Shoals	1990	MP	
	II	Marine National Park	Dampier	2012	CMR	Managed for nature conservation, where only non-fishing related tourism and recreation is allowed.
			Kimberley	2012	CMR	
			Ningaloo	1987	MP	
MPA - MU		Recreational Use	Ashmore Reef	1983	CMR	Managed for nature conservation, where recreational fishing and fishing-related tourism is allowed.
			Montebello Islands	2004	MP	
			Ningaloo	1987	MP	
				2012	CMR	
			Rowley Shoals	1990	MP	
	IV	Habitat Protection	Barrow Island	2004	MMA	Managed to maintain, conserve and restore species and habitats, where commercial and recreational fishing using pelagic gear is allowed.
			Dampier	2012	CMR	
			Gascoyne	2012	CMR	
			Kimberley	2012	CMR	
			Montebello Islands	2004	MP	
			Ningaloo	1987	MP	
			Rowley Shoals	1990	MP	
	VI	Multiple Use	Argo-Rowley Terrace	2012	CMR	Managed for sustainable use with minimal impact on biological diversity, where commercial and recreational fishing using pelagic gear or traps is allowed.
			Barrow Island	2004	MMA	
			Eighty Mile Beach	2012	CMR	
				2013	MP	
			Gascoyne	2012	CMR	
			Joseph Bonaparte Gulf	2012	CMR	
			Kimberley	2012	CMR	
			Lalang-garram/ Camden Sound	2012	MP	
			Montebello	2012	CMR	
			Montebello Islands	2004	MP	
			Muiron Islands	2004	MMA	
			Ningaloo	1987	MP	
			Oceanic Shoals	2012	CMR	
			Roebuck	2012	CMR	
			Rowley Shoals	1990	MP	

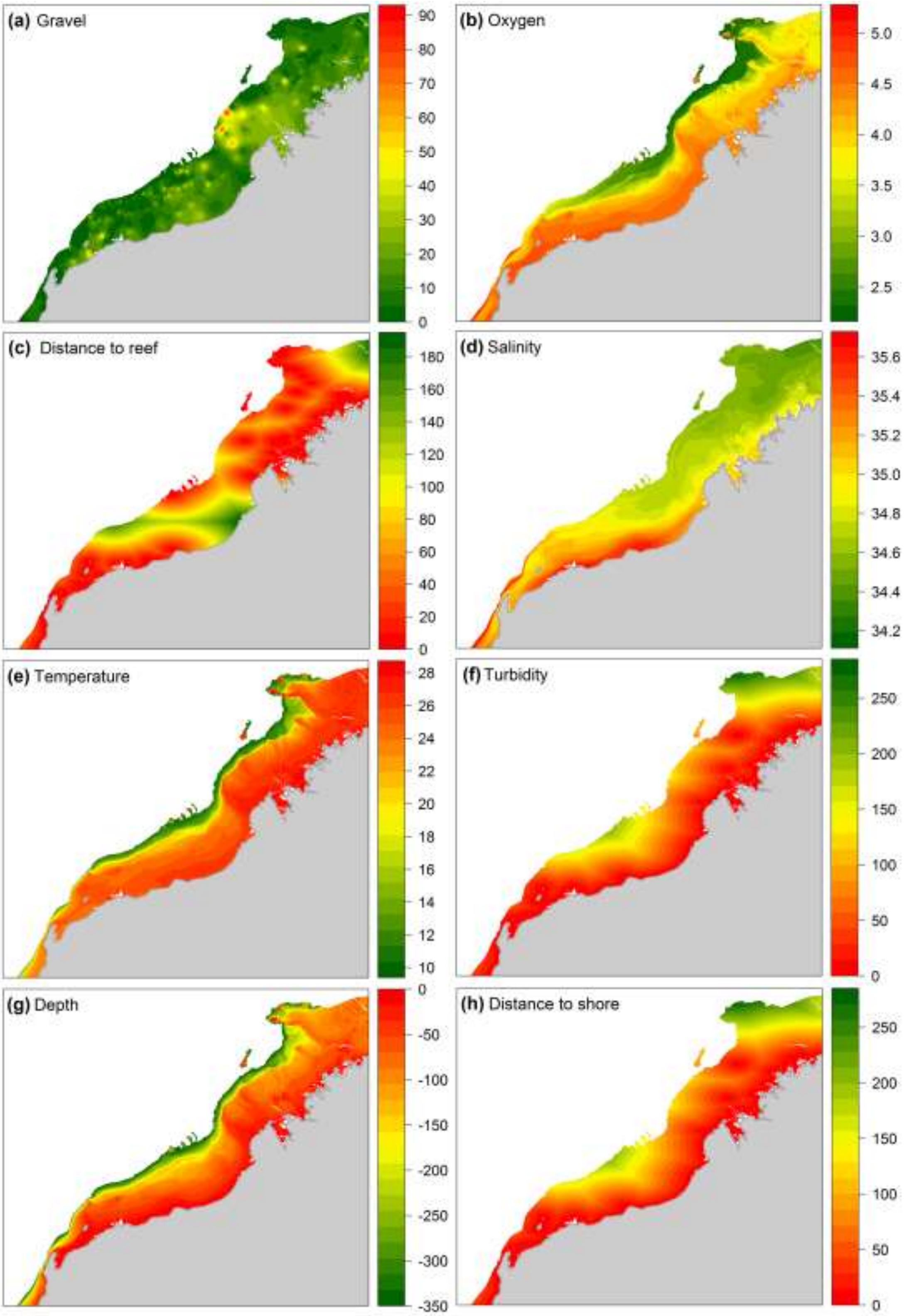

Figure S3.7 Maps of NW Australia showing patterns of variation in (a) gravel, (b) oxygen, (c) distance to reef, (d) salinity, (e) temperature, (f) turbidity, (g) depth and (h) distance to shore. The description and source of each predictor is summarised in Table S3.3.

Chapter 4 Contrasting patterns of residency and space use of coastal sharks within a communal shark nursery

Abstract: The benefits of marine protected areas (MPAs) are difficult to attain for mobile species, but the effectiveness of MPAs can be increased if they protect essential habitats such as nursery areas. We examined movements of juvenile blacktip reef (*Carcharhinus melanopterus*) and sicklefin lemon sharks (*Negaprion acutidens*) in a coastal nursery in northern Australia. Telemetry-derived data were modelled using Brownian bridges and overlaid with maps of habitats and no-take zones. Juvenile *N. acutidens* were typically residents (≥ 30 days) of the nursery with small core space use (< 1.3 km^2), while juvenile *C. melanopterus* were non-residents (< 30 days) with large space use (< 3.6 km^2). Both species displayed positive selection for sandflats and mangroves, and avoidance of deeper lagoonal and slope habitats. Monthly patterns were examined only for resident *N. acutidens*, where residency decreased with increasing shark length and varied seasonally for males but not females, while space use showed weak declines with increasing tidal range, and slight increases with mean air pressure, rainfall and shark length. Protecting sandflat and vegetated habitats can increase the efficacy of no-take zones for juvenile *N. acutidens* that display residency and affinity to these features, but will offer limited benefit for juvenile *C. melanopterus* with low residency and larger movements.

4.1 Introduction

Marine protected areas (MPAs) are important tools for spatial management (Edgar *et al.*, 2014) to counter the rapid loss of biodiversity resulting from overexploitation by fisheries and habitat degradation (Worm *et al.*, 2006). Benefits to species are maximised in MPAs that are no-take, well-enforced, old (>10 years since establishment), large in area (>100 km^2) and isolated. When these criteria are met, MPAs can support five times more large fish and fourteen times more shark biomass than fished areas (Edgar *et al.*, 2014). Small-scale MPAs could also be effective for species that have restricted ranges or key life stages linked to predictable or fixed habitat features (Garla *et al.*, 2006; Schofield *et al.*, 2013). As many sharks are highly mobile and tend to make large-scale movements (>100 km) (Heupel *et al.*, 2010), most MPAs are often too small (median size = 4.6 km^2, Wood et al., 2008) to encompass the range of movements of large adults (Green et al., 2015). Small MPAs may offer protection for smaller-bodied species that have restricted movements over their full life cycle (Munroe et al., 2015; Escalle et al.,

2016) or species that occupy coastal nurseries for their early life stages (Heupel *et al.*, 2007) but disperse more widely on reaching maturity. This is particularly important for the resilience of shark species, since most tend to grow slowly, mature late and produce few young (Cortés, 2002; Heithaus, 2007).

Young sharks typically segregate from adults in shallow, coastal nurseries, which are defined as areas that: i) support higher abundances of neonates (age < 1 year), ii) are used over extended periods of time and iii) are used over multiple years (Heupel et al. 2007). Such nurseries are thought to promote the survivorship of young sharks through protection from predators and increased foraging success (Cortés, 2002; Heithaus, 2007; Guttridge *et al.*, 2012). The former might be facilitated by the increased availability of micro-habitats such as mangroves, sandflats and seagrass beds in inshore nurseries (Chin *et al.*, 2012; Munroe *et al.*, 2014; Escalle et al., 2016). The use of these shallow habitats might also increase foraging success of sharks, with ebbing high tides forcing smaller fishes and other prey off intertidal sandflats (Papastamatiou *et al.*, 2009, 2015). For many species, the use of nurseries coincides with warmer water temperatures (e.g. Grubbs & Musick, 2007; Conrath & Musick, 2008). Aggregation by juveniles (Guttridge *et al.*, 2009) in a nursery might also improve foraging success through social learning (Guttridge *et al.*, 2013) or dilution of predation risk (Heupel & Simpfendorfer, 2005b). Tide-mediated selection for these shallow habitats has also been proposed as a strategy for predator avoidance (Wetherbee *et al.*, 2007; Guttridge *et al.*, 2012). However, competition for limited food resources could result in habitat partitioning between species in communal nurseries (Kinney et al. 2011). Given the susceptibility of inshore, coastal habitats to anthropogenic impacts and climate change (Field *et al.*, 2009b; Chin *et al.*, 2010), increased understanding of the ecological factors that influence the use of coastal nurseries is needed to enhance the management and conservation of sharks.

Although nurseries for coastal sharks have been identified and characterised in the north-western Atlantic Ocean, Gulf of Mexico and Caribbean Sea (Keeney *et al.*, 2005; Chapman *et al.*, 2009; Conrath & Musick, 2010; Norton *et al.*, 2012), very limited information about nurseries exists for the Indian Ocean. Ningaloo Reef in the eastern Indian Ocean is the world's largest fringing coral reef system and a United Nations World Heritage Site that supports a wide variety of habitats and is a global hotspot of shark diversity (Lucifora *et al.*, 2011). Extensive surveys indicated that Mangrove Bay, a shallow (water depths < 10 m) mangrove-lined tidal embayment in the north of the Ningaloo Reef Marine Park (NMP), had the highest sighting rates for six species of shark and rays within the Marine Park (Stevens *et al.*, 2009). There is some evidence that Mangrove Bay is a communal nursery for juveniles, however the delineation of nursery habitats within the Bay remains unclear (Cerutti-Pereyra *et al.*, 2014; Speed *et al.*, 2016). Furthermore, the zoning plan of the NMP was not developed to protect these species (Escalle et al., 2016; Speed et al., 2016) and therefore the suitability of existing spatial management strategies for conservation and management of shark and ray nurseries is poorly understood.

Our study addresses these issues using acoustic telemetry to examine spatial and temporal patterns in the movements of young blacktip reef (*Carcharhinus melanopterus*) and sicklefin lemon (*Negaprion acutidens*) sharks at Mangrove Bay. We hypothesised that: i) both species would display patterns of long-term residency (>6 months) and restricted space use, consistent with the use of Mangrove Bay as a shark nursery; ii) residency would decrease and space use increase with increasing shark size, thus decreasing the degree of protection afforded to both species by existing no-take MPAs; iii) because factors such as temperature (Conrath & Musick, 2008; Froeschke *et al.*, 2010), proximity to tidal inlets (Froeschke *et al.*, 2010) and barometric pressure (Heupel *et al.*, 2003; Udyawer *et al.*, 2013) are known to be important determinants of habitat use by juvenile sharks, the presence of young sharks in Mangrove Bay would be influenced by environmental variables (tides, water temperatures, air pressure, wind etc.); and iv) given the similarities in their dependency on coastal producers (Speed et al., 2012), young sharks of these species would be likely to partition habitats within the nursery to coexist and decrease inter-species competition.

4.2 Materials and methods

4.2.1 Study site

Ningaloo Reef (21.9°S, 113.9°E) extends for 320 km along the north-west coast of Western Australia (WA) and has been protected by the multiple-use NMP, covering a total area of 5070 km_2, since 1996 (Figure 4.1; LeProvost Dames & Moore 2000; Department of Conservation and Land Management, 2005). Commercial fishing is prohibited within the NMP, but recreational fishing is allowed in all zones with the exception of sanctuary zones which comprise 34% of the NMP. Shark capture and tagging for this study was concentrated at Mangrove Bay within the NMP (Figure 4.1), a tidal embayment encompassing small mangrove-lined inlets and a fringing reef at the seaward edge. The bay contains the Mangrove Bay Sanctuary Zone, a no-take area ~11.4 km^2 in size, established to protect a small area of mangrove forest within the NMP and its associated ecosystems (Department of Conservation and Land Management, 2005; Smallwood et al., 2012). Habitats within Mangrove Bay include coral reefs, bare rocky reefs, mangroves, algae and turf covered reefs interspersed with sand flats (Figure 4.1; Bancroft 2003). The mean monthly tidal range is approximately 2.0 m, with the Bay drying at lowest tide levels. The prevailing wind is from south to south west (Table 4.1) and the region is periodically subjected to severe cyclonic wind and floods (Lovelock *et al.*, 2011). Mean monthly water temperature is approximately 25.3 °C (Table 4.1).

4.2.2 Shark tagging and receiver array

Blacktip reef (*C. melanopterus*) and sicklefin lemon sharks (*N. acutidens*) were captured from shore within the Mangrove Bay Sanctuary zone using gillnets or handlines with barbless, 6/0 circle hooks baited with pilchard or squid. Captured sharks were transferred to a holding tank filled with seawater and identified to species, sexed, measured, photographed, assessed for clasper calcification and examined for umbilical scar condition and wounds. We measured fork (distance from snout to fork of the tail) and stretched total length (distance from snout to the tip of the upper lobe of the caudal fin) to the nearest cm and classified sharks as either neonate based on the presence of umbilical scars (Chin *et al.*, 2015) or juvenile using length-at-age data (Last & Stevens, 2009). We implanted 13 *C. melanopterus* (8 females, 5 males) and 23 *N. acutidens* (11 females, 12 males) with a uniquely-coded microchip (Trovan FDX-A, Microchips Australia) at the base of left dorsal to minimise the possibility of double-tagging with acoustic tags. We then inverted sharks to induce tonic immobility (Kessel & Hussey, 2015) and implanted an acoustic tag (V13-1H; Vemco Ltd, Canada) into the abdominal cavity through a 2 cm incision using a scalpel along the ventral midline that was subsequently closed using absorbable surgical sutures (Ethicon 2-0). Each tag transmitted a unique identification code with a transmission delay that varied randomly from 110–250 s and a battery life of 514–540 days. Sharks were held for 5–10 min from capture to completion of surgery, after which individuals were monitored until recovery (i.e. the individual could swim away from gentle restraint) for 5–15 min and released at the site of capture. All procedures were approved under Department of Parks and Wildlife licences (SF009588, 163165, CE004244), Department of Fisheries WA exemptions (2150, 2355), and University of Western Australia Animal Ethics Committee (UWA AEC; RA 3/100/1168).

An array of 85 acoustic receivers (VR2 and VR2W; Vemco Ltd, Canada) deployed as part of a national network of receivers (www.imos.org.au/aatams.html) was used to monitor movements of sharks tagged in Mangrove Bay (Figure 4.1; See Table S1; available as Supporting Information for this paper). The array consisted of 70 receivers at Mangrove Bay and two cross-shelf lines of 8 receivers at Tantabiddi and 7 receivers at Turquoise Bay (Figure 4.1). Receivers were secured to metal pickets either hammered directly into the reef or mounted in custom-built cement blocks (0.013 m^3) deployed on the reef. The receivers were placed within movement corridors including inlets, natural constrictions and channels. Various factors can influence spatial and temporal variability in the detection range of receivers, including depth, temperature, wind and ambient noise (Kessel *et al.*, 2014; Huveneers *et al.*, 2016). To establish the effective detection range of receivers in intertidal areas of Mangrove Bay, we anchored receivers in a straight line at approximately 0, 50, 100, 150, 175, 200, 225, 250 and 275 m away from a submersed, fixed delay interval V13-1H range-test tag (with a mean transmission interval of 10 s). Range tests were conducted in the intertidal zone of Mangrove Bay in March 2013 when wind speeds ranged from 0 – 49.0 km h^{-1} (median = 20.3 km h^{-1}), and in the lagoon in August 2012 following the methods described by Pillans et al. (2014). The detection probability of a receiver was calculated by dividing the number of detections by the expected mean number of transmissions over the range testing period. The effective detection range was defined as the distance at which detection probability was 50% (D_{50}) and estimated using a loess smoother fitted in R (R Core Team, 2015). Range testing showed that the effective detection range (D_{50}) for the receivers in the intertidal bay was 175 m (see Figure S4.8), and in the lagoon was 300 m (Pillans *et al.*, 2014). Receivers were spaced 150–300 m apart in the intertidal zone adjacent to mangroves (2 m depth) and 200–800 m apart in the lagoon (2-10 m depth), channel (10-15 m depth) and open shelf (15-40 m depth; Figure 4.1). Receivers were downloaded every 6 to 9 months and acoustic monitoring of tagged sharks occurred from March 2013 to May 2015. To assess temporal variation in receiver performance (Payne *et al.*, 2010), we deployed a V13-1H sentinel tag (with a transmission delay of 550–650 s) at fixed distances from two receivers (1 and 153 m respectively) located in areas of greatest shark activity between November 2013 and January 2015 (Figure 4.1). We assessed the influence of environmental variables on detection probability of these two receivers using generalised additive models (Section 4.6.2.1 and Table S4.7; available as Supporting Information for this paper).

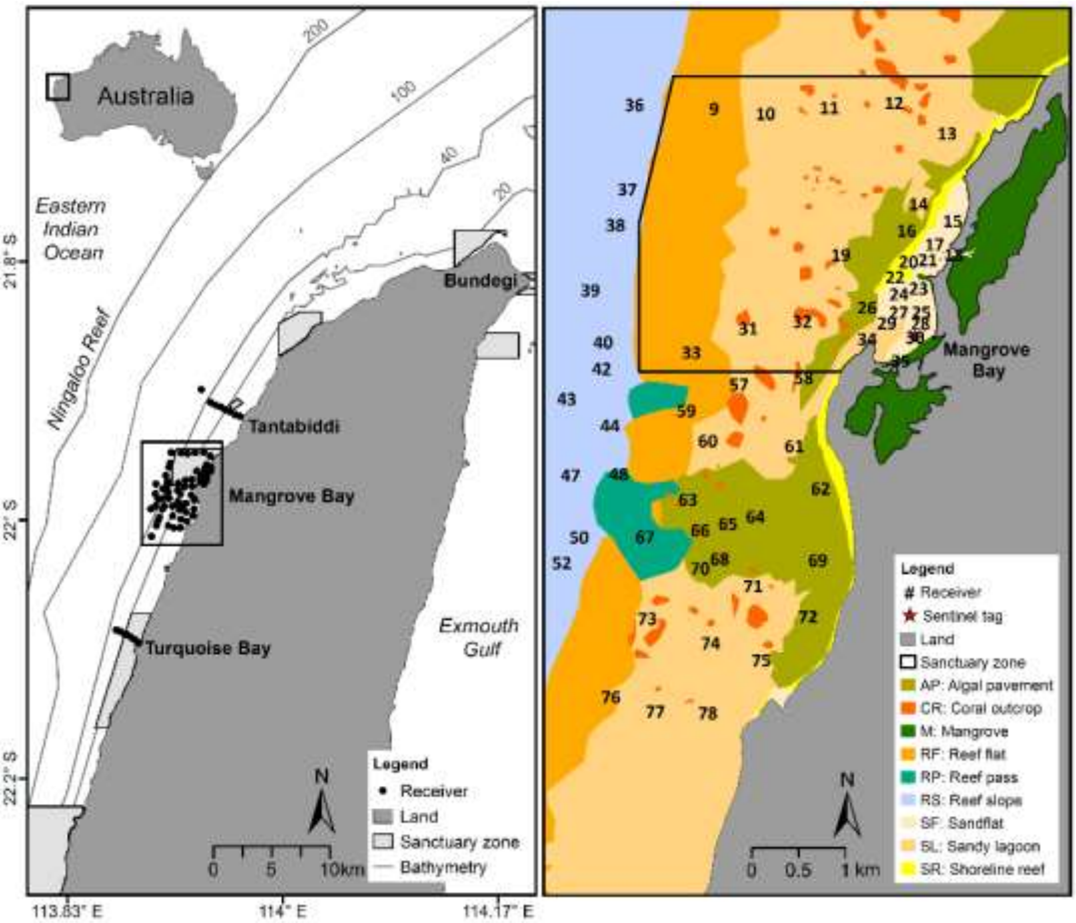

Figure 4.1 Map of Mangrove Bay, in the northern Ningaloo Reef Marine Park showing the location of acoustic receivers (*points on the left plot and numbers on the right plot*), bathymetry (*grey lines*), sanctuary zones (*solid lines*) and inset map of Australia. Benthic habitats are coloured by habitat type.

4.2.3 Residency and space use

Prior to analysis, we removed false detections from the data set, which were defined as single detections recorded within a 24 h period, or when two detections recorded by different receivers were within too short a time frame for an individual to travel the distance separating the receivers (Pincock, 2012). Sharks were assumed to move at a constant speed and the maximum swimming speed of carcharhinid sharks from the literature (1 m s^{-1}; Webb & Keyes 1982, Sundstrom *et al.* 2001, McCauley *et al.* 2012) was used to estimate maximum distance travelled within a time frame. To examine patterns of residency, we considered a shark as present within the Mangrove Bay array if two or more detections were recorded on a receiver within an hour on a given day following Papastamatiou *et al.*, (2010). We calculated a residency index (RI) as the number of days a shark was present within the full array as a proportion of the total number of days monitored. As individuals were released on different days, the projected battery life of each tag was used as a standard reference value for the total number of days monitored. All sharks were likely to have survived the tagging process (Buray *et al.*, 2009; Chin *et al.*, 2015) and thus sharks not detected by the array were assumed to have departed. Residency index values ranged from 0 (no residency) to 1 (high residency). Drawing upon descriptions of one of the criteria for a shark nursery (Heupel et al., 2007), we classified individuals as either non-residents that were present within the array for days to weeks (< 30 days; RI < 0.06) or residents that were predictably present within the array for months to years (≥ 30 days; RI ≥≤ 0.06).

Table 4.1 List of explanatory variables included in models of residency index (RI), core and total kernel area (50% & 95% KA respectively) and residency index of *N. acutidens* at Mangrove Bay. Details include description, source, mean (± SD) calculated from monthly values from March 2013 – May 2015, unit of measure for each continuous variable or category levels for categorical predictors (marked *). All variables were included as fixed effects apart from tag number which was included as a random effect in all models.

Variable	Description	Source	Units/Levels	Range
Environmental				
PressAV	Mean air pressure	Milyering weather station	hectopascal	1004.1-1017.1
PressR	Air pressure range	Milyering weather station	hectopascal	0 – 14.8
TempAV	Mean water temperature	Temperature logger	°C	23.0 – 28.2
TempR	Water temperature range	Temperature logger	°C	2.4 – 7.4
TideAV	Mean tide height	Regional Oceanic Modelling System	m	1.42 – 1.66
TideR	Tidal height range	Regional Oceanic Modelling System	m	1.78 – 2.17
WspeedAV	Mean wind speed	Milyering weather station	$km.h^{-1}$	0 – 22.7
WspeedR	Wind speed range	Milyering weather station	$km\ h^{-1}$	0 – 49.0
WdireAV	Mean wind direction	Milyering weather station	°	0 – 257.2
RainAV	Mean cumulative rainfall	Milyering weather station	mm	0 – 17.8
Biological				
TL	Stretched total length	Observer	mm	63.0 – 116.9
Tag*	Tag identification number	Observer; Vemco Ltd. (Canada)	B1 – 13; L1 – 23	–
Sex*	Sex	Observer	female, male	–
Temporal				
Month	Month	Calendar	month	1 – 12

We first tested for differences in shark length and number of days detected between species (*C. melanopterus* and *N. acutidens*) and sexes using generalised linear models (GLMs) and an information theoretic approach to model selection (Burnham & Anderson, 2002). For each response variable (shark length and number of days detected), we used a Gaussian error distribution with identity link and compared the slope model with the intercept-only (null) model according to the sample-corrected Akaike's Information Criterion (AIC_C) and corresponding AIC_C weight ($wAIC_C$) that assigns relative strengths of evidence to the different competing models. The information theoretic approach uses a multi-model framework to provide a more robust method than standard regression techniques for comparing alternative hypotheses (Burnham & Anderson, 2002) and was used in all subsequent model evaluation. We examined the residuals of the models within 2 AICC points of the top-ranked model to verify that the appropriate distribution was applied.

