Chondrichthyan conservation in marine protected areas: Elucidating species associations in two chondrichthyan hotspots using non-invasive techniques

by

Geoffrey J. Osgood
B.Sc., University of Calgary, 2014

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We acknowledge with respect the Lekwungen peoples on whose traditional territory the University stands and the Songhees, Esquimalt and W̱SÁNEĆ peoples whose historical relationships with the land continue to this day.

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Abstract

Chondrichthyans—sharks, rays, skates, and chimaeras—influence top down control of food webs and connect disparate ecosystems, yet populations of many species around the world have experienced sharp declines in abundance. Marine protected areas (MPAs) have a long history of conserving marine biodiversity, but their effectiveness to protect representative and critical habitat for threatened species on a global scale is controversial and hindered by a lack of biological and ecological data for the majority of chondrichthyan species. In this thesis, I use non-invasive baited remote underwater video (BRUV) and citizen science diver data to explore diverse chondrichthyan communities in two countries, South Africa and Costa Rica, with data-poor chondrichthyan fisheries and limit conservation funding, and the relationships of these chondrichthyans to biotic and abiotic factors in their habitats in and around MPAs. First, through a literature review, I find substantial taxonomic and geographic biases in understanding of reef shark biology, ecology, and conservation, which impair ability to implement effective conservation measures for these species. After identifying these research gaps, I used BRUVs to explore the diversity of a chondrichthyan hotspot in South Africa, finding many poorly understood endemic chondrichthyans. I discovered strong associations of the chondricthyan community to different habitat types (sand versus reef and kelp habitat), which resulted in poor diversity within one of the region's larger MPAs—a whale sanctuary whose focus on large charismatic whales left mostly poorer quality sand habitat protected. However, a high occurrence of chondrichthyans within a neighbouring MPA suggested even small MPAs can conserve a high abundance of smaller species, especially if residency can be demonstrated. I then used the BRUV data to examine the relationships amongst these chondrichthyans and the community of other marine animals within the region, finding strong co-occurrence patterns that suggest chondrichthyans, particularly the endemic catsharks, could serve as effective ‘umbrella’ species for conservation in this region where little other information is available for conservation planning and monitoring. Finally, at Cocos Island, an MPA off Costa Rica, I discovered similarly strong, species-specific associations to another aspect of habitat: temperature. I found significant and species-specific responses to the El Niño–Southern Oscillation (ENSO). For example, the scalloped hammerhead *Sphryna lewini* counts declined by 224.7% during strong El Niño conditions and by 14.7% with just a 1°C rise in SST, while the benthic whitetip reef shark *Triaenodon obesus* had a weaker response, dropping by only 7.9% and 4.4%, respectively. In general, strong El Niño events reduced sightings within the MPA, providing some of the first indications of how a rising frequency and intensity of these events will impact the spatial distribution of both chondrichthyans and their habitat in the Eastern Tropical Pacific. Overall, this thesis provides insight into the factors influencing chondrichthyan abundance and diversity, demonstrating the importance of considering both biotic and abiotic factors during MPA design and the need to study these factors across diverse taxonomic groups and ecosystems.

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Dedication

To Janice, Glenn, and Julie,

for supporting me and my shark-chasing dreams

Chapter 1 – Introduction

Marine predators can stabilize food webs, enhance ecosystem resilience, instigate top-down trophic control, inspire fear effects in their prey, and connect ecosystems (Duffy 2003, Bascompte et al. 2005, Shaffer et al. 2006, Heithaus et al. 2008, McCauley et al. 2012b). For instance, in Australia's Shark Bay, the apex tiger shark *Galeocerdo cuvier* instils such a fear response in its herbivorous dugong and turtle prey that primary productivity of the local seagrass increases in its presence, even without consumptive effects, since these prey animals alter their habitat use (Heithaus et al. 2012). Other mobile shark species transport nutrients across ecosystems by feeding in one habitat and resting in another (Howey et al. 2016, Williams et al. 2018), and iron defecation by foraging sperm whales *Physeter macrocephalus* enhances primary productivity in the deep ocean (Lavery et al. 2010). Orca whales *Orcina orca* have such a high energy demand and mobility that predation from as few as five whales can lead to severe declines in multiple prey species (Williams et al. 2004). Marine predators, with diverse habitat requirements on large spatial scales, can also serve as both umbrella species and indicators of ecosystem health (Zacharias and Roff 2001, Sergio et al. 2006, Hazen et al. 2019), making them as important for marine conservation as they are ecologically for marine ecosystems.

Large predators, however, are also some of the most threatened taxa in the ocean, as anthropogenic threats increasingly overlap with hotspots of predator diversity (Halpern et al. 2008b). Overfishing, pollution, and climate change all impact marine predators on both global and local scales (Myers and Worm 2003, Estes et al. 2011, Davidson et al. 2012). Predators concentrate their trophic productivity into fewer, albeit larger, individuals compared to producers and herbivores (Barnes et al. 2010, Trebilco et al. 2013), and large body size is often associated with traits, such as low fecundity and late age of maturity, that enhance extinction risk from exploitation (Cardillo 2003, Reynolds et al. 2005, Olden et al. 2007). Additionally, many marine predators make long distance migrations that can expose them to multiple anthropogenic threats and complicate their management (Block et al. 2011, Costa et al. 2012, Harrison et al. 2018). On reef ecosystems, for example, high abundances of apex and mesopredators are mostly restricted to remote reefs; these refuges should be targets of measures like marine protected areas (MPAs) (Nadon et al. 2012, Edgar et al. 2014, Letessier et al. 2019).

1.1 **Marine protected areas as conservation tools**

Marine protected areas may act to conserve predator populations by restricting fishing pressure and other anthropogenic disturbances in certain areas (Lester et al. 2009, Gaines et al. 2010), and as such, they could also restore predation to ecosystems impacted by fishing (Cheng et al. 2019). Although the benefits of MPAs vary in accordance with species-specific traits, MPAs often boost populations of large marine predators (Micheli et al. 2004, Claudet et al. 2010). This is especially true for large, isolated MPAs that protect pristine habitat covering most of a predator’s home range (Toonen et al. 2013, Edgar et al. 2014) or protect important and reliably used foraging or breeding sites (Werry et al. 2014). For example, even in remote Palau, its extensive Protected Area Network had a five-fold increase of predator biomass within MPAs compared to fished areas, particularly in the larger MPAs (Friedlander et al. 2017). Marine protected areas, due to their apparent simplicity in implementation and apparent successes (Dulvy 2013), are attractive conservation measures in developing countries, many of which are also hotspots of marine biodiversity (Davidson and Dulvy 2017). As such, MPAs were incorporated into the Aichi Targets (10% of coastal and marine areas in MPAs by 2020) agreed on by countries party to the Convention on Biology Diversity in 2010 (Gannon et al. 2019). The declaration of MPAs has recently increased to meet this target, particularly in the form of large MPAs (Lubchenco and Grorud-Colvert 2015, Jones and De Santo 2016), and recent projections suggest this target will be met (Gannon et al. 2019).

Marine protected areas, however, have also failed for many species, and, in some countries they are shrouded in uncertainty that arises from poor monitoring, management, and enforcement (Mora et al. 2006, Edgar et al. 2014, Gill et al. 2017). For instance, only three of fifteen Italian marine reserves were sufficiently enforced to have biodiversity benefits for large predators (Guidetti et al. 2008), and illegal fishing can occur even with enforcement and patrolling (Davis and Harasti 2020). Many hotspots of marine predator diversity are outside MPAs (Letessier et al. 2019) and poor knowledge of critical habitat for threatened species hinders MPA prioritization (Briscoe et al. 2016), especially in developing countries where threatened diversity can be high but research effort low (Briggs 2003, 2005, Ban et al. 2009, White and Kyne 2010). Despite large MPAs generally considered the most effective—covering diverse habitat and a high proportion of threatened species' home ranges (Edgar et al. 2014)—the recent push for very large and remote MPAs associated with meeting the Aichi Target has shifted attention away from the smaller MPAs that benefit impacted ecosystems around human population centers, where they are also direly needed (Devillers et al. 2015, Jones and De Santo 2016). Thus, modern MPA design and placement is often based on political, economic, and social ease of implementation rather than on biological criteria and the need to protect representative habitat or migration corridors (Dulvy 2013, Devillers et al. 2015, Letessier et al. 2019).

Marine protected areas will also not protect any species from the full suite of threats they may face (Mora et al. 2006, Maxwell et al. 2013). Even large MPAs cannot protect all the habitat used by large mobile species, which regularly MPA boundaries (Grüss et al. 2011, Pérez-Jorge et al. 2015, Dwyer et al. 2020). Additionally, threats from climate change are not easily addressed with MPAs (Roberts et al. 2017, Bruno et al. 2018). Climate change threatens marine predators by altering thermal habitat, destroying coral reefs, and shifting their populations into new areas where fisheries may be more intense or habitat less suitable (Perry et al. 2005, Hazen et al. 2013).

Beyond these considerations, not all MPAs afford the same level of protection for all taxa (Mora et al. 2006). All MPAs restrict fishing activity to some degree; many allow activities such as recreational diving and boating but disallow fishing, while a small percent restrict human access completely (Giakoumi et al. 2017). Other MPAs have zones for limited fishing and recreational activity and core zones set aside as no-access or no-take (Denny and Babcock 2004, Halpern et al. 2008a, Rife et al. 2013a). The most successful MPAs, with the highest abundance of fishes, are no-take, restrict human access, and have long-lasting zoning regulations and strong enforcement (Robbins et al. 2006, Aburto-Oropeza et al. 2011, Giakoumi et al. 2017, Juhel et al. 2018); other zones or MPAs with less strict regulations typically show little difference in fish populations to sites outside MPAs (Denny and Babcock 2004, Lester and Halpern 2008, Rife et al. 2013a). In fact, no-entry reserves also keep predators behaving and hunting as they would naturally in a setting without human presence (Juhel et al. 2019). Regardless of the strength of restrictions, in countries with a limited capacity or political drive for enforcement, many MPAs become “paper parks”, existing only in legislation that is not enforced (Rife et al. 2013b). This is especially true for very large and remote MPAs, whose pace of designation exceeds that of capacity development for enforcement (Jones and De Santo 2016), including many of the MPAs developed to meet the Aichi Target (Gill et al. 2017, Gannon et al. 2019). Less than 10% of

MPAs are no-take globally, further exacerbating uncertainty over their role in protecting biodiversity (Costello and Ballantine 2015). Ultimately, a diversity of MPA types is needed, from small to large and from remote to well-connected, to represent the diversity of ecosystems, species needs, and threats currently existing in the ocean (Jones and De Santo 2016).

Coupled with effective designs and enforcement, assessing MPA success to protect predators relies on long-term monitoring of their populations (Micheli et al. 2004, White 2019). Many long-term surveys are fisheries-independent, but use fishing techniques like longlining to estimate relative abundance of a species in an area (Froeschke et al. 2010, Hansell et al. 2017), while others rely on fisheries-dependent catches (Baum et al. 2003). Due to their destructive nature, however, such surveys, oppose the conservation goals of MPAs while providing limited insight on habitat and species of lower catchability (Mallet and Pelletier 2014). Reliance on fisheries catches also limits data to areas of economic importance and would be absent or limited from within MPAs (Briscoe et al. 2016). Underwater visual censes have been used extensively to reduce the population impact of monitoring, but diving limits the depths, timing, and duration of observations, and human presence can alter fish behaviour (Dickens et al. 2011, Mallet and Pelletier 2014, Rizzari et al. 2014a). Lacking these limitations, baited remote underwater video (BRUV) has emerged as a non-invasive method to gauge the relative abundance and diversity of predators (Mallet and Pelletier 2014). Bait attracts fish and other carnivores to a camera on which they can be counted and identified, enabling accurate estimation of species richness, especially for communities with mobile, elusive predators (Colton and Swearer 2010, Ebner et al. 2015). Citizen science is also an emerging tool for conservation and monitoring (Dickinson et al. 2010). Although precision and bias of citizen science data can be affected by involving a large number of relatively unskilled observers, such issues can be modelled statistically (Bird et al.

2014), and the potential to develop long-term data sets outweigh its costs, especially for charismatic and easily identified species like many marine predators (Dickinson et al. 2010, White et al. 2015). In the Caribbean, citizen science data detected the extirpation of large sharks from areas around human population centers, demonstrating its potential as a monitoring tool through both space and time (Ward-Paige et al. 2010). Long-term data are required for both the statistical power and accuracy of monitoring data sets (White 2019); by operating regularly and consistently with motivated participants, the dive industry is an ideal source for citizen science, particularly in MPAs (White et al. 2015, Freiwald et al. 2018).

1.2 Chondrichthyans: marine predators in need of conservation

Chondrichthyans—sharks, rays, skates, and chimaeras—are charismatic marine predators in great need of non-invasive monitoring and citizen science. Although there is variation in life history traits, compared to most teleost species, most chondrichthyans grow slowly, mature late, and have small litters, and so they have slow population growth rates that hinder recovery from anthropogenic impacts, such as overexploitation and habitat destruction (Schindler et al. 2002, García et al. 2008, Gallagher et al. 2012). Chondrichthyan populations have declined around the world (Baum et al. 2003, Dulvy et al. 2008a, Ferretti et al. 2010, Worm et al. 2013), but some populations have recovered through a variety of management measures, including many within large, well-enforced no-take MPAs (Bond et al. 2012, Shiffman and Hammerschlag 2016, Speed et al. 2018), such as on the Great Barrier Reef (Robbins et al. 2006). Some countries, such as the Bahamas and Palau, have also introduced shark sanctuaries that prohibit the fishing of all sharks, although fishing of other species is still allowed and bycatch still possible (Davidson 2012, Ward-Paige 2017).

Despite these successes, we lack the knowledge needed to design effective MPAs for many species (Dwyer et al. 2020). Although all chondrichthyans have been assessed by the IUCN, almost half are still data deficient (Dulvy et al. 2014). Species-specific knowledge is critical to MPA design, as chondrichthyans differ in behaviour and ecology (Casselberry et al. 2020); some are highly migratory and mobile, while others are highly resident, resting often in the same habitats on the ocean floor (Whitney et al. 2012a, Dwyer et al. 2020). Thus, MPAs can be effective for some species but not others (Shiffman and Hammerschlag 2016, Dwyer et al. 2020), and even reef-associated species such as *Triaenodon obesus, Carcharhinus amblyrhynchos*, and *C. melanopterus,* often display some degree of large-scale dispersal or movements (Whitney et al. 2012a, Chin et al. 2013a, White et al. 2017). Due to their strong dispersal ability, many chondrichthyans will also shift their distribution in response to climate change (Perry et al. 2005), and such an ever-changing kaleidoscope of chondrichthyan regional diversity would complicate the role of static MPAs in their conservation (McLeod et al. 2009). Additionally, hotspots of both chondrichthyan diversity and fishing occur in developing countries (Davidson and Dulvy 2017); such places would be targets for MPA placement, if they were not also centers of our ignorance.

Understanding species-habitat associations is critical for MPA placement and planning and for monitoring success (Agardy et al. 2011). For instance, many chondrichthyan species have strong site fidelity to specific locations and habitats used for foraging and reproduction that can be protected, even when wide-ranging and migratory (Barnett et al. 2012, Werry et al. 2014, Daly et al. 2018). Proper protection of critical habitat could ensure MPAs still benefit both large, mobile species and more resident populations (White et al. 2017, Heerah et al. 2019, Yurkowski et al. 2019), but only if detailed knowledge of habitat use and how it varies by species is acquired and used (Graham et al. 2016, Yates et al. 2016). A lack of prior knowledge of species-habitat associations will lead to ineffective MPAs if they leave out important portions of a species range or critical habitats (Agardy et al. 2011, Barnett et al. 2012, Davidson and Dulvy 2017). If these habitat associations are established, chondrichthyans could also serve as indicators of ecosystem diversity and health (Hazen et al. 2019). Thus, there is a need to study how different chondrichthyan species associate with different habitat and environmental variables, such as temperature, to optimize chondrichthyan conservation (Byrne et al. 2019, Casselberry et al. 2020, Dwyer et al. 2020). Knowledge of habitat associations will be especially important in the design of smaller MPAs that do not cover the same range of habitat diversity as larger MPAs (Agardy et al. 2011, Toonen et al. 2013).

In summary, despite recent advances studying chondrichthyan conservation in MPAs, our understanding of chondrichthyan ecology, spatial protection, and indicator potential would benefit from improved information on the relationship between chondrichthyan species and their abiotic and biotic environments. Large charismatic species attract most research attention, with nearly 90% of all chondrichthyan species receiving little to no research effort (Huveneers et al. 2015, Shiffman et al. 2020). These gaps are exacerbated in developing countries (Griffiths and Dos Santos 2012); most studies of chondrichthyan species-environment relationships focus on developed nations (Huveneers et al. 2015, Shiffman et al. 2020), such as Australia (Espinoza et al. 2014, Yates et al. 2015) or countries with strong dive-based tourism industries like Belize or the Bahamas (Bond et al. 2012, Brooks et al. 2013, Shipley et al. 2018) and a few well-studied atolls like Palmyra (Papastamatiou et al. 2009b). Developing countries are also falling behind in the push for MPA coverage due to weak, institutional capacity, political instability, a lack of funds, and social concerns, creating a need to assess current MPAs and conduct research to better ensure any further MPA efforts succeed in these countries (Failler et al. 2019). In addition to a focus on charismatic species, a lack of diversity exists among studied MPAs; chondrichthyans within smaller MPAs are rarely studied in detail with research focus heavily skewed toward larger protected areas (e.g. Dale et al. 2011a, Espinoza et al. 2014, White et al. 2017). Yet, continuing debate about the benefits of large MPAs over smaller ones suggests the role of MPA size in promoting biodiversity can depend on local factors (Lester et al. 2009, Edgar et al. 2014, Rojo et al. 2019). A failure to identify and fill taxonomic and geographic gaps in research effort underlies these issues (Griffiths and Dos Santos 2012).

1.3 Thesis overview

To address these gaps, my thesis uses non-lethal underwater survey methods (BRUVs and citizen science divers) to investigate the relationship between MPAs and chondrichthyan diversity in two developing countries—South Africa and Costa Rica—situated in global hotspots of chondrichthyan diversity, with the ultimate goal of elucidating spatial and temporal patterns of chondrichthyan diversity relative to abiotic and biotic factors. I draw comparisons across taxa in the same system to help generalize conclusions about chondrichthyan habitat associations within MPAs. As a first step, in chapter 2, I conducted a literature review on reef shark biology, ecology, and conservation to identify knowledge gaps for this group of sharks. Marine protected areas are increasingly important for reef sharks, as many species inhabit heavily impacted coastal ecosystems (Ward-Paige et al. 2010, Nadon et al. 2012). Additionally, many reef sharks, such as *Carcharhinus melanopterus* and *Triaenodon obesus,* display high residency and restricted movements on their home reefs, which imply well-placed MPAs would be effective for their conservation (Barnett et al. 2012, Speed et al. 2016). In fact, many of the large, remote MPAs recently implemented by countries to help them meet their Aichi Targets protect reef ecosystems

(Toonen et al. 2013, Jones and De Santo 2016), and some of the most well-studied MPAs are in and around the Great Barrier Reef and Hawaii, where the first BRUV surveys occurred (Cappo et al. 2003). Thus, reef sharks serve as an excellent case study to summarize current knowledge on chondrichthyans potentially impacted by MPAs and to identify knowledge gaps that could influence conservation. I review every published research article (as of September 2015) written on twenty-nine species of shark whose primary habitat is tropical coral reefs and discover gross imbalances in the literature. One genus, *Carcharhinus*, is the focus of most studies, and in only a few locales: the Caribbean, Australia, and a few Pacific Islands like Palmyra and Hawaii. Biodiversity hotspots in the Indo-Pacific and smaller endemic species are left uncertain despite their great need for biological and ecological information to inform and motivate chondrichthyan conservation. However, reef shark science is advancing rapidly, and the research on these *Carcharhinus* species should allow updates to their IUCN status and conservation needs. I suggest a few avenues for future studies on reef sharks, synthesizing work from genetics, movement research, and population ecology,

In chapters 3 and 4, I use BRUVs to fill knowledge gaps in a chondrichthyan community dominated by poorly studied, endemic species in South Africa, which has both an expensive network of small MPAs and also intense fisheries that take a large biomass of chondrichthyans every year (da Silva et al. 2015). I collaborated with the South African Shark Conservancy (SASC) to collect and analyze BRUVs over two years across two different MPAs: the Betty's Bay MPA and the Walker Bay Whale Sanctuary. Both are small MPAs near Hermanus, South Africa, but they differ in their management history and purpose. The Walker Bay Whale Sanctuary was designated only in the early-2000s to protect breeding southern right whales *Eubalaena australis* and provides strict, albeit seasonal, protection. In contrast, the Betty's Bay

MPA was established in the 1970s to conserve commercial fish and abalone and operates year round. I worked with SASC to deploy over 400 BRUVs at sites within these MPAs and at unprotected sites outside them.

In chapter 3, I use these BRUVs to quantify the diversity and relative abundance of chondrichthyans in relation to the two neighbouring MPAs, revealing strong, yet varying, habitat associations among the diverse chondrichthyans. I also discover an ecosystem impacted by fishing: large high trophic level shark species are depauperate while mesopredatory sharks abound. I provide the first assessment of endemic chondrichthyan diversity within the Walker Bay Whale Sanctuary, demonstrating that habitat conservation for large species like whales is not always optimal for chondrichthyan diversity. I emphasize the imperative to assess the habitat needs of the local biodiversity and the distribution of that habitat before assuming MPAs will succeed. However, I also show small MPAs can benefit endemic diversity, even when not designed explicitly for them, when placed in accordance with quality habitat, as the small Betty's Bay MPA, dense with kelp and reef habitat, had a high abundance of mesopredatory sharks and rays.

In chapter 4, I expand on my analysis of chondrichthyan diversity in and around these South African MPAs by examining the biotic relationships between chondrichthyans and other marine fish and invertebrate taxa. Given the importance of understanding habitat to MPA success, and the lack of such knowledge in poorly funded developing countries, shortcuts to identifying sites of high biodiversity would help prioritize space-based conservation. If strong relationships hold between chondrichthyans and other taxa in their communities, perhaps they could serve as an indicator of ecosystem diversity and productivity (Zacharias and Roff 2001, Gilby et al. 2017). As such, I turn again to BRUVs to assess the capacity of chondrichthyans to serve as umbrella species. Borrowing methods from social networking theory, I discover South Africa's endemic scyliorhinid shark species are strong candidates for an umbrella species complex due to their connections to other taxa in the community, including species of conservation, economic, and social importance. These sharks are also easily caught and located in their ecosystem, enhancing their utility as indicators, and are ecologically diverse as a group, expanding the types of habitats about which they can inform. Through simulating reserve networks, I also show these sharks are good indicators of diversity and are thus candidates for informing MPA placement in the region.

In chapter 5, I investigate one final aspect of chondrichthyan habitat with the potential to affect their relationship to MPAs: temperature. Since most chondrichthyans are ectothermic, they maintain optimal body temperatures through behavioural thermoregulation. Thus, studying a range of chondrichthyan species that vary in their ecology and behaviour could help the search for generalizations about how temperature and other environmental variables influence chondrichthyan populations. Such knowledge of the association with abiotic variables is increasingly important under climate change, as changes to environmental gradients could cascade to behavioural and distributional shifts in species (Perry et al. 2005, Pistevos et al. 2017) that hinder the effectiveness of MPAs (Bruno et al. 2018). Cocos Island—an old MPA located off Costa Rica—is a hotspot of shark and ray diversity, including mobile apex predators like the scalloped hammerhead *Sphyrna lewini* and the tiger shark *Galeocerdo cuvier*, and smaller benthic species like the whitetip reef shark *T. obesus* and the marbled ray *Taeniurops meyeni* (White et al. 2015). The island is also regularly affected by the El Niño Southern Oscillation (ENSO), which, in addition to causing month-long cycles in the sea surface temperature anomaly, alters productivity in the Eastern Tropical Pacific (Lavín et al. 2006, Wolff et al. 2012).

Using 27 years of citizen science data collected by a dive company, I find strong relationships between chondrichthyans and temperature, as well as with the El Niño, that vary by species, although most species respond negatively to both. The most mobile species show the strongest responses to changes in temperature and the El Niño. Relative abundance of the mobile *S. lewini* declined over two-fold during strong El Niño events, while the relatively sedentary *T. obesus* had a weak response. Overall, I demonstrate the potential for chondrichthyans to respond to changes in temperature and productivity, in some cases over a 14% decrease in relative abundance with a one degree change in SST, highlighting the importance of considering these effects when predicting future abundance change within static MPAs.

In sum, my thesis aims to elucidate patterns of diversity in relation to habitat and MPAs for chondrichthyans, one of the most threatened taxa worldwide, and to advance our understanding of their association to the biotic and abiotic factors of their environment. The biodiversity crisis is ongoing and increasingly compounded by climate change. We need to understand how MPAs affect chondrichthyans, from poorly understood benthic sharks to charismatic apex predators, and look for general patterns in their habitat associations if we are to conserve them effectively in the face of global environmental change. In the hunt for this knowledge, the diversity within developing nations should be a research priority. Using non-invasive techniques to establish monitoring of the associations between diversity and habitat within MPAs is a critical first step.

Chapter 2 – Reef sharks: recent advances in ecological understanding to inform conservation

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Author contributions: J.K.B conceived of the review. G.J.O. read and synthesized the literature and wrote the manuscript with input from J.K.B.

2.1 Abstract

Sharks are increasingly being recognized as important members of coral-reef communities, but their overall conservation status remains uncertain. Nine of the 29 reef shark species are designated as data deficient in the IUCN Red List, and three-fourths of reef sharks had unknown population trends at the time of their assessment. Fortunately, reef shark research is on the rise. This new body of research demonstrates reef sharks' high site restriction, fidelity and residency on coral reefs, their broad trophic roles connecting reef communities and their high population genetic structure, all information that should be useful for their management and conservation. Importantly, recent studies on the abundance and population trends of the three classic carcharhinid reef sharks (grey reef shark *Carcharhinus amblyrhynchos*, blacktip reef shark *Carcharhinus melanopterus* and whitetip reef shark *Triaenodon obesus*) may contribute to reassessments identifying them as more vulnerable than currently realized. Because over half of the research effort has focused on only these three reef sharks and the nurse shark *Ginglymostoma cirratum* in only a few locales, there remain large taxonomic and geographic gaps in reef shark knowledge. As such, a large portion of reef shark biodiversity remains uncharacterized despite needs for targeted research identified in their red list assessments. A research agenda for the future should integrate abundance, life history, trophic ecology, genetics, habitat use and movement studies, and expand the breadth of such research to understudied species and localities, in order to better understand the conservation requirements of these species and to motivate effective conservation solutions.

2.2 Introduction

Sharks are large predators on coral reefs, and yet these species, and their ecological role in these ecosystems, were often overlooked until recently. For example, neither Sale's (1991) classic book nor the follow-up edition (Sale 2006) make any mention of sharks. This might be attributed to the long exploitation history on coral reefs, which resulted in the virtual elimination of these predators on many coral reefs around the world long before modern scientific studies were conducted in these ecosystems (Jackson et al. 2001, Pandolfi et al. 2003). Coral reefs are, however, used by a variety of shark species (White and Sommerville 2010) and they form critical habitat for those sharks that remain resident on reefs throughout their life cycle, here termed reef sharks. Fishing surveys on the Great Barrier Reef, Australia, for example, have found that most surveyed shark species occurred at or near reefs, particularly at sites with hard-coral cover, emphasizing the importance of coral-reef habitat to these species (Chin et al. 2012, Espinoza et al. 2014). Scientific research focused on reef sharks has increased substantially in the past few decades, and along with growing recognition of the importance of these species there is also recognition that they face many threats. Most notably, as coral reefs have been degraded over the past century, reef sharks have continued to face exploitation pressure and habitat loss (Jackson et al. 2001, Pandolfi et al. 2003, Bellwood et al. 2004, Hoegh-Guldberg et al. 2007, Sandin et al. 2008). Recently, climate change has also been postulated to pose an additional threat to these species through effects on physiology and the suitability of coral-reef habitat (Chin et al. 2010).

Directed research effort is required to ensure the design and implementation of effective conservation measures that encompass the suite of reef shark diversity. The IUCN Red List is the primary tool used to define global shark extinction risk and conservation statuses, and has been important for shark conservation, as evidenced by the recent CITES listings of five shark species listed as vulnerable and endangered by the Red List (Vincent et al. 2014, CITES 2015). Up to date knowledge of reef shark diversity, ecology and population statuses is critical for conservation prioritization, and as such, the current ability of reef shark research to serve as aids for conservation needs to be assessed. This review (1) presents the first synthesis of the scientific literature on reef sharks focusing specifically on ecological research, (2) assesses the extent to which current knowledge may contribute to IUCN Red List evaluations and (3) identifies gaps in reef shark research and suggests priority research directions to foster reef shark conservation.

2.3 Methods

Reef sharks were defined as those species that use shallow tropical coral reefs as their primary habitat. The final species list was determined primarily using the habitat descriptions by Compagno et al. (2005), following initial consideration of each species whose habitat description included ‘reef’ or ‘coral’, those species with multiple habitat types indicated, and for which tropical coral reefs were not their primary habitat, were removed. As such, those large pelagic sharks that frequent coral reefs but are not reef-restricted and those sharks that inhabit only rocky reefs were excluded. Additionally, the following species were removed because coral reefs are not their primary habitat: bluegrey carpetshark *Heteroscyllium colcloughi*, blind shark *Brachaelurus waddi*, brownbanded bambooshark *Chiloscyllium punctatum*, nervous shark *Carcharhinus cautus*, spot-tail shark *Carcharhinus sorrah* (A. Chin, pers. comm.), spotted *Orectolobus maculatus*, ornate *Orectolobus ornatus* and cobbler *Sutorectus tentaculatus* (C. Huveneers, pers. comm.). For some species, there was insufficient information to confidently assess them as reef sharks, but if the little information available suggested that they live on coral reefs, they were retained.

For each reef shark species, a Web of Science (WoS) search was conducted on 19 April 2015 using the species' scientific and common names as search terms, including synonyms. Abstracts from conference proceedings and papers that only briefly referenced the species were removed. Reef shark papers that were not located in the original WoS search but were referenced elsewhere in the literature were also included. Three additional studies were found in September 2015 during a follow-up search.

Each paper was classified based on the subject matter of the study; papers on multiple subjects were classified into multiple categories. 'Physiology' was used for any study on the physiology or biochemistry of reef sharks and their proteins and cells. 'Behaviour' includes studies of the use of senses, mating, aggression, reaction to humans and locomotory behaviour. 'Habitat use' includes use of nursery or mating grounds, habitat preferences and characteristics, aspects of their distribution and studies of movement and spatial use. 'Basic biology' is a broad category that includes general descriptions of the species' biology and natural history; studies of form, function and general external morphology (including teeth and feeding mechanics); reproductive biology studies (such as egg case descriptions) not included in the physiology, behaviour or habitat use categories; interactions with other species that do not include predation or parasitism; growth studies and studies of condition. 'Diet' includes studies of feeding, including stomach content and stable-isotope analysis. 'Genetics' include studies of population genetics and structure as well as multiple paternity, genetic aspects of parthenogenesis, characterization of genomes and genes, microsatellite identification and sequencing and investigations of polyploidy. 'Parasites' include all references pertaining to parasites found in the target species, including bacterial disease. 'Abundance' was used for studies providing estimates or indications of a species' abundance or density in an area or through time, including fishing surveys. The ‘socio-economic and conservation’ (SEC) category includes studies discussing a human dimension or aspect of conservation, including fisheries and shark eco-tourism. The category ‘captive’ was used for studies on husbandry and keeping of sharks in captivity. ‘Taxonomy’ was used for studies discussing reef shark taxonomic units or redefining reef shark taxonomy, and for accounts of fossils. ‘Other’ was used for anything else, including reviews, studies of methodology and records of first occurrence.

2.4 Reef shark diversity and overview of recent advances

In total, 29 reef shark species are considered here (Table 2.1). These species are taxonomically and functionally diverse spanning three orders [Heterodontiformes (bullhead sharks), Orectolobiformes (carpet sharks) and Carcharhiniformes (ground sharks)] and seven families (Table 2.1, Figure 2.1). From a life-history perspective, reef sharks are also a diverse group of fishes, with estimated maximum total lengths (L_T) ranging from 60 to 370 cm and estimated trophic levels ranging from 3·1 to 4·2 (Table 2.1).

The total number of studies on reef sharks has risen rapidly, particularly over the past 30 years, with a total of 1101 studies identified in the literature review (Figure 2.2a). Physiological studies of the nurse shark *Ginglymostoma cirratum* (*n*=366), a model organism, are most common in this body of literature (Figure 2.3a). Without considering any physiology studies, there are a total of 604 reef shark studies (Figure 2.2a). The taxonomic focus of these reef shark studies is highly uneven, with over half focused on just four species: *G. cirratum* (*n*=167) and the three classic carcharhinid reef sharks [blacktip reef shark *Carcharhinus melanopterus*

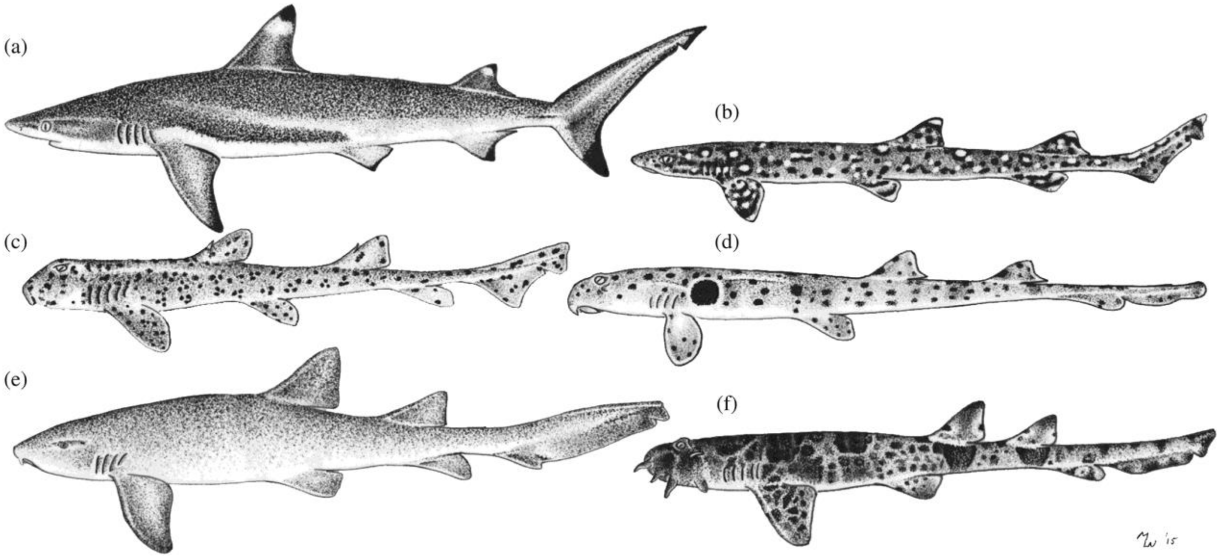

Figure 2.1 Representative sharks from each reef shark Family considered, except for Stegostomatidae, which is similar in form to Orectolobidae. (a) Carcharhinidae: *Carcharhinus melanopterus*; (b) Scyliorhinidae*: Atelomycterus marmoratus*; (c) Heterodontidae: *Heterodontus quoyi*; (d) Hemiscylliidae: *Hemiscyllium ocellatum*; (e) Ginglymostomatidae: *Ginglymostoma cirratum*; (f) Orectolobidae: *Orectolobus wardi*. Drawings by M. Nikoo.