We applied a suite of generalised additive models (GAMs) to evaluate the effects of shark length, sex and possible two-way interactions on three response variables: residency index (RI) core and total kernel area (50% KA and 95% KA respectively), separately for each species. We modelled RI as the frequency of presence (i.e. number of days a shark was present or absent) using a binomial error distribution with logit link and 50% and 95% KA using Gaussian error distributions with identity link. Shark total length (TL) was modelled using a cubic regression spline (bs = "cr"), with the basis dimension "k" restricted to < 4 to avoid overfitting. We specified a maximum of one term per model for *C. melanopterus* due to the small sample size (n = 10) and three terms for *N. acutidens* due to the relatively larger sample size (n = 21). Hence, we used in a candidate set of three models for *C. melanopterus* and five models for *N. acutidens* that included all possible combinations of variables, which were ranked according to AICC and $wAIC_C$ (Table 4.3). For each response variable, a confidence set of models that were within 2 AIC_C points of the top-ranked model were considered equivalent and if these models did not include the null model, we used model averaging to calculate relative variable importance (RVI) (Burnham & Anderson, 2002) from the sum of wAICC across the confidence set. Models containing only highly influential variables (i.e. determined as those preceding a sharp decline in RVI) were used for graphical representation of variable effects.

4.2.4 Monthly patterns of residency and space use

We calculated and analysed monthly metrics of residency and space use only for *N. acutidens* that were resident within the receiver array for over 30 days (*n* = 16). It was not possible to perform temporal analysis for *C. melanopterus* due to the low number of resident individuals (n = 3). To examine biological and environmental effects on monthly patterns of residency and space use, we compiled a suite of relevant explanatory variables including water temperature, air pressure, rainfall, tidal height, wind speed and direction, month, sex and total length of shark (Table 4.1). We assessed multi-collinearity between pairs of variables using Pearson correlation coefficients (*r*) and retained one variable from correlated pairs (r > 0.6) to minimise the possibility of over-fitting models (Dormann et al., 2013). To account for the growth of tagged sharks over the monitoring period, we estimated monthly total length (TL) based on the initial size at capture and published growth rates of juvenile *N. acutidens* reported in the Indian Ocean (Stevens, 1984). Water temperature was recorded at Tantabiddi using HOBO Pro V2 data loggers (calibrated at the Australian Institute Marine Science; AIMS) sampling at 30-min intervals, which were periodically downloaded and replaced every 3-12 months. Daily values for air pressure (hPA), rainfall totals (mm), wind speed (m s^{-1}) and direction (°) were obtained from a weather station at Milyering (10 m elevation; 22.03°S, 113.92°E) situated 6.8 km south of Mangrove Bay (http://data.aims.gov.au/). Predicted tidal height data was obtained through the Regional Oceanic Modelling System (https://www.myroms.org/). Values of monthly mean and range were computed for all variables from March 2013 to May 2015 and chronologically matched with shark movement data across the monitoring period.

We used generalised additive mixed-effect models (GAMMs) with binomial error distributions with logit link to model RI and Gaussian error distributions to model square root-transformed (to normalise the distribution) 50% and 95% kernel areas. To account for repeated observations made for each shark, tag number was included as a random effect in the models (Bolker *et al.*, 2008). All explanatory variables were modelled with a cubic regression spline except for month and wind direction which were modelled with a cyclic cubic regression spline, i.e. a penalised cubic regression spline whose ends match up to second derivative. As the latter smoother includes shrinkage by default, the shrinkage version of the cubic regression spline was also implemented here. We restricted the basis dimension “k” to < 4 to avoid overfitting. We specified a maximum of four fixed effects per model due to relatively small sample sizes and applied the rule of marginality including interactions only in models with both main effects. This resulted in a set of 96 candidate models, with model selection and averaging undertaken using the same approach described for GAMs. Standard diagnostic plots were made to assess the validity of models in the confidence set and we also checked for temporal autocorrelation in the residuals. We then presented the top six models for each response, except when more than six models were within two AICC points, in which case all models within the confidence set were presented. All models were implemented using the *lme4* (Bates *et al.*, 2015), *MuMIn* (Barton, 2015), *mgcv* and *gamm4* (Wood & Scheipl, 2015) packages in R (R Core Team, 2015).

4.3 Results

Tagged sharks were monitored for 2–544 days between March 2013 and May 2015 (Table 4.2; Figure 4.2). All of the tagged sharks were neonates with umbilical scars in various stages of healing (age <1 year) with the exception of one *C. melanopterus* that was a juvenile female. Mean total lengths of *N. acutidens* were slightly larger (75.2 ± 10.0 cm; *n* = 23) than *C. melanopterus* (63.9 ± 16.7 cm; *n* = 13), with higher statistical support for the generalised linear model (GLM) that included species (wAICC = 0.59) than the intercept-only model (wAICC = 0.41). We found no evidence for a difference in total length between sexes for both *C. melanopterus* (females, 65.2 ± 20.6 cm; males, 61.8 ± 9.0 cm; wAICC = 0.89 for the intercept-only model) and *N. acutidens* (females, 75.5 ± 11.0 cm; males, 75.0 ± 9.5 cm; wAICC = 0.77 for the intercept-only model).

Table 4.2 Tagging and detection details of 13 *C. melanopterus* and 23 *N. acutidens* monitored at Mangrove Bay from March 2013 – May 2015. Details include sex (F: female, M: male), life stage (N: neonate, J: juvenile), stretched total length in cm (TL), residency category (RC; R: resident, NR: non-resident), total monitoring days (TMD; based on the projected battery life of the tag), days detected (DD), consecutive days detected (CDD), the number of receivers on which a tagged shark was detected (No. receivers), residency index (RI), core and total kernel area (50% and 95% KA respectively). *Shark L5 and L19 were moving around the array until 26-May-2013 and 20-Jan-2014. After these dates, the tags were stationary close to one receiver. Residency index for these sharks were calculated from data prior to the tag becoming stationary. **Shark L3 was recaptured by fishermen in the recreational use zone within the array on 21-Jul-2013 and its tag was subsequently implanted into **Shark L9.

Tag	Sex	Stage	TL	RC	Date tagged	Date last detected	TMD	DD	CDD	No. receivers	RI	50% KA	95% KA
C. melanopterus													
B1	F	N	88	R	27-Nov-13	16-Feb-15	540	395	148	39	0.73	1.70	22.89
B2	F	N	56	R	04-Dec-13	31-May-15	540	407	90	5	0.75	0.16	0.95
B3	M	N	74	R	02-Dec-13	04-Nov-14	540	45	6	13	0.08	4.14	27.21
B4	F	N	53.5	NR	25-Nov-13	02-Dec-13	540	8	8	15	0.01	0.36	1.41
B5	F	J	107	NR	29-Nov-13	04-Dec-13	540	6	6	10	0.01	5.51	31.47
B6	F	N	55.5	NR	14-Dec-13	15-Dec-13	514	2	2	13	0.00	0.65	2.76
B7	F	N	55	NR	15-Dec-13	12-Jan-14	514	9	4	2	0.02	0.07	0.33
B8	F	N	51	NR	17-Dec-13	23-Dec-13	514	7	7	16	0.01	3.00	18.72
B9	F	N	55.5	NR	17-Dec-13	21-Dec-13	514	5	5	8	0.01	4.89	17.92
B10	M	N	56	NR	27-Nov-13	na	na	na	na	na	na	na	na
B11	M	N	59	NR	05-Dec-13	23-Dec-13	514	16	11	4	0.03	0.09	0.45
B12	M	N	52	NR	10-Dec-13	03-Jan-14	514	12	10	15	0.02	1.05	7.80
B13	M	N	68	NR	17-Dec-13	11-Jan-14	514	9	8	12	0.02	0.15	0.94
N. acutidens													
L1	F	N	70.5	R	21-Mar-13	17-Oct-13	540	185	156	18	0.34	0.20	1.18
L2	F	N	67	R	21-Mar-13	29-Jun-13	540	101	101	29	0.19	0.12	1.10
L3**	F	N	70	R	24-Mar-13	21-Jul-13	120	105	57	17	0.88	0.19	2.15
L4	M	N	75	R	21-Mar-13	12-Nov-13	540	230	223	12	0.43	0.11	0.57
L5*	M	N	65	R	21-Mar-13	02-Aug-13	65	65	67	19	1.00	0.86	11.33
L6	M	N	69.5	R	22-Mar-13	05-Aug-13	540	136	135	30	0.25	0.33	2.77
L7	M	N	63	R	23-Nov-13	08-Jan-14	540	47	8	8	0.09	0.13	0.70
L8	M	N	72	R	26-Nov-13	23-Dec-14	540	391	327	17	0.72	0.43	2.22
L9	M	N	70	R	27-Nov-13	01-Aug-14	248	75	11	9	0.30	0.73	7.29
L10	M	N	81	R	27-Nov-13	21-May-14	540	159	80	20	0.29	0.99	5.60
L11	M	N	90	R	30-Nov-13	11-Apr-14	540	131	129	16	0.24	0.19	1.06
L12	M	N	90.5	R	11-Dec-13	27-May-15	514	512	470	21	1.00	0.34	2.40
L13**	F	N	75.5	R	25-Nov-13	05-Aug-14	540	236	112	30	0.44	1.81	13.91
L14	F	N	74.5	R	28-Nov-13	27-Jul-14	540	242	242	15	0.45	0.20	0.75
L15	F	N	101	R	02-Dec-13	10-Mar-15	540	440	370	20	0.81	0.63	3.76
L16	F	N	69	R	17-Dec-13	31-May-15	514	517	123	15	1.00	0.32	1.71
L17	F	N	73	NR	12-Dec-13	03-Jan-14	514	23	23	16	0.04	0.42	1.94
L18	F	N	64.5	NR	12-Dec-13	15-Dec-13	514	4	4	14	0.01	0.23	1.47
L19*	F	N	74	NR	16-Dec-13	05-Jun-14	514	37	37	4	0.07	0.13	0.86
L20	F	N	91.5	NR	16-Dec-13	24-Dec-13	514	8	6	16	0.02	2.19	13.02
L21	M	N	85	NR	25-Nov-13	30-Nov-13	540	4	3	8	0.01	0.58	2.01
L22	M	N	66.5	NR	10-Dec-13	24-Feb-14	514	28	7	19	0.05	2.50	24.15
L23	M	N	72	NR	14-Dec-13	23-Dec-13	514	10	10	16	0.02	0.59	1.97

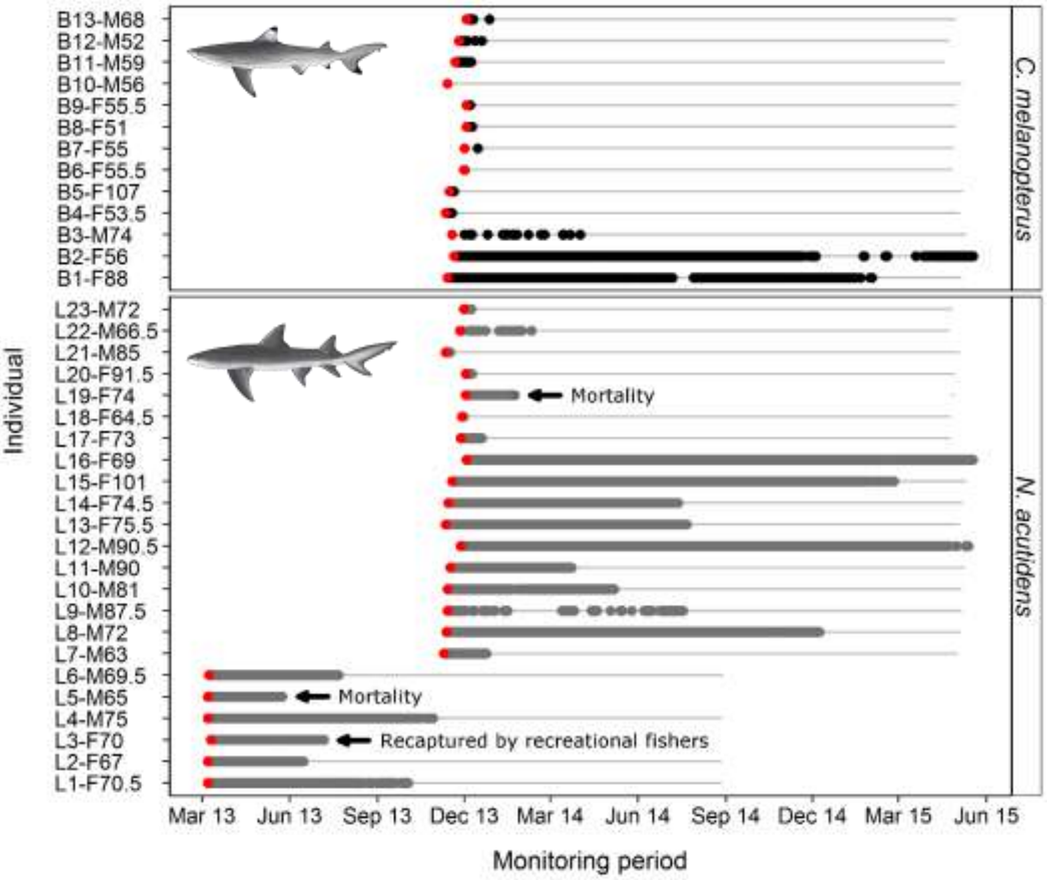

Figure 4.2 Daily presence of individual *C. melanopterus* (*black circles*) and *N. acutidens* (*grey circles*) released with acoustic transmitters in Mangrove Bay from March 2013 to May 2015. Individuals are identified by sex (M *males*; F *females*) and stretched total length (cm). The tagging dates are indicated by *red circles* and *grey lines* represent the availability of the shark for detection based on tagging date and battery life of the tag.

4.3.1 Residency and space use

Nine *C. melanopterus* and five *N. acutidens* were detected within the array between 2–23 days after tagging but ceased to be detected after January 2014 (Table 4.1). The remaining three *C. melanopterus* were detected for a maximum of 45–407 days (77 ± 152 days) and 18 *N. acutidens* were detected between 47–517 days (166 ± 160 days), with higher statistical support for the model that included species ($\mathrm{wAIC_C} = 0.84$) relative to the intercept-only model ($\mathrm{wAIC_C} = 0.16$). We found no evidence for differences in the number of days detected between the sexes of both species (*C. melanopterus*, $\mathrm{wAIC_C} = 0.80$ for the intercept-only model; *N. acutidens*, $\mathrm{wAIC_C} = 0.77$ for the intercept-only model). One of the tagged *C. melanopterus* (B10) was never detected following its release (Figure 4.4). Two of the eighteen *N. acutidens* (L5 and L19) were assumed to have died close to a receiver after 65 and 37 days respectively resulting in the tag being continuously detected by 1 or more overlapping receivers (Figure 4.4). We retrieved a tag from one *N. acutidens* (L3) that was recaptured by a recreational fisher outside of the Mangrove Bay Sanctuary Zone, and subsequently deployed it into another *N. acutidens* (L9). Throughout the detection period, 74% of tagged sharks were detected on more than 10 receivers (15 ± 8 receivers) (Table 4.2). One *C. melanopterus* (B1) and three *N. acutidens* (L13, L15 and L22) were detected by the receiver curtains off Tantabiddi (~ 10km north) and Turquoise Bay (~ 15 km south), a part of the array that was designed to detect such long-range movement (Figure 4.1). We found strong evidence for an effect of species on residency index with the slope model having highest statistical support ($wAIC_C = 1$) and *N. acutidens* having higher residency (0.42 ± 0.34) than *C. melanopterus* (0.17 ± 0.30).

For *C. melanopterus* residency, the additive model including TL had the highest statistical support (GAM, $wAIC_C = 1$; Table 4.3) and accounted for 88% of the variance in the response, indicating a positive trend in residency when TL increased from 60 – 90 cm (Figure 4.3a). For *N. acutidens* residency, we found highest support for the model including sex, TL and the interaction between sex and TL (GAM, $wAIC_C = 1$; Table 4.3), indicating increased residency among smaller (≤ 70 cm TL) neonate females and decreased residency with increasing TL of larger (> 70 cm TL) neonate females (Fig. 3b). In contrast, there was no apparent change in residency with increasing TL for males (Figure 4.7c). However this model accounted for less than 1% of the variance in the response ($R^2 = 0.7$).

4.3.2 Space use

Core and total kernel areas (50% and 95% KA respectively) of 10 *C. melanopterus* and 21 *N. acutidens* largely overlapped within nearshore waters of Mangrove Bay (Figure 4.4). We found evidence that core kernel areas differed between species with the slope model having higher statistical support ($wAIC_C = 0.72$) than the intercept-only model ($wAIC_C = 0.28$) (mean ± SD; 1.6 ± 2.0 km^2 for *C. melanopterus* and 0.6 ± 0.7 km^2 for *N. acutidens*) (Table 4.3). There was also evidence for a species difference in total kernel areas with the slope model having higher statistical support (wAICc = 0.66) than the intercept-only model (wAICC = 0.34). Total kernel areas of *C. melanopterus* (11.2 ± 12.5 km^2) were larger than those for *N. acutidens* (4.8 ± 6.1 km^2). We found no evidence for a difference in overall core space use of *C. melanopterus* with either shark sex or TL with the intercept-only model having majority support (wAIC$_C$ = 0.80). Similarly, there was limited evidence for an effect of total length or sex on total space use, as the intercept-only model ranked highest (Table 4.3). There was also no evidence for a difference in core and total space use of *N. acutidens* with either shark sex or TL with the intercept-only model most parsimonious (Table 4.3). The proportion of total space use within sanctuary zones was higher for *N. acutidens* (0.86 ± 0.19) relative to *C. melanopterus* (0.71 ± 0.30), with the slope model having complete support (wAIC$_C$ = 1) over the intercept-only model.

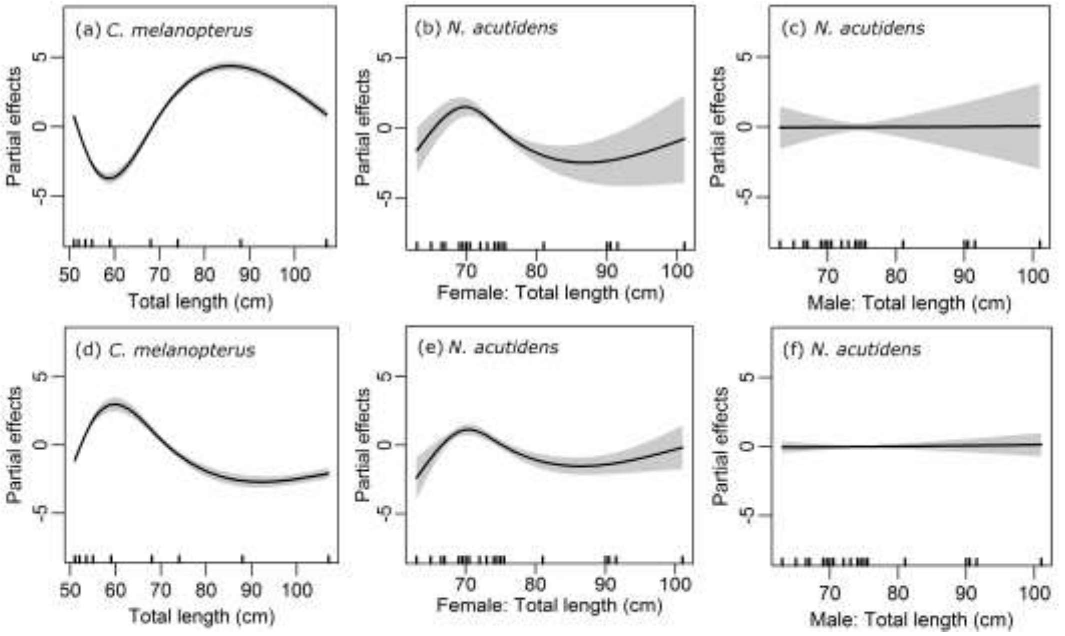

Figure 4.3 Partial residual plots showing the relationship between the dependent variables (residency index (a-c) and the relative proportion of 95% kernel area (d-f) in no-take MPAs) and the independent variables in the top ranked additive models for *C. melanopterus* (a and d) and *N. acutidens* (b, c, e and f). Black line represents the fitted line and grey shaded areas represent the 95% confidence intervals.

In terms of the proportion of total kernel area within no-take zones, the additive mixed model including TL had the highest statistical support for *C. melanopterus* (wAIC$_C$ = 1; Table 4.3) and accounted for 60% of the variance in the response, indicating a negative trend in the protection of total space use when TL exceeded 60 cm for *C. melanopterus* (Figure 4.7d). For *N. acutidens*, the highest statistical support was for the model including sex, TL and the interaction between sex and TL (wAIC$_C$ = 1; Table 4.3) and accounted for 24% of the variance. The proportion of total space use within no-take zones was marginally higher for females between 65 and 75 cm TL, but was consistent for males across the range of TL sampled (Figure 4.7e-f). There was no difference in the proportion of habitat types used between species (50% KA, $\chi^2_8 = 1.14$, p = 1.00; 95% KA, $\chi^2_8 = 13.21$, p = 0.10), and across space use metrics within species (*C. melanopterus*, $\chi^2_8 = 5.22$, p = 0.73; *N. acutidens*, $\chi^2_8 = 1.71$, p = 0.99). Core and total space use of both species primarily focused on sandflats (>34 % and >21 % respectively) and sandy lagoon habitats (>30 % and >26 % respectively). We found that neonates selected disproportionately for inshore sandflats, followed by mangroves, algal pavement and shoreline reefs (*C. melanopterus*, $\chi^2_8 = 29.57$, $p < 0.001$; *N. acutidens*, $\chi^2_8 = 106.78$, $p < 0.001$) (Figure 4.3). Mean selection values revealed that reef slope and sandy lagoon habitats were consistently avoided by *C. melanopterus* and by *N. acutidens* (Figure 4.5).

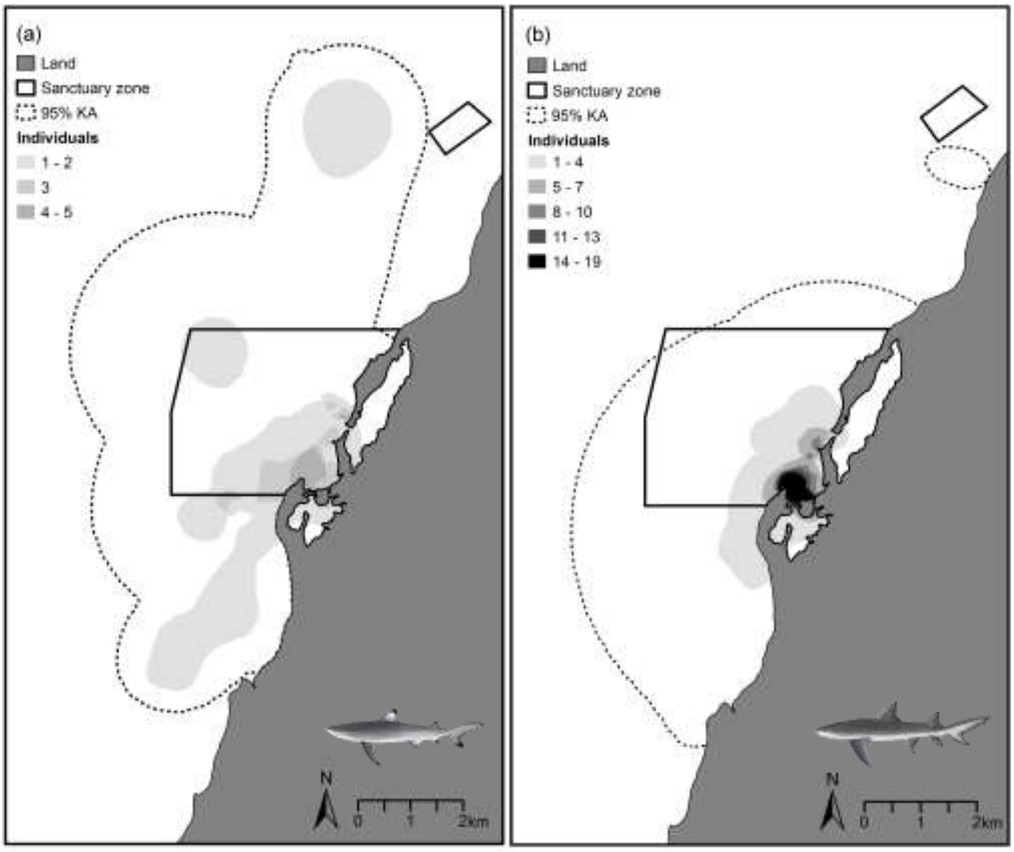

Figure 4.4 Maps of 50% and 95% kernel area (KA) of (a) *C. melanopterus* and (b) *N. acutidens* monitored within Mangrove Bay for at least five days. Contours of 95% KA (*dashed lines*) and relative densities of 50% KA (*shaded areas*) are shown for combined individuals.