(*n*=119), grey reef shark *Carcharhinus amblyrhynchos* (*n*=110) and whitetip reef shark *Triaenodon obesus* (*n*=101)] (Figures 2.2b, 2.3b). Fewer studies have been devoted to the Caribbean reef shark *Carcharhinus perezi* (*n*=53), the Galapagos shark *Carcharhinus galapagensis* (*n*=51), the zebra shark *Stegostoma fasciatum* (*n*=47), the epaulette sharks (family Hemiscylliidae, *n*=44; although most of these studies (72%) focused on a single species, the epaulette shark *Hemiscyllium ocellatum*), the silvertip shark *Carcharhinus albimarginatus* (*n*=39) and other ginglymostomids besides *G. cirratum* (*n*=38) (Figures 2.2b, 2.3b). The heterodontids, orectolobids and scyliorhinids remain understudied: <10% of reef shark studies examined any of these groups even though they comprise over one third of the species; most of their studies (56%) were published recently (Figure 2.2b).

Besides physiology studies, most reef shark research has focused on habitat use (21%) or basic organismal biology (20%, Figure 2.2c), with data typically obtained from fisheries catches or underwater observations. Studies pertaining to reef shark abundance have risen rapidly in the past decade and now comprise the third highest research focus (15%) (Figure 2.2c). There has been a steady focus on reef shark behaviour (12%) over time, with most of these studies describing agonistic displays and behaviour towards humans, foraging behaviour, locomotory performance, the use of the senses or mating behaviour; almost all behaviour studies (93%) were of *G. cirratum* or the carcharhinid species. In addition, numerous studies have characterized the diversity and biology of reef shark parasites (11%) (Figure 2.2c), covering all reef shark groups besides Scyliorhinidae. Characterization of reef shark parasites could open a new avenue of research in which parasites are used to assess contemporary and historical movement patterns of their hosts (Caira and Euzet 2001). There has also been a steady rise in the studies dealing with reef shark taxonomy (8%) (Figure 2.2c), reflective of taxonomic uncertainties and recent discoveries of new species in Orectolobidae and Hemiscylliidae (Last et al. 2006, Allen and Erdmann 2008, Goto 2008, Corrigan and Beheregaray 2009). Fewer studies to date have examined reef shark genetics (6%) or diets (5%) (Figure 2.2c).

Table 2.1 Reef shark species of the world. Their estimated size (Max TL = maximum total length, from Compagno *et al*., 2005 except where otherwise indicated), and trophic level (T.L., from Froese & Pauly, 2015), as well as information derived from the IUCN Red List: the current status (Vu=Vulnerable, NT=Near Threatened, LC=Least Concern, DD=Data deficient and year of most recent assessment (regions and years on a second line refer to separate regional assessments of the species in addition to the global status assessment), population trend (as indicated in most recent IUCN Red List report: **↓** indicates a decreasing trend, — indicates a stable trend, and ? indicates an unknown trend), distribution (Au=Australia, EA=Eastern Atlantic, EP=Eastern Pacific, IP=Indo-Pacific (excluding Australia), Med=Mediterranean, WA=Western Atlantic WI=West Indian Ocean, WP=Western Pacific (Northern Asia)), and fisheries use (targeted, bycatch:Y=Yes, N=No).

ORDER/ Family[1]	Species	Common Name	Max TL (cm)	T.L.	IUCN Red List Status	Trend	Distribution	Targeted	Bycatch
HET/He	*Heterodontus mexicanus*	Mexican hornshark	70	4.2	DD - 2006	**?**	EP	N	Y
	H. quoyi	Galapagos bullhead shark	61	3.5	DD - 2004	**?**	EP	N	Y
ORE/Or	*Eucrossorhinus dasypogon*	Tasselled wobbegong	>125		NT-2003	□	IP/Au	Y	Y
	Orectolobus japonicus	Japanese wobbegong	>107	3.8	DD-2007	**?**	WP	Y	Y
	O. wardi	Northern wobbegong	63	4.0	LC-2003	—	Au	N	N
	O.hutchinsi	Western wobbegong	200	4.0	DD-2008	**?**	Au	N	Y
	*O.floridus**	Floral banded wobbegong	75	3.8	DD-2008	**?**	Au	N	Y
	*O. reticulatus**	Network wobbegong	Unk	3.7	DD-2011	**?**	Au	N	N
ORE/Hs	*Chiloscyllium arabicum**	Arabian carpetshark	54	4.1	NT-2008	**?**	WI	N	Y
	Hemiscyllium freycineti	Indonesian speckled carpetshark	72	3.4	NT-2011	**?**	IP (New Guinea)	Y	Y
	H. michaeli	Michael's epaulette shark	69[1]	3.5	NT-2012	**?**	IP (New Guinea)	N	N
	H. ocellatum	Epaulette shark	107	3.4	LC-2003 IP: NT-2003	—	IP/Au	Y	Y
	H. henryi	Henry's epaulette shark	81.5[2]	3.5	DD-2012	**?**	IP-NG	N	N
	H. strahani	Hooded carpetshark	80	3.4	Vu-2003	**?**	IP-NG	N	N
	H. trispeculare	Speckled carpetshark	79	3.5	LC-2003	**?**	Au	N	N
	*H.hallstromi**	Papuan epaulette shark	77	3.5	Vu-2003	**?**	IP-NG	N	N
	*H.galei**	Cenderwasih epaulette shark	>57[2]	3.4	DD-2012	**?**	IP-Indonesia	N	N

ORDER/ Family[1]	Species	Common Name	Max TL (cm)	T.L.	IUCN Red List Status	Trend	Distribution	Targeted	Bycatch
ORE/Gi	*Ginglymostoma cirratum*	Nurse shark	300	4.2	DD-2006 WA: NT-2006	**?**	WA/EA/EP	Y	Y
	Nebrius ferrugineus	Tawny nurse shark	320	4.1	Vu-2003 Au: LC-2003	□	IP/Au	Y	Y
	Pseudoginglymostoma brevicaudatum	Shorttail nurse shark	75	3.8	Vu-2004	**?**	WI	N	Y
St	*Stegostoma fasciatum*	Zebra shark	354	3.1	Vu-2003 Au: LC-2003	□	IP/Au	Y	Y
CAR/Sc	*Atelomycterus marmoratus*	Coral catshark	70	4.1	NT-2003	**?**	IP	Y	Y
	*Aulohalaelurus labiosus**	Blackspotted catshark	67	4.1	LC-2003	**?**	Au	N	N
CAR/Ca	*Carcharhinus albimarginatus*	Silvertip shark	300	4.2	NT-2007	**?**	WI/IP/EP	Y	Y
	C. amblyrhynchos	Grey reef shark	255	4.1	NT-2005	**?**	IP/WI/Au/EP/ WP	Y	Y
	C. melanopterus	Blacktip reef shark	<200	3.9	NT-2005	□	WI/IP/Med/EP /WP/Au	N	Y
	C. perezi	Caribbean reef shark	295	4.5	NT-2006	□	WA	N	Y
	C. galapagensis	Galapagos shark	370	4.2	NT-2003 Au: DD-2003	**?**	EA/WA/WI/E P/IP/Au	Y	Y
	Triaenodon obesus	Whitetip reef shark	200	4.2	NT-2005	**?**	WI/IP/Au/WP/ EP	Y	Y

*Indicates a little known species that is most likely a reef shark. 1 Orders: Het=Heterodontiformes, Ore=Orectolobiformes, Car=Carcharhiniformes. Families: He=Heterodontidae, Or=Orectolobidae, Hs=Hemiscylliidae, Gi=Ginglymostomatidae, St=Stegostomidae, Sc= Scyliorhinidae, Ca=Carcharhinidae. [1]Allen & Dudgeon, 2010. [2]Allen & Erdmann, 2008.

Here, a review of the reef shark literature deemed most relevant to conserving these species is undertaken, namely studies focused on reef shark ecology (habitat and diet), genetics, abundance, socio-economics and conservation. Although there is still much to learn, research in these areas has increased substantially in the past decade (Figure 2.2c), making a synthesis of this new knowledge now possible.

2.5 Habitats, movement, and home ranges

Reef sharks are coastal species with preference for the structurally complex habitats of reefs with high coral cover (e.g. Chin et al. 2012, Espinoza et al. 2014, Rizzari et al. 2014b). Beyond this general characterization, interspecific habitat preferences vary widely. The tawny nurse shark *Nebrius ferrugineus*, *H. ocellatum, S. fasciatum* and *C. melanopterus* prefer shallow habitat in lagoons and on sand and reef flats and ledges (Heupel and Bennett 2007, Papastamatiou et al. 2009a, 2009b, 2010, Speed et al. 2011, 2015, Chin et al. 2013b, Rizzari et al. 2014b). In contrast, *C. galapagensis* (e.g. Holzwarth et al. 2006, Lowe et al. 2006, Papastamatiou et al. 2015), *C. perezi* (Garla et al. 2006, Chapman et al. 2007) and *C. amblyrhynchos* (e.g. McKibben and Nelson 1986, Dale et al. 2011b, Rizzari et al. 2014b) prefer deeper sites with strong currents on exposed forereef slopes, crests and channels. Similarly, *C. amblyrhynchos* is fairly restricted to reef habitat (Chin et al. 2012, Espinoza et al. 2014) while *C. albimarginatus* has preferences for deeper sites further offshore (Stevens 1984, Espinoza et al. 2014). As a benthic species, *T. obesus* can be widespread across habitat with high coral cover that provides rock ledges and coral heads for refuges and foraging (Randall 1977, Whitney et al. 2012a, Espinoza et al. 2014). Although reef sharks may select habitat partially based on environmental variables such as coral cover, depth, complexity, and temperature (Papastamatiou et al. 2009a, Vianna et al. 2013, 2014,

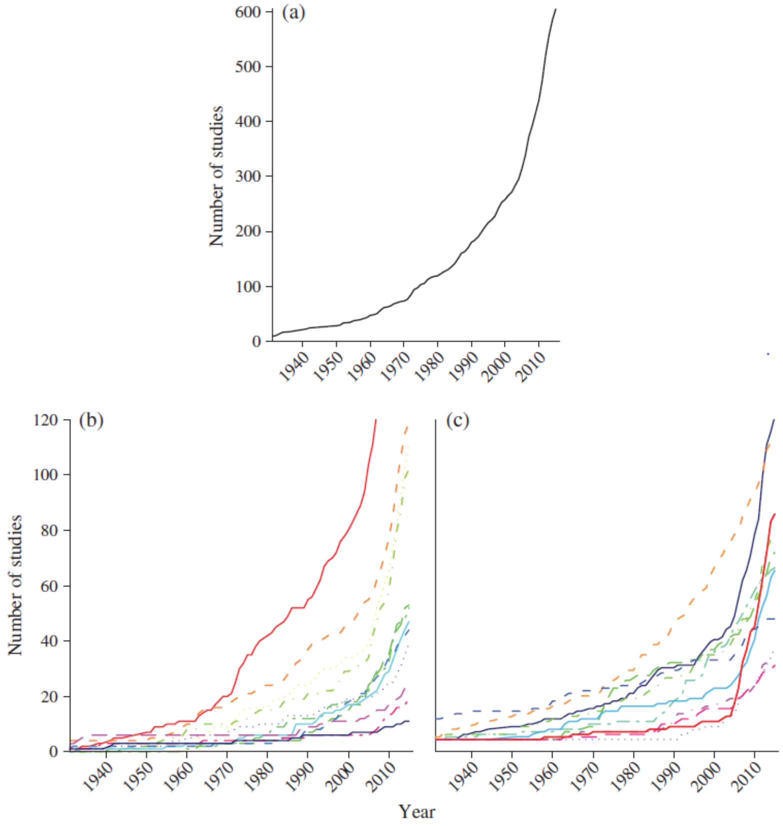

Figure 2.2 The cumulative number of studies on reef sharks (excluding physiology studies) published in peer-reviewed journals by year. (a) for all species and topics combined, (b) by species (or Family), and (c) by topic. Other Ginglymostomatidae includes *Nebrius ferrugineus* and *Pseudoginglymostoma brevicaudatum*. Each x-axis starts at 1931 although nine taxonomic studies occurred earlier, from 1867. The y-axis on (b) and (c) only extends to 120, but on (b) *Ginglymostoma cirratum* increases to 167 and on (c) Habitat use extends to 126. For (b) and (c) lines are ordered from categories with the greatest to the least number of studies. *Ginglymostoma cirratum* (—), *C. melanopterus* (- - -), *C. amblyrhynchos* (····), *T. obesus* (– -), *C. perezi* (– –), *C. galapagensis* (–-), *S. fasciatum* (—), Hemiscylliidae (- - -), *C. albimarginatus* (····), other Ginglymostomatidae (- -), Scyliorhinidae (– –), Orectolobidae (–-), and Heterodontidae (—). Habitat use (—), basic biology (- - -), abundance (—), other (– -), behaviour (– –), parasites (–-), socio-economics conservation (—), taxonomy (- - -), genetics (- - -), captive (– -), and diet (– –). Figure A1 displays similar data but with all reef shark physiology studies included.

Espinoza et al. 2014), recent evidence suggests these effects are relatively weak and that biological factors such as competition may be more important (Heupel and Simpfendorfer, 2014, Espinoza et al. 2015a).

Tagging and telemetry methods have been increasingly used over the past decade to track reef shark movements and to delineate their habitat use, home ranges and long-distance

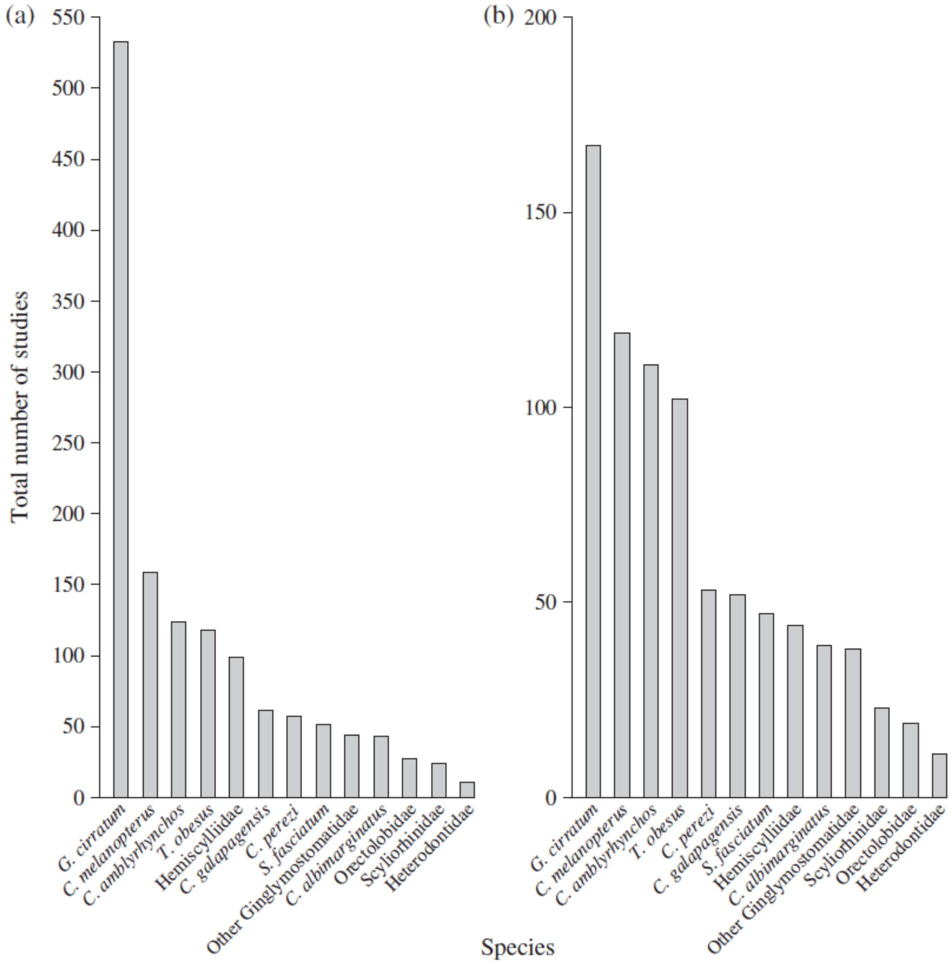

Figure 2.3 Frequency distribution of peer-reviewed reef shark studies (excluding physiology studies) by species (or group). Other Ginglymostomatidae includes *Nebrius ferrugineus* and *Pseudoginglymostoma brevicaudatum.* Figure A2 displays similar data but with all reef shark physiology studies included.

movements. Thus far, these studies have focused on 10 reef shark species: *C. amblyrhynchos* (*n*=14 studies), *C. melanopterus* (*n*=13), *C. galapagensis* (*n*=8), *C. perezi* (*n*=6), *G. cirratum* (*n*=6), *T. obesus* (*n*=5), *S. fasciatum* (*n*=2), *C. albimarginatus* (*n*=3), *N. ferrugineus* (*n*=1) and *H. ocellatum* (*n*=1). Most of these studies have employed acoustic telemetry (Maljkovic and Côté, 2011, Espinoza et al. 2015b, Heupel and Simpfendorfer 2015), including the placement of acoustic receivers and transmitters on the sharks themselves (Holland et al. 2009). Other methods include tagging for mark–recapture or resighting (Stevens 1984, Garla et al. 2006, Chin et al. 2013b), pop-off satellite archival transmitting (PSAT) tags for studying depth use (Chapman et al. 2007) and Argos satellite tracking (Meyer et al. 2010, Papastamatiou et al. 2010, Friedlander et al. 2012). Additionally, movement has been studied directly using photo-identification surveys (Dudgeon et al. 2008, Mourier et al., 2012, Whitney et al. 2012a).