Table 4.3 Ranked additive models of residency index (RI), core and total kernel area (50% and 95% KA respectively) and the proportion of total kernel area within no-take zones (*p.* 95% KA in no-take) of *C. melanopterus* and *N. acutidens* explained by the biological variables (see Table 4.1 for an explanation of each variable). All models fitted for each response are shown; the best-supported model is highlighted in bold. Details include the estimated degrees of freedom (*edf*), the sample-corrected Akaike's Information Criterion (AICc), increase in AICc relative to the model with the lowest AICc value (ΔAICc), relative AICc weight (wAICc) and goodness of fit (Adjusted R^2).

No.	Response	Model	*edf*	AICc	ΔAICc	wAICc	Adjusted R^2
C. melanopterus							
m3	RI	TL	3.00	331.26	0.00	1	88.0
m2	RI	sex	1.00	1471.35	1140.09	0	6.1
m1	RI	1	0.00	1665.93	1334.67	0	0.0
m1	sqrt (50% KA)	1	0.00	26.20	0.00	0.90	0.0
m2	sqrt (50% KA)	sex	1.00	30.60	4.40	0.10	9.3
m3	sqrt (50% KA)	TL	2.78	36.08	9.88	0.01	54.2
m1	sqrt (95% KA)	1	0.00	43.85	0.00	0.86	75.3
m2	sqrt (95% KA)	sex	1.00	48.20	4.35	0.10	8.7
m3	sqrt (95% KA)	TL	2.92	49.94	6.09	0.04	0.00
m3	p. 95% KA in no-take	TL	2.99	159.68	0.00	1	59.7
m2	p. 95% KA in no-take	sex	0.00	456.49	296.81	0	10.8
m1	p. 95% KA in no-take	1	1.00	463.76	304.08	0	0.0
N. acutidens							
m5	RI	sex × TL	6.96	3526.32	0.00	1	0.7
m4	RI	sex + TL	4.00	4244.19	717.87	0	4.0
m3	RI	TL	3.00	4244.21	717.89	0	1.8
m2	RI	sex	1.00	4906.25	1379.93	0	4.2
m1	RI	1	0.00	4946.41	1420.09	0	0.0
m1	sqrt (50% KA)	1	0.00	21.84	0.00	0.33	0.0
m3	sqrt (50% KA)	TL	0.00	21.84	0.00	0.33	0.0
m5	sqrt (50% KA)	sex × TL	2.67	23.25	1.42	0.16	16.1
m2	sqrt (50% KA)	sex	1.00	24.50	2.66	0.09	4.8
m4	sqrt (50% KA)	sex + TL	1.00	24.50	2.66	0.09	4.8
m1	sqrt (95% KA)	1	0.00	69.02	0.00	0.35	0.0
m3	sqrt (95% KA)	TL	0.00	69.02	0.00	0.35	0.0
m2	sqrt (95% KA)	sex	1.00	71.46	2.44	0.10	3.7
m4	sqrt (95% KA)	sex + TL	1.00	71.46	2.44	0.10	3.7
m5	sqrt (95% KA)	sex × TL	1.87	71.55	2.53	0.10	3.8
m5	p. 95% KA in no-take	sex × TL	5.59	630.86	0.00	1	23.8
m4	p. 95% KA in no-take	sex + TL	3.85	664.67	33.81	0	20.9
m3	p. 95% KA in no-take	TL	2.69	667.37	36.51	0	13.2
m1	p. 95% KA in no-take	1	0.00	676.48	45.62	0	0.0
m2	p. 95% KA in no-take	sex	1.00	677.49	46.63	0	5.0

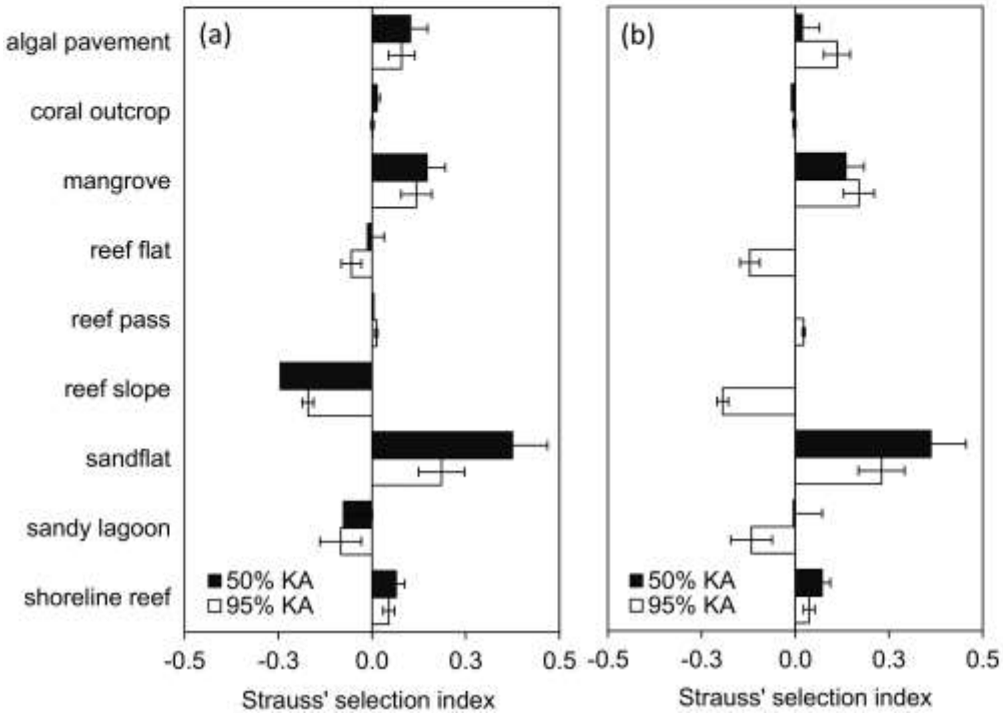

Figure 4.5 Values of mean Strauss' selection index (S_i) based on 50% and 95% kernel area of a) *C. melanopterus* and b) *N. acutidens* across the habitat types detailed in Figure 4.1.

4.3.3 Monthly patterns of residency and space use

A detection span sufficient (>30 days) to allow the estimation of monthly space use (50% and 95% kernel areas) and residency index was obtained for 3 *C. melanopterus* and 16 *N. acutidens* (Table 4.2). However, the generalised additive mixed models described were only fitted for *N. acutidens* but not *C. melanopterus* due to the small sample size (n = 3). This modelling revealed that the confidence set ($< 2\ \Delta AIC_C$) included one model where residency index was the response, 12 models where 50% kernel area was the response and two models where 95% kernel area was the response (Table 4.4). For residency index, the model containing TL and the interaction between month and sex had the highest statistical support ($wAIC_C = 1$, $R^2 = 4.8\%$) (Figure 4.7a-c). We found only weak relationships between 50% kernel area and explanatory variables for all 12 models within the confidence set (R^2 ranged from 0.1–2.8%; Table 4.4). Of these, relative variable importance values (RVI) derived from model averaging indicated that tidal height range, mean air pressure and TL had the most influence on core space use (Figure 4.6) and the models containing (model 19, 13 and 2; Table 4.4) are shown in Figures 4.7d-f. For 95% kernel area, model averaging indicated that TL and mean rain accumulation had the most influence on total space use (Fig. 6) and the model containing these variables (model 25; wAIC$_C$ = 0.26, R^2 = 8.2%; Table 4.4) are shown in Figures 4.7g-h. Estimated total lengths of *N. acutidens* at the end of the detection period ranged from 64.8 – 114.8 cm, indicating that all resident individuals were still immature.

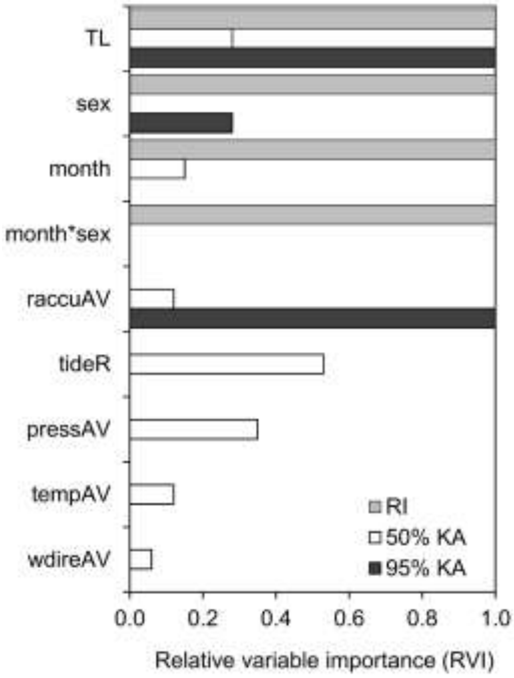

Figure 4.6 Relative variable importance (RVI) values of the independent variables in additive mixed models of monthly patterns of residency index, 50% and 95% kernel area of *N. acutidens*. Variables that were common within the confidence set (i.e. models with < 2 ΔAIC$_C$) have a RVI value of 1.0.

There was a negative trend in the monthly residency of immature *N. acutidens* across the range of TL sampled (Figure 4.7a). Monthly residency indices of *N. acutidens* were sex-specific (Figure 4.7b-c). Females were resident throughout the year (Figure 4.7b), while males were found to have longer residency in winter and spring (June to September) than in summer and autumn (Figure 4.7c). Core space used by *N. acutidens* increased by 0.02 km^2 when mean air pressure was greater than 1012 hPa, and decreased by 0.05 km^2 when monthly tidal height range was exceeded 2.0 m (Figures 4.7d and f). Core and total space used by *N. acutidens* increased by 0.1 km^2 and 0.5 km^2 respectively when TL exceeded 88 cm (Figures 4.7e and h). Total space use of *N. acutidens* increased marginally as mean rainfall increased from 0 to 7 mm and then stabilised (Figure 4.7g).

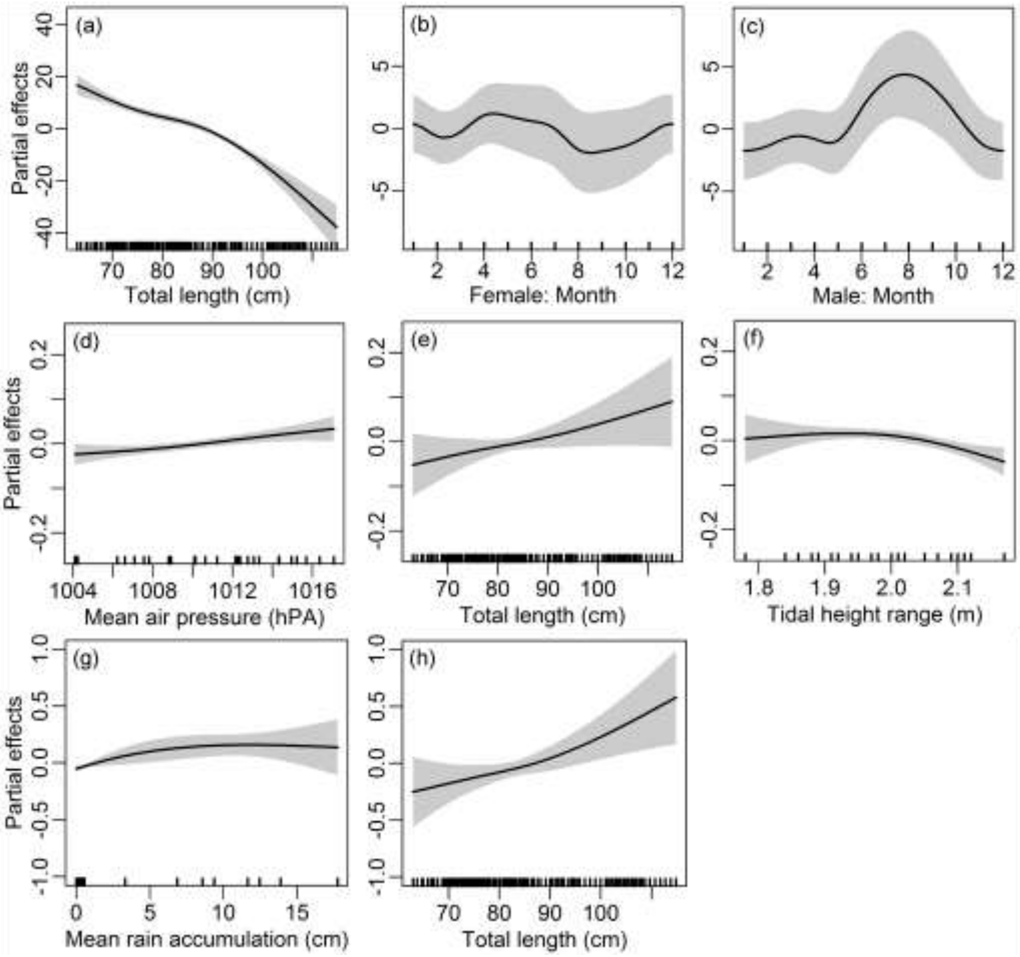

Figure 4.7 Partial residual plots relative to the independent variables in the top ranked additive mixed models for residency index (a-c), 50% (d-f) and 95% kernel area (g-h) of *N. acutidens* (see Table 4.4 for an explanation of each model). Each column represents the influence of a variable on each response. Black line represents the fitted line and grey shaded areas represent the 95% confidence intervals.

Table 4.4 Ranked additive mixed models of monthly core residency index (RI), core and total kernel area (50% and 95% KA respectively) of *N. acutidens* explained by the independent variables (see Table 4.1 for an explanation of each variable). The top six models for each response are shown; if more than six models are within 2 AICc points, all these models are shown. Tag number was treated as a random effect in all models; the model(s) containing the most influential variables and used for graphical representation are highlighted in bold. Details for each model include the estimated degrees of freedom (edf), the sample-corrected Akaike's Information Criterion (AIC_C), increase in AIC_C relative to the model with the lowest AIC_C value ($\Delta\text{AIC}_\text{C}$), relative AIC_C weight (wAIC_C) and goodness of fit (Adjusted R^2).

RainAV	Response	Model	*edf*	AIC_C	$\Delta\text{AIC}_\text{C}$	wAIC_C	Adjusted R^2
Residency index							
m11	RI	TL + month × sex	17.88	592.67	0.00	1.00	4.8
m7	RI	TL + month	11.81	661.58	68.91	0.00	4.3
m10	RI	TL + sex + month	12.81	663.47	70.80	0.00	4.5
m12	RI	month + sex × TL	14.43	666.71	74.04	0.00	4.4
m23	RI	TL + pressAV	4.90	696.62	103.95	0.00	4.1
m43	RI	sex × TL + pressAV	5.90	698.58	105.91	0.00	4.2
50% kernel area							
m84	sqrt (50% KA)	temp + tideR	3.62	-236.03	0.00	0.06	0.6
m19	sqrt (50% KA)	tideR	2.65	-235.98	0.05	0.06	0.2
m13	sqrt (50% KA)	pressAV	1.21	-235.61	0.42	0.05	1.5
m66	sqrt (50% KA)	pressAV + tideR	3.39	-235.43	0.60	0.05	1.2
m4	sqrt (50% KA)	month	3.04	-235.24	0.79	0.04	2.0
m29	sqrt (50% KA)	TL + tideR	3.41	-235.17	0.86	0.04	2.8
m79	sqrt (50% KA)	rainAV + tideR	3.59	-235.12	0.91	0.04	1.1
m7	sqrt (50% KA)	TL + month	3.98	-235.06	0.97	0.04	1.5
m23	sqrt (50% KA)	TL + pressAV	3.17	-234.97	1.06	0.04	1.8
m92	sqrt (50% KA)	tideR + wdireAV	3.39	-234.80	1.24	0.03	0.4
m2	sqrt (50% KA)	TL	2.37	-234.72	1.31	0.03	2.4
m64	sqrt (50% KA)	pressAV + pressR	2.95	-234.45	1.58	0.03	1.5
m63	sqrt (50% KA)	pressAV + rainAV	3.09	-234.15	1.88	0.03	2.4
95% kernel area							
m25	sqrt(95% KA)	TL + rainAV	3.07	129.39	0.00	0.26	8.2
m45	sqrt(95% KA)	TL + sex + rainAV	4.08	130.83	1.44	0.13	12.7
m15	sqrt(95% KA)	rainAV	1.58	131.65	2.26	0.08	2.4
m35	sqrt(95% KA)	sex + rainAV	2.58	133.14	3.75	0.04	6.2
m76	sqrt(95% KA)	rainAV + tempAV	2.3	133.16	3.77	0.04	3.2
m79	sqrt(95% KA)	rainAV + tideR	2.13	133.61	4.22	0.03	2.9

4.4 Discussion

Our study is the first to quantify residency and patterns of space use of neonate *C. melanopterus* and *N. acutidens* in the eastern Indian Ocean. Differences in the residency patterns between these species implied that for *N. acutidens* the nearshore waters of Mangrove Bay meet the proposed criteria of Heupel *et al.* (2007) for a nursery, but it is apparent that additional data is required for *C. melanopterus*. Neonates of *N. acutidens* had relatively small activity spaces (mean 95% KA = 4.8 km^2), a pattern consistent with earlier studies both at Ningaloo (Speed *et al.*, 2011, 2016) and elsewhere (Filmalter *et al.*, 2013b) and we also found evidence of ontogenetic expansions in space use among neonates of this species.

While our study does not provide quantitative data on increased neonate abundance in Mangrove Bay (one of the criteria for a nursery area), our high capture rates and extensive in-water surveys from Stevens et al. (2009) suggest that Mangrove Bay supports higher abundances of both species. The presence of open and partially healed umbilical scars (age < 1 week; Chin et al. 2015) on both *C. melanopterus* and *N. acutidens* captured between November and February over two seasons indicates that neonates of these species are pupped in or near to Mangrove Bay in autumn and summer and some remain there for up to 17 months. We found highly variable patterns in the residency of neonate and juvenile *C. melanopterus* (mean ± SD; 0.2 ± 0.3), consistent with reported variability in residency of juveniles of this species (0.3 ± 0.3) in East Australia (Chin et al., 2016). Our findings for *C. melanopterus* contrasted with patterns of long-term residency we found for *N. acutidens* and corroborate increasing evidence that although extended residency in shark nurseries is common (Chapman *et al.* 2009; DeAngelis *et al.*, 2008; Legare *et al.*, 2015; Knip *et al.* 2011), it is not universal in juvenile sharks (Chin et al., 2016; Munroe et al., 2016). Our results suggest that although Mangrove Bay may provide suitable pupping grounds for *C. melanopterus*, it does not appear to function as a long-term nursery habitat for this species. Prolonged residency and site attachment has been recorded for adult *C. melanopterus* on isolated coral atolls (Papastamatiou *et al.*, 2009; Mourier *et al.*, 2012), whereas large-scale dispersal (>80 km) has been documented for neonates and juveniles in archipelagic systems (Chin *et al.*, 2013a, 2016). The shallow depth of the lagoon at Mangrove Bay (< 4 m) and availability of contiguous reef habitat along Ningaloo Reef may facilitate the dispersal of neonate *C. melanopterus* along the reef system. Two of the nine *C. melanopterus* (B5 and B9) that permanently departed the array were last recorded on the receivers at the northern limit of the array at Tantabiddi that indicate a minimum linear dispersal distance of 10 km. Alternatively, or in addition, low apparent residencies of neonate *C. melanopterus* could also reflect high mortality rates, as have been documented for juvenile blacktip

(Heupel & Simpfendorfer, 2002), lemon (Gruber *et al.*, 2001) and scalloped hammerhead *Sphyrna lewini* (Duncan & Holland, 2006) sharks elsewhere. In contrast, 70% of tagged *N. acutidens* had relatively high residency and displayed repeated use of nearshore, shallow sandflats, consistent with patterns reported for this species at atolls in the western Indian Ocean (Filmalter *et al.*, 2013b) and habitat selection in other similar-sized carcharhinids (Papastamatiou *et al.*, 2009; Chin *et al.*, 2012; Rizzari *et al.*, 2014a).

As expected, our temporal models revealed a progressive decline in monthly residency and increase in monthly space use with ontogeny for resident individuals of *N. acutidens*. Ontogenetic expansion in space use (Garla *et al.*, 2006; Dicken *et al.*, 2007; Knip *et al.*, 2011), followed by reduced nursery residency (Hussey *et al.*, 2009; Conrath & Musick, 2010) has been observed in many sharks, and is thought to reflect foraging optimisation in association with reduced predation risk as sharks grow in size (Heupel *et al.*, 2004; Matich & Heithaus, 2015). The relationship with total length and overall residency of *N. acutidens* showed the opposite trend to monthly residency, with an increase in overall residency for the larger neonates. These differences might suggest that other factors besides ontogeny drive residency, however it would seem that our temporal modelling approach which incorporated monthly increases in shark total length was more appropriate for examining the relationship between ontogeny and residency.

Estimates of total space use by neonate and juvenile *C. melanopterus* (95% KA; 0.3 – 31.5 km^2) were consistent with estimates in East Australia (95% KA; 10.9 – 30.1 km2) (Chin et al., 2016), and larger than those found in older juveniles (Minimum convex polygons (MCP); 5.8 – 8.5 km^2) and adults (MCP; 3.5 – 21.8 km^2) in this region (Speed *et al.*, 2016). Our findings support recent evidence that coastal habitat use by *C. melanopterus* (Chin et al., 2016) differs from conspecifics on coral reefs (Papastamatiou et al., 2011; Mourier et al., 2013b) and do not conform to the characteristic patterns of classical nursery use where neonates demonstrate highly restricted movements before undergoing ontogenetic expansions in space use. Our results combined with previous studies reflect ecological flexibility of *C. melanopterus* in being to adapt movement patterns to optimise the use of local environments and suggest that this behaviour may be innate. In any event, our results must be treated with caution due to the low sample size (n = 10) of tagged *C. melanopterus* and the relatively short durations of monitoring.

Consistent with previous observations of overlap in nursery habitat use by *C. melanopterus* and *N. acutidens* in the Pacific Ocean (Papastamatiou et al., 2009; Mourier et al., 2013a), both species in our study showed positive selection for nearshore sandflat and vegetated (mangrove and algal pavement) habitats indicating low levels of habitat partitioning. This absence of habitat partitioning and space use overlap between and within species may reflect opportunistic use of abundant refuges or prey resources (Frisch *et al.*, 2016) within sandy flats and vegetated habitats where parturition occurs (Papastamatiou et al., 2009; Mourier et al., 2013a). Alternatively, strong selection for inshore mangroves and sandflats may relate to reduced predation risk within physical refuges (Guttridge *et al.*, 2012), increased chances of finding prey on shallow sandflats (Papastamatiou *et al.*, 2009) or behavioural thermoregulation (Papastamatiou *et al.*, 2015). Avoidance of deeper lagoonal and reef slope habitats by neonate sharks may reduce predation risk or competition with other species, as larger predators such as adult *C. melanopterus*, sub-adult *N. acutidens*, grey reef sharks *C. amblyrhynchos* and tiger sharks *Galeocerdo cuvier* frequent these habitats (Ferreira et al., 2015; Speed et al., 2016).

Our modelling of temporal patterns indicated that environmental variables influenced space use of *N. acutidens* on a monthly basis, but had no influence on monthly residency. Along with expansions in space use with ontogeny, we found a weak negative influence of tidal range on core space use of neonate *N. acutidens*, consistent with the hypothesis of tide-mediated selection of shallow or familiar habitats as a strategy for predator avoidance, as seen in juvenile lemon sharks *N. brevirostris* (Guttridge *et al.*, 2012). At Mangrove Bay, the high-use area at the southern part of the Bay contained a shallow sandflat adjacent to a mangrove-fringed inlet that remained flooded at low tides. Our telemetry data and capture locations confirmed that at high tide, neonate *N. acutidens* often remained within the complex of mangrove root systems that probably afforded a physical refuge for these juveniles from larger predators. Alternatively, or in addition, reduced space use may also be a strategy for optimizing foraging efficiency as a consequence of tidally-driven prey migrations via discrete corridors (Friedlander & Monaco, 2007; Papastamatiou *et al.*, 2009). Consistent with evidence of behavioural responses of a range of Carcharhinid shark species to changing barometric pressure (Heupel et al., 2003; Udyawer et al., 2013), we also detected slight increases in core space use of *N. acutidens* with increases in barometric pressure. Increases in total space use of *N. acutidens* with increasing rainfall, may reflect avoidance of freshwater inflows or the re-dispersion of prey from core parts of the habitat. Alternatively, freshwater inflows were hypothesised to contribute to increased niche separation of juvenile sharks from adults (Heupel & Simpfendorfer, 2008) and to expand available habitat for juvenile bull sharks *C. leucas* (Matich & Heithaus, 2015). The minimal influence of environmental variables on residency suggests that local conditions and the availability of prey resources may be favourable year-round for this species in the nursery. The lack of seasonality in the residency of neonate *N. acutidens* females was consistent with patterns seen in older juveniles (Filmalter *et al.*, 2013b), however, we found increases in the residency of neonate *N. acutidens* males in winter months. Differences in residency patterns between sexes in adult sharks may be driven by sex-specific differences in thermoregulatory requirements (Hight & Lowe 2007), avoidance of sexual harassment in females (Wearmouth *et al.*, 2012) or sex-specific dietary preferences (McCord & Campana, 2003). The latter hypothesis could be verified by future studies examining differences in diet between the sexes. Our observations of sex-specific patterns residency in neonate and juvenile *N. acutidens* suggest that sex-specific behaviour may be innate.

Analysis of movements based on acoustic telemetry requires a number of assumptions to be made regarding equipment performance and cessation of detections from tagged animals. Contrary to other studies (Gjelland & Hedger, 2013; Mathies *et al.*, 2014; Huveneers *et al.*, 2016), we found no evidence of temporal variations in receiver performance due to ambient noise from wind or rain, changes in air pressure or water temperature. As movement and behaviour was not observed directly, an abrupt end in detections could have resulted from a number of possible causes including premature transmitter failure, tagging-associated mortality (predation or transmitter expulsion), natural or fishing mortality and dispersal of the tagged animal from the study area. Characteristic detection patterns indicated natural mortality of two *N. acutidens*, that were assumed to have died or been consumed close to a receiver after 65 and 17 days of tagging, resulting in the tag being continuously detected by one or more overlapping receivers. There was also one instance of fishing mortality, with one *N. acutidens* recaptured by recreational fishers. High rates of wound healing and survival of internally tagged individuals of our two focal species (Buray *et al.*, 2009; Filmalter *et al.*, 2013b; Chin *et al.*, 2015) and multiple recaptures of sharks between 2 – 19 days from release (17%) indicated that declines in detections of tagged sharks likely reflect dispersal to other sites, high rates of natural or fishing mortality or a combination of both, rather than tagging mortality.

4.4.1 Conservation and management

No-take zones in our study encompassed large proportions (>70 %) of total space use areas for neonate populations of *N. acutidens*, and *C. melanopterus* to a lesser extent, and provide some support for the use of small-scale no-take MPAs for effective management of the vulnerable, early life stages of carcharhinids (Garla *et al.*, 2006; Heupel *et al.*, 2010). To effectively protect mobile species, no-take zones should ideally be at least twice the size of the 95% kernel area of focal species (Green *et al*. 2015). Although total space use estimates of both species are largely encompassed by existing no-take zones, there was evidence of short-term residency and declining spatial protection for neonate *C. melanopterus* when their total lengths exceeded 60 cm, thus supporting our hypothesis of lower protection for larger-sized sharks. Conversely, protection afforded by no-take zones was seen to increase with body size of neonate, male *N. acutidens*. Both our study and a previous study suggests considerable rates of recapture (2.9% and 4.2% respectively) of tagged reef sharks by recreational fishers in the NMP (Speed *et al.*, 2016), indicating that areas within (Smallwood *et al.*, 2012) or adjacent to sanctuary zones may still be vulnerable to anthropogenic impacts. A southward extension of the Mangrove Bay sanctuary zone would enhance protection for neonate populations of *C. melanopterus* and *N. acutidens*. Our results indicate that similar scale no-take zones may provide some protection for other neonate populations of *C. melanopterus* along the Ningaloo Reef coast and increase the species' resilience at seascape scales (Mumby, 2006). Given that Ningaloo Reef extends over 320 km of coastline, it is unlikely that Mangrove Bay is the only potential nursery, although equivalent habitats with fringing mangroves are rare along this coastline (Smallwood *et al.*, 2012). Future work should focus on identification of key nursery and pupping locations and possible connectivity between these nurseries.

The short-term residency and higher dispersal capacity of *C. melanopterus* seen in our study and elsewhere (Chin *et al.*, 2013a, 2016) suggests that this species is able to utilise a wider variety of habitats for development than *N. acutidens*, particularly shallow reef environments within the region (Vanderklift *et al.*, 2014). In contrast, the intensive use of small areas by *N. acutidens* has implications for the vulnerability of the species due to increased exposure to coastal threats such as fisheries, pollution and habitat loss or degradation (Knip *et al.*, 2010). *C. melanopterus* is currently classified as “Near Threatened” globally by the International Union for the Conservation of Nature (Heupel, 2009), while *N. acutidens* is classified as “Least Concern” in Australia but “Vulnerable” globally (Pillans, 2003), providing opportunity to protect one of the last strongholds for the species. Although we have identified potential drivers of space use and residency for *C. melanopterus* and *N. acutidens* in their natal environments, further studies of reef shark movement and behaviour involving an expanded acoustic array, active tracking in shallow micro-habitat, standardized surveys and genetic assessment of parentage (Mourier & Planes, 2012; Mourier *et al.*, 2013a) will aid in clarifying the significance of particular nursery habitats for population maintenance in contiguous coastal systems.

4.5 Acknowledgements

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4.6 Supporting Information

Table S4.5 Summary of the location, habitat type and detections of the acoustic receivers deployed in the Mangrove Bay array.

Receiver	Longitude	Latitude	Deployment		Habitat	MPA zoning	Site zoning	Total detections	% detections
			Start	End					
Tantabiddi									
1	-21.899	113.937	01-Mar-14	01-Jun-15	Coral reef		1	1	0.00
2	-21.909	113.944	19-Mar-13	01-Jun-15	Coral reef		1	17	0.00
3	-21.911	113.948	19-Mar-13	01-Jun-15	Coral reef		1	4	0.00
4	-21.915	113.956	01-Mar-14	19-Oct-14	Sandflat		1	0	0.00
5	-21.912	113.952	19-Mar-13	01-Jun-15	Rocky reef		1	1	0.00
6	-21.916	113.959	19-Mar-13	01-Jun-15	Sandflat		1	4	0.00
7	-21.918	113.963	19-Mar-13	01-Jun-15	Rocky reef		1	4	0.00
8	-21.920	113.967	19-Mar-13	01-Jun-15	Rocky reef		1	12	0.00
Mangrove bay									
9	-21.948	113.921	19-Mar-13	01-Jun-15	Coral reef	SZ	2	20	0.00
10	-21.949	113.926	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	0	0.00
11	-21.948	113.933	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	0	0.00
12	-21.948	113.939	19-Mar-13	01-Jun-15	Coral reef	SZ	2	0	0.00
13	-21.950	113.944	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	65	0.01
14	-21.957	113.941	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	970	0.19
15	-21.959	113.944	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	1845	0.36
16	-21.960	113.940	25-Mar-13	01-Jun-15	Algal reef	SZ	2	764	0.15
17	-21.961	113.943	25-Mar-13	31-May-15	Rocky reef	SZ	2	2322	0.46
18	-21.962	113.945	26-Mar-13	31-May-15	Rocky reef	SZ	2	4615	0.91
19	-21.962	113.934	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	231	0.05
20	-21.963	113.940	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	6707	1.33
21	-21.963	113.942	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	30593	6.05
22	-21.964	113.939	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	2018	0.40
23	-21.965	113.941	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	4006	0.79
24	-21.966	113.939	08-Dec-14	31-May-15	Rocky reef	SZ	2	112	0.02
25	-21.967	113.941	19-Mar-13	31-May-15	Rocky reef	SZ	2	5673	1.12
26	-21.967	113.936	19-Mar-13	01-Jun-15	Algal reef	SZ	2	2729	0.54
27	-21.968	113.939	19-Mar-13	01-Jun-15	Sandflat	SZ	2	4407	0.87
28*	-21.969	113.941	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	39054	7.72
29	-21.969	113.938	19-Mar-13	31-May-15	Sandflat	SZ	2	135477	26.79
30*	-21.974	113.941	19-Mar-13	31-May-15	Sandflat	SZ	2	75768	14.98
31	-21.969	113.925	19-Mar-13	01-Jun-15	Coral reef	SZ	2	1582	0.31
32	-21.969	113.930	19-Mar-13	01-Jun-15	Rocky reef	SZ	2	156	0.03
33	-21.972	113.919	19-Mar-13	01-Jun-15	Coral reef	SZ	2	92	0.02
34	-21.970	113.936	19-Mar-13	01-Jun-15	Sandflat	SZ	2	161182	31.87
35	-21.972	113.939	26-Mar-13	31-May-15	Mangrove	SZ	2	18401	3.64
36	-21.948	113.914	19-Mar-13	01-Jun-15	Coral reef		3	1	0.00
37	-21.956	113.913	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00
38	-21.959	113.912	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00
39	-21.966	113.910	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00
40	-21.971	113.911	19-Mar-13	01-Jun-15	Coral reef		3	2	0.00

41	-21.972	113.902	19-Mar-13	24-May-13	Rocky reef		3	0	0.00
42	-21.973	113.911	19-Mar-13	01-Jun-15	Coral reef		3	1	0.00
43	-21.976	113.907	08-Mar-14	24-Oct-14	Rocky reef		3	0	0.00
44	-21.979	113.912	19-Mar-13	01-Jun-15	Coral reef		3	5	0.00
45	-21.980	113.902	08-Mar-14	01-Jun-15	Rocky reef		3	1	0.00
46	-21.984	113.904	08-Mar-14	24-Oct-14	Rocky reef		3	0	0.00
47	-21.983	113.908	08-Mar-14	01-Jun-15	Coral reef		3	0	0.00
48	-21.983	113.912	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00
49	-21.989	113.902	19-Mar-13	02-Mar-14	Rocky reef		3	26	0.01
50	-21.989	113.909	19-Mar-13	22-Oct-14	Coral reef		3	1	0.00
51	-21.991	113.898	19-Mar-13	19-Oct-14	Rocky reef		3	6	0.00
52	-21.992	113.907	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00
53	-21.998	113.905	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00
54	-22.001	113.903	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00
55	-22.005	113.902	19-Mar-13	01-Jun-15	Coral reef		3	0	0.00
56	-22.013	113.899	19-Mar-13	26-Oct-14	Coral reef		3	0	0.00
57	-21.975	113.924	19-Mar-13	01-Jun-15	Coral reef		4	763	0.15
58	-21.974	113.930	19-Mar-13	01-Jun-15	Algal reef		4	3144	0.62
59	-21.977	113.919	19-Mar-13	01-Jun-15	Coral reef		4	23	0.00
60	-21.980	113.921	19-Mar-13	01-Jun-15	Coral reef		4	13	0.00
61	-21.980	113.929	19-Mar-13	01-Jun-15	Sandflat		4	2119	0.42
62	-21.985	113.932	19-Mar-13	01-Jun-15	Coral reef		4	509	0.10
63	-21.986	113.919	19-Mar-13	01-Jun-15	Coral reef		4	1	0.00
64	-21.987	113.925	19-Mar-13	01-Jun-15	Coral reef		4	12	0.00
65	-21.988	113.923	02-Mar-14	01-Jun-15	Coral reef		4	0	0.00
66	-21.989	113.920	19-Mar-13	01-Jun-15	Coral reef		4	0	0.00
67	-21.989	113.915	19-Mar-13	01-Jun-15	Coral reef		4	2	0.00
68	-21.991	113.922	19-Mar-13	01-Jun-15	Coral reef		4	0	0.00
69	-21.991	113.931	19-Mar-13	01-Jun-15	Algal reef		4	183	0.04
70	-21.992	113.920	19-Mar-13	01-Jun-15	Coral reef		4	0	0.00
71	-21.994	113.925	19-Mar-13	01-Jun-15	Algal reef		4	13	0.00
72	-21.997	113.931	19-Mar-13	01-Jun-15	Rocky reef		4	45	0.01
73	-21.997	113.915	19-Mar-13	01-Jun-15	Coral reef		4	15	0.00
74	-21.999	113.921	19-Mar-13	01-Jun-15	Coral reef		4	6	0.00
75	-22.001	113.926	19-Mar-13	01-Jun-15	Coral reef		4	5	0.00
76	-22.005	113.912	19-Mar-13	01-Jun-15	Coral reef		4	4	0.00
77	-22.006	113.916	19-Mar-13	01-Jun-15	Rocky reef		4	12	0.00
78	-22.006	113.921	19-Mar-13	01-Jun-15	Coral reef		4	0	0.00
Turquoise bay									
79	-22.085	113.871	19-Mar-13	01-Jun-15	Rocky reef		6	0	0.00
80	-22.086	113.874	19-Mar-13	01-Jun-15	Rocky reef		6	0	0.00
81	-22.088	113.877	19-Mar-13	01-Jun-15	Coral reef		6	0	0.00
82	-22.089	113.880	19-Mar-13	01-Jun-15	Coral reef	SZ	5	0	0.00
83	-22.091	113.883	19-Mar-13	01-Jun-15	Coral reef	SZ	5	0	0.00
84	-22.093	113.886	19-Mar-13	01-Jun-15	Coral reef	SZ	5	4	0.00
85	-22.095	113.888	19-Mar-13	01-Jun-15	Coral reef	SZ	5	3	0.00

Table S4.6 Summary of the effects of varying sig2 values on estimates of 50% and 95% kernel areas of one *N. acutidens* individual. Monthly tracks of the shark #L1, which had the median value for 50% kernel area, were used to estimate kernel area range.

Sig2 value	Detection probability	Kernel area (KA) range	
		50% KA (km2)	95% KA (km2)
285.2	0.20	0.24 – 0.51	0.96 – 1.84
263.2	0.25	0.22 – 0.49	0.9 – 1.75
252.3	0.30	0.21 – 0.47	0.84 – 1.67
229.8	0.40	0.18 – 0.44	0.73 – 1.51
175.0	0.50	0.12 – 0.36	0.51 – 1.56
129.6	0.60	0.08 – 0.34	0.36 – 2.77
106.7	0.70	0.07 – 0.34	0.34 – 3.85
97.0	0.75	0.07 – 0.34	0.34 – 4.33
87.5	0.80	0.06 – 0.34	0.33 – 4.8

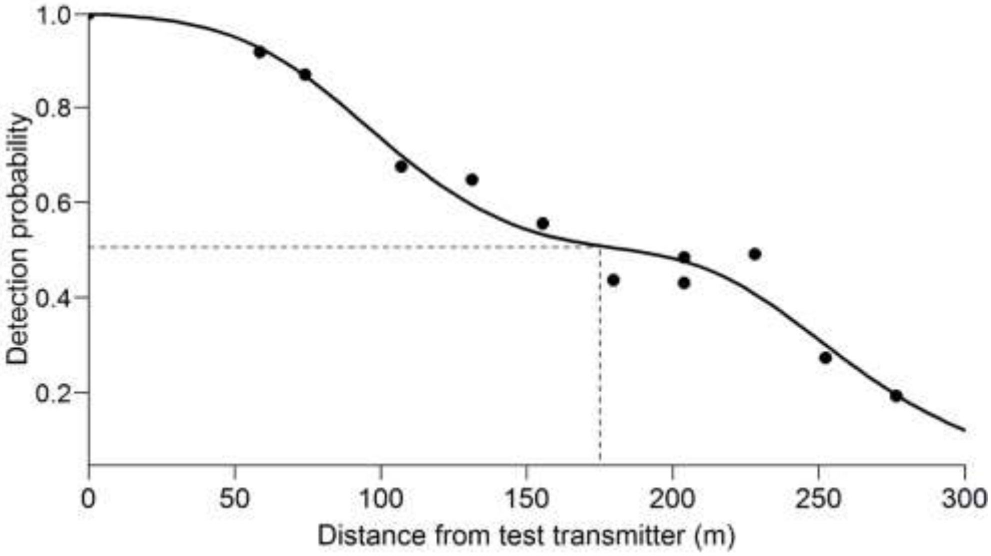

Figure S4.8 Detection probabilities recorded on acoustic receivers placed in intertidal areas, at increasing distances from a test transmitter at Mangrove Bay in March 2013. Data were fitted using a loess smoothing curve and *dashed lines* represent the effective detection range at which 50% of the transmissions were detected (D_{50} = 175 m).

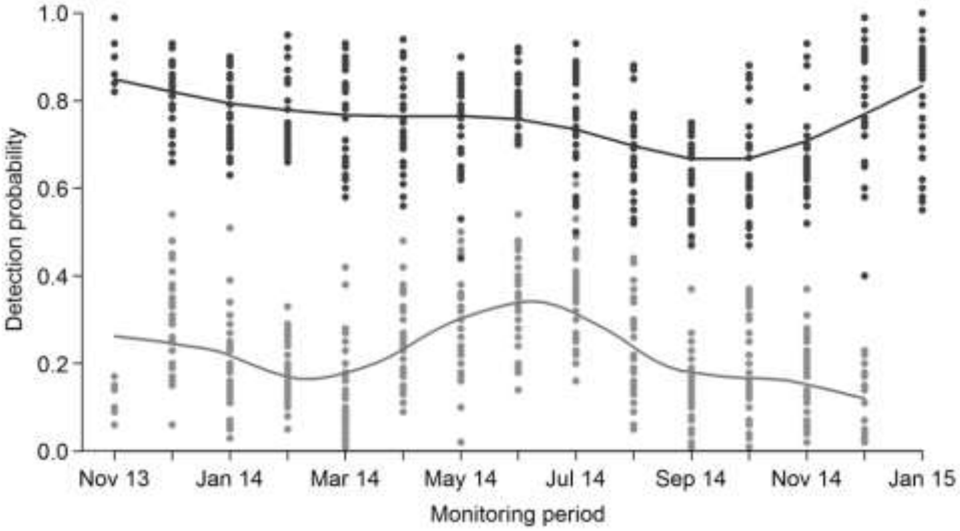

Figure S4.9 Monthly detection probabilities recorded on acoustic receivers placed 1 m (*black circles*; receiver #30) and 153 m (*grey circles*; receiver #28) from a sentinel transmitter used to monitor detection efficiency in Mangrove bay. Data were fitted using a loess smoothing curve and *circles* represent daily detection probabilities.

4.6.1 Methods

4.6.1.1 Variables influencing receiver efficiency

To examine environmental effects on monthly patterns of detection efficiency of two acoustic receivers placed 1 and 153 m from a V13-1H sentinel transmitter, we compiled a suite of explanatory variables including water temperature, air pressure, rainfall, tidal height, wind speed and direction, month, sex and total length of shark (Table 4.1). Water temperature was recorded at Tantabiddi using HOBO Pro V2 data loggers (calibrated at the Australian Institute Marine Science; AIMS) sampling at 30-min intervals, which were periodically downloaded and replaced every 3-12 months. Daily values for air pressure (hPA), rainfall totals (mm), wind speed (m s^{-1}) and direction (°) were obtained from a weather station at Milyering (10 m elevation; 22.03°S, 113.92°E) situated 6.8 km south of Mangrove Bay (http://data.aims.gov.au/). Predicted tidal height data were obtained through the Regional Oceanic Modelling System (https://www.myroms.org/). Values of monthly mean and range were computed for all variables from November 2013 to January 2015 and chronologically matched with detection data of the sentinel tag across the monitoring period. We used generalized additive mixed models (GAMMs) with binomial error distributions to model detection probability. We modelled month as a random effect in all models and fitted all environmental variables with a cubic regression spline, restricting the basis dimension "k" to < 4 to avoid overfitting. A maximum of one fixed term per model was specified due to relatively small sample sizes (*n* = 12). This resulted in a set of 11 candidate models (Table S4.7) which were ranked according to the sample-corrected Akaike's Information Criterion (AIC_C) and relative AIC_C weight ($wAIC_C$).

4.6.2 Results

4.6.2.1 Variables influencing receiver efficiency

Atmospheric pressure, water temperature, rainfall, wind speed and direction were not found to be important drivers of receiver performance (Table S4.7). Therefore, we found no evidence that the monthly patterns in residency and space use of tagged sharks in our study were an artefact of ambient noise from wind or rain or changes in air pressure or water temperature. We found the highest statistical support for model 7 ($wAIC_C = 1$) which showed a negative influence of tidal height on detection probabilities of the station located 1 m from the sentinel tag and model 8 ($wAIC_C = 1$) which showed negative influence of tidal range on detection probabilities at the station located 153 m from the sentinel tag (Table S4.7; Figure S4.10).

Table S4.7 Summary of the effects of environmental variables on detection probabilities recorded on acoustic receivers placed 1 m (receiver #30) and 153 m (receiver #28) from a sentinel transmitter used to monitor detection efficiency in Mangrove Bay. Month was treated as a random effect in all models; details for each model include the estimated degrees of freedom (*edf*), the sample-corrected Akaike's Information Criterion (AIC_C), relative AICC weight ($wAIC_C$) and goodness of fit (Adjusted R^2).

No.	Model	Receiver #30				Receiver #28			
		edf	AIC_C	$wAIC_C$	Adjusted R^2	*edf*	AIC_C	$wAIC_C$	Adjusted R^2
m1	1	0.00	5244.06	0	0	0	3938.69	0	0
m2	days.detected	9.87	4768.45	0	2.6	9.22	3853.48	0	21.4
m3	pressAV	2.76	5065.04	0	7.8	2.83	3892.54	0	5.1
m4	rainAV	1.90	5209.43	0	0.6	2.19	3852.26	0	0
m5	tempAV	2.89	5026.28	0	12.4	2.45	3931.24	0	1.8
m6	tempR	2.91	5189.72	0	0.4	0.43	3940.56	0	0.1
m7	tideAV	2.92	4185.76	0	27.6	2.96	3724.17	1	5.4
m8	tideR	2.92	3860.27	1	31.8	2.7	3770.69	0	2.4
m9	wdireAV	1.95	5186.17	0	0.8	1.74	3934.78	0	5.4
m10	wspeedAV	2.66	5238.57	0	0.4	2.9	3809.00	0	8.6
m11	wspeedR	2.31	5206.21	0	0.7	2.84	3925.91	0	0

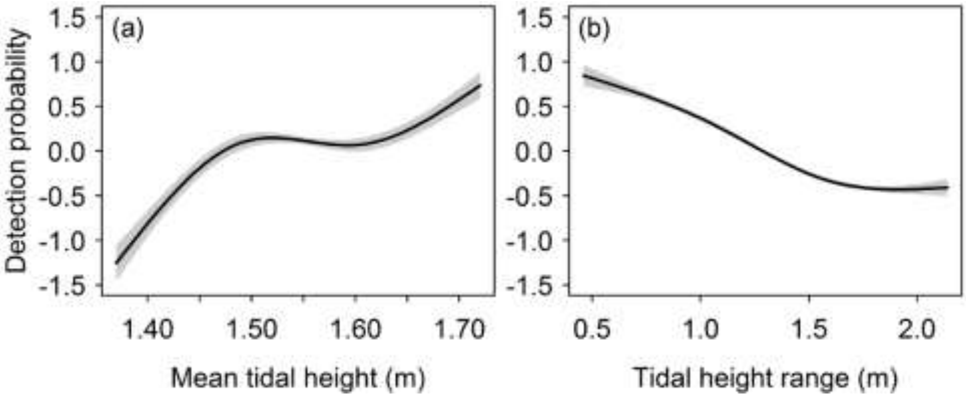

Figure S4.10 Partial residual plots of the effects of environmental variables on detection probabilities recorded on acoustic receivers located a) 1 m and b) 153 m from a sentinel tag placed within an area with highest shark activity (see Table S4.7 for an explanation of each model). Each column represents the influence of a variable on each response. *Black lines* represents the fitted smoother and *grey shaded areas* represent the 95% confidence intervals.

Chapter 5 Overlap and ontogenetic shifts in the diet of sympatric sharks in a coastal nursery ecosystem

Abstract: Resource partitioning allows sympatric species with similar niche requirements to coexist. Overlap in the distribution of many shark species that utilise coastal nurseries suggests they must partition food resources to share space. We analysed stable isotopes of δ^{13}C and δ^{15}N in tissues of blacktip reef (*Carcharhinus melanopterus*), nervous (*Carcharhinus cautus*) and sicklefin lemon sharks (*Negaprion acutidens*) of neonate, juvenile and adult age classes to model trophic niche space, size-related diet shifts and diet composition. Mean δ^{13}C was –9.7 (± 0.5 SE) for adults and ranged between –10.5 (± 0.6 SE) and –13.8‰ (± 1.2 SE) for neonates and juveniles, suggesting that reliance on coastal food webs decreased with ontogeny. Juvenile blacktip reef sharks exhibited the widest niche breath of δ^{13}C and used multiple carbon sources, whereas nervous and sicklefin lemon sharks partitioned coastal food webs within a relatively restricted range of δ^{13}C. Inter-specific differences in mean δ^{15}N and trophic position were preserved across age classes, consistent with a higher trophic role of sicklefin lemon sharks (range, 11.2–13.1 ‰) relative to blacktip reef (10.7–11.7 ‰) and nervous sharks (10.2–11.4 ‰). We found evidence of slight increases in δ^{13}C with body size of all species, presumably as foraging develops in neonates, while shifts in δ^{15}N with size varied among species. Nervous sharks fed at higher trophic levels, blacktip reef sharks had no change in δ^{15}N and young sicklefin lemon sharks displayed a decrease in δ^{15}N with size. Mixing models suggested similarities in shark diets and that herbivorous and some carnivorous fishes were proportionally more important prey than planktivores. Trophic overlap was presumably mediated by intra-specific partitioning in δ^{15}N niche space by diet specialists such as nervous and sicklefin lemon sharks and in δ^{13}C space by diet generalists such as blacktip reef sharks. Vulnerability to resource fluctuations may be greater for specialists than generalists.

5.1 Introduction

Resource partitioning, whether by habitat or diet, is a fundamental component that allows multiple species to co-exist within the same environment (Pianka, 1974). Partitioning in space and time, and by trophic level can reduce niche overlap and competitive pressure within and between species with similar niches (Schoener, 1974).