Recent movement studies are providing compelling evidence of reef sharks' high site fidelity, residency and restricted home ranges over multiple years, even after seasonal and diel migrations (e.g. Speed et al. 2010, Field et al. 2011, Bond et al. 2012; Chapman et al. 2015, Espinoza et al. 2015a, 2015b). Home ranges vary from <1 to 10km^2 in the smaller more sedentary, site-restricted species such as *C. melanopterus*, *T. obesus* and *G. cirratum* (e.g. Papastamatiou et al. 2010, Whitney et al. 2012a, Ferreira et al. 2013) up to tens of km^2 in size in the larger, more mobile species such as *C. amblyrhynchos* and *C. perezi* (e.g. McKibben and Nelson 1986, Garla et al. 2006, Heupel and Simpfendorfer 2015). Despite high residency, some individuals of *C. amblyrhynchos*, *C. galapagensis*, *C. perezi*, *T. obesus*, *S. fasciatum* and *G. cirratum* have been shown to make longer movements or migrations over tens of km throughout and between wider reef systems (e.g. McKibben and Nelson 1986, Chapman et al., 2005; Lowe et al. 2006, Heupel et al. 2010, Whitney et al. 2012a, Dudgeon et al. 2013).

In addition, movement studies are revealing interspecific and intraspecific variation in reef shark habitat use, degree of movement and home range size. *Carcharhinus amblyrhynchos* movement is generally less restricted on continuous to semi-isolated reef habitat (Heupel et al. 2010, Espinoza et al. 2015a; Speed et al. (2011) and Heupel and Simpfendorfer (2014) provide examples of site restriction in these systems) than it is on isolated oceanic islands and atolls separated by deep water (Field et al. 2011, Barnett et al. 2012, Speed et al. 2012). *Carcharhinus perezi* does not show the same year-long residency on reefs in the Bahamas, which presumably have less seasonal temperature fluctuations, as it does on reefs further south (Garla et al. 2006, Bond et al. 2012, Brooks et al. 2013). Body size, which can influence energy requirements, also affects interspecific and intraspecific habitat variation. For *C. amblyrhynchos*, *C. melanopterus* and *C. perezi*, activity space appears to increase with size and juveniles typically use shallower habitat closer to shore such as lagoons (e.g. Garla et al. 2006, Chin et al. 2013a, Rezzolla et al. 2014). On the Great Barrier Reef, the larger *C. albimarginatus* displays wider movements, is less site attached and more likely to move between management zones than either *C. amblyrhynchos* or *T. obesus* (Barnett et al. 2012, Espinoza et al. 2015b). Similarly, in Fiji, one *C. albimarginatus* displayed pelagic behaviours in addition to its reef-associated habits (Bond et al. 2015). Finally, there is also variation by sex, with females tending to be more resident and philopatric, and sometimes showing different spatial and temporal habitat use patterns from males (e.g. Speed et al. 2011, 2012, Whitney et al. 2012a, Brooks et al. 2013). For example, female *C. melanopterus* off Moorea, French Polynesia use lagoons while males preferentially use the forereef (Mourier et al. 2012). Males may show greater movement than females due to dispersal or searching out females during mating season (e.g. Field et al. 2011, Whitney et al. 2012a, Espinoza et al. 2015a, 2015b).

The wealth of new information about reef shark habitat and movement could help to inform effective management strategies for these species. Marine protected area (MPA) design, for example, will benefit from information about home-range size, habitat selection and exposure to anthropogenic stressors in different zoning regions (Chapman et al. 2007, Wiley and Simpfendorfer 2007, Espinoza et al. 2015b). Movement studies can serve to evaluate MPA placement and design by evaluating the fidelity and residency of reef shark species to particular protected zones (Heupel et al. 2010, Bond et al. 2012, Speed et al. 2016). Moreover, tagging studies that include vertical movement reveal that certain reef shark species prefer deeper waters and may exhibit seasonal or diel shifts in depth that could bring them out of MPAs around shallower reef habitat (Chapman et al. 2007, Vianna et al. 2013, Papastamatiou et al. 2015). The occasional long-range movements identified in reef sharks also informs about wider population connectivity, with implications for reducing extinction vulnerability (Heupel et al. 2010, Whitney et al. 2012a, Mourier and Planes 2013). The variation in habitat use between species, sizes and sexes should be further characterized using a combination of tagging, telemetry and population genetic techniques, and then incorporated into management plans as this variation may determine the effectiveness of MPAs.

2.6 Diets and trophic ecology

Diet studies also provide an important window into the ecological role of reef sharks. About 30 studies have examined reef shark diets and trophic ecology to date, most of which focused on carcharhinid reef sharks and utilized stomach content analysis of specimens captured during fisheries surveys. Carcharhinid reef sharks are generalists consuming a wide variety of reef-associated teleosts, cephalopods, crustaceans as well as the occasional elasmobranch

(Stevens 1984, Stevens and McLoughlin 1991, Salini et al. 1992, Wetherbee et al. 1997, Papastamatiou et al. 2006, Zhang et al. 2006, Tavares 2009). Apart from the Carcharhinidae, stomach content analysis of *H. ocellatum* found worms and crabs to be most important, followed by other crustaceans and small fishes (Heupel and Bennett 1998). Also, one tasselled wobbegong *Eucrossorhinus dasypogon* was observed consuming another elasmobranch on the Great Barrier Reef (Ceccarelli and Williamson 2012). Two stomach-content analyses revealed that *N. ferrugineus* consumes cephalopods and sea snakes (Smale 1996, Masunaga et al. 2008).

To date, only eight studies have employed stable-isotope analyses, but these studies have already shed light on reef shark trophic ecology. Stable isotopes have, for example, been used to detect ontogenetic diet shifts, along with individual variation in these shifts, both directly by repeated measures of the same individuals through time and indirectly by relating stable isotopes to body size (Papastamatiou et al. 2010, Speed et al. 2012, Matich et al. 2015). This approach also has provided evidence of competition in reef shark communities: stable-isotope data for *C. perezi* at a provisioning site in the Bahamas showed that a few individuals with enriched δ15N values were monopolizing the feeding (Maljkovic and Côté 2011). Stable-isotope data have revealed interspecific differences in niche width between *C. perezi* and *G. cirratum* in Belize, including differences in δ13C values that suggest resource partitioning despite similar trophic levels (Tilley et al. 2013). At Ningaloo Reef, Australia, *C. melanopterus*, *C. amblyrhynchos* and *T. obesus* have largely overlapping trophic levels, but *T. obesus* still feeds at a slightly lower trophic level, and it is believed to rely more on benthic herbivores and invertivores than piscivory (Speed et al. 2012).

In addition, stable-isotope studies can help elucidate reef shark habitats and prey bases (Borrell et al. 2011, Speed et al. 2012), thus providing complementary information to movement studies and new insights into these species' ecological roles on reef ecosystems. Diet information has already been used to parameterize models that suggest sharks play an important role in coral-reef food webs (Bascompte et al. 2005). Recent studies have revealed that reef sharks can connect distinct reef habitats through their foraging, which, in addition to their omnivory, is hypothesized to help to confer stability to these ecosystems (Bascompte et al. 2005, Rooney et al. 2006). In the north-west Hawai'ian Islands, for example, an analysis of δ13C coupled with telemetry work revealed that although *C. galapagensis* primarily inhabits and forages on shallow reefs, about one third of its resources are derived from deeper mesophotic reefs (Papastamatiou et al. 2015). On Palmyra atoll, in the northern Line Islands, *C. amblyrhynchos* is the dominant shark on the forereef, but derives most of its resources from offshore pelagic sources, whereas adult *C. melanopterus*, which are smaller and less abundant, do forage mainly on the forereef (McCauley et al. 2012b). A related study, combining telemetry with stable isotopes, revealed both low levels of mixing and distinct trophic ecologies (δ15N and δ13C) and foraging success, as evidenced by body condition, between *C. melanopterus* living in Palmyra's eastern and western lagoons (Papastamatiou et al. 2010).

2.7 Genetics

Reef shark genetics represent an emerging research area (Figure 2.2c), although only nine studies have focused on the most relevant information for assessing reef shark conservation status, namely reef shark genetic population structure and gene flow and assessing cryptic biodiversity. With respect to the latter, Karl et al.'s (2012) *G. cirratum* study revealed that its Pacific populations may in fact be a different species from its heavily studied Atlantic populations. Other reef shark studies have examined multiple paternity in *C. galapagensis* (Daly-

Engel et al. 2006) and *G. cirratum* (Saville et al. 2002, Heist et al. 2011), or sequenced genes and microsatellite loci for the Japanese wobbegong *Orectolobus japonicus* Regan 1906 (Chen *et al.*, 2013), *G. cirratum* (Heist et al. 2003), *S. fasciatum* (Dudgeon et al. 2006) or *C. amblyrhynchos* (Momigliano et al. 2014), as well as other sharks related to the carcharhinid reef sharks (Keeney and Heist 2003, Fitzpatrick et al. 2011b), which should enable population genetic work in the future.

Population genetic studies thus far have provided evidence of high genetic structure and low genetic diversity for populations of four reef shark species, *G. cirratum* (Karl *et al.*, 2012), *S. fasciatum* (Dudgeon et al. 2009), *C. melanopterus* (Mourier and Planes 2013, Vignaud et al. 2013, 2014) and *T. obesus* (Whitney et al. 2012b). One study of *C. amblyrhynchos* on the Great Barrier Reef found, however, very low genetic structure that is indicative of substantial dispersal for these populations (Momigliano et al. 2015). Although these results are expected based on the residency patterns of these species, they should still help in assessments of their conservation status. First, the information could help to justify effort for reef shark conservation assessments at finer spatial scales (Dudgeon et al. 2009). Second, these studies suggest there is limited potential for depleted populations of these reef sharks to be rescued from other regions with more abundant populations (Dudgeon et al. 2009) while demonstrating a high potential for inbreeding. For instance, genetic diversity of *C. melanopterus* is greater on the large well-connected reefs of the Red Sea and the Great Barrier Reef, which promote dispersal, than on the fragmented reefs of French Polynesia, where it exhibits high genetic structure and low effective population size, probably due to inbreeding resulting from high natal philopatry of females to nursing grounds (Mourier and Planes 2013; Vignaud et al. 2013, 2014). These findings underscore the need for interconnected systems of MPAs for conservation of reef shark genetic diversity (Vignaud et al. 2014; Momigliano et al. 2015). Further genetic work, however, is still required to quantity the benefits of dispersal as well as the severity and consequences of inbreeding depression for reef sharks. Finally, genetic studies can provide information on effective population size to aid in monitoring genetic diversity and abundance for shark populations (Dudgeon and Ovenden 2015). Genetic studies can also complement the results of tagging and telemetry by demonstrating gene flow, dispersal and philopatry over longer time frames (Whitney et al. 2012b, Mourier and Planes 2013, Momigliano et al. 2015).

2.8 Abundance

Studies aimed at quantifying reef shark baselines, abundances and densities, and how these have changed over time, have increased greatly in the past decade (*n*=89) (Figure 2.2c), but because of the dearth of available data there are still serious geographic and taxonomic gaps in understanding. Carcharhinid reef sharks were the focus of most (81%) abundance studies, with the three classic Indo-Pacific reef sharks (*C. amblyrhynchos*, *C. melanopterus* and *T. obesus*) accounting for 59% of these studies, and for two-thirds of those that inferred temporal or spatial (space-for-time) trends in abundance. Even for these well-studied species, however, abundance is well characterized only for Australia and some selected islands in the western and central Pacific, including Hawai'i and the Line Islands; little information exists about their Indian and western Pacific Ocean populations (Figure 2.4a-c). *Ginglymostoma cirratum* was investigated in 23% of all abundance studies, of which only one third inferred any temporal or spatial trends. Its abundance has only been studied in any detail in the western Atlantic Ocean, particularly in the Caribbean, despite a distribution that spans the eastern Pacific and eastern Atlantic Oceans (Figure 2.4d). The remaining reef shark species were included in only 16% of abundance studies, and although 61% of those inferred trends in abundance, most were based on aggregate counts over multiple species (Heupel et al. 2009, Nadon et al. 2012, Rizzari et al. 2015) or on small sample sizes (Joshi et al. 2008, Chin et al. 2012, Goetze and Fullwood 2013).

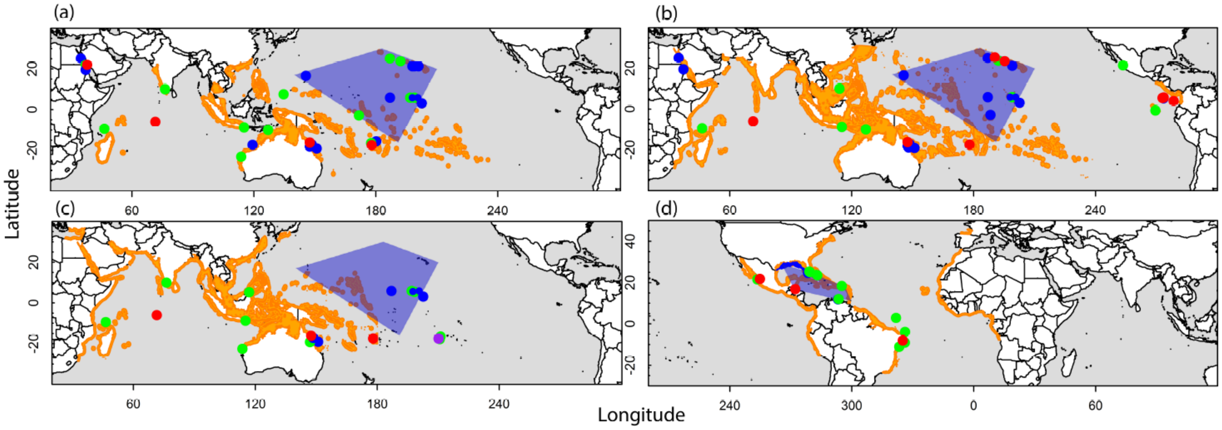

Figure 2.4 Geographic location of 'abundance' studies for the four best studied reef shark species. (a) grey reef shark *Carcharhinus amblyrhynchos*, (b) whitetip reef shark *Triaenodon obesus*, and (c) blacktip reef shark *C. melanopterus*, (d) nurse shark *Ginglymostoma cirratum* overlaid on maps of their global ranges (represented in orange), based on spatial data from the IUCN Red List (IUCN, 2015). Red circles denote studies of abundance, blue circles denote spatial studies, purple indicates a demographic analysis from genetic data, and green circles denote studies including only estimates of density or abundance from a single location and time. Larger blue polygons were used for studies that examined a wider region rather than only a single, smaller locality. Maps made with Natural Earth and the R package *PBSmapping* (http://www.r-project.org; cran.r-project.org/web/packages/PBSmapping/index.html).

A diversity of survey and analytical methods has been used to study reef sharks. Reef shark abundances have been quantified using fisheries-dependent data (48% of studies), underwater visual censuses (UVC) by divers (40%; of which 22% collected data through tourist operations) and video, including baited remote underwater videos (BRUV; 9%). Five studies

(6%) used mark–recapture to estimate population size in their study area (Stevens 1984, Heupel and Bennett 2007, Dudgeon et al. 2008, McCauley et al. 2012a, Zanella et al. 2012). Despite the variety of survey methods, the analysis of abundance data has been largely limited to basic statistical methods, with most studies (n=51) using linear regression or simpler methods to examine abundance, including 46% of the studies that inferred temporal or space-for-time trends, despite the largely non-normal nature of count data. The recognized importance of environmental covariates in affecting reef shark abundance will mean that appropriate statistical techniques will be crucial for inferring trends in abundance (Nadon et al. 2012, Richards et al. 2012, Brooks et al. 2013, Afonso et al. 2014, Espinoza et al. 2014, White et al. 2015). The importance for robust modelling approaches driven by data from long-term programs has already been recognized in temperate contexts (Rutterford et al. 2015). Robust statistical analysis and long-term monitoring programs should be made common practice for tropical reef systems as well.