In marine systems, intra- and inter-specific partitioning of resources is widespread among mobile species that often co-exist within dynamic environments, such as seals, seabirds, whales and sharks (Page *et al.*, 2005; Cherel *et al.*, 2008; Friedlaender *et al.*, 2009; Tillett *et al.*, 2014). Resource use may differ between species and within species with respect to age classes and sexes, as a result of body size or condition, habitat domain and morphology (Bethea *et al.*, 2004; MacNeil *et al.*, 2005; Lewis *et al.*, 2006; Brischoux & Shine, 2011; Hussey *et al.*, 2011; Tillett *et al.*, 2014). Changes in energy requirements, foraging efficiency, swimming speed, jaw size, tooth morphology and vulnerability to predators through ontogeny often lead to shifts in habitat and resource use as individual needs and the nature of trade-offs change (Werner & Gilliam, 1984). The realized trophic niche of species likely reflects trade-offs between the diversifying effects of intra-specific competition and the constraints imposed by interspecific competition (Roughgarden, 1972; Bolnick *et al.*, 2010).

Dietary strategies exist on a spectrum from generalists that have large trophic niches and use multiple resources to obligate specialists that have small trophic niches and use a narrow range of resources (Futuyma & Moreno, 1988; Irschick *et al.*, 2005; Munroe *et al.*, 2014). Generalists can adapt to novel resources to compensate for declines in prey availability and maintain higher fitness in unstable environments (Chapman & Mackay, 1984; Richmond *et al.*, 2005; Heithaus *et al.*, 2006; Meyer *et al.*, 2010; Matich & Heithaus, 2013, 2015), but incur higher energetic costs (DeWitt *et al.*, 1998). In contrast, specialists can increase foraging efficiency and energy assimilation when environmental conditions are optimal and stable, but have reduced capacity to adapt to environmental change (Chin *et al.*, 2010). Improved understanding of the trophic niche of species is thus crucial to a clear definition of their role and vulnerability in their environment, and for developing effective management approaches under changing environmental conditions.

As ubiquitous predators in marine ecosystems, many sharks play important roles in energy transfer and trophic dynamics (McCauley *et al.*, 2012), although there is increasing recognition of high dietary variation and functional redundancy among species (Munroe *et al.*, 2013; Frisch *et al.*, 2016). The plasticity in dietary strategies, combined with evidence of individual variation, ontogenetic and spatio-temporal changes in diet, complicates our understanding of niche ecology in this functionally diverse group (Matich & Heithaus, 2013, 2015). Furthermore, the relatively low abundance, large size and mobile nature of many sharks has likely limited our ability to assess resource partitioning and competitive exclusion in this predatory guild (Papastamatiou *et al.*, 2006).

The vulnerable, early life stages of many sharks face unique foraging challenges when they aggregate in coastal nursery areas. These essential habitats are typically occupied by juveniles of multiple species (Bethea *et al.*, 2004; Kinney *et al.*, 2011; Tillett *et al.*, 2014) that have restricted home ranges and extended periods of residency, and may be frequented by large predatory sharks if they are energetically productive environments (Heithaus, 2007). Competition for limited resources may cause generalised species to become highly specialised (Bush & Holland, 2002; Papastamatiou *et al.*, 2006). Conversely, resource-rich nurseries may be frequented by larger predatory sharks forcing juveniles to forage sub-optimally to reduce predation risk (Heithaus & Dill, 2002; Guttridge *et al.*, 2012). Competition and predation can regulate selection pressures on the foraging efficiency of juvenile sharks, with some evidence that selection against large size and high condition may occur in environments with increased predation risk (DiBattista *et al.*, 2007). Communal nursery areas therefore offer an appropriate model for investigating the dynamics of niche differentiation in shark communities.

The evaluation of diet among sympatric species is challenging when attempts employ stomach content data that allow only for dietary snap-shots (Bearhop *et al.*, 2004), occur over short time scales that may not capture spatio-temporal variations in resource use (Matich & Heithaus, 2013) or focus on specific age groups (Bethea *et al.*, 2004). Given these issues, many studies now employ stable isotope analyses, which provide a cost-effective tool to resolve the dietary strategies of sharks (MacNeil *et al.*, 2005), assess trophic niche breadth (Tilley *et al.*, 2013), and detect inter- and intra-specific resource partitioning (Kinney *et al.*, 2011; Tillett *et al.*, 2014) and ontogenetic trophic shifts (Matich & Heithaus, 2015). Although lacking the taxonomic resolution of stomach content analysis, stable isotope analysis can concurrently track energy transfer through ecological communities and capture complex predator-prey interactions, thereby offering robust information on long-term trophic niche size (Bearhop *et al.*, 2004). However, maternal interference on the isotopic signatures of neonate (age–0) individuals, particularly placentatrophic species, can complicate interpretation of trophic niche parameters (McMeans *et al.*, 2009; Hussey *et al.*, 2010a; Olin *et al.*, 2011; Belicka *et al.*, 2012). Thus, studies investigating the trophic niche of early life stages through ontogeny are necessary to assess how maternal influences may affect the interpretation of isotopic data.

In this study, we used stable isotope analysis to examine species-specific patterns in isotope niche metrics, resource use and trophic position within a coastal shark community. The system consisted of three species with differences in growth rates (total length per year; TL/year) and body size at maturity (TL_M): nervous *Carcharhinus cautus* (~24 cm TL/year; TL_M, females ≤101 cm and males ≤91 cm), blacktip reef *Carcharhinus melanopterus* (*ca.* 6.5 cm TL/year; TL_M, females, ≤133.5 cm; males, ≤105 cm) and sicklefin lemon sharks *Negaprion acutidens* (12-15 cm TL/year; TL_M, ≤220 cm) to provide a broad picture of niche specialisation (White *et al.*, 2002; Chin *et al.*, 2013c; Ebert *et al.*, 2013). We hypothesized that: i) sharks of these species are generalists that do not partition dietary resources, consistent with theory of resource abundance within productive coastal nurseries (Simpfendorfer & Milward, 1993; Rojas *et al.*, 2014); ii) trophic position ($\delta^{15}N$) would increase and carbon enrichment ($\delta^{13}C$) would decrease with increasing body size in accordance with ontogenetic shifts in diet within species (Olin et al. 2011, Matich & Heithaus 2015, Matich et al. 2015) and iii) the isotopic niche and trophic diversity of sharks, as indicators of dietary strategy (Munroe *et al.*, 2013), would vary by species and age class.

5.2 Methods

5.2.1 Study site

This study was conducted at Mangrove Bay, which forms part of the multiple-use Ningaloo Marine Park (NMP) in north-west Australia (Leprovost Dames & Moore, 2000; CALM & MPRA, 2005). All fishing is prohibited in no-take sanctuary zones that encompass over 33% of the reef (5,070 km^2), but recreational fishing is permitted in surrounding multiple-use zones. Mangrove Bay consists of shallow, mangrove-lined, lagoonal ecosystems that are protected by the Mangrove Bay Sanctuary Zone (11 km^2). Habitats in this system include coral outcrops, mangroves, algal-covered pavement interspersed with expanses of sandflats (Figure 5.1).

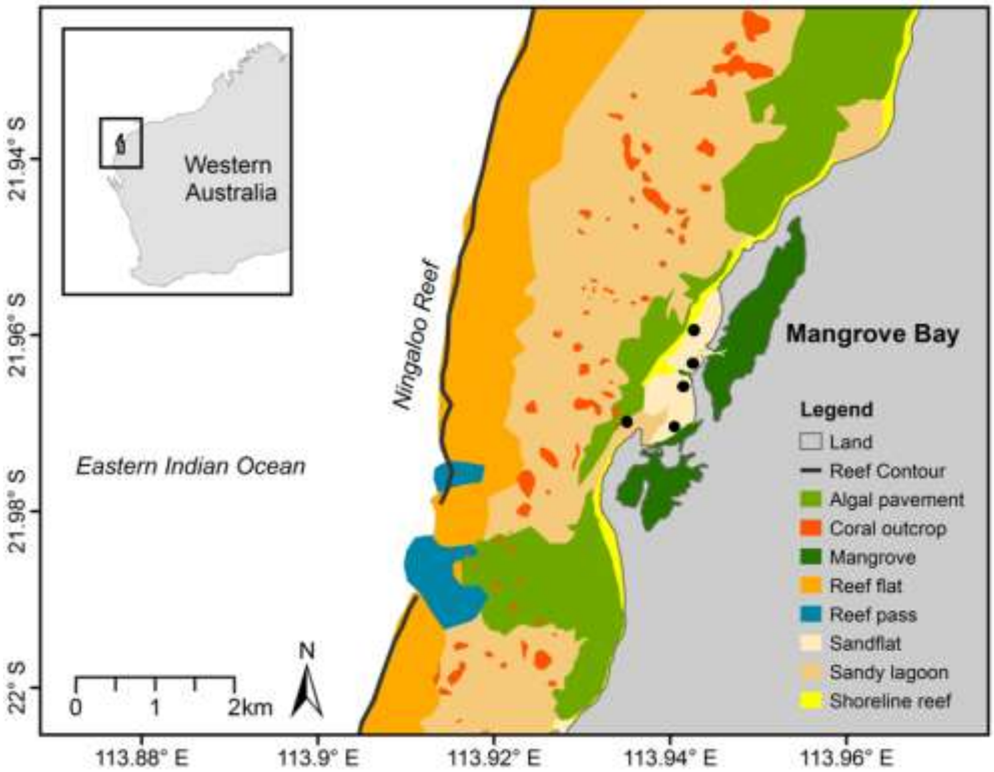

Figure 5.1 Main capture locations (*black circles*) of *C. cautus, C. melanopterus* and *N. acutidens* from which muscle samples were collected between March to December 2013 in Mangrove Bay, Ningaloo Reef, Western Australia.

5.2.2 Sample collection

Sharks and predatory fishes were captured using handlines and baited barbless circle hooks during the austral summer months (November to March) between November 2012 and December 2013. We sexed, measured stretched total length (TL) to the nearest 0.1 cm during each capture and classified sharks into age groups using observations of umbilical scars, clasper calcification (for males) and length-at-age data. Neonate sharks had unhealed umbilical scars, juveniles had healed umbilical scars and were ≤ length at 50% maturity, and adults were ≥ length at 50% maturity (White *et al.*, 2002; McAuley *et al.*, 2007; Last & Stevens, 2009; Chin *et al.*, 2013c) or had calcified claspers. Isotopic values (see below) of neonates were analysed separately to those of juveniles to discern the effect of maternal feeding on stable isotope signatures (Olin *et al.*, 2011). Approximately 0.3 cm^3 of white muscle was collected from the anterior dorsal region of each shark using a sterilized biopsy punch and scalpel blade, and care was taken to ensure that skin, cartilage (or bone) and connective tissue was excluded from the sample. White muscle tissue (~1 cm^3) from various teleost fish species (Supporting Information, Table S5.5) was also collected from the abdomen of each fish. Clippings of algae and mangrove leaves were collected by hand from sites throughout the bay. Water samples of zooplankton were also collected by towing a plankton net (333-µm mesh) horizontally at the surface (2 min at ~ 30 m min^{-1}) in calm conditions at high tide, to minimise contamination with suspended sediment or organic matter. The carbon content of algae was used to define reef-associated food webs, mangrove was used to characterise the base of inshore food webs and zooplankton used to characterise pelagic food webs. A total of 39 algae, 20 mangrove and 5 zooplankton samples and 43 muscle samples from 14 teleost fishes (Supporting Information, Table S5.5) were collected. All samples were stored on ice during transport and immediately frozen (below -20°C) on return to the laboratory. This study followed procedures approved under Department of Parks and Wildlife licences (SF009588, 163165, CE004244), Department of Fisheries WA exemptions (2150, 2355), and University of Western Australia Animal Ethics Committee (UWA AEC; RA 3/100/1168).

5.2.3 Laboratory preparation and isotope analysis

All samples were thawed, rinsed in deionised water and inspected visually for sources of contamination. Sections of plant tissue (i.e., non-calcareous algae and mangrove leaf) were cleaned of visible residue and epiphytes and removed from the thallus or stem respectively. Zooplankton (>333 µm) was filtered onto Whatman GF/F filters (0.7 µm pore size), oven-dried and exposed to 12 M hydrochloric acid fumes in a desiccator (Lorrain *et al.*, 2003). All samples were then oven-dried at 60°C for 48 hours and homogenized using either hand-held polypropylene pestles or a Mixer Mill MM 200 with 6.4-mm ball bearings. Aliquots of 0.6–0.7 mg of dried fish muscle and 1.1–12 mg of dried plant material were weighed to the nearest 0.001 mg into sterilized tin capsules and analysed for carbon (^{13}C) and nitrogen (^{15}N) content at two facilities. Isotopic content (12% of samples) were analysed initially using a 20–22 IRMS isotope-ratio mass spectrometer coupled to an ANCA-GSL elemental analyser (Sercon Limited/United Kingdom) at the Edith Cowan University Natural Isotopes Laboratory. Following closure of this facility, the remaining samples (88%) were analysed using a continuous flow system consisting of a Delta V Plus isotope-ratio mass spectrometer connected to a Thermo Flush 1112 via Conflo IV (Thermo-Finnigen/Germany) at the University of Western Australia, Western Australian Biogeochemistry Centre (WABC). Stable-isotope ratios were expressed in δ-notation (‰) relative to Vienna Pee Dee Belemnite ($\delta^{13}C$) and atmospheric N_2 ($\delta^{15}N$). Multi-points normalisation were used to reduce raw values to fit the international scale (Thompson *et al.*, 2005; Paul *et al.*, 2007), which were in turn based on Coplen et al. (2006). Samples analysed at the WABC were standardised against secondary reference samples (ANCA5 L-glut and WABC4 Glut), which were in turn standardised against primary analytical standards obtained from the International Atomic Energy Agency, Vienna ($\delta^{13}C$ –NBS22, USGS24, NBS19, LSVEC; and for $\delta^{15}N$ – N1, N2, N3 and laboratory standards). Based on laboratory and international standards, the analytical precision was 0.1 for both $\delta^{13}C$ and $\delta^{15}N$. To ensure sufficient tissue mass for isotopic analysis, we did not extract lipids from shark muscle samples. Instead, we applied a lipid correction factor ($\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.22 + 0.99 \times C:N$), following the methodology of (Post *et al.*, 2007) to $\delta^{13}C$ values. As shark samples had fairly low C:N ratios (2.92 ± 0.38; mean ± SD) (Hussey *et al.*, 2010b), lipid correction had minimal effects on $\delta^{13}C$ values (Table 5.1).

5.2.4 Data analysis

We applied a multi-model inference framework, tailored to each set of explanatory variables. Generalised linear models (GLMs) were used to model categorical variables and generalised additive models (GAMs) were used to model combinations of categorical and continuous variables. Sampling variations of total length between species, sexes, sampling year and site were examined using GLMs with Gaussian error distributions. For each explanatory variable, we compared the slope model with the intercept-only (i.e. null) model. We then evaluated the biological influence of shark species, sex and total length (TL) on $\delta^{13}C$ and $\delta^{15}N$ values using a candidate set of 14 GAMs with Gaussian error distributions. Total length was modelled using a cubic regression spline (bs = "cr"), with the basis dimension "k" restricted to < 4 to avoid overfitting. We specified a maximum of four fixed effects per model due to relatively small sample sizes and applied the rule of marginality including interactions only in models with both main effects. Following our tailored modelling framework, we used a unified, information-theoretic approach for model selection, ranking models according to the sample-corrected Akaike's Information Criterion (AIC_C) and evaluating strength of evidence based on the relative AIC_C weight ($wAIC_C$) (Burnham & Anderson, 2004). If several models fell within two AIC_C points of the best model, the most parsimonious model (i.e. with the least number of model terms) was used for graphical representation of variable effects. All analyses used the packages *mgcv* (Wood & Scheipl, 2015) and *MuMIn* (Barton, 2015) in R (R Core Team, 2015).

Sharks were assigned to one of seven species–age groups for subsequent analyses (Table 5.1). We quantified the trophic position (TP) of sampled shark groups assuming constant (Post et al. 2002) and scaled (Hussey *et al.* 2014a, b) diet-tissue fractionation. We used the equations: $TP_{constant} = \lambda + (\delta^{15}N_{shark} - \delta^{15}N_{base}) / \Delta_n$ and $TP_{scaled} = \lambda + \log_e(\delta^{15}N_{lim} - \delta^{15}N_{base}) - (\delta^{15}N_{lim} - \delta^{15}N_{shark}) / k$. The λ is the trophic position of a known baseline consumer, $\delta^{15}N_{shark}$ and $\delta^{15}N_{base}$ are the direct estimates of the mean $\delta^{15}N$ in each shark and baseline consumer respectively, Δ_n is the diet-tissue discrimination factor of sharks, $\delta^{15}N_{lim}$ is the saturating isotope limit, *k* is the average rate at which consumer isotope values approach $\delta^{15}N_{lim}$ per trophic step. We used a shark-specific value of 2.29 % for Δ_n and fish-specific values of 21.9% and 0.137 for $\delta^{15}N_{lim}$ and *k* respectively (Hussey *et al.*, 2010b, 2014a, 2014b).

To account for uncertainty in the suitability of any particular base group, we estimated TP using three base groups encompassing a range of λ values, including the detritivore *Mugil cephalus* (λ = 2.5), demersal predator *Lethrinus* spp. (λ = 3.8) and the large pelagic predator *Caranx ignobilis* (λ = 4.2). Consumers are typically used as baseline indicators rather than primary producers because they exhibit less temporal variability (Post et al. 2002). Trophic positions of fishes were based on published records derived from stomach content analyses (Farmer & Wilson 2011, Froese & Pauly 2014; <www.fishbase.org>). To determine the mean TP of sharks, each estimate of $TP_{constant}$ and TP_{scaled} was then weighted according to the respective λ used (rounded to the nearest integer), which accounted for increases in uncertainty with each trophic level due to potential error in estimates of diet-tissue fractionation (Hussey *et al.*, 2014).

Isotope data were plotted in $\delta^{13}C$–$\delta^{15}N$ space, and niche size and diet overlap were quantified with Bayesian standard ellipse areas (SEA_B) generated in the packages *SIBER* and *SIAR* in R (R Core Team, 2015). Bayesian ellipses corrected for small sample sizes (SEA_C) were used to account for potential bias in sampling effort when performing comparative analysis between species and age groups. The size of Bayesian ellipses provided a measure of isotopic diversity within each group and the proportion of overlap of ellipses between paired groups, calculated as an index of probability (0–1), provided a measure of niche overlap.

The relative contributions of potential prey species to the diet of sharks at Mangrove Bay was estimated using the Bayesian stable isotope mixing model *MixSIAR* GUI (Stock & Semmens, 2016) in R (R Core Team, 2015). To capture the range of potential prey items taken by sharks (Frisch *et al.*, 2016), we included mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values of samples collected by our study and also from samples collected (in 2007) and analysed by Wyatt et al. (2010). Prey samples were collected during the same season (May–November) that sharks were sampled. MixSIAR uses Markov Chain Monte Carlo simulations to repeatedly estimate the probability distributions (5th, 25th, 50th, 75th and 95th) of the dietary proportions of each potential prey item until the best fit is found. It allows sources of uncertainty, larger numbers of sources and individual-specific trophic fractionation values ($\Delta\delta^{13}C$ and $\Delta\delta^{15}N$) to be incorporated in the analysis (Phillips *et al.*, 2014). We used trophic fractionation values that were directly quantified for a variety of fishes at Ningaloo Reef (Wyatt *et al.*, 2010). We calculated individual-specific trophic fractionation values for each prey item using the equation developed by Caut et al. (2008), where $\Delta\delta^{13}C = - 0.213(\delta^{13}C) - 2.85$ and $\Delta\delta^{15}N= -0.261(\delta^{15}N) + 4.90$ following the approach of Cardona et al. (2012). We ran the model including neonate, juvenile and adult sharks as the consumers and potential teleost fish prey as sources. Only sharks with isotopic signatures that fell within the convex hull polygon formed by prey items were included in the *MixSIAR* model runs. The Bayesian model used vague, non-informative priors and was built using three Markov chains with 3,000,000 steps per chain, a discarded burn-in of 1,500,000 iterations and a thinning interval of 500. Chain mixing trace plots, autocorrelation values and convergence diagnostics (Gelman & Rubin, 1992) were used to access each applied version of the models. All Bayesian analyses were implemented using the packages *R2jags* (Su & Yajima, 2015) in R (R Core Team, 2015) and JAGS v 4.2.0.

5.3 Results

Sixty-four sharks from three species: 36 sicklefin lemon, 20 blacktip reef and 10 nervous sharks, were analysed for isotopic content (Table 5.1). A broad range of shark sizes were sampled (TL, 52–174 cm), comprising of 22 neonate, 35 juvenile and 9 adult individuals (Table 5.1). Of the nine adult sharks sampled, six were nervous and three were blacktip reef sharks. No adult sicklefin lemon sharks were sampled (Table 5.1).

Table 5.1 Summary of isotopic metrics of adult (A), juvenile (J) and neonate (N) nervous (CC), blacktip reef (CM) and sicklefin lemon (NA) assigned to seven species-age groups based on umbilical scar presence and published length-at-age data. Details include mean and range values of total lengths (TL), carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope, trophic position, ellipse areas and non-overlapping ellipse area (unique area) for sampled groups of sharks. Ellipse areas were not examined for adult blacktip reef sharks (CM-A) due to small sample sizes. Trophic position (TP) was calculated relative to the TP of different base groups, assuming constant diet tissue fractionation as detailed in Hussey et al. 2010. Mean values of base $\delta^{15}N$ were derived from teleost species sampled in Mangrove Bay: *Mugil cephalus* (detritivore), *Lethrinus* spp. (demersal predator) and *Caranx ignobilis* (pelagic predator) and base trophic positions (λ) were derived from Farmer and Wilson (2011).

Group	Species – age group	n	Sex ratio (F: M)	Mean TL (cm ± SE)	Range TL (cm)	Mean $\delta^{13}C$ (‰ ± SE)	Range $\delta^{13}C$ (‰)	Mean $\delta^{15}N$ (‰ ± SE)	Range $\delta^{15}N$ (‰)	Mean C:N (‰ ± SE)	Ellipse area (‰^{2})	Unique area (‰^{2})	Mean TP (± SE)
CC-A	Nervous shark - Adult	6	4:2	108.8 ± 4.3^{a}	96 – 120	-9.7 ± 0.5	3.0	11.4 ± 0.3	1.8	2.82 ± 0.12	2.75 ± 0.01	0.43	4.3 ± 0.09
CC-J	Nervous shark - Juvenile	4	4:0	91.3 ± 4.5^{ab}	80 – 100	-10.5 ± 0.6	3.0	10.2 ± 0.2	0.8	3.09 ± 0.21	2.40 ± 0.01	0.31	3.7 ± 0.07
CM-A	Blacktip reef shark - Adult	3	2:1	117.0 ± 13.2^{a}	97 – 142	-9.7 ± 0.9	3.1	11.2 ± 0.3	1.0	3.31 ± 0.17	–	–	4.2 ± 0.09
CM-J	Blacktip reef shark - Juvenile	9	6:3	82.3 ± 6.4^{bc}	62 – 122.5	-11.5 ± 1.6	13.4	10.7 ± 0.4	3.8	2.99 ± 0.14	15.0 ± 0.04	6.63	4.0 ± 0.09
CM-N	Blacktip reef shark - Neonate	8	5:3	55.9 ± 1.3^{c}	52 – 63	-13.8 ± 1.2	9.2	11.7 ± 0.2	1.8	2.86 ± 0.09	6.79 ± 0.02	4.34	4.4 ± 0.07
NA-J	Sicklefin lemon shark - Juvenile	22	11:11	98.7 ± 6.0^{ab}	69.5 – 174	-12.1 ± 0.3	5.7	11.2 ± 0.2	3.5	2.9 ± 0.06	4.87 ± 0.01	0.00	4.1 ± 0.07
NA-N	Sicklefin lemon shark - Neonate	14	9:5	66.9 ± 1.3^{bc}	56 – 75	-11.3 ± 0.5	5.3	13.1 ± 0.1	1.4	2.7 ± 0.04	3.02 ± 0.01	3.02	5.0 ± 0.07

Mean (± SE) total lengths were largest for adult nervous (108.8 ± 4.3 cm) and blacktip reef sharks (117.0 ± 13.2 cm), and smallest for neonate blacktip reef sharks (55.9 ± 1.3 cm), with higher statistical support for the slope model that included species-age group ($wAIC_C = 1$) than the intercept-only model (Table 5.1).

We found no evidence for a difference in total length between sexes for all species ($wAIC_C = 0.9$ for the intercept-only model). There was evidence of an effect of sampling location ($wAIC_C = 0.8$ for the slope model) and year ($wAIC_C = 0.94$ for the slope model) on total length, therefore only total length was retained in subsequent modelling of isotopic content.

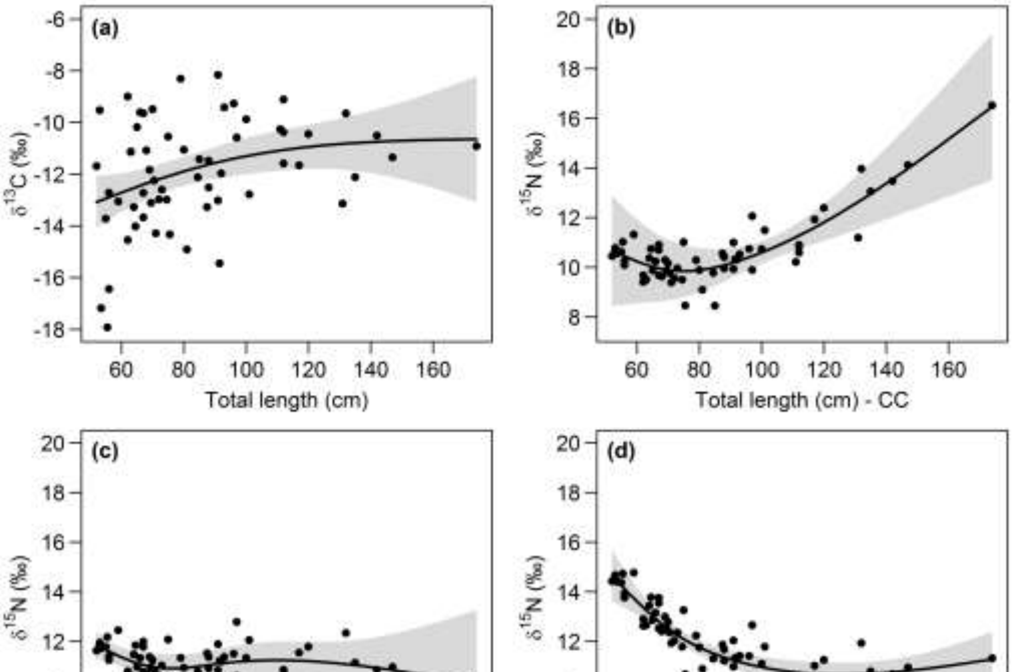

Figure 5.2 Partial residual plots showing the relationship between (a) carbon $\delta^{13}C$ and (b-d) nitrogen $\delta^{15}N$ isotope and the independent variables in the top ranked, most parsimonious additive model. *Black line, black circles* and *grey shaded areas* represent the fitted line, partial residuals and 95% confidence intervals respectively.

Our generalised additive models revealed equal statistical support (< 2 ΔAIC_C) for three models where $\delta^{13}C$ was the response and two models where $\delta^{15}N$ was the response (Table 5.2). For $\delta^{13}C$, the most parsimonious model included total length ($wAIC_C = 0.15$, DE = 13%), indicating a shift towards a more $\delta^{13}C$-enriched food source as TL increased within the size range examined (Table 5.2; Figure 5.2). The most parsimonious model for

$\delta^{15}N$ included species, TL and the interaction between species and TL (wAIC$_C$ = 0.49, DE = 67%), revealing species-specific trends in $\delta^{15}N$ with size. We found a strong shift towards a more $\delta^{15}N$-enriched diet with increasing body size of nervous sharks, no influence of body size on $\delta^{15}N$ of blacktip reef sharks, and a marked decline in $\delta^{15}N$ with increasing body size of sicklefin lemon sharks which stabilised when TL exceeded 100 cm (Figure 5.2). Our GAM analysis excluded three sharks (two blacktip reef and one sicklefin lemon sharks) that were notable outliers.

Table 5.2 Ranked generalised additive models of $\delta^{13}C$ and $\delta^{15}N$ of sampled sharks explained by the independent variables. The top six models for each response are shown; values in bold indicate the most parsimonious model. Details for each model include the estimated degrees of freedom (*edf*), the sample-corrected Akaike's Information Criterion (AIC$_C$), increase in AIC$_C$ relative to the model with the lowest AIC$_C$ value (ΔAIC$_C$), relative AIC$_C$ weight (*w*AIC$_C$) and percent deviance explained (DE; %).

No.	Response	Model	*edf*	AIC$_C$	ΔAIC$_C$	*w*AIC$_C$	DE (%)
m8	δ13C	species + TL + TL x species	6.54	259.28	0.00	0.31	30.8
m7	δ13C	species + TL	4.69	260.05	0.76	0.21	24.0
m4	**δ13C**	**TL**	**1.62**	**260.76**	**1.47**	**0.15**	**13.1**
m13	δ13C	species + sex + TL + TL x species	7.53	262.09	2.81	0.08	30.8
m10	δ13C	sex + TL + TL x sex	3.80	262.38	3.10	0.07	18.1
m11	δ13C	species + sex + TL	5.69	262.56	3.28	0.06	24.2
m13	δ15N	species + sex + TL + TL x species	8.79	138.91	0.00	0.51	68.2
m8	**δ15N**	**species + TL + TL x species**	**7.90**	**139.02**	**0.11**	**0.49**	**66.7**
m11	δ15N	species + sex + TL	4.90	162.20	23.30	0.00	44.3
m14	δ15N	species + sex + TL + TL x sex	5.95	163.30	24.40	0.00	45.8
m7	δ15N	species + TL	3.92	163.42	24.51	0.00	40.8
m12	δ15N	species + sex + TL + species*sex	6.89	167.48	28.57	0.00	44.3

Coastal sharks were broadly distributed through $\delta^{13}C$–$\delta^{15}N$ space (Figure 5.3), indicating a wide range of trophic diversity in foraging. Juvenile blacktip reef sharks displayed the largest range of $\delta^{13}C$ (13.4 ‰) and also of $\delta^{15}N$ (3.8 ‰), indicating a high degree of trophic diversity among individuals in this age class (Table 5.1). Mean $\delta^{13}C$ values were highest for adult nervous (-9.7 ± 0.5 ‰) and blacktip reef sharks (-9.7 ± 0.9 ‰), and lowest for neonate blacktip reef sharks (-13.8 ± 1.2 ‰). Mean $\delta^{15}N$ values were lowest for juvenile nervous sharks (10.2 ± 0.2 ‰) and highest for neonate sicklefin lemon sharks (13.1 ± 0.14 ‰), with mean trophic position (TP), calculated using a constant discrimination factor (TP$_{constant}$), ranging from 3.7 ± 0.07 in the former to 5.0 ± 0.07 in the latter. There was little variation in estimates of TP calculated using the scaled approach, except that mean TP$_{scaled}$ of neonate blacktip reef and sicklefin lemon sharks increased to 4.7 and 5.7 respectively (Supporting Information, Table S5.6). Isotopic niches of the seven species and age-specific groups differed in size and position, indicating a continuum of narrow to wide isotopic niches (Figure 5.3). Mean ellipse area (SEA$_C$) was smallest for juvenile nervous sharks (2.40 ± 0.01 ‰^{2}), and largest for juvenile blacktip reef sharks (15.0 ± 0.04 ‰^{2}; Table 5.1), with a significantly higher degree of trophic specialisation in the former groups relative to the latter group (SIBER, $p < 0.01$; Table 5.3, Figure 5.4). Unique ellipse area was consequently largest for juvenile blacktip reef sharks (6.63 ‰^{2}) and absent for juvenile sicklefin lemon sharks (0 ‰^{2}), with a higher degree of trophic partitioning in the former relative to the latter (Table 5.1, Figure 5.3). Overlap in isotopic niche, an indicator of trophic competition, was greatest between juveniles of blacktip reef and nervous sharks (87.3%), and absent between neonate sicklefin lemon sharks and all other groups (Table 5.3, Figure 5.3).

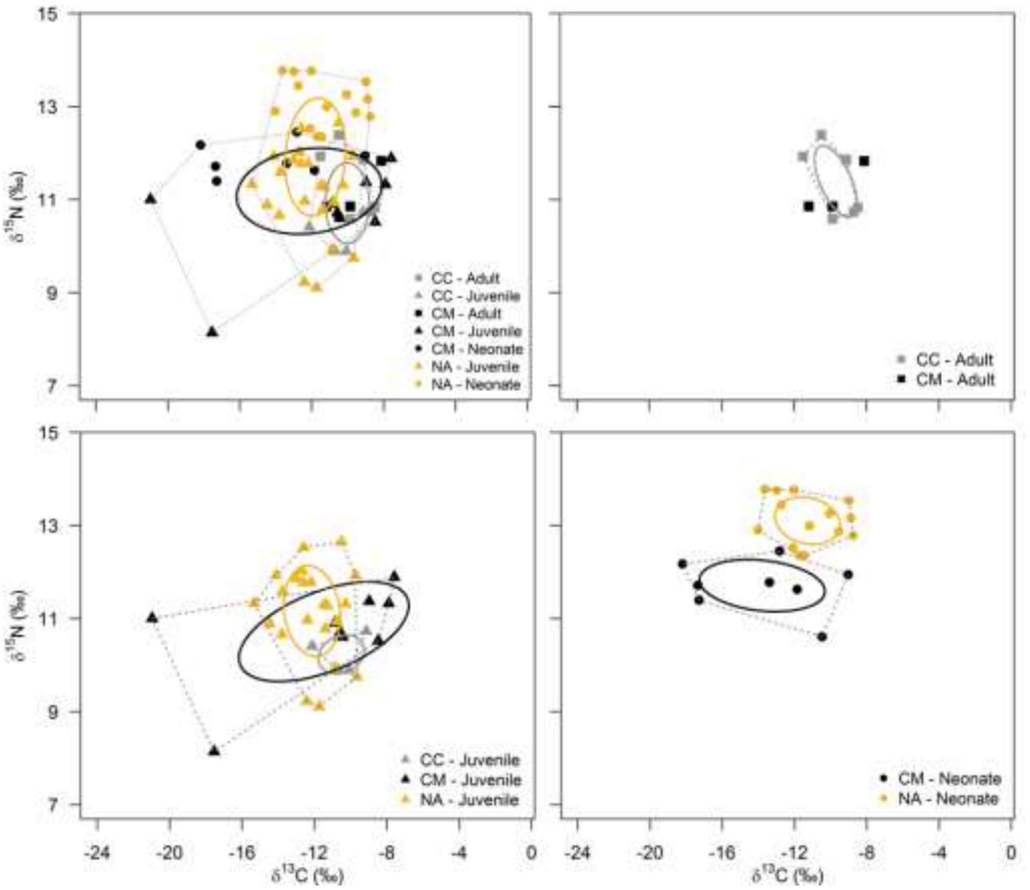

Figure 5.3 Isotopic (δ^{13}C-δ^{15}N) niches of nervous (CC; *grey symbols*), blacktip reef (*black symbols*) and sicklefin lemon (*yellow symbols*) represented as sampled-corrected Bayesian ellipses (*solid lines*) and convex hulls (*dotted lines*). *Squares*, *triangles,* and *circles* represent adult, juvenile and neonate age classes.

The MixSIAR mixing model indicated that prey items with isotopic signatures resembling the convict surgeonfish (*Acanthurus triostegus*) contributed most to the diet of six shark groups (34.9 – 77.8 %), whereas fishes with isotopic signatures similar to the reef-associated reticulated damselfish (*Dascyllus reticulatus*) contributed most to the diet of neonate sicklefin lemon sharks (17.1%; Table 5.4). Fishes with similar isotopic signatures to the spangled emperor (*Lethrinus nebulosus*) and giant trevally (*Caranx ignobilis*) had relatively small contributions to the diet of the six shark groups (1.1–3.5 % and 1.3–4.0 % respectively) as compared to neonate sicklefin lemon sharks that had greater contributions from fishes isotopically similar to these species (13.1% and 11.2% respectively; Table 5.4). The variation in the contribution of *Acanthurus triostegus* to shark diets was higher within shark groups (11.4–78.0%; maximum range of 5th–95th percentile) than between shark groups (34.9–77.8%; maximum range of mean) (Table 5.4). Seven juvenile (one nervous, four blacktip reef, two sicklefin lemon sharks) and two adult nervous sharks were excluded from the model runs as their positioning in δ^{13}C–δ^{15}N space violated the assumptions of the mixing model (Figure 5.5).

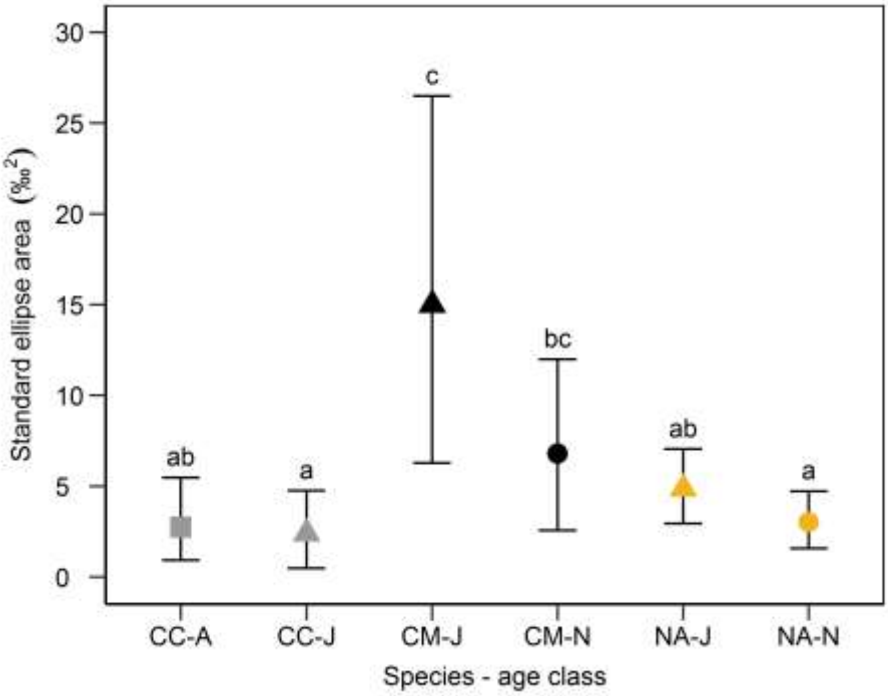

Figure 5.4 Variation in the sample-corrected Bayesian standard ellipse areas (SEA$_C$) of nervous (CC, *grey symbols*), blacktip reef (CM, *black symbols*) and sicklefin lemon sharks (NA, *yellow symbols*). *Squares*, *triangles*, and *circles* represent adult, juvenile and neonate age classes. Groups with the same letter did not have significantly different posterior distributions of SEA$_C$ based on pair-wise multiple comparisons.

Table 5.3 Overlap (%) of sample-corrected Bayesian standard ellipse areas (SEA$_C$) and probability that the SEA$_C$ of one species-age group is larger than the SEA$_C$ of another species-age group (in parentheses). Data should be interpreted as the percentage of SEA$_C$ of group 1 that is occupied by the SEA$_C$ of group 2. Values in bold indicate a significant difference in SEA$_C$ between the two groups when $\alpha = 0.01$.

Group 1	Group 2					
	CC-A	CC-J	CM-A	CM-J	NA-J	NA-N
CC-A	–	0.31 (0.3)	35.49 (0.48)	**79.83 (1.00)**	0.79 (0.89)	0 (0.6)
CC-J	0.36	–	9.95 (0.66)	**87.3 (1.00)**	14.83 (0.94)	0 (0.79)
CM-J	14.62	13.96	14.98	–	**24.28 (< 0.01)**	**0 (< 0.01)**
CM-N	5.71	0	0	23.06	36.1 (0.26)	0 (0.04)
NA-J	0.45	7.31	12.01	74.83	–	0 (0.08)
NA-N	0	0	0	0	0	–

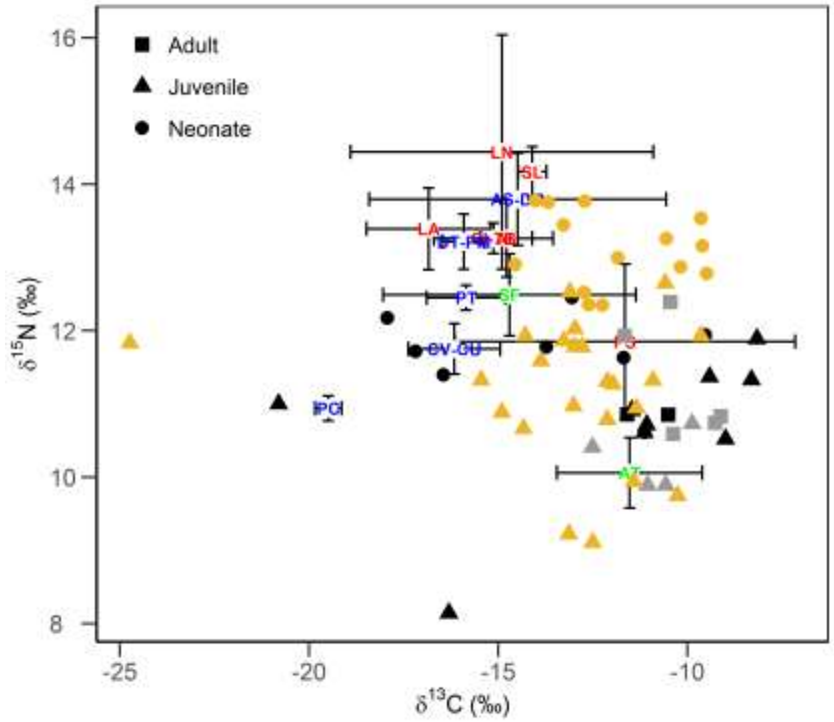

Figure 5.5 Isospace plot of potential prey items that contributed to the diet of (*grey symbols*), blacktip reef (*black symbols*) and sicklefin lemon (*yellow symbols*) sampled in Mangrove Bay. Prey item codes are detailed in Table S5.5 and Wyatt *et al.* 2010. Values (mean ± SD) were adjusted for isotopic discrimination between diet and tissue – functional groups include carnivores (*red*), planktivores (*blue*) and herbivores (*green*). All sampled sharks are shown for comparison, but only sharks whose isotopic values were within the convex hull polygon formed by prey items were included in the stable isotope mixing model (MixSIAR) runs. AL, *Acanthopagrus latus;* CI, *Caranx ignoblis;* LN, *Lethrinus nebulosus;* LA, *Lutjanas argentimaculatus;* PS, *Parupeneus signatus;* SL, *Scomberoides lysan;* TB, *Trachinotus botla;* AT, *Acanthurus triostegus*; CU, *Chrysiptera unimaculata;* SF, *Stegastes fasciolatus;* AS, *Abudefduf sexfasciatus;* CV, *Chromis viridis;* DA, *Dascyllus aruanus;* DR, *Dascyllus reticulatus;* DT, *Dascyllus trimaculatus;* PC, *Pomacentrus coelestis;* PM, *Pomacentrus moluccensis;* PT, *Pterocaesio tile*.

Table 5.4 Stable isotope mixing (MixSIAR) model results with mean percent diet contributions (5th – 95th percentile) of each potential prey item compared to δ^{13}C-δ^{15}N isotopic values of adult (A), juvenile (J) and neonate (N) age classes of nervous (CC), blacktip reef (CM) and sicklefin lemon (NA). Only shark samples with δ^{13}C-δ^{15}N that fell within the convex hull formed by the potential prey items were included in the model run. Values in bold indicate the contributions of major prey items.

Potential prey species	CC-A	CC-J	CM-A	CM-J	CM-N	NA-J	NA-N
Acanthopagrus latus	2.4 (0.1-7.3)	0.9 (0-3.7)	1.7 (0-6.9)	1.4 (0-5.1)	3.0 (0.1-12.1)	2.3 (0.1-8.9)	2.5 (0-10)
Caranx ignoblis	4.0 (0.1-12.7)	1.3 (0-4.9)	2.5 (0-9.5)	2.5 (0-10.3)	3.6 (0.1-13.3)	3.1 (0.1-11.3)	13.1 (0.1-59.9)
Lethrinus nebulosus	3.5 (0.1-11.6)	1.1 (0-4.2)	2.2 (0-8.6)	2.1 (0-9.4)	3.0 (0.1-11)	2.7 (0.1-9.9)	11.2 (0.1-48)
Lutjanas argentimaculatus	1.9 (0.1-5.7)	0.7 (0-3)	1.4 (0-5.3)	1.0 (0-3.6)	2.7 (0-11.6)	1.9 (0-7.5)	1.7 (0-6.7)
Parupeneus signatus	12.3 (0.5-32.9)	5.5 (0.1-19.7)	10.9 (0.2-43.1)	20.4 (0.2-67.3)	8.1 (0.3-25.3)	8.1 (0.2-26.6)	10.3 (0.2-31)
Scomberoides lysan	2.4 (0.1-7.1)	0.9 (0-3.2)	1.6 (0-6.1)	1.4 (0-5.3)	2.5 (0.1-9.8)	2 (0.1-7.7)	4.5 (0.1-23.1)
Trachinotus botla	2.7 (0.1-8.3)	0.9 (0-3.6)	1.8 (0-7.1)	1.5 (0-5.9)	2.7 (0.1-10.8)	2.3 (0.1-8.5)	5.5 (0.1-30.7)
Acanthurus triostegus	**41.9 (23.7-56.7)**	**77.8 (58.2-92)**	**58.0 (20.7-82.9)**	**53.6 (11.4-78.0)**	**34.9 (13.3-52.7)**	**50.7 (33-63.8)**	11.3 (2.9-23.5)
Chrysiptera unimaculata	2.8 (0.1-8.4)	1.2 (0-4.7)	2.2 (0-9.3)	1.4 (0-5.2)	5.1 (0.1-23.5)	3.2 (0.1-13.2)	2.0 (0.1-6.9)
Stegastes fasciolatus	2.8 (0.1-8.5)	1.1 (0-4.3)	1.9 (0-7.4)	1.4 (0-5.2)	4 (0.1-17.5)	2.7 (0.1-11.2)	2.4 (0.1-8.9)
Abudefduf sexfasciatus	2.7 (0.1-8.3)	0.9 (0-3.5)	1.8 (0-7)	1.5 (0-5.7)	2.8 (0.1-10.6)	2.4 (0.1-9)	5.0 (0.1-27.2)
Chromis viridis	2.7 (0.1-7.9)	1.1 (0-4.5)	2.0 (0-8.3)	1.3 (0-5.1)	5.2 (0.1-24.7)	2.9 (0.1-11.9)	1.9 (0.1-6.6)
Dascyllus aruanus	3.6 (0.2-10.9)	1.3 (0-4.8)	2.6 (0.1-10.6)	2.3 (0-8.9)	4.2 (0.1-16.7)	3.3 (0.1-12.9)	4.0 (0.1-16.2)
Dascyllus reticulatus	5.2 (0.2-15.7)	1.6 (0-5.9)	3.1 (0.1-12.4)	3.8 (0.1-16)	3.9 (0.1-13.6)	3.5 (0.1-11.8)	**17.1 (0.1-58.3)**
Dascyllus trimaculatus	2.1 (0.1-6.3)	0.8 (0-3.1)	1.5 (0-5.7)	1.1 (0-4.1)	2.9 (0.1-12.2)	2.1 (0-8.1)	2.0 (0-7.6)
Pomacentrus coelestis	2.2 (0.1-6.3)	1.0 (0-4.1)	1.6 (0-6.4)	1.0 (0-3.5)	4.2 (0.1-17.9)	2.3 (0-8.5)	1.4 (0-4.6)
Pomacentrus moluccensis	2.2 (0.1-6.6)	0.8 (0-3.3)	1.5 (0-6)	1.1 (0-4.3)	3.0 (0.1-12.8)	2.2 (0-8.7)	2.0 (0-8)
Pterocaesio tile	2.5 (0.1-7.3)	1.0 (0-3.6)	1.8 (0-6.9)	1.3 (0-5)	3.9 (0.1-17)	2.5 (0.1-9.9)	2.0 (0.1-7.7)

5.4 Discussion

Dependency on coastal producers and dietary specialization has potentially important implications for the vulnerability of coastal sharks and efficacy of existing conservation approaches (Munroe *et al.*, 2014). We found multiple lines of evidence to support the long-standing hypothesis of resource abundance within a coastal shark nursery (Heupel *et al.*, 2007). Firstly, mixing model results were consistent with previous research that the shark community were feeding on prey with similar isotopic signatures (White *et al.*, 2004; Farmer & Wilson, 2011; Frisch *et al.*, 2016), with the exception of neonate sicklefin lemon sharks. Secondly, restricted movement and overlap in space use by nervous, blacktip reef and sicklefin lemons in Mangrove Bay (Chapter 4; Escalle et al. 2015), suggests that these species are likely using similar coastal, benthic habitats for foraging. Thirdly, adult blacktip reef and nervous sharks were encountered within Mangrove Bay (Escalle et al. 2015; Speed *et al.*, 2016) and share similarities in diet composition and energy sources as juvenile conspecifics, suggesting that Mangrove Bay may supply ample resources for larger species and or that sharks partition prey by size class. Lastly, trophic overlap was mediated by intra-specific resource partitioning in $\delta^{15}N$ niche space by nervous and sicklefin lemon sharks, and in $\delta^{13}C$ space by blacktip reef sharks. Our results suggest that differences in trophic position and dietary strategy as a function of inter-specific differences in life-histories facilitate coexistence by multiple shark species and age classes using a shared environment.