Despite a paucity of time-series data to examine reef shark trends in abundance, 17 such studies have been published, all but one in the past decade. Only seven of these studies, however, used time series longer than ten years, and three of them analyzed aggregate counts of multiple species some of which included just occurrence data (Heupel et al. 2009, Ruppert et al. 2013, Torres-Herrera and Tovar-Avila 2014), reflecting the difficulty of obtaining good quality long-term data. Temporal studies have found a mixture of trends for all studied reef shark species, with eight reporting declines, 10 finding evidence for positive population trends and five identifying population stability in at least some of their studied species. Two studies have demonstrated positive trends for the carcharhinid reef sharks (except for *C. albimarginatus*) and *N. ferrugineus* in the Great Barrier Reef Marine Reserve (Heupel et al. 2009; Espinoza et al.

2014). In contrast, there have been general declines for these same species (again except for *C. albimarginatus* which increased) at the Chagos Archipelago, Indian Ocean, over 30years (Graham et al. 2010). Declines were seen for both *T. obesus* and *C. albimarginatus* at Cocos Island in the eastern Pacific Ocean, although *C. galapagensis* occurrence appears to be increasing; also their populations appear stable at the nearby Malpelo Island (Soler et al. 2013, White et al. 2015). Elsewhere in the Pacific Ocean, temporal studies are known only from provisioned tourism enterprises at Fiji and Hawai'i, which found proportions of some species visiting the sites, such as *C. galapagensis*, *C. melanopterus* and *T. obesus* increasing with time at the expense of other species such as *C. albimarginatus* (Meyer et al. 2009b, Brunnschweiler et al. 2014).

Most studies have either examined abundance across spatial scales spanning multiple islands or reef systems (*n*=34) or only indicate abundance for a particular region or reef system (*n*=34) without inferring temporal or spatial trends for some of the studied species. About 22 studies have used space-for-time analyses to infer historical population trends in areas lacking temporal data by comparing sites with fewer anthropogenic pressures to more heavily affected ones. Every space-for-time study found lower abundance (or occurrence) in areas with higher anthropogenic effect or fishing pressure. For instance, UVCs provide evidence that populations of *C. amblyrhynchos*, *C. galapagensis*, *C. melanopterus*, *T. obesus* and *N. ferrugineus* in the central-western Pacific Ocean (DeMartini et al. 2008, Nadon et al. 2012) and *C. perezi* and *G. cirratum* in the Caribbean (Ward-Paige et al. 2010) are depressed on reefs around areas of high human density. Reef shark populations have potentially declined to <10% of baseline levels on Pacific reefs (Nadon et al. 2012). UVCs suggest that top predators, including sharks, make up a large portion of fish biomass at the reefs of the more remote north-west Hawai'ian Islands and

Palmyra Atoll, while at the more populated main Hawai'ian Islands and Fanning Island, reef sharks are rarer and in some instances large species such as *C. amblyrhynchos* were either observed only rarely or not at all (Wetherbee et al. 1997, Friedlander and DeMartini 2002, Stevenson et al. 2007). Similarly, these sorts of studies can also reflect the influence of fishing pressure on reef sharks, finding substantially higher abundances of populations inside reserves with stricter fishing regulations, including for those of *C. perezi* in Belize (Pikitch et al. 2005) and *C. amblyrhynchos*, *C. melanopterus* and *T. obesus* on the Great Barrier Reef (Robbins et al. 2006, Espinoza et al. 2014, Rizzari et al. 2015).

A global picture of reef shark abundance remains difficult to formulate both because of the dearth of studies and because caution is needed when comparing conclusions amongst studies and sites. Survey methods can, for example, greatly influence density estimates (McCauley et al. 2012a; Nadon et al. 2012). For instance, UVCs conducted at smaller scales can overestimate true densities, which can lead to potentially erroneous conclusions about the role of sharks on reefs (McCauley et al. 2012a, Trebilco et al. 2013). Towed-diver surveys over a larger scale appear to provide more accurate estimates of reef shark abundances (Richards et al. 2011; McCauley et al. 2012a): in the Line Islands, these surveys (Nadon et al. 2012) estimated one tenth as many reef sharks as smaller transect surveys conducted in the same locations (Sandin et al. 2008). Methods with higher detection abilities, but lower accuracy, such as baited video surveys, may also be desired when reef sharks are rarer, as found at heavily fished localities or if only presence–absence or relative abundance data are desired for studies of species richness or composition (Dennis et al. 2005, Heagney et al. 2007, Brooks et al. 2011, Bond et al. 2012, McCauley et al. 2012a, Ruppert et al. 2013, Espinoza et al. 2014, Rizzari et al. 2014a). Video surveys can also be used if estimates of total biomass are desired given the ease and accuracy of measuring size on video (Goetze and Fullwood 2013, Rezzolla et al. 2014). BRUVs are only slightly less accurate and efficient than typical fisheries-dependent methods of estimating abundance and are also non-invasive (Brooks et al. 2011). Mark–recapture may be the best approach for estimating absolute abundances, but is of course a much more effort-intensive approach than BRUVs (McCauley et al. 2012a). Estimating effective population size from a sample of microsatellite loci may provide an effective alternative when estimates of absolute abundance cannot be achieved (Dudgeon and Ovenden 2015). If the few studies that estimated abundance in relatively isolated areas, such Aldabra Atoll, the northwest Hawai'ian Islands, the Line Islands and areas in the Red Sea (Stevens 1984, Holzwarth et al. 2006, Papastamatiou et al. 2009a, Dale et al. 2011b, Hussey et al. 2011, Obura et al. 2011, McCauley et al. 2012a), are to be useful in temporal or spatial comparisons or for setting baselines, both oceanographic variables and survey methodology will need to be carefully considered.

Habitat selection of the target species can also introduce bias into abundance estimates if not properly considered. For instance, the deepwater preferences of *C. albimarginatus* may require baited underwater remote cameras to overcome the depth limitations of divers in order to get systematic counts (Espinoza et al. 2014). The shallower preferences of *C. melanopterus* (Hobson 1963, Stevens 1984, Papastamatiou et al. 2009a, 2009b, Rizzari et al. 2014b) compared with other carcharhinid reef sharks mean that surveys in shallower reefs and lagoons will find them aplenty even when the forereef community is dominated by larger, more deepwater sharks (Papastamatiou et al. 2009a, McCauley et al. 2012b). Seasonal or diel changes in habitat use can also affect abundance estimates if these factors are not incorporated into survey design (Brooks et al. 2013, Vanderklift et al. 2014).

In lieu of time series or spatial data, other studies have used demographic models parameterized by estimates of mortality (Dudgeon et al. 2008, Hisano et al. 2011) and genetic models of effective population size based on microsatellite DNA diversity and mutation rates (Vignaud et al. 2014) to infer population trends and the negative influences that fishing and human presence may have on reef sharks. Analysis of historical records has also proved useful in demonstrating the potential extinction of *C. galapagensis* at Saint Paul's Rocks, an archipelago in the central Atlantic Ocean, where it was once quite abundant (Luiz and Edwards 2011). Interviews with fishermen could also prove to be another useful tool for estimating historical abundance when no other options exist (Teh et al. 2007).

Even with the rapid rise in reef shark abundance knowledge, there is still a need for quality geographically and taxonomically diverse abundance data, particularly over long temporal scales, if the conservation status of reef sharks is to be reliably assessed. These monitoring programs ideally should have standardized designs based upon the study species that account for the biases of the chosen survey methods. Lack of species specificity is also a widespread problem not only for fisheries-dependent data (Heupel et al. 2009, Torres-Herrera and Tovar-Avila 2014), but also has happened in UVC studies (Sandin et al. 2008, Williams et al. 2011, Ruppert et al. 2013), particularly when a species is counted too rarely to support independent analysis (Ward-Paige et al. 2010, Nadon et al. 2012). Citizen science is a logistically feasible, effective and relatively inexpensive alternative to standardized surveys that can collect abundance data over large spatial and temporal scales as long as tourism operators have training and links to researchers with statistical expertise (Huveneers et al. 2009, Ward-Paige et al. 2010, Vianna et al. 2014).

2.9 Threats

Fishing currently poses the greatest threat to reef shark species globally (Dulvy et al. 2014), but most exploitation has occurred in the absence of fisheries data, and as such the effects of fishing on reef shark populations remain poorly understood. Overall, there have been reports of fishing pressure, both targeted and as by-catch, for reef sharks in each family except Scyliorhinidae and Hemiscyllidae (e.g. Heupel et al. 2009, Tavares 2009, Meneses et al. 2011, Aguilar et al. 2014). Amongst species, the threat posed by fishing differs depending on life-history characteristics (Hutchings et al. 2012) as well as by habitat preferences and associated exposure to fishing pressure. For instance, *T. obesus* is not as susceptible to fishing pressure as other reef sharks such as *C. amblyrhynchos*, partially because of its preference for shallow reef habitat which limits its capture in longline fisheries (Dennis et al. 2005, Dale et al. 2011b, Chin et al. 2012). Reef shark fisheries records are sporadic: high catches of *C. amblyrhynchos* and *N. ferrugineus* have been reported from India (Joshi et al. 2008, Kumar et al. 2015), and for these species and *T. obesus* in Indonesia (White 2007). Studies have also documented high landings in largely unreported artisanal fisheries, including in Madagascar, the Seychelles, Brazil and Mexico (Nageon de Lestang 1999; Smith et al. 2009, Meneses et al. 2011, Robinson and Sauer 2013, Furlong-Estrada et al. 2014). For instance, *G. cirratum* and *T. obesus* experience an intermediate ecological risk from artisanal gillnets and longlines in the Gulf of California (Furlong-Estrada et al. 2014). Additionally, several recent studies have uncovered and assessed quantitative time series or spatial data on reef shark populations, from which inferences about fisheries effects on reef shark populations have been made. Other perceived threats to reef shark species include pollution, biomagnification (the concentration of pollutants up the food chain) (Lyle 1986, Al-Hassan et al. 2000, Dulvy et al. 2014) and disturbances to nursery grounds

(Carrier and Pratt 1998). These, in addition to habitat destruction, have been identified as important in the IUCN Red List assessments, but remain unstudied and under discussed in the current literature (Dulvy et al. 2014, IUCN 2015).

2.10 Conservation status

The IUCN Shark Specialist Group (SSG) has assessed all reef shark species, and although the conservation status of most species was uncertain at the time of their assessment and many assessments are now a decade old, little new information is available to alleviate these uncertainties. Overall, five reef shark species are assessed as vulnerable, 11 as near threatened, four as least concern and nine as data deficient (Table 2.1). Given the difficulty of assessments, it is not surprising that the majority of reef shark species (59%) were last assessed in or before 2005 (Table 2.1); but this was also the year when studies of abundance began to rise rapidly (Figure 2.2b). As such, most abundance studies (e.g. *C. amblyrhynchos*: 89%, *C. melanopterus*: 92%, *T. obesus*: 88%, *C. galapagensis*: 80%, *C. albimarginatus*: 79%, *C. perezi*: 75% and *G. cirratum*: 72%) have been published since a species' last red list assessment. Yet despite the rise of abundance studies there remains little information on long-term reef shark population trends, often because studies were based upon short time series or low sample sizes with insufficient power to detect trends in abundance; the only species assessed in the last 5 years were newly described wobbegong and epaulette shark species. Uncertainty in reef shark conservation status is reflected in the fact that at the time of assessment, 22 of the 29 species had uncertain population trends; five species (two vulnerable and three near threatened) had declining population trends while only two (listed as least concern) had stable populations (Table 2.1). It is also suspected that as a group reef sharks may be more threatened and require more conservation attention than the current red listings suggest. As examples, global conservation assessments may mask conservation concerns at the regional or sub-regional level, reef shark data collected at coarse taxonomic scales could mask declines in individual species, and many reef shark population declines probably occurred prior to modern data collection (Jackson et al. 2001).

The five reef shark species (two ginglymostomatids [*N. ferrugineus* and the short-tail nurse shark *Pseudoginglymostoma brevicaudatum*], two hemiscylliids [hooded carpet shark *Hemiscyllium strahani* and Papuan epaulette shark *Hemiscyllium hallstromi*] and *S. fasciatum*), red listed as vulnerable in 2003 and 2004 (Table 2.1), were assessed as such on the basis of limited ranges, habitat destruction and exploitation (Heupel and Kyne 2003a, 2003b, Pillans 2003a, Pillans and Simpfendorfer 2003, Nel et al. 2004). Of these, only *N. ferrugineus* and *S. fasciatum*'s population trends were known. Along with reports of local *N. ferrugineus* extinctions in Thailand and India (Pillans 2003a), there is now also evidence of its populations declining at Chagos Archipelago (Graham et al. 2010), Fiji (Brunnschweiler et al. 2014) and outside of the Great Barrier Marine Reserve (Espinoza et al. 2014). Six studies have quantified *S. fasciatum* abundance, but only one, which used demographic models parameterized by mark–recapture data (Dudgeon et al. 2008), documented temporal trends. There are no abundance studies of *P. brevicaudatum*, and no research effort has been devoted to the two hemiscylliid species possibly due to their small size and cryptic nature.

Since 2005, when *C. amblyrhynchos*, *C. melanopterus* and *T. obesus* were assessed as near threatened (Table 2.1) based primarily on their restricted habitat, life-history characteristics and exploitation history (Smale 2005, 2009, Heupel 2009), evidence has accumulated suggesting that each of these species faces a heightened risk of extinction and might be found to be more vulnerable when a new assessment is completed. Although population trends were unknown at the time of their assessments, numerous studies have since quantified *C. amblyrhynchos* (*n*=38) and *T. obesus* (*n*=35) abundance, providing evidence of populations declines in both (Robbins et al. 2006, Heupel et al. 2009, Graham et al. 2010, Nadon et al. 2012, Clarke et al. 2013, Espinoza et al. 2014, Rizzari et al. 2015, White et al. 2015), except for a few protected populations in Australia (Heupel et al. 2009; Espinoza et al. 2014). For *C. amblyrhynchos*, in addition to two temporal studies suggesting declines exceeding 90% (Graham et al. 2010; Clarke et al. 2013), 16 studies have shown high abundance at remote reefs and low abundance in affected areas and are evidence of historical declines. Moreover, *C. amblyrhynchos* population simulations show declines even under scenarios of moderate fishing pressure (Hisano et al. 2011). Nine studies examining *T. obesus* population trends show a mix of positive and negative trends, whereas the 12 space-for-time studies consistently indicate declines. *Triaenodon obesus* is estimated to have declined by over 90% in the past 30years at Chagos (Graham et al. 2010) and by 77% over 20years at Cocos in the eastern Pacific Ocean (White et al. 2015). In contrast, populations appear to be stable at Malpelo Island in the eastern Pacific Ocean (Soler et al. 2013) and increasing on the Great Barrier Reef (Espinoza et al. 2014). Of the five studies that have examined *C. melanopterus* population trends, declines were found only at Chagos (Graham et al. 2010). A recent population bottleneck was inferred in Moorea, French Polynesia, based on genetic evidence (Vignaud et al. 2014). Such genetic studies also provide information on the low gene flow, inbreeding and susceptibility to habitat fragmentation in *C. melanopterus* populations in the Indo-Pacific, which is useful for conservation planning (Mourier and Planes 2013, Vignaud et al. 2013, 2014). Moreover, five studies show that *C. melanopterus* remains abundant at some remote and protected areas (Stevenson et al. 2007, Papastamatiou et al. 2009a, Obura et al. 2011, McCauley et al. 2012a, 2012b, Vanderklift et al. 2014). Overall, given that large populations of these three species have been observed recently only within MPAs or on uninhabited or remote reefs, reassessments of these three species in particular would be useful.

Although many of the remaining eight near threatened species were assessed about a decade ago (Table 2.1), there is little new information about them in the scientific literature that could inform new red-list assessments. In general, the near threatened designation emphasizes research need since it often has arisen either from a paucity of information rather than a lack of threat or from balancing suspected threats in data-poor areas with lower extinction risk in protected parts of a species' range. For example, *E. dasypogon*, the Arabian carpetshark *Chiloscyllium arabicum* and *C. albimarginatus* were each assessed as near threatened due to suspected population declines or suggested threats (Pillans 2003b, Moore 2009, Pillans et al. 2009). The other five species, the coral catshark *Atelomycterus marmoratus*, the Indonesian speckled carpetshark *Hemiscyllium freycineti*, Michael's epaulette shark *Hemiscyllium michaeli*, *C. perezi* and *C. galapagensis,* might have also been classified in a threatened category had more information been available (Bennett et al. 2003, White 2003, Rosa et al. 2006b, Kyne and Heupel, 2011, Dudgeon et al. 2012). Uncertainty surrounding the conservation status of *C. albimarginatus*, *C. perezi* and *C. galapagensis,* in particular, contrasts with the three carcharhinid reef shark species previously discussed. The few studies that have been carried out provide evidence of extirpation, or nearly so, over parts of these species' ranges (Dennis et al. 2005, Stallings 2009, Ward-Paige et al. 2010, Luiz and Edwards 2011, Ruppert et al. 2013). *Carcharhinus albimarginatus* is especially understudied, probably because its preference for deeper waters on outer forereefs prevents easy monitoring (Stevens 1984, Friedlander et al. 2012, Espinoza et al. 2014) and so far it has typically only been analyzed in taxonomically aggregated shark counts (e.g. Heupel et al. 2009, Goetze and Fullwood 2013, Shawky and De Maddalena 2013).

The conservation status of the 13 reef shark species currently designated as least concern or data deficient remains uncertain despite goals for research on their population statuses identified in their red-list assessments. Notably, *G. cirratum*, the most studied reef shark, is still designated as data deficient because its population dynamics are seldom studied: only four of the 18 abundance studies provide information useful for assessment. The abundance of any species within Heterodontidae has been studied only twice (Galván-Magaña et al. 1989; Smith et al. 2009) and within Hemiscyliidae only once (Heupel and Bennett 2007), but none allowed for inference about population trends. No abundance, movement or population genetic studies have been conducted for reef sharks of the families Scyliorhinidae and Orectolobidae. Some of this trouble is due to the fact that species such as the floral banded wobbegong *Orectolobus floridus* Last & Chidlow 2008 and the network wobbegong *Orectolobus reticulatus* are known from only a few specimens (Last and Chidlow 2008, Last et al. 2008, Huveneers and McAuley 2009a, Corrigan and Huveneers 2011). *Orectolobus reticulatus* may have satisfied criterion B for a threatened category due to its limited distribution (Corrigan and Huveneers 2011), but having been only recently described (Last et al. 2008) data were still limited at the time of its assessment. Based on their life-history characteristics and geographic extent, *G. cirratum*, the western wobbegong *Orectolobus hutchinsi*, the Mexican hornshark *Heterodontus mexicanus* and the Galapagos bullhead shark *Heterodontus quoyi*, all of which are currently Data Deficient (Kyne et al. 2004, Garayzar 2006, Rosa et al. 2006a, Huveneers and McAuley 2009b), are also predicted to be threatened (Dulvy *et al.*, 2014).

Conservation-relevant reef shark research remains focused on a few species and regions (Table 2.1), even though most related red-list assessments identified uncertainties years ago that could have helped guide research focus. Even for well-studied species, geographic gaps still exist, particularly for populations outside Australia, the central Pacific Ocean or Caribbean. For instance, *C. galapagensis* has been mainly studied in Hawai'i despite populations across the Pacific Ocean, including Australia, and possible extirpation at St Paul's Rocks in the Atlantic Ocean (Luiz and Edwards 2011) and *C. perezi* has been mainly studied at Glover's Reef in Belize. The IUCN Red List uses broad regional categories and only five reef shark species received additional designations beyond their global assessment. For example, *G. cirratum* was designated as near threatened in the western Atlantic Ocean (a combination of its vulnerable status off South America and its least concern status in the Caribbean) (Rosa et al. 2006a), but most of the work on it has been in the Caribbean, leaving a relatively poor understanding of the eastern Atlantic, Pacific and South American populations that may be more under threat (Castro and Rosa 2005, Afonso et al. 2014). Similarly, the near threatened populations of *H. ocellatum* in New Guinea have been left unstudied despite almost meeting IUCN Red List criterion A3cde for vulnerable in 2003 (Bennett and Kyne 2003). The overall lack of understanding of fine-scale reef shark conservation statuses is problematic because of the high site fidelity and residency of reef shark populations, which can lead to high degrees of population segregation and structure (Dudgeon et al., 2009, Karl et al. 2012, Vignaud et al. 2014), but research still needs to expand geographically before the IUCN SSG will be able to undertake more regional assessments.

2.11 Protecting reef sharks

Give the high site fidelity and residency typical of reef sharks, MPAs and shark sanctuaries could be effective conservation measures for these species provided their capacity for movement outside of reserves during dispersal, and seasonal and diel migrations, is understood and accounted for (Chapman et al. 2005, 2007, Wiley and Simpfendorfer 2007, Heupel et al. 2010, Espinoza et al. 2015b, Speed et al. 2016). Starting in 2009 with Palau's Shark Haven Act, which prohibited all fishing of sharks in this country's exclusive economic zone, there has been a recent surge in the establishment of shark sanctuaries (Hoyt 2014). There has also been a recent trend to explicitly include provisions for shark conservation in the management and design of sanctuaries and MPAs, including the Great Barrier Reef Marine Park in Australia, Papahānaumokuākea Marine National Monument in the Pacific and the Galapagos Marine Reserve in Ecuador (Hoyt 2014). Already, there is evidence from eastern Australia that MPAs can promote recovery of fished reef shark populations (Heupel et al. 2009, Espinoza et al. 2014). In general, MPAs covering a single reef could suffice for the conservation of juveniles or populations of small site-restricted species such as *H. ocellatum*, *T. obesus* or *C. melanopterus*, particularly on isolated reef systems, whereas protection of larger, wider roaming species such as *C. albimarginatus* and *C. amblyrhynchos*, will probably require an interconnected system of protected reefs (Chapman et al. 2005, Heupel and Bennett 2007, Heupel et al. 2010, Espinoza et al. 2015b, Speed et al. 2016). The latter also will be required where promoting gene flow and reducing inbreeding is of concern (Mourier et al. 2013, Vignaud et al. 2013).

In addition to biological considerations, the conservation success of MPAs will depend on their quality, as measured by degree of community and fisher support, enforcement, monitoring, research and fragmentation, rather than their quantity (Hoyt 2014). Reef shark declines have been observed at ill-enforced protected areas (White et al. 2015), and carcharhinid reef sharks have significantly lower abundance at no-take compared with no-entry sites on the Great Barrier Reef, which indicates that even limited human activities can contribute to population depletion (Robbins et al. 2006, Rizzari et al. 2015). In addition to effective enforcement, consistent monitoring would not only provide long-term information on the trends of populations in reserves, but could also provide extra surveillance for illegal fishing. Variable MPA benefits amongst species also compel an expansion of the taxonomic breadth of research effort so that knowledge exists to craft MPAs that are effective for more than just the few well-known charismatic species. Integration of multi-species and ecosystem-based management approaches should be the primary approach to MPA design in the future (Hoyt 2014). Finally, evidence to date suggests that MPAs have limited spillover effects, indicating that other regulations will be necessary to effectively conserve reef sharks (Ward-Paige et al. 2010, Espinoza et al. 2014), although few details of fisheries regulations were found in the literature review (Nageon de Lestang (1999) provide an example). As such, there is a need to expand research of other management options beyond MPAs as MPAs alone cannot effectively conserve shark species on a global scale without the regulation and reduction of fishing effort (Baum et al. 2003; Kinney and Simpfendorfer 2009 Vignaud et al. 2013).

Shark diving tourism is lucrative and serves as one additional tool that could motivate reef shark conservation (Vianna et al. 2012, Dicken, 2014). Although some changes in behaviour can occur as sharks interact with diving operations (González-Pérez and Cubero-Pardo 2010, Cubero-Pardo et al. 2011, Fitzpatrick et al. 2011a), this eco-tourism should have minimal effect on their populations (Maljkovic & Côté 2011, Vianna et al. 2014). Sharks have been found to avoid areas of high human use, but this pattern is probably more reflective of fishing pressure and may be abated by the establishment of shark sanctuaries that incorporate conservation-minded diving practices (Garla et al. 2006, Stallings 2009, Ward-Paige et al. 2010, Shawky and De Maddalena 2013).

2.12 Future research needs

Understanding both the population status and ecological role of reef sharks are proposed as priority research foci given the potential for such research to inform conservation and to motivate management measures of reef shark populations potentially suffering declines. Overall, the current conservation statuses of reef sharks worldwide are only poorly understood from both geographic and taxonomic standpoints. A comprehensive global assessment of reef shark conservation statuses would be built most effectively through a combination of integrated new research targeted on populations' abundance, movement patterns, trophic ecology and genetics. Most importantly, high quality long-term species-specific monitoring data are urgently required for reef shark populations around the world: the continuation of existing monitoring programs is strongly encouraged, as is the development of new programs for data-poor areas and species.Additionally,taggingandtelemetrystudiescouldhelpinformpopulationabundance assessments by revealing mechanisms behind spatial abundance gradients (Garla et al. 2006, Heupel et al. 2010), validating the methods and findings of abundance studies and evaluating if higher abundances within reserves are transient in nature or related to biases in sampling (Wiley and Simpfendorfer 2007, Bond et al. 2012, Vianna et al. 2014, Espinoza et al. 2015b).

Knowledge of reef shark population segregation by size and sex from movement and abundance studies could also aid in the design of MPAs that have specific goals to protect particular shark life-history stages from fisheries exploitation. Reef shark conservation would also benefit from new genetic research to elucidate cryptic reef shark diversity, as well as genetic structure and gene flow between populations (Dudgeon et al. 2012, Chapman et al. 2015). Genetic studies could also help to demonstrate whether high residency on single reefs leads to inbreeding (Mourier and Planes 2013) and could give indications of longer-term dispersal in reef sharks, information that is inaccessible from telemetry data alone (Whitney et al. 2012b, Vignaud et al. 2014). Conservation prioritization could also benefit from knowledge of effective population sizes and the likelihood of reef shark population rescue from localized depletion even when trends in abundance are available.

Over the past decade, conservation groups have promoted the importance of sharks to healthy ecosystems as a motivator for shark conservation, but such claims are premature given the current lack of knowledge about the role sharks play on coral reefs. If conservation is to be motivated in this way, convincing demonstrations of the ecological role of reef sharks are needed. To date, the few studies examining community consequences of shark losses have found little evidence of top–down control of reef fish communities by reef sharks (Ruppert et al. 2013; Rizzari et al. 2015). More studies examining reef shark trophic interactions are needed, as are new stable-isotope analyses as these could elucidate both the how and why of reef shark movement and demonstrate the extent to which mobile reef shark species connect different reef habitats (Papastamatiou et al. 2015).

Within the framework of the priority research foci proposed here, reef shark research needs to expand both in taxonomic and geographic scope. Studies of the lesser known reef shark species on diverse Indo-Pacific coral reefs, as well as in the less diverse eastern Pacific and western Atlantic Oceans, are required as are genetic studies to help illuminate cryptic reef biodiversity. The restricted spatial nature and high genetic structure of reef shark populations underscores the fact that regional assessments on the scale of ocean basins will probably not suffice to summarize the local conservation status for most reef shark species, specifically those having large geographic distributions. Although recognizably difficult given geographic gaps in knowledge, a more nuanced approach where possible would make clearer geographic variation in reef shark conservation statuses. Ultimately, there needs to be tighter feedback between the conservation needs of reef shark populations and the research devoted to them. Research has responded rapidly in the last few years to deficiencies in reef shark knowledge, but researchers are encouraged to pay greater attention to IUCN Red List assessments, particularly data deficiencies. Conversely, conservation assessors should be helped to update reef shark assessments as soon as possible so that conservation efforts are based upon the best and most recent available scientific evidence.

2.13 Conclusions

Research effort relevant to reef shark conservation is relatively recent but is increasing rapidly in concert with the growing recognition of the importance of sharks on coral reefs. Most research has focused on *G. cirratum* and the three classic carcharhinid species, and studies of these are still geographically restricted, with most in Australia, the Line Islands, Hawai'i and the Caribbean. Consequently, there remain significant taxonomic and geographic research gaps, which need to be filled if global reef shark conservation goals are to be set and achieved, and only a few species can currently be considered for reassessment by the IUCN Red List. Although available evidence suggests that reef shark abundances are now substantially lower than historical baselines and that declines are ongoing, much uncertainty remains about current population trends because of the paucity of abundance data and focused research effort in this area. Existing reef shark monitoring programs need to be supported and continued, and new programs focusing on data-poor species and areas should be developed. The latter could be integrated with dive tourism and citizen science. MPAs should remain an important tool for reef shark conservation, although research should be expanded into other management options. Research programs that achieve a critical synthesis of biodiversity, genetic, abundance, trophic ecology and movement knowledge will be best prepared to assess reef shark susceptibility to extinction, the effectiveness of protected areas for these species and the consequences that depletions in reef shark populations will have for their ecosystem.

Chapter 3 – Using baited remote underwater videos (BRUVs) to characterize chondrichthyan communities in a global biodiversity hotspot

Adapted from Geoffrey J. Osgood[1], Meaghen E. McCord[2], & Julia K. Baum[1] (2019). *PLoS ONE* 14(12): e0225859, DOI: 10.1371/journal.pone.0225859.

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3.1 Abstract

Threatened chondrichthyan diversity is high in developing countries where scarce resources, limited data, and minimal stakeholder support often render conservation efforts challenging. As such, data on many species, including many evolutionarily distinct endemics, is poor in these countries and their conservation status and habitat needs remain uncertain. Here, we used baited remote underwater videos (BRUVs; n=419) conducted at 167 sites over two years to assess the frequency of occurrence (FO), relative abundance, diversity, and structure of chondrichthyan assemblages in one of the world's chondrichthyan biodiversity and endemism hotspots, South Africa. We compared chondrichthyan assemblages across three habitat types, and between unprotected and protected areas (a small marine protected area [MPA] and a larger, seasonal whale sanctuary). Although in total we observed 18 chondrichthyan species (11 families), over half of all observations were of just two species from the same family of mesopredatory endemic catsharks; only 8.8% were larger shark species. These mesopredatory species do not appear to be threatened, but some skates and larger shark species, including some endemics, were much rarer. Overall chondrichthyan FO was high (81% of all BRUVs); FO was higher in kelp (100% of BRUVS) and reef (93%) sites than at sites in sandy habitat (63%), which had a distinct chondrichthyan community. Independent of habitat, the chondrichthyan community did not relate strongly to protection. Because sites with kelp and reef habitat were rare in the whale sanctuary, this protected area had a lower chondrichthyan FO (67% of BRUVs) than either unprotected sites (81%) or those in the small MPA (98%), as well as having lower chondrichthyan relative abundance and species richness. Our study provides evidence of the importance of distinct habitat types to different chondrichthyan species, and suggests that even

small MPAs can protect critical habitats, such that they may provide safe refuge for endemic species as anthropogenic pressures increase.

3.2 Introduction

Threats from overfishing, habitat degradation, and pollution are heightened for many chondrichthyan (sharks, skates, rays, and chimaeras) species because their life history characteristics, including a late age of sexual maturity and small litter sizes, correspond to slow population growth rates (García et al. 2008, Dulvy et al. 2014). These threats have already resulted in significant chondrichthyan population declines in many regions, especially for coastal species (Worm et al. 2013, Dulvy et al. 2014). For most species, however, a paucity of data hinders management by stock assessment or assessment of their conservation status (Dulvy et al. 2014). Marine protected areas (MPAs), where fishing, and often other human activities, are either restricted or illegal, have been employed to promote chondrichthyan conservation in some regions (Shiffman and Hammerschlag 2016), with some success, particularly on coral reef systems (Goetze and Fullwood 2013, Bond et al. 2017, Speed et al. 2018). It is recognized, however, that additional tools to effectively conserve shark populations are likely required, and that conservation measures would benefit from species-specific biological data (Dulvy et al. 2017).

In many developing countries chondrichthyan biodiversity and endemism are high, but a lack of resources to study and manage the species means their conservation status remains unknown (Goetze and Fullwood 2013, Dulvy et al. 2017). Typically the data required to conduct population (stock) assessments is lacking for chondrichthyans, meaning spatial protections may instead be relied upon for their conservation, especially when multiple threats, from habitat destruction to fishing pressure, need to be managed (Sobel and Dahlgren 2004, Bräutigam et al. 2015, Davidson and Dulvy 2017). However, MPA design also requires species-specific knowledge, as even related chondrichthyans show considerable variation in residency patterns and in preferred depths and habitat types (Espinoza et al. 2014, Speed et al. 2016). Since research effort is often concentrated on a few charismatic chondrichthyan species, many species, particularly endemics, remain poorly understood globally with little information on their populations (Dulvy et al. 2014, Osgood and Baum 2015). Managers require this information to assess what management measures may be appropriate for a broad range of taxa, including both mesopredators and more mobile apex predators, and to decide if MPAs protect sufficient critical habitat (Sale et al. 2005, Agardy et al. 2011). Therefore, there is a need to assess the diversity and conservation status of overlooked but threatened chondrichthyan species and to relate that diversity to habitat characteristics and current management schemes in developing countries. Local knowledge in these hotspots scales is critical if global chondrichthyan diversity is to be conserved.

South Africa, a global biodiversity hotspot with high chondrichthyan endemism (~30% species), exemplifies the challenges associated with chondrichthyan conservation. Although shark and ray species have significant cultural and natural heritage value in the region (Bräutigam et al. 2015, Ebert and van Hees 2015), they are both threatened by multiple stressors, including coastal development, pollution, and heavy fishing pressure (Sink et al. 2012, Mead et al. 2013, da Silva et al. 2015, Ebert and van Hees 2015), and poorly studied, such that knowledge of the abundance and distribution is limited for most species. Although MPAs now cover almost a quarter of South Africa’s coast, the extent to which they protect biodiversity from both fishing and other threats is still unknown, as most were established without clear management objectives or ecological information (Attwood et al. 1997, Solano-Fernández et al. 2012). Additionally, corruption, poverty and stakeholder conflict limit the success of many conservation measures in the country (Sowman and Sunde 2018).