The relatively high degree of $\delta^{13}C$ overlap observed for blacktip reef, nervous and sicklefin lemon sharks at Mangrove Bay and use of shared habitat by these three species during most life stages (White *et al.*, 2004; Papastamatiou *et al.*, 2006; Speed *et al.*, 2012a, 2016; Mourier *et al.*, 2013a; Frisch *et al.*, 2016), suggests competition for prey was likely consistent through ontogeny. The enriched $\delta^{13}C$ signatures of the shark community indicated that they are sustained by multiple benthic sources obtained from algae- (-13.8 ± 1.7 ‰; mean ± SD) or mangrove-based (-29.0 ± 1.5 ‰) food webs. Movement studies in Mangrove Bay indicate strong affinity for mangrove and algal pavement habitats by resident sicklefin lemon and nervous sharks, and a relatively small proportion of resident blacktip reef sharks (Chapter 4; Escalle *et al.*, 2015). Nervous sharks and to a lesser extent sicklefin lemon sharks had a relatively narrow range of $\delta^{13}C$

values, implying a reliance on algae- or seagrass-derived carbon that is consistent with earlier work (Heithaus *et al.*, 2013; Matich & Heithaus, 2015; Frisch *et al.*, 2016). Juvenile blacktip reef sharks exhibited the widest δ^{13}C niche breadth, with the most divergent δ^{13}C values indicating a reliance on mangrove-derived carbon by some individuals. The broad δ^{13}C niche breath is consistent with large-scale movements of some juvenile blacktip reef sharks seen at this site (Oh, unpublished data) and in East Australia (Chin *et al.*, 2013a) and is indicative of a generalist predator that uses a diversity of foraging habitats and prey (Munroe *et al.*, 2014). Wide variation in δ^{13}C for juvenile blacktip reef sharks may potentially result from individual specialisation in diet within a population of generalists (Papastamatiou et al. 2010; Matich *et al.*, 2011; Vaudo & Heithaus, 2011), although larger sample sizes and tissues with higher turnover rates will be needed to confirm this.

Inter-specific differences in δ^{15}N values were preserved across age groups, consistent with sicklefin lemon sharks having a relatively high trophic role compared to blacktip reef and nervous sharks (Speed *et al.*, 2012a; Heithaus *et al.*, 2013; Matich *et al.*, 2015; Frisch *et al.*, 2016). Species-specificity in δ^{15}N signatures likely reflect differences in life-histories, where neonate sicklefin lemon sharks are born at and attain larger sizes (56–75 cm; this study) than blacktip reef sharks (52–63 cm; this study) and nervous sharks (45–49 cm; White 2002). Mean δ^{15}N values for juvenile sicklefin lemon sharks (11.2) fell within the range of earlier studies (11.2 – 11.9) (Speed *et al.*, 2012a; Heithaus *et al.*, 2013; Frisch *et al.*, 2016). The elevated δ^{15}N and TP signature of nervous sharks at Mangrove Bay (10.2 – 11.4) relative to the only other study of the species at Shark Bay (8.7; >300 km south of Ningaloo Reef) may reflect increased food chain length in fringing mangrove bays relative to seagrass systems, more optimal feeding resulting from lower predation pressure or differences in δ^{15}N values of baseline consumers (Heithaus *et al.*, 2013; Bornatowski *et al.*, 2014b). While sub-adult and adult reef sharks often utilise the shark nursery at Mangrove Bay (Speed et al. 2016, Oh, unpublished data), the diversity of the shark community at Shark Bay suggests that small-bodied sharks likely face a higher predation risk in Shark Bay than Mangrove Bay, leading to differences in δ^{15}N and TP profiles between these sites. Geographic variations in δ^{15}N and TP values indicate that trophic interactions may be context-dependent and may result from variations in predation pressure, environmental conditions or resource availability (Matich &

Heithaus, 2015).

Contrary to our hypothesis of increasing $\delta^{15}N$ with ontogeny, we found considerable inter-specific variation in $\delta^{15}N$ shifts with ontogeny, but no effect of sex. Declines in long-term trophic level (i.e., $\delta^{15}N$) were observed in all species when sharks were below 75 cm in size, which likely reflects a transition from reliance on maternal energy sources to self-foraging (Matich *et al.,* 2010; 2015). Size-related shifts in $\delta^{15}N$ signatures beyond 75 cm were fastest for relatively fast-growing nervous sharks (~24 cm TL/year), followed by sicklefin lemon sharks (12-15 cm TL/year) and slowest for relatively slow-growing blacktip reef sharks (*ca.* 6.5 cm TL/year), regardless of the direction of change. Congruency of species-specific growth rates and size-based rates of change in $\delta^{15}N$ corroborates hypotheses that tissue incorporation rates depend on a variety of factors such as an organism's growth rate, body size or metabolic activity (as reviewed in Martinez *et al.*, 2009). Size-based increases in $\delta^{15}N$ profiles of nervous sharks, probably reflected an interplay of factors, including improved foraging experience, reduced predation risk, larger gape size and hence the ability to acquire prey of higher trophic levels by adults relative to juveniles (Lowe, 1996; McElroy *et al.*, 2006). In contrast, the lack of any change in $\delta^{15}N$ of blacktip reef sharks across the size range we examined was consistent with previous studies (Speed *et al.*, 2012a; Frisch *et al.*, 2016). For sicklefin lemon sharks, ontogenetic declines in $\delta^{15}N$ values coupled with the higher $\delta^{15}N$ and TP observed in neonates, was indicative of maternal contamination of the isotopic signature of neonates (Olin *et al.*, 2011, 2013; Matich & Heithaus, 2015; Matich *et al.*, 2015) and may imply that large pregnant females (>220 cm), forage at much higher trophic levels. The limited size range and absence of sub-adult and adult sicklefin lemon sharks at our study site precluded observations of ontogenetic changes in $\delta^{15}N$ at body sizes larger than 180 cm. Overall, the magnitude and direction of change in $\delta^{15}N$ with ontogeny varied among species, but appears to be consistent across locations, indicating that species-specific studies across a broad size range are needed to clarify the complex trophic roles that predatory sharks will have on their respective ecosystems.

5.4.1 Dietary contributions

Consistent with their dependency on algal food webs, mixing model results indicated that herbivores with isotopic signatures similar to the convict surgeonfish *Acanthurus triostegus* made up the largest proportion of diet within the shark community, with the exception of neonate sicklefin lemon sharks. Neonate sicklefin lemon sharks appeared to consume a wider variety of prey items with isotopic signatures similar to the giant trevally *Caranx ignoblis* and reticulated damsel *Dascyllus reticulatus*. As maternal feeding likely contributed to the relatively higher trophic position (δ^{15}N) seen for neonate sicklefin lemon sharks, our mixing model results imply that pregnant females may consume both benthic and pelagic prey and link these environments. Although isotope signatures may not provide the taxonomic resolution of stomach content analysis, they do suggest that herbivorous and mesopredatory fish consistently form an important proportion of the diet of all three species over time, as suggested by earlier studies (White and Potter 2004; Papastamatiou et al. 2010; Farmer and Wilson 2011; Frisch et al. 2016; S. Barley, unpublished data). A notable caveat to this approach is that prey items cannot be identified to species, rather they should be considered as indicative of broader classes of prey with similar isotopic signatures. Considering the diverse range of prey that reef sharks are known to consume, the spectrum of prey items in our study may have been under-represented and may include cephalopods and herbivores such as abalone as suggested by stomach content data (Farmer & Wilson, 2011; Frisch *et al.*, 2016). However, the limited contribution by pelagic-based sources such as phytoplankton consumers to the diet of the sharks in our study was consistent with earlier work that suggest these species derive the majority of their carbon from reef-based sources (Frisch *et al.*, 2016). Similarities in the long-term diet composition among the shark community and the relatively high degree of niche overlap by age class, suggest that prey resources are not limiting at Mangrove Bay or alternatively that predation rates may maintain small-bodied (<1 m) shark populations at levels below which food becomes limiting (Vaudo & Heithaus, 2011). Our findings demonstrate the importance of vegetated coastal food webs for shark populations that use non-reef habitats during all or some life stages, particularly within the Ningaloo Reef region where equivalent nursery habitats such as fringing mangroves are rare (Smallwood *et al.*, 2012).

5.4.2 Implications of dietary strategies on trophic role and vulnerability

The degree of dietary and habitat specialization are strong predictors of the functional role of a species (Munroe *et al.*, 2013). Trophic niche size, was smallest for nervous and sicklefin lemon sharks (Fig 3) and largest for juvenile blacktip reef sharks, and in line with activity space sizes (50% KUD, 0.7, 1.3 and 3.6 km^2 respectively) at Mangrove Bay (Escalle et al. 2015; Chapter 4). Although sympatric sharks overlap in their habitat occupancy (Chapter 4), fine-scale partitioning in their use of coastal food webs suggest that their predatory role within their respective marine communities may be functionally different (Rosenblatt *et al.*, 2013). Our findings suggested that nervous and sicklefin lemon sharks may exert a stronger predatory influence when they spend more time within a narrow foraging range. Individual variation in the diets of juvenile blacktip reef sharks suggests that they move or forage differently from conspecifics and hence potentially play a different ecological role within the same ecosystem. Given that similar predatory assemblages are present in other Indo-Pacific nurseries (Mourier *et al.*, 2013a), the dietary strategies observed in this study are likely to hold in other contexts and thus more effort is necessary to understand density-dependent effects of predatory assemblages on community function and structure. Recent research has highlighted the role of predatory sharks in regulating carbon cycles within vegetated coastal habitats and for buffering climate change (Atwood *et al.*, 2015). These processes may be complex and further investigation of inter-population and individual variability in resource use will help to resolve the pathways through which coastal carbon supports sharks.

By providing information on ontogenetic shifts in isotopic niches of coastal shark species, this study enhances understanding of the implications associated with the sharing of space by multiple species and age classes. Although ontogenetic shifts to feeding at higher trophic levels were observed for nervous and sicklefin lemon sharks, their dependency on coastal food webs and restricted niche suggests that these dietary specialists may be less resilient to environmental disturbances that alter the composition of coastal fish communities. Vulnerability to climate-related stressors (Chin *et al.*, 2010) is therefore expected to be higher for nervous and sicklefin lemon sharks and moderately lower for blacktip reef sharks due to their ability to exploit multiple sources of production. Our results must be treated with caution as the small sample sizes limit the resolution of our inferences of prey choice and trophic dynamics. Nevertheless, the generalist dietary strategy of juvenile blacktip reef sharks, coupled with the reported plasticity in movement patterns across different systems (Papastamatiou *et al.*, 2010; Speed *et al.*, 2012a; Chin *et al.*, 2016) and their high dispersal capacity (Chin *et al.*, 2013a) provide strong evidence of the ecological flexibility of the species and imply reduced sensitivity to localised disturbances. Given the susceptibility of coastal ecosystems to resource depletion and environmental change (Chin *et al.*, 2010; Knip *et al.*, 2010), knowledge of the trophic dynamics of sympatric sharks and their dependency on vegetated coastal environments provides an important foundation for future research and management action.

5.5 Acknowledgements

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5.6 Supporting Information

This document includes a table of isotope metrics of primary producers, secondary consumers and teleost fish species sampled in Mangrove Bay (Table S5.5) and a table of trophic position of sampled shark groups relative to the trophic position of different base groups (Table S5.6).

Table S5.5 Summary of isotope metrics of primary producers (algae), secondary consumers (zooplankton), teleost fish and shark species sampled in Mangrove Bay. Details include mean and range values of fork length (FL), carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopes and trophic position (TP) derived from www.fishbase.org.

Species	Code	Common name	n	Mean FL (cm ± SE)	Range FL (cm)	Mean δ^{13}C (‰ ± SE)	Range δ^{13}C (‰)	Mean δ^{15}N (‰ ± SE)	Range δ^{15}N (‰)	Mean TP (± SE)
Algae										
Acanthopora spicifera	AS	Rhodomelaceae	7	–	–	-15.8 ± 0.2	1.5	5.3 ± 0.1	0.6	1
Caulerpa lamourouxii	CR	Caulerpaceae	5	–	–	-11.5 ± 0.2	1.2	5.5 ± 0.2	0.9	1
Cystoseria trinodis	CT	Fucaceae	5	–	–	-14 ± 0.5	3.2	3.4 ± 0.3	1.6	1
Dictyota ciliolata	DC	Dictyotaceae	5	–	–	-15 ± 0.4	2.5	1.9 ± 0.4	2.3	1
Distromium flabellatum	DF	Dictyotaceae	6	–	–	-13.7 ± 0.4	2.6	1.8 ± 0.3	2.1	1
Helminthocladia australis	HA	Nemaliales	5	–	–	-12.7 ± 0.7	4.1	1.7 ± 0.3	1.7	1
Udotea argentea-flabellum	UA	Udoteaceae	6	–	–	-13 ± 0.5	3.2	3.6 ± 0.4	2.1	1
Mangrove										
Avicennia marina	AM	Grey mangrove	10	–	–	-29.4 ± 0.6	6.2	2.8 ± 0.2	1.9	1
Rhizophora stylosa	RS	Stilted mangrove	10	–	–	-29.2 ± 0.6	6.8	0.4 ± 0.6	6.3	1
Zooplankton										
Zooplankton	ZC	Zooplankton	4	–	–	-20.5 ± 1.6	7.0	8.1 ± 0.3	1.1	1
Teleost fish										
Acanthopagrus latus	AL	Yellowfin seabream	5	22.1 ± 0.7	21 - 25	-15 ± 0.3	1.7	10.3 ± 0.2	1.4	3.3*
Caranx ignoblis	CI	Giant trevally	3	31.7 ± 3.8	26 - 39	-13.2 ± 1.1	3.7	11 ± 0.04	0.1	4.2 ± 0.4
Lethrinus nebulosus	LN	Spangled emperor	1	44	–	-11.8 ± 0	0.0	10.2 ± 0	0.0	3.8 ± 0.2
Lethrinus olivaceus	LO	Long-nose emperor	1	–	–	-10.5 ± 0	0.0	10 ± 0	0.0	4 ± 0.4
Lutjanas argentimaculatus	LA	Mangrove red snapper	16	26.1 ± 1	21 - 38	-17.7 ± 0.4	6.0	10.4 ± 0.1	2.1	3.6 ± 0.5
Mugil cephalus	MC	Flathead grey mullet	2	22.5	22.5	-14.3 ± 0.2	0.4	8.4 ± 5.7	-8.2	2.5 ± 0.2
Platycephalus indicus	PI	Bartail flathead	2	33	33 - 33	-14.5 ± 2.9	5.7	10.5 ± 0.4	0.7	3.6 ± 0.6
Pseudocaranx georgianus	PD	White trevally	1	–	–	-14 ± 0	0.0	9.2 ± 0	0.0	3.9 ± 0.6
Rhabdosargus sarba	RS	Goldlined seabream	1	22	–	-13.2 ± 0	0.0	10.7 ± 0	0.0	3.4 ± 0.6
Scomberoides lysan	SL	Double-spotted queenfish	3	41 ± 8	32 - 57	-14.1 ± 0.3	0.9	11.5 ± 0.2	0.7	4.4 ± 0.7
Sillago vittata	SV	Banded sillago	1	–	–	-11.4 ± 0	0.0	10.2 ± 0	0.0	3.5 ± 0.2
Sphyraena novaehollandiae	SN	Australian barracuda	1	36 ± 0	36	-15.8 ± 0	0.0	10.5 ± 0	0.0	4.5 ± 0.8
Trachinotus botla	TB	Largespotted dart	4	32.5 ± 2.2	27 - 36	-13.9 ± 0.7	3.2	11.2 ± 0.2	0.6	3.2 ± 0.4

Table S5.6 Trophic position (TP) of sampled shark groups relative to the TP of different base groups, assuming constant and scaled (in parentheses) diet tissue fractionation as described by Hussey et al. 2010. Mean values of base δ^{15}N were derived from teleost species sampled in Mangrove Bay: *Mugil cephalus* (detritivore), *Lethrinus* spp. (demersal predator) and *Caranx ignobilis* (pelagic predator) and base trophic positions (λ) were derived from Farmer & Wilson (2011).

Group	Base group			Mean TP (± SE)
	Detritivore (λ = 2.5)	Demersal predator (λ = 3.8)	Pelagic predator (λ = 4.2)	
NS-A	3.8 (4.3)	4.4 (4.6)	4.4 (4.4)	4.3 ± 0.09 (4.4 ± 0.09)
NS-J	3.3 (3.6)	3.8 (3.9)	3.8 (3.7)	3.7 ± 0.07 (3.7 ± 0.09)
CM-A	3.7 (4.2)	4.3 (4.5)	4.3 (4.3)	4.2 ± 0.09 (4.3 ± 0.09)
CM-J	3.5 (3.9)	4.1 (4.2)	4.1 (4.0)	4.0 ± 0.09 (4.0 ± 0.09)
CM-N	4.0 (4.6)	4.5 (4.9)	4.5 (4.7)	4.4 ± 0.07 (4.7 ± 0.09)
NA-J	3.7 (4.2)	4.2 (4.5)	4.2 (4.3)	4.1 ± 0.07 (4.3 ± 0.09)
NA-N	4.6 (5.6)	5.1 (5.9)	5.1 (5.7)	5.0 ± 0.07 (5.7 ± 0.09)

Chapter 6 General discussion

Predicting species distributions through space and time is central to addressing biogeographic knowledge gaps (Elith & Leathwick, 2009), otherwise known as the Wallacean shortfall. Accurate predictions are also fundamental to conservation planning, particularly for data-deficient taxa with elevated risks of extinction. In this thesis, I applied a multi-disciplinary approach to predict elasmobranch distributions and determine patterns in shark movements and diet as a function of abiotic (i.e. static and dynamic) and biotic factors at continental, regional and local scales. Static abiotic factors included spatial (i.e. latitude, longitude, distance-to-domain) and non-spatial attributes (i.e. bathymetry and habitat). Dynamic abiotic factors included attributes that change through space and time (i.e. salinity and temperature). Biotic factors are attributes of the animals (i.e. species, size and sex). Static abiotic attributes such as bathymetry and distance-to-domain (geographical position in relation to e.g. shore, reef or mangrove) were generally important influencers of continental-scale abundance and species richness (Chapter 2), regional-scale occurrence (Chapter 3) and local-scale movement patterns (Chapter 4). This conclusion contrasts to suggestions that the distribution of mobile species is less likely to be predicted by static attributes of seascapes (Tittensor *et al.*, 2010).

My results indicate that the static abiotic variables, bathymetry and distance-to-domain, are cost-effective surrogates in the prediction of elasmobranch community structure or species-specific occurrence of mobile coastal sharks at broad spatial scales (Chapters 2-3). Abiotic effects were usually strong but not uniformly so, indicating that the relative utility of static abiotic surrogates may vary with environmental conditions or species. Biotic effects such as body size, sex and age of individuals were also important influencers, operating in synergy with abiotic effects to moderate patterns in habitat and resource use of coastal sharks at finer spatial scales (Chapters 4-5). A hierarchical conservation biogeography and ecology approach using non-lethal avenues of enquiry such as remote videography (Chapters 2-3), passive acoustic telemetry (Chapter 4) and isotopic analysis (Chapter 5) was valuable in providing distributional and ecological knowledge for threatened and elusive animals. My thesis provides evidence that abiotic factors are important in structuring species pools at large-scales (Chapters 2-3), but that local-scale assembly of communities was mediated through biotic factors (Chapters 4-5). The findings of this thesis will help guide future management priorities in the coastal ocean, and may also aid in refining present conservation approaches, such as the placement and zoning scheme of MPA networks.

6.1 The role of abiotic factors

Patterns of elasmobranch distribution and shark occurrence were consistently predictable at continental and regional scales, indicating that bathymetry, latitude, longitude, and distance-to-domain were important influencers of distribution at large scales (Chapters 2-3). While bathymetry is a simple metric for topography (Bouchet *et al.*, 2015), it provides a robust surrogate for vertical niche and has accordingly provided useful insight on elasmobranch richness (Lucifora *et al.*, 2011; Guisande *et al.*, 2013), and extinction risk (Dulvy *et al.*, 2014). Bathymetric features such as shelf breaks are known to serve as navigational guides during the foraging trips of bottom-dwelling yellow-eyed penguins (*Megadyptes antipodes,* Mattern et al. 2007), or as stepping stones along the path of seasonal migration for swordfish (*Xiphias gladius,* Sedberry & Loefer 2001). Spatial gradients in elasmobranch distribution may also reflect the combined effects of environmental gradients such as latitudinal variation in temperature (Tittensor *et al.*, 2010) or cross-shelf gradients in salinity or chlorophyll-a (Chapter 3, Liston et al. 1992, Strom et al. 2006, Guerrero et al. 2014) that structure assemblages of teleost fish prey (Mellin *et al.*, 2010; Parravicini *et al.*, 2013). Our findings thus align with both theory and empirical data (Mellin *et al.*, 2010; Reiss *et al.*, 2010; Last *et al.*, 2011; Woolley *et al.*, 2013) suggesting that bathymetry and spatial factors such as distance to reef, shore or mangrove, provide a cost-effective surrogate for the combined effects of environmental factors when predicting coastal elasmobranch distributions at broad scales (Chapters 2-3).

Foundation species such as corals and mangroves increase habitat complexity, with complexity known to enhance the survivorship and density of other taxa connected to foundation species (Mumby, 2006). Continental-scale peaks in elasmobranch abundance and richness were identified at locations between 110 – 180 km from mangroves (Chapter 2), which may reflect the productivity of mangrove-lined coasts that function as nursery grounds for potential recruits (Chapters 4-5) to offshore adult habitats. The presence of juvenile habitats such as mangroves in the vicinity of coral reefs was seen to exert a profound impact on community structure by enhancing the adult biomass of several teleost species of parrotfishes, grunts and snappers on reefs (Mumby, 2006; Olds *et al.*, 2013; Nagelkerken *et al.*, 2014). Although habitat selectivity indices cannot reveal the importance of a habitat (Chapter 4), only its relative use, my findings are consistent with the use of mangrove-lined coastal bays by juvenile elasmobranch populations in the Indo-Pacific (Chin *et al.*, 2013b, 2016; Cerutti-Pereyra *et al.*, 2014; Escalle *et al.*, 2015; Yates *et al.*, 2015b; Speed *et al.*, 2016) and Atlantic oceans (Jennings *et al.*, 2008; Chapman *et al.*, 2009; Legare *et al.*, 2015). Understanding the abiotic features of nursery areas that support habitat quality for sharks will facilitate their protection or even the rehabilitation of areas that have been degraded as nursery habitat.

Realized distribution patterns reflect synergistic controls that environmental forcing exerts on survival, growth and reproduction (Hortal *et al.*, 2015). While bathymetry and spatial factors were important in predicting multivariate and community-level patterns in elasmobranchs, they ranked poorly in predicting the occurrence of some individual species (Chapters 2-3), underscoring the inter-dependence between static and dynamic abiotic factors in shaping species' habitat utilisation. Dynamic abiotic factors such as salinity, temperature, and turbidity proved to be important predictors of juvenile shark occurrence at regional scales (Chapter 3) and have been linked with juvenile shark distribution in the Pacific (Yates *et al.*, 2015a) and Atlantic oceans (Froeschke *et al.*, 2010; Ward-Paige *et al.*, 2014). Indeed, while persistent associations with static seascape features have been shown for grey reef (*Carcharhinus amblyrhynchos,* Barnett et al. 2012), silvertip (*Carcharhinus albimarginatus*, Barnett et al. 2012)*,* tiger (*Galeocerdo cuvier,* Werry et al. 2014), thresher (*Alopias pelagicus*, Oliver et al. 2011) and whitetip reef sharks (*Triaenodon obesus,* Barnett et al. 2012), predictable shifts in depth use have also been linked with environmental variations in temperature for grey reef (Vianna *et al.*, 2013) and sandbar (*Carcharhinus plumbeus*, Conrath & Musick 2008) sharks. Environmental variables might vary in their performance as predictors depending on the spatial scale at which species respond to environmental heterogeneity as well as the degree of connectivity of habitats that may serve as barriers to movement (Field *et al.*, 2011; Mourier *et al.*, 2013b; Schlaff *et al.*, 2014; Espinoza *et al.*, 2015). There is also evidence of regional variability in the responses of species to ambient conditions, with conspecific sharks responding differently to tropical storms on two continents (Udyawer *et al.*, 2013). My work adds to the growing body of research (Froeschke *et al.*, 2010; Ward-Paige *et al.*, 2014; Yates *et al.*, 2015a) highlighting the importance of investigating habitat preferences across conditions, populations and species, as the effectiveness of abiotic surrogates will be dependent on species and spatial scale (Mellin *et al.*, 2011).