We focus herein on the sub-temperate Cape Whale Coast in the Western Cape of South Africa, a stretch of coastline that is home to at least sixty chondrichthyan species, many of which are endemic (e.g. the spotted gully shark *Triakis megalopterus*, pyjama catshark *Poroderma africanum*, leopard catshark *P. pantherinum*, dark shyshark *Haploblepharus pictus*, and puffadder shyshark *H. edwardsii*). The few studies that have investigated the biology of these species suggest that these chondrichthyans use a diversity of coastal habitats, from sandy bays to kelp forests and temperate rocky reefs (da Silva et al. 2013, De Vos et al. 2014), although knowledge of species-specific habitat preferences is limited.

The conservation status of chondrichthyans on the Cape Whale Coast, and the role of MPAs in protecting the region's chondrichthyan biodiversity is uncertain. The region currently includes two small protected areas: the small Betty's Bay MPA (20 km^2), which has year-round prohibition of boat-based activity (albeit with shore-angling allowed) and Walker Bay Whale Sanctuary, a larger, seasonal MPA located in the inner 113 km^2 of Walker Bay. Betty's Bay MPA was established initially in 1973 to protect South African abalone *Haliotis midae* and linefish stocks, and is now important for the conservation of Endangered African penguin *Spheniscus demersus* (du Toit and Attwood 2009). The Walker Bay Whale Sanctuary was established in 2001 under South Africa's *Marine Living Resources Act* (Act No. 18 of 1998) to protect the southern right whale *Eubalaena australis*, and is only in effect during their calving season (July to December), when all vessels except permitted whale watching boats are prohibited. To date, only a year-long preliminary survey of the fishes and benthic invertebrates in Betty’s Bay has been done, showing weak to no effects of protection (Roberson et al. 2015).

Overall, the Cape Whale Coast is heavily impacted by fishing pressure and coastal development, with unknown consequences for the area’s chondrichthyans. A century-old line fish fishery collapsed in the late-1990s (Attwood et al. 1999), and considerable small-scale fishing and commercial line and seine fishing continues to occur (Moloney et al. 2013, da Silva et al. 2015), and is common around the two MPAs when pilchard *Sardinops sagax* and snoek *Thyrsites atun* are running. Larger sharks, including the soupfin shark *Galeorhinus galeus,* common smoothhound shark *Mustelus mustelus*, and bronze whaler *Carcharhinus brachyurus* are targeted in commercial and recreational fisheries (100-400 t per year), whereas most smaller mesopredatory chondrichthyans are caught incidentally (1-10 t per year) in linefish and lobster fisheries or by recreational anglers, most of which is catch-and-release (da Silva et al. 2015). Small, endemic catsharks are taken as bycatch in small shore-based recreational and subsistence fisheries targeting valuable reef fish and large sharks within the Walker Bay Whale Sanctuary and the Betty’s Bay MPA (M. McCord, pers. obs.). Although only a few catsharks are retained for local consumption and illegal sale, poor catch and release practices and improper handling likely result in high post-release mortality rates of those sharks that are released (M McCord, pers. obs). Few data on the population trends of these endemic species exist, and data required for stock assessments exist for less than 10% of the chondrichthyans found in the region (da Silva et al. 2015). Thus, the impacts of incidental fishing on South Africa’s endemic sharks remain unknown. Coastal development and pollution also threaten these endemic species to an unknown extent, particularly *H. edwardsii,* which is currently listed as Near Threatened on the IUCN Red list (Human 2009).

Given an overwhelming paucity of data to support chondrichthyan management and conservation in South Africa, this study employed baited remote underwater video (BRUV), a common, non-invasive technique for monitoring mobile and rare species (Espinoza et al. 2014, Mallet and Pelletier 2014), to provide first insights into the ecology of local chondrichthyan species—with a focus on endemic sharks—in relation to habitat and protected areas, in this important biodiversity hotspot. We quantified the abundance and diversity (in terms of species, higher level taxonomy, and trophic levels) of chondrichthyans, and characterized their community structure, across three habitat types inside and outside of each of the two protected areas, and then modelled how these factors varied amongst habitats and across protection levels. Finally, we evaluated if habitat differences across protection zones accounted for differences in diversity in order to assess the future potential of these MPAs for conserving South Africa's rich and diverse chondrichthyan heritage. We hypothesized that mesopredatory endemic chondrichthyans would dominate the abundance and diversity of the community in all habitats and protection zones, being released from predation due to likely declines of larger sharks in fisheries. We further hypothesized that chondrichthyan diversity, relative abundance, and community composition would not vary with protection, but instead be driven primarily by habitat type as neither MPA is no-take, both are small, and both were designed based on the ecological needs of other taxa.

3.3 Methods and materials

3.3.1 Sampling design

Over a two-year period (July 2016 – July 2018), in both winter-spring (June–November) and summer-fall (December–May), we deployed a total of 419 BRUVs at 167 sites along the

South African coastline in two regions: Betty’s Bay and Walker Bay (Figure 3.1b, Table B1). We made efforts to sample each site once in each season, but constraints due to weather and equipment sometimes prevented this. At least some sites in each region and level of protection were sampled in each season. Ultimately, a total of 233 BRUV drops occurred in the summer-fall and 186 BRUV drops in the winter-spring (Table B1). A BRUV drop represents a replicate at a site, and between one to five (mean = 2.5) drops occurred per site. Sites were randomly placed stratified among the Walker Bay Whale Sanctuary (n = 40 sites total, 109 total drops) and Betty’s Bay MPA (n = 29 sites total, 85 total drops), and areas outside each in Walker Bay (n=69, 131 total drops) and Betty’s Bay (n=29, 94 total drops) (Figure 3.1a, Table B4). We note that the sites sampled in Betty’s Bay were the same as previously sampled by colleagues (Roberson et al. 2015). Sampling sites were 500 m apart except for within the Betty’s Bay MPA where, due to the smaller area sampled, sites were at minimum 100-200 m apart. Whenever possible, sites closer than 500 m apart were not sampled on the same day. The depths of sampled sites ranged between 3 m and 55 m (mean = 25.3 m, standard deviation (SD) = 12.2 m). We made efforts to sample across all habitat types (kelp forest, sand and rocky reef) within each region and protected area, but relied on random sampling to reflect the habitat frequency within each region, since there are no detailed data on distributions of habitat in either region.

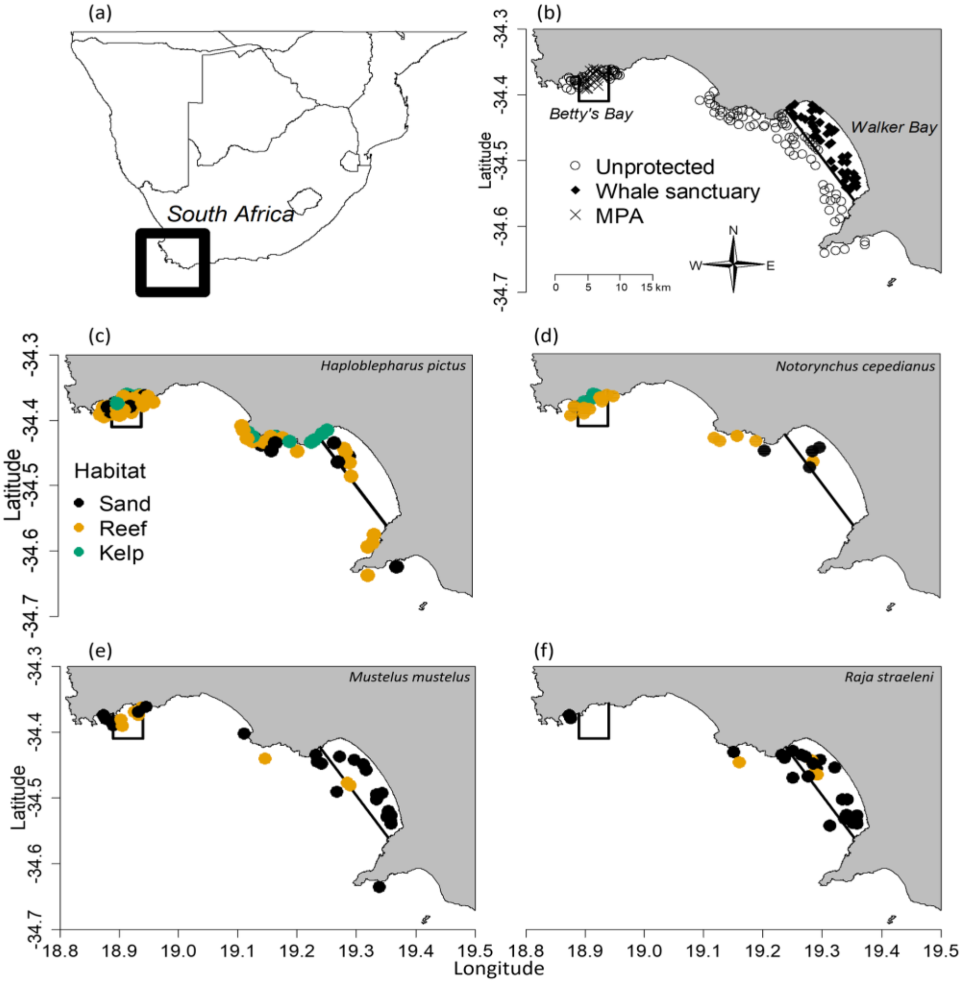

Figure 3.1 Maps of sampling sites showing protection levels and locations and habitats of commonly observed species. (a) The study area within southern Africa (black circle); (b-f) maps of the study area showing (b) the two protected areas (Walker Bay Whale Sanctuary; Betty's Bay MPA) with all BRUV sites categorized by protection level; observations of five representative species categorized by habitat type: (c) dark shyshark *Haploblepharus pictus* (most abundant shark); (d) broadnose sevengill shark *Notorynchus cepedianus* (most abundant high trophic level shark); (e) common smooth-hound shark *Mustelus mustelus* (most abundant triakid); and (f) biscuit skates *Raja straeleni* (most abundant endemic batoid). Legend for habitat colour in (c) applies to (d-f).

3.3.2 Baited remote underwater video (BRUV) design and analysis

Each BRUV rig was composed of a mild-steel cross-shaped base with a bait canister and camera set 110 cm apart. The bait canister and camera were raised 20-30 cm off the rig's bottom by bending the ends of steel arms 90° vertically. One meter of stainless steel chain attached the rig to a rope leading to a surface buoy. One kilogram of chopped, defrosted sardine (*Sardinops sagax*) was placed into each bait canister. We used GoPro® cameras (Hero 1, Hero 2, Hero 3 Silver Edition, Hero+) set to 720p.

All BRUVs were deployed between 8:00 and 15:00, at least half an hour after sunrise and three hours before sunset. Water visibility varied between 0.5 m and approximately 20 m at each site. Target deployment time was 67 minutes, allowing bait to disperse and leaving 60 minutes of footage to analyze, but due to field conditions and camera failure, actual recording time ranged from 20.7 minutes to 103.2 minutes (mean=62.7, SD= 10.7).

For each BRUV at each site, we recorded the percentage of BRUV drops on which a chondrichthyan occurred (frequency of occurrence or FO), and the maximum number of individuals observed together for one species at any one time on the entire video (MaxN; following Cappo et al. 2004). MaxN is a commonly used conservative measure of species' relative abundance in BRUV analyses because it avoids double-counting (Cappo et al. 2012, Espinoza et al. 2014). The shyshark *H. edwardsii* was distinguished from the closely related *H. pictus* using the former's broad head and distinct dark-margined dorsal saddles, often with orange-yellow coloration inside. From each BRUV, we recorded the dominant (>50% cover) habitat type (sand, rocky reef, kelp) and visibility in broad categories, using the distance to the bait canister as a guide (1 = <1 m; 2 = 1-5 m; 3 = 5-10 m; 4 = >10 m). We recorded depth and sea surface temperature (SST) using a HDS-8m Gen2 Lowrance chartplotter for deployments in

Betty’s Bay. In Walker Bay, we recorded depth using one meter markings on the BRUV rope and daily SST as the GOES-POES 5-km Blended SST from PacIOOS (http://www.pacioos.hawaii.edu/voyager/#). For each species we observed, we retrieved trophic levels from FishBase, which were determined from mean trophic level of diet items.

All observations of live animals were authorized by the University of Victoria Animal Care Committee (AUP 2016-032(1)) for this study and conducted under the authority of a joint research permit issued by the South African Department of Agriculture, Forestry and Fisheries and Department of Environmental Affairs: Oceans and Coasts Branch (RES2017-31 and RES2018-59).

We used available catch data from three sources to compare with the species composition found on the BRUVs. We obtained data on chondrichthyan recreational catches collected by volunteer anglers to the Cooperative Fish Tagging Project of South Africa’s Oceanographic Research Institute (ORI) since 2012 in Betty’s Bay. We also obtained data from four Rock and Surf Super Pro League (RASSPL) recreational angling competitions over the last ten years in the Betty’s Bay MPA. Finally, we used the South African Shark Conservancy’s (SASC) database of chondrichthyans tagged during biological sampling from both shore and boat handline fishing in the Walker Bay region since 2010. These data were the only available, but have the following caveats: 1) anglers participating in the ORI tagging project typically do not tag or record endemic sharks due to their perceived lack of importance; 2) RASSPL anglers generally only record larger sharks; and 3) the SASC dataset does not include the Betty’s Bay MPA. Therefore these analyses were qualitative due to sampling biases and associated analytical constraints.

3.3.3 Statistical analysis

We analyzed the effects of protection and habitat on chondrichthyan FO, relative abundance (summed MaxN across all species), and species richness using generalized linear mixed models (GLMM), with a binomial error distribution for FO and a Poisson error distribution for the latter two. Although we initially considered a negative binomial error structure for the relative abundance and species richness models, residual versus fitted plots and likelihood ratio tests revealed that it did not provide a better fit and we therefore used the Poisson distribution for each. For each model, we included region (Walker Bay versus Betty's Bay), protection (inside or outside MPA), the interaction of region and protection, habitat type (sand, temperate rocky reef, kelp forest), SST, depth, visibility, year, and seasonality (sine and cosine of study Julian day divided by 365) as fixed effects, and site as a random effect. We also included duration of the video as an offset. We included the interaction of region and protection to account for differing effects of the two MPAs (one seasonal, one allowing shore fishing); we removed the interaction if it was not significant. We used a likelihood ratio test to determine if protection and habitat, and their interaction, significantly improved the likelihood of each GLMM. To ascertain the significance of other variables, and to determine which individual levels of protection and habitat were significant, we used a Wald's Z test on the coefficients of each GLMM. We also examined residual versus fitted plots to check for major model misspecification.

We then repeated the FO and relative abundance analyses described above on three species groups of interest: the endemic mesopredatory catsharks (the most abundant sharks in the region); larger-bodied sharks as a group (broadnose sevengill shark *Notorhyncus cepedianus*, *T. megalopterus, G. galeus, M. mustelus, C. brachyurus,* hammerhead shark *Sphyrna* sp.); and batoids. As the most batoids we observed at once was two, we focus only on FO GLMMs for the batoids.

Next, to assess how protection and habitat influenced chondrichthyan community structure, we used two complementary multivariate statistical techniques. First, we constructed multivariate regression trees (MRT) using the R package *mvpart* (De'ath 2014). We used this clustering technique to evaluate which variable (protection, habitat, depth, season, SST, visibility) best differentiated chondrichthyan communities (based on their MaxN values) at different sites. We then calculated Dufrêne-Legendre Indicator (DLI) values to determine which species served as indicators of each cluster identified in the MRT. Significance of DLI was determined with a permutation test with 1000 permutations and we deemed species with a DLI > 0.15 to be important indicators. Second, we implemented a recently developed ordination technique (*boral* package, Hui 2016) that enabled us to visualize the variation in chondrichthyan community composition across sites, to identify individual chondrichthyan species that distinguished sites, and to verify the clusters identified by the MRT. To construct the ordination, the *boral* package uses Bayesian latent variable models in which the ordination axes represent the two most important latent variables fitted to the community at each site (Hui 2016). The corresponding latent variable coefficients, which represent the contribution of each species to that axis, are plotted with their scores to make a biplot. We included a site-level random effect to focus on community composition rather than variation in abundance, since this allows for the fact that communities at different sites with identical species compositions could have different abundances. We also included total video duration as an offset. Bayesian latent variable models are appropriate for multivariate data with correlated response variables and a strong mean-variance relationship, such as our count and presence-absence data, and are preferred to distance-based analyses (eg. PCA, MDS), which have low power to detect differences except for species with high variance, even after transformations, and harder to evaluate methodological assumptions (Warton et al. 2012, Hui 2016).

To account for potential spatial autocorrelation between sites, we calculated spatial eigenfunctions using distance-based Moran's eigenvector maps, staggered for Walker Bay and Betty’s Bay, using the R function create.dbMEM.model in the package *adespatial* (Dray et al. 2018). We kept eigenvectors corresponding to positive spatial autocorrelation for use in each of our multivariate and univariate models, besides the MRT.

We verified complete sampling of the chondrichthyan community in our BRUVs by constructing a species accumulation curve for the data in each of the three protection levels, randomizing the order of samples and calculating an average curve from 999 permutations with the specaccum function of the package *vegan* (Oksanen et al. 2013).

We conducted all analyses in R version 3.5.0 (R Core Team 2018). We used the package glmmADMB to run the generalized linear mixed models (Fournier et al. 2012) and the function *indval* in the package labdsv to calculate DLI values (Roberts 2016). Data are available online (https://zenodo.org/badge/latestdoi/194944885).