6.2 The role of biotic factors

Biotic factors such as species, size and sex are likely to be effective predictors of fine-scale habitat use as abiotic factors are often stable at these local scales. Indeed, Mangrove Bay in northern Australia offers suitable nursery habitat for early juvenile stages of coastal sharks and the extent of habitat use was species-, size- and sex-specific (Chapters 4-5). Long residence times, restricted movements and dependency on coastal food webs by neonate and juvenile *N. acutidens* suggest that mangrove-lined coastlines provide suitable nursery and foraging habitat for this species (Chapters 4-5). Adult and juvenile *C. cautus* displayed residency (Escalle *et al.*, 2015) and affinity for coastal resources (Chapter 5) in Mangrove Bay, consistent with observations elsewhere in northern Australia that suggest this species spends its entire life within coastal environments (Lyle, 1987; White & Potter, 2004; Heithaus *et al.*, 2013). For *C. melanopterus*, short residence times, longer range movements (>10 km) and small sample sizes precluded the designation of nursery habitat (Chapter 4). Nevertheless, our observations were consistent with recent evidence showing *C. melanopterus* use turbid, coastal bays as pupping sites and that juveniles were generally short-term residents capable of dispersal over large (>80 km) distances, particularly in contiguous systems (Chin *et al.*, 2013a, 2016). The conventional nursery model suggests females enter coastal nurseries for pupping and then depart leaving an aggregation of neonates to mature within the nursery (Springer, 1967; Simpfendorfer *et al.*, 2011b). Overall, I found a spectrum of life-history strategies ranging from larger-bodied (>2.5 m) *N. acutidens* with an extended nursery strategy, to medium-bodied (>1.5 m) *C. melanopterus* with movements atypical of a conventional nursery strategy, to smaller-bodied (<1.5 m) *C. cautus* with no nursery strategy and all life stages occupying the same system (Chapters 4-5). Differences in trophic position and dietary strategy as a function of inter-specific differences in life-histories (Chapter 5) may facilitate the co-existence of multiple shark species and age classes occupying shared natal environments as predicted by niche theory (Werner & Gilliam, 1984).

Expansions in space use and declines in residency of juvenile *N. acutidens* (Chapter 4) likely reflect the combined effects of changes in resource needs (Chapter 5) or improved foraging experience and reduced predation risk with increasing body size (Werner & Gilliam, 1984; Heupel *et al.*, 2004; Grubbs, 2010; Matich *et al.*, 2015). Ontogenetic shifts in habitat and resource requirements (Chapters 4-5) will dictate how abiotic drivers of movements and distribution are manifested (as reviewed in Nagelkerken et al. 2014), highlighting the need to examine size classes (i.e. juvenile and adult) independently in predictive models of distribution (Chapter 3). My results revealed differences in movement strategies of juvenile *C. melanopterus* across different systems (Chapter 4, Speed et al. 2011, Chin et al. 2016), as has been reported for blacktip (*Carcharhinus tilstoni,* Legare et al. 2015, Munroe et al. 2016), and sandbar sharks (*Carcharhinus plumbeus*, Grubbs & Musick 2007, McAuley et al. 2007). Such differences in movements may reflect variations in habitat structure or other biotic interactions such as competition and predation that regulate habitat use.

6.2.1 The role of competition and predation

Overlap in trophic niches and diet composition, and the presence of adults and juveniles of focal species at Mangrove Bay (Chapter 5, Escalle et al. 2015, Speed et al. 2016) suggest that this area is likely both resource- and predator-rich. Subtle mechanisms of resource partitioning were identified along a spectrum of ecological specialisation, from specialists such as *C. cautus* and *N. acutidens* to generalists such as *C. melanopterus* (Chapter 5). Competition between juveniles of specialist species may be mediated in part by subtle partitioning of resource pools and differences in trophic level between species and also among conspecifics based on size within Mangrove Bay (Chapter 5). The suitable conditions for young sharks (Chapters 4-5, Escalle et al. 2015) and rays (Cerutti-Pereyra *et al.*, 2014) suggest that mangrove-lined bays present an energetically productive foraging habitat accessible at higher tides to cannibalistic, larger-bodied sharks (Speed *et al.*, 2016). Neonate and juvenile *C. melanopterus* and *N. acutidens* displayed strong avoidance of deeper reef flat, sandy lagoon and reef slope habitats (Chapter 4), that may present a higher predation risk for young sharks as larger sharks frequented these areas (Speed *et al.*, 2016). This avoidance of deeper habitats was further supported by evidence of smaller activity spaces of resident *N. acutidens* with increasing tidal range, that may reflect the preference of young sharks to remain within shallow habitats for longer when higher tides allow larger sharks to access intertidal habitats (Chapter 4, Wetherbee et al. 2007, Guttridge et al. 2012). This research adds to the growing body of literature (Gruber *et al.*, 2001; Heupel & Simpfendorfer, 2002, 2011; de Freitas *et al.*, 2009; Guttridge *et al.*, 2012; Knip *et al.*, 2012b) that challenges the central paradigm of nursery areas as resource-rich and predator-poor environments that promote juvenile survival (Beck *et al.*, 2001). Understanding resource availability and patterns of use is a key component in the valuation and management of nursery areas.

6.3 Lessons in coastal shark conservation and management

The ability to prioritise key habitats for conservation is critical given coastal ecosystems are deteriorating worldwide, with associated negative impacts on the many economically and ecologically important services they provide (Worm *et al.*, 2006; Barbier & Hacker, 2011; Halpern *et al.*, 2015). Marine protected areas (MPAs) offer a solution to counter the rapid erosion of marine biodiversity and their value in protecting sedentary and site-attached species is established (Claudet *et al.*, 2008; Lester *et al.*, 2009; Babcock *et al.*, 2010; Gaines *et al.*, 2010a). Less well understood is whether and how they can enhance management and conservation of relatively mobile coastal sharks. Some studies claim large (>100 km^2), old (>10 years), remote (i.e. isolated by deep water or sand), no take and well-enforced MPAs offer greater conservation benefits (Koldewey *et al.*, 2010; Edgar *et al.*, 2014), while others support the view that small (<20 km^2), no-take and coastal MPAs are indispensable tools for the protection of mobile sharks (Chapman *et al.*, 2005; Garla *et al.*, 2006; Bond *et al.*, 2012; Knip *et al.*, 2012a; Francis, 2013). These comparative viewpoints are reminiscent of the single large or several small (SLOSS) debate on terrestrial reserves (Diamond, 1975). Reflecting the now-recognised false dichotomy of the terrestrial 'SLOSS' debate (Kremen, 2015), my thesis suggests that no-take MPAs both large and small can be used to maximize conservation benefits for mobile sharks provided robust abiotic and biotic surrogates are identified and used to prioritize areas for protection. In many contexts, it may not be possible to establish MPAs that are large enough to encompass the full range of species occurring within a region (Green *et al.*, 2015). However, information on how different sizes of MPAs may benefit different species provides a foundation for MPA design against which feasibility trade-offs (e.g. socio-economic factors) can be explicitly assessed. My thesis thus provides an important and timely examination of the habitat features that underpin MPA effectiveness for coastal sharks at multiple scales that can be used to evaluate priorities for management and conservation.

6.3.1 Large MPAs and shark conservation

Increasing evidence supports the value of large MPAs (>10,000 km^2) for protecting wide-ranging predators such as cetaceans (Gormley *et al.*, 2012), marine turtles (Scott *et al.*, 2012) and seabirds (Young *et al.*, 2015), despite some counter arguments (e.g. Fletcher et al. 2015). The data required to examine this for sharks at scales pertinent to conservation planning are however lacking for many species, as is the baseline information needed to evaluate effectiveness of large MPAs for shark conservation. Bioregional planning is often used to support conservation planning (*cf*. Commonwealth of Australia 2006, Barr & Possingham 2013); however, the challenge is to determine the degree to which chosen bioregions reflect the biogeography of multiple taxa of concern. My analysis revealed that the structure of elasmobranchs along the northern Australian margin (Chapter 2) was less finely resolved than existing bioregions delineated using bathymetry and demersal fish distributions (Last *et al.*, 2011). Thus, static abiotic features provided an effective blueprint to identify bioregions that will allow the representation of distinct elasmobranch assemblages (Chapter 2) within the boundaries of large MPAs (Commonwealth of Australia, 2006). Results from my research can thus help guide investment in biodiversity conservation at large scales. For instance, the north-west corner of the eastern Indian Ocean would be a critical ocean basin in which to consider establishment of large MPAs given the elevated abundance, richness and occupancy by multiple species (Chapters 2-3) and its proximity to waters of expanding illegal, unreported and unregulated (IUU) fishing for sharks (Field *et al.*, 2009a).

Although larger and generalised, these areas provide a starting point for the prioritisation of management and monitoring efforts.

There is emerging evidence that conservation plans designed without appropriate biological information will miss important habitats for mobile species, as has been shown for loggerhead turtles (*Caretta caretta*) in the Mediterranean (Mazor *et al.*, 2016) and dugongs (*Dugong dugon*) in New Caledonia (Cleguer *et al.*, 2015). Although bioregions may serve to capture representative assemblages (Chapter 2), the highly protected no-take zones within the existing network of State and Commonwealth MPAs along north-west Australia significantly under-represent the most suitable habitats for juvenile sharks at both coarse and fine taxonomic resolutions (Chapter 3). Although, MPAs in the region were not specifically designed to target the protection of sharks, sharks represent a useful surrogate for multispecies conservation because they often occupy large habitats and are of high economic value (Vianna et al. 2012, Dent & Clarke, 2015). Acknowledging that while all life stages should be considered for successful conservation planning for sharks (Kinney & Simpfendorfer, 2009), the importance of juvenile habitats is well recognised (Heithaus, 2007) and is a key driver for the identification of essential fish habitat in the United States (Froeschke *et al.*, 2013) and Europe (Vasconcelos *et al.*, 2014). While future work is necessary to further validate model predictions, in the interim, maps of habitat suitability for juvenile sharks across un-sampled locations provide foundational data (Chapter 3) needed to inform trade-offs of decisions in the design of large MPAs.

Monitoring of large MPAs is also difficult by simple virtue of their size. Standardised methods such as baited remote underwater video systems (BRUVS), in either single or stereo configuration offer a cost-effective solution to assist large-scale management and conservation (Chapter 2-3). As non-lethal, information-rich tools, BRUVS are especially appropriate for data-deficient predatory species and use in MPAs where extractive activities are prohibited. The increasing application of BRUVS on a global scale confirms the broad utility of remote videography and widespread effort in advancing this field of research (Bond *et al.*, 2012; Goetze & Fullwood, 2012; Rizzari *et al.*, 2014b; Jaiteh *et al.*, 2016). Developments in camera technology coupled with increased economy of camera systems (Letessier *et al.*, 2015) will enable the scaling up of ecological data over larger ocean areas with enormous potential for the monitoring and assessment of MPAs at large scales. This thesis demonstrates that BRUVS can serve as appropriate platforms for the construction of predictive models through elucidating relationships between mobile species and physical habitats (Chapters 2-3) to provide priorities for inclusion in large MPAs.

6.3.2 Small-scale MPAs and shark conservation

Small MPAs (<20 km^2) may be the only viable spatial management tool in some areas where socio-political factors may hinder the protection of large habitat units or water bodies (Alcala & Russ, 2006). My analysis suggests that small MPAs can support shark conservation by targeting productive coastal systems that serve a nursery function for mobile species (Chapter 2). Identifying essential habitats such as nursery areas where young sharks aggregate and face increased vulnerability to exploitation can be useful for MPA design at smaller scales (<20 km^2). In this context, regional-scale (>400,000 km^2) maps of habitat suitability will be useful for identifying candidate sites with suitable abiotic conditions (Chapter 3), where dedicated studies using acoustic and isotopic tools will assist to resolve the importance of specific microhabitats (Chapters 4-5). At this scale, biotic surrogates are useful for the strategic placement of small MPAs (Chapters 4-5). Although synergistic controls by abiotic and biotic processes may influence inter-specific variation in MPA function, juvenile sharks that are site-attached to restricted areas are likely to benefit from sub-bay size coastal MPAs (<20 km^2) if they encompass areas of high spatial use (Chapter 4) and vegetated, coastal resources used for feeding (Chapter 5). Consideration of the connectivity of priority habitats such as sand flats, mangroves and algal pavements (Chapter 4) can therefore guide the design of small MPAs to enhance protection of all microhabitats that fall within the larger nursery seascape. Knowledge of essential microhabitats at small scales can aid in protecting not only habitats with feeding or shelter functions (i.e. algae pavements and mangroves), but also secondary habitats (i.e. sand flats) that may not play a role for feeding or shelter, but are part of an animals’ activity space (Chapters 4-5). Understanding foraging site fidelity and the energetic value of seascapes is an essential aspect in the emerging discipline of conservation physiology (Homyack, 2010; Braithwaite *et al.*, 2015) and can reveal functionally connected habitats within the larger nursery seascape (Mumby, 2006; Sheaves, 2009; Nagelkerken *et al.*, 2014; Sheaves *et al.*, 2014) to be incorporated in the design of multiple small MPAs.

Synthesis of the movements of 210 reef-associated species led to recommendations that MPAs be at least twice the size of the 95% kernel utilisation distribution (95% KUD) of focal species (Green *et al.*, 2015). Reflecting these recommendations, the no-take zone at Mangrove Bay (11 km^2) affords the minimum level of adequate protection for *N. acutidens* (95% KUD = 4.8 km^2), but would need to be doubled in size to adequately encompass the wider movements of *C. melanopterus* (95% KUD = 11.5 km^2). Although the battery life of tags used in our study did not permit data collection for more than 1.5 years (Chapter 4), tracking studies of the allopatric lemon shark *Negaprion brevirostris* suggests that dispersal from natal sites occurs at a slow rate (Chapman *et al.*, 2009). Small MPAs may thus offer protection to site-attached *N. acutidens* for several years (>3 years), even after leaving the narrower confines of the nursery. For species such as *C. melanopterus* that may display high behavioural and dietary plasticity within the population (Chapters 4-5), small MPAs will only protect part of the juvenile population in regions where wide-ranging movements occur (Chapter 4, Chin et al. 2013a, 2016). In this context, acoustic monitoring and isotopic analyses provide a useful platform for investigating the importance of site-specific features that underpin nursery function and also the minimum MPA sizes needed to accommodate movements of focal predators (Chapters 4-5).

6.3.3 The case for species-specific data acquisition

Information on the distribution, movement and diet of populations of key species can also guide species-specific management strategies (Chapters 2-5) where MPAs are either insufficient (i.e. species with large home ranges) or unfeasible (i.e. areas with socio-political constraints). Recent research on ocean health has found the abundance of top predators to be an important component of ecosystem structure and process (Heithaus *et al.*, 2012; Ruppert *et al.*, 2013; Atwood *et al.*, 2015), despite high variation in the ecological role among shark species (Heupel *et al.*, 2014; Roff *et al.*, 2016). While taxa- or species-specific benefits may be viewed as side benefits of an ecosystem approach, it is important to ensure preservation of significant habitat types for key species such as elasmobranchs. Many elasmobranchs have experienced strong population declines (Worm *et al.*, 2013). Thus, species-specific information will be crucial to guide dedicated recovery strategies such as fishery management, habitat restoration, bycatch mitigation or policy instruments (see extensive review in Ward-Paige et al. 2012; Worm et al. 2013) that help rebuild exploited populations. For instance, vital information on the trophic niche of *C. cautus* (Chapter 5) will aid in assessment of extinction risk for this currently "Data Deficient" species (Bennett & Kyne, 2003). Additionally, predicted distributions (Chapter 3) provide a baseline against which future changes in species distributions, management actions and the effects of climate change (Jones & Cheung et al. 2015) may be monitored and compared.

Species-specific vulnerabilities in their environment can be evaluated by assessing the interactions of three distinct components: (1) exposure to risk, (2) sensitivity to exposure and (3) adaptive capacity to potential impacts (Chin *et al.*, 2010). While integrated risk assessments for species will require information on impacts at relevant spatial and temporal scales (Maxwell *et al.,* 2013; Halpern *et al.*, 2015), behavioural data on movement and diet (Chapter 4-5) can contribute to this assessment by informing on the: (1) overlap between risks (i.e. fishing mortality) and species' activity spaces (exposure), (2) movement and habitat use patterns of vulnerable life stages (sensitivity) and (3) dietary and habitat plasticity, mobility and distribution (adaptive capacity). Species with narrow niches along both habitat and trophic axes such as *N. acutidens* and *C. cautus* (Chapter 4-5, Escalle et al. 2015) will have increased sensitivity to localised impacts from fisheries, pollution and habitat loss or degradation (Munroe *et al.*, 2013, 2014). For instance, fishing within the 5 km^2 area of Mangrove Bay (Chapter 4), if permitted, would cause localised depletion of early life stages, removing a source of *N. acutidens* shark recruits to other coastal areas and offshore coral reefs. Reliance on coastal productivity, specialised diets and restricted movements suggest low adaptive capacity of these *C. cautus and N. acutidens* to localised impacts (Chapters 4-5). Indeed, conservation of coastal nursery habitats will be important for long-term management of *N. acutidens*. This species is classified as "Vulnerable" globally by the International Union for the Conservation of Nature but "Least Concern" in Australia (Pillans *et al.* 2003), providing opportunity to protect one of the last strongholds for these species. Given their rapid range reductions at the global scale, vulnerability to local extirpations (Pillans, 2003), and site-restricted coastal nature (Chapter 4), it is unlikely that populations will be replenished by transoceanic dispersal (Schultz *et al.*, 2008; Mourier *et al.*, 2013b). While exposure to risks may be mitigated in part through the strategic placement of small MPAs (Chapters 4), other management criteria may also be required to protect important habitats for specialist species such as improved land use to protect mangroves and adjacent habitats (Sanchirico & Mumby, 2009) or the protection of early juveniles using minimum size limits. In contrast, generalists such as *C. melanopterus* that utilise both mangrove-lined bays (Chapters 4-5, (Chin *et al.*, 2016; Speed *et al.*, 2016) and coral reefs (Papastamatiou *et al.*, 2009; Speed *et al.*, 2011, 2012a), may face increased exposure to cumulative pressures in the different habitats. High site-fidelity, restricted movements of *C. melanopterus* (Papastamatiou *et al.*, 2009; Speed *et al.*, 2011) and reproductive philopatry by females (Mourier & Planes, 2012) can increase their sensitivity to localised impacts. At regional scales, exposure and sensitivity to risks may be moderated by the abundance (Vanderklift *et al.*, 2014), and adaptive capacity of *C. melanopterus* (Chapters 4-5, Chin et al. 2016), where population declines in one area could be mitigated by movement to new locations and recruitment from other locations through juvenile dispersal (Chin *et al.*, 2013a). Given the variability in the habitat associations, movement and diet strategies of coastal sharks (Chapters 2-5), the development of effective conservation and management strategies will require species-specific data. My analysis at regional scales showed that habitat suitability models based on the occurrence of all shark species performed poorly and may reflect the decoupling of shark-habitat linkages, whereas those incorporating specific-species data will be more accurate and precise (Chapter 3).

6.4 Future directions

The models presented in this thesis represent shark distributions largely as a function of abiotic variables. Sharks also respond to a suite of internal controls that include group living and sociality (Jacoby *et al.*, 2012; Mourier *et al.*, 2012), learning memory processes (Papastamatiou *et al.*, 2011), competition (Papastamatiou *et al.*, 2006; Kinney *et al.*, 2011), and predator avoidance (Guttridge *et al.*, 2012). Environmental forcing alone is rarely so strong as to prevail over all these drivers and thus cannot be expected to entirely explain the biogeography of coastal sharks. A new suite of dynamic models known as population distribution models (PDMs), hold potential for better integrating empirical knowledge of a wider range of influential factors, including life-history traits, physiological tolerances, energy requirements, swimming capacities or relationships with congeners (but see Planque et al. 2011). Much of this information is still lacking for sharks (Dulvy *et al.*, 2014; Osgood & Baum, 2015), but can be obtained in part by using BRUVS. The ease of use, standardization, and non-extractive and cost-efficient nature of BRUVS (Letessier *et al.*, 2015) can drive the generation of high volumes of data across large regions, and when combined with advanced statistical techniques, may allow for the development of global-scale models.

An important focus should be to test the assumption that species-habitat relationships are invariant to population density and quantify variations of habitat use across gradients of population growth or decline (Matthiopoulos *et al.*, 2015). In this context, abundance data from BRUVS teamed with agent-based models and validated with acoustic telemetry may prove a useful approach for estimating shark densities, where direct observations are difficult (Vanderklift *et al.*, 2014).

Animal mobility presents substantial challenges for conservation (Martin *et al.*, 2007; Runge *et al.*, 2014), as the location of an individual at any point in time is a reflection of the conditions it has encountered. Behavioural plasticity of sharks may mask the animals' true habitat preferences by allowing displacement into, or temporary occupation of less-suitable or non-suitable habitats in response to human activities (Morton & Symonds, 2002; Rako *et al.*, 2013). Long-term surveys are needed so that species distribution models incorporate inter-annual variability and facilitate the identification of robust hotspots within a dynamic planning environment.

Individual-level indices such as body size, age and maturity stage allow inferences on anti-predation investment to be drawn at local-scales. However concurrent telemetry tracking of both predator and prey is needed to clearly resolve the influence of predation on habitat use. In this context, novel acoustic tags that change in signal when a tagged individual is consumed (www.htisonar.com), hold promise for estimating predation mortality and generating reliable survival estimates. Such information is in turn needed to assess the relative contributions of juvenile populations to the adult stock, which is a central component of the value of nursery habitats (Beck *et al.*, 2001).

Primary movement corridors that facilitate movements from one habitat to another should be identified through ontogeny as has been explored for *C. amblyrhynchos, C. albimarginatus* and *C. leucas* (Espinoza *et al.*, 2015). Connectivity models allow the development of 'resistance surfaces' that describe the relative probability of an animal moving through different seascape features (e.g. coral reefs, algal flats or seagrass beds) and validated using empirical (Mumby, 2006; Olds *et al.*, 2013; Espinoza *et al.*, 2015) or genetic data (McRae, 2006), will facilitate the identification and protection of connectivity corridors within MPA networks that has been advocated for sea turtles, pinnipeds and cetaceans (Hooker *et al.*, 2011; Hays *et al.*, 2014; Pendoley *et al.*, 2014). Approaches such as investigating the genetic connectivity (i.e. parentage analysis) among populations will provide insight into breeding patterns (Mourier & Planes, 2012; Mourier *et al.*, 2012), connectivity and the value of nurseries in terms of, for instance, female philopatry (as reviewed in Chapman et al. 2015), which could assist in the understanding of population dynamics and optimization of MPA networks to assist population recovery.

Given the array of anthropogenic threats to shark populations (Chin *et al.*, 2010; Knip *et al.*, 2010), the spatial footprint of human activities in coastal and offshore environments (c.f. Selig et al. 2014, Halpern et al. 2015) could be coupled with spatially-explicit model outputs to understand the vulnerability of different habitats. Model outputs can also guide the identification of potential synergistic cumulative impacts (e.g. Davidson et al. 2012; Anthony et al. 2015) to anticipate where they may occur, thereby adopting the precautionary principle and planning for resilience. This is especially important given the elevated richness, abundance and occurrence of sharks close to the Indo-Australian border (Chapters 2-3) where small-scale IUU fisheries are expanding (Field *et al.*, 2009a). As both the east and west coasts of Australia are global hotspots of shark biodiversity (Lucifora *et al.*, 2011) and conservation priority (Dulvy *et al.*, 2014), spatial information on impacts is urgently needed. Although many sharks are targeted for the global trade of fins and meat (Worm *et al.*, 2013), elasmobranchs caught as bycatch in other fisheries often exceed the catch of targeted species (Molina & Cooke, 2012). Predictions of habitat suitability for sharks (Chapter 3) could be overlayed with maps of fishing effort to identify areas of high occupancy and high bycatch for protection. Such maps of impacts have been successfully assembled at broad scales for cetaceans, marine turtles, pinnipeds and seabirds (Maxwell *et al.*, 2013; Lewison *et al.*, 2014), but remain lacking for sharks. The combination of model outputs with additional activity layers (Chapters 2-3) or global climate change scenarios adds another dimension to the model and contextualises model projections with respect to current management issues and could enable the planning of suitable adaptation strategies for exploited species (Cheung *et al.*, 2012; Sequeira *et al.*, 2014). Lastly, it would be of tremendous value to combine modelling outputs with biological traits (e.g. growth rates, longevity, fragility) to map ecosystem structure and function.

6.5 Concluding remarks

The conservation and management of exploited species requires the identification of areas essential to long-term population persistence. As 'true baselines' of shark distribution become increasingly problematic to establish (Lotze & Worm, 2009), with simultaneous losses of coastal ecosystems and shark populations (Worm *et al.*, 2006; Barbier & Hacker, 2011), assessing species-habitat associations is one way of refining distribution maps to provide substantive inputs to conservation planning and adaptive management in the marine realm. This thesis demonstrates the benefit of a multi-scale approach in evaluating the importance of habitat to coastal elasmobranchs through (i) a continent-wide view of distribution that facilitates the prioritization of areas for future research and conservation, (ii) regional habitat suitability maps that can support the tracking of responses and impacts, and (iii) fine-scale inference of important foraging and refuge habitats that can guide the identification of functionally connected habitats within a larger nursery seascape. More importantly, establishing habitat associations highlighted the need for species-specific data acquisition that will inform spatial planning and complementary management efforts beyond MPA boundaries that are needed to fully protect specific species. Our findings on coastal elasmobranchs represent one example of an approach relevant to mobile species generally. In this context, sampling programs need to accommodate multi-disciplinary designs that are systematic, species-specific and scale-appropriate, while integrating advances in statistical modelling that account for missing data. Configurations of MPAs will ultimately depend on other ecological design criteria and be applied within different, context-dependent, socioeconomic and governance settings. Hence, my findings do not represent explicit recommendations, but rather provide fundamental information to assess planning trade-offs, and perspective on the value of both large and small MPAs as well as species-specific data acquisition for coastal elasmobranchs.

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