3.4 Results

Overall, we counted 1166 chondrichthyans on 419 videos. These included 18 chondrichthyan species from 11 families: 14 species of shark, 3 species of batoid, and one species of holocephalan (Table 3.1). Half of the observed chondrichthyan species, spanning five families, are endemic to southern Africa (Table 3.1). Despite this taxonomic and phylogenetic diversity, two species (*H. pictus* and *P. poroderma*) and one family (Scyliorhinidae) of mesopredatory sharks dominated our observations, accounting for 53% and 82% of all chondrichthyans, respectively (Table 3.1, Figure 3.2). These two species occurred throughout each region and in all habitats, although most were observed within the Betty's Bay MPA (Table 3.1, Figure 3.1c). Only 8.8% of the counted chondrichthyans were larger shark species, and of those *M. mustelus* was the most frequently observed (10% of BRUVs), particularly in the MPAs (Figure 3.1e), where it collectively occurred on 17% of sand sites. We also commonly observed *N. cepedianus* in the Betty's Bay MPA (15% of BRUVs, Figure 3.1d) and biscuit skates *Raja straeleni* in the Walker Bay Whale Sanctuary (18% of BRUVs, Figure 3.1f). The rarest species were *C. brachyurus*, *Sphyrna* sp., and shortnose spurdog *Squalus megalops*, each observed on only one occasion. The mean trophic level (+/- SD) of all counted individuals was 4.20 +/- 0.35 due to the high abundance of mesopredatory catsharks (trophic level 3.6 to 4.2) (Table 3.1). One third of the observed species are listed as data deficient on the IUCN Red List, while four species (22%) are threatened (Table 3.1). Species accumulation curves in each area, and overall, reached an asymptote, indicating complete sampling of the chondrichthyan community (Figure B1).

The RASSPL recreational catch and SASC tagging data had a similar relative abundance of Scyliorhinidae over other chondrichthyan species in the region, comprising 76% and 93% of these records, respectively (Table B2). In contrast, the ORI tagging database was dominated by *T. megalopterus* and *N. cepedianus* (68% and 26% of 243 records, respectively), with no records of Scyliorhinidae in its seven years. *Notorynchus cepedianus* was the second most abundantly caught species (1.6% of 1850 records) after scyliorhinids in the SASC database (none were captured from shore). However, triakids as a group were the most commonly captured after Scyliorhinidae when considering all databases (Table B2). *Triakis megalopterus* was abundant in RASSPL (7.7% of 310 records), but less so in SASC records (0.5% of 1138 records from shore, 0.65% of 1850 total). In the SASC database, for which species-specific data is most reliable, *H. pictus* were the most abundantly captured chondrichthyan (46% of 1850 records). Only a few records of the brown shyshark *Haploblepharus fuscus* and ragged tooth shark *Carcharias taurus* were species not on the BRUVs (Table B2).

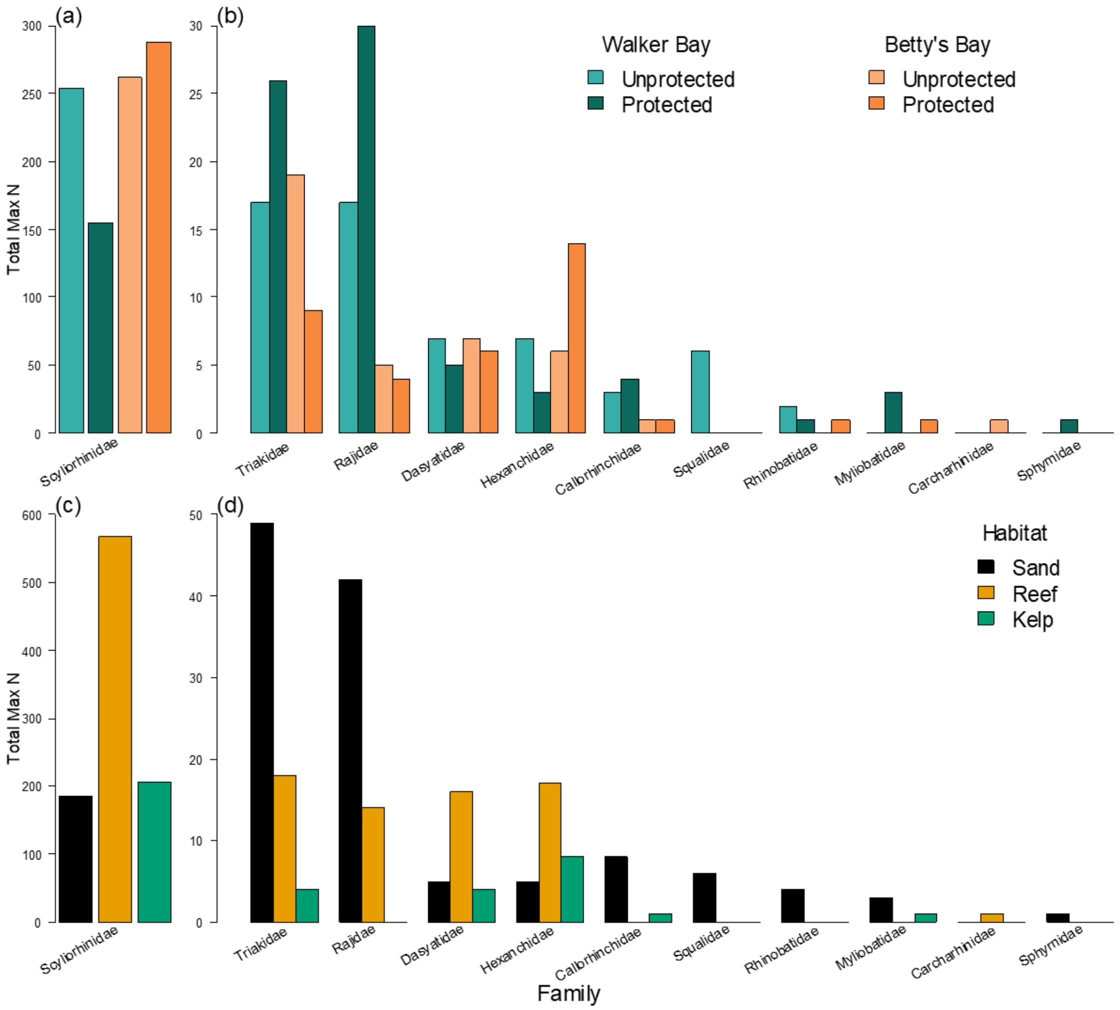

Figure 3.2 Max N summed for all chondrichthyans species in each family over all BRUVs by (a,b) protection level in each region and (c,d) by habitat. (a, c) The most commonly observed chondrichthyan family, the scyliorhinid catsharks. (b, d) The remaining chondrichthyan families. Note the different scales on the y-axes.

Table 3.1 Summary of the taxonomy, endemism, IUCN Red List status, population trend on the IUCN Red List (Version 2019-2), trophic level, and relative abundance (FO, MaxN)[a] of the chondrichthyan species observed on BRUVs, ordered from highest to lowest FO within each taxonomic group (Sharks, Batoidea, Holocephali).

							Walker Bay				Betty's Bay			
							Unprotected sites		Whale Sanctuary		Unprotected sites		MPA	
Species	Common name (abbreviation)	Family	Endemic (Y/N)	Trophic level[b]	IUCN[a]	Population trend	FO	Max N	FO	Max N	FO	Max N	FO	Max N
Sharks														
Haploblepharus pictus	Dark shyshark (DS)	Scyliorhinidae	Y	4.2	LC	Unknown	0.34	1.51	0.14	1.60	0.81	1.39	0.89	1.72
Poroderma africanum	Pyjama catshark (PJ)	Scyliorhinidae	Y	3.6	NT	Unknown	0.27	1.60	0.22	2.75	0.54	1.59	0.61	1.65
Haploblepharus edwardsii	Puffadder shyshark (PA)	Scyliorhinidae	Y	3.8	NT	Unknown	0.21	3.11	0.15	2.25	0.21	1.20	0.16	1.36
Poroderma pantherinum	Leopard catshark (LP)	Scyliorhinidae	Y	4.1	DD	Unknown	0.21	1.21	0.08	1.33	0.30	1.43	0.42	1.22
Mustelus mustelus	Common smooth-hound (CS)	Triakidae	N	3.8	VU	Decreasing	0.08	1.00	0.15	1.25	0.11	1.30	0.06	1.00
Halaelurus natalensis	Tiger catshark (TC)	Scyliorhinidae	Y	4.2	DD	Unknown	0.06	1.50	0.13	1.21	0.09	1.38	0.06	1.60
Notorynchus cepedianus	Broadnose sevengill (BG)	Hexanchidae	N	4.7	DD	Unknown	0.05	1.00	0.03	1.00	0.05	1.20	0.15	1.08
Galeorhinus galeus	Soupfin shark (SF)	Triakidae	N	4.3	VU	Decreasing	0.05	1.00	0.04	1.00	0.04	1.00	0.02	1.00
Triakis megalopterus	Spotted-gully shark (SG)	Triakidae	Y	4.0	NT	Unknown	0.00	0.00	0.02	1.00	0.02	1.00	0.02	1.00
Squalus megalops	Shortnose spurdog (SD)	Squalidae	N	4.3	DD	Unknown	0.01	6.00	0.00	0.00	0.00	0.00	0.00	0.00
Carcharhinus brachyurus	Bronze whaler (BW)	Carcharhinidae	N	4.5	NT	Unknown	0.00	0.00	0.00	0.00	0.01	1.00	0.00	0.00
Sphyrna sp.	Hammerhead shark (SH)	Sphyrnidae	N	4.9	VU	Decreasing	0.00	0.00	0.01	1.00	0.00	0.00	0.00	0.00
Batoidea														
Raja straeleni	Biscuit skate (BS)	Rajidae	Y	4.0	DD	Unknown	0.06	1.13	0.18	1.15	0.02	1.00	0.00	0.00
Rostroraja alba	Spearnose skate (SN)	Rajidae	N	4.4	EN	Decreasing	0.06	1.00	0.06	1.00	0.03	1.00	0.05	1.00
Bathytoshia brevicaudata	Short-tail stingray (SR)	Dasyatidae	N	3.9	LC	Stable	0.05	1.00	0.05	1.00	0.07	1.00	0.07	1.00
Rhinobatos annulatus	Lesser guitarfish (LG)	Rhinobatidae	Y	3.4	LC	Unknown	0.02	1.00	0.01	1.00	0.00	0.00	0.01	1.00
Myliobatis aqulia	Eagle ray (ER)	Myliobatidae	N	3.6	DD	Unknwon	0.00	0.00	0.03	1.00	0.00	0.00	0.01	1.00
Holocephali														
Callorhinchus capensis	St. Joseph shark (SJ)	Callorhinchidae	Y	3.5	LC	Stable	0.02	1.00	0.04	1.00	0.01	1.00	0.01	1.00

[a] Abbreviations: LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered; DD, data deficient; FO, frequency of occurrence (ie . proportion of videos observed on); MaxN, maximum number of individuals observed per species per video averaged across sites where the species occurred.

[b] Trophic levels taken from FishBase (www.fishbase.org)

3.4.1 Chondrichthyan frequency of occurrence and relative abundance

We observed chondrichthyans in 81% of all BRUVs and at 88% of all sites, but FO was higher in reef and kelp sites (93% and 100% of BRUVs, respectively) than in sandy habitat (63%). Chondrichthyan FO was high in Betty's Bay, both within the MPA (98% of BRUVs) and outside of it (95% of BRUVs), compared to Walker Bay, where it was much lower, both inside the Whale Sanctuary (67% of BRUVs) and outside it (72% of BRUVs). Across both regions, chondrichthyans were observed at 81% of BRUVs at unprotected sites. Both habitat (LRT, χ^2 = 15.48, df = 2, $p<0.001$) and region (LRT, χ^2 = 5.17, df = 1, $p=0.023$) improved the FO model fit, but protection did not (LRT, χ^2 = 0.286, df = 1, $p=0.59$) (Table B3).

The relative abundance of chondrichthyans varied significantly by habitat (LRT, χ^2 = 22.1, df = 2, $p<0.001$), with a predicted 59% and 63% more chondrichthyans observed in reef and kelp, respectively, compared to sandy habitat (Figure 3.3b, Table B3). Protection had a smaller significant effect on relative abundance that varied by region (LRT, χ^2 = 5.1, df = 1, $p=0.024$): the Betty's Bay MPA had a predicted 11% greater relative abundance of chondrichthyans compared to its adjacent unprotected sites, whereas the Walker Bay Whale Sanctuary had a predicted 50% lower relative abundance compared to its adjacent unprotected sites, based on model coefficients once other variables (region, depth, etc.) were controlled for (Figure 3.3a). Directly comparing the two protected areas, the Betty's Bay MPA had a significantly greater chondrichthyan abundance per BRUV (predicted increase of 126%) than the Walker Bay Whale Sanctuary (LRT, χ^2 = 16.5, df = 2, $p<0.001$).

For catsharks and larger shark species only region and habitat significantly affected FO and mean total relative abundance (Table B3); protection was not significant, despite qualitative differences, such as a high FO of large sharks (*N. cepedianus* FO in Betty's Bay MPA: 15%) and

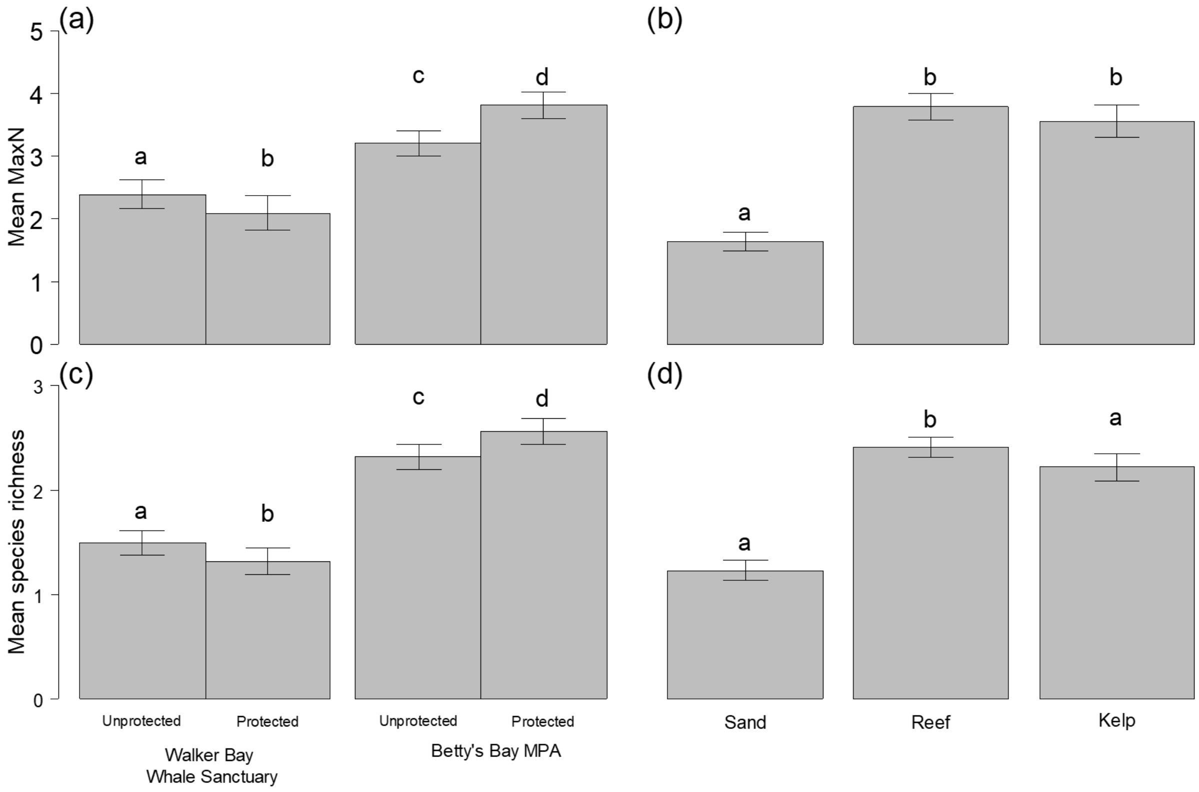

Figure 3.3 Mean chondrichthyan relative abundance and richness by protection and habitat. (a, b) Mean summed MaxN per BRUV and (c,d) mean species richness per BRUV, compared across: (a, c) protection level in each region and (b, d) habitat type. Bars are +/- SE. Comparisons with the same letter were not significantly different.

the only observation of *Sphyrna* sp. recorded in the MPAs. Catsharks had a significantly higher mean relative abundance (LRT, χ^2 = 26.3, df = 2, p<0.001) and FO (LRT, χ^2 = 45.4, df = 2, p<0.001) on reef (mean MaxN = 3.4, FO = 93%) and kelp sites (mean MaxN = 3.3, FO = 98%), compared to sand sites (mean MaxN = 0.98, FO = 41%) (Table B3). In contrast, larger sharks had a marginally greater relative abundance (LRT, χ^2 = 7.132, df = 2, p=0.028) and FO (LRT, χ^2 = 6.36, df = 2, p=0.042) on sand sites (mean MaxN = 0.29, FO = 23%) compared to reef (mean MaxN = 0.22, FO =19%) and kelp sites (mean MaxN = 0.19, FO = 17%). Protection, region, and habitat were not significant in our batoid FO model (Table B2). Although batoid FO appears significantly less in kelp habitat, overall habitat did not improve model fit (LRT, χ^2 = 5.0, df = 2, p=0.08).

3.4.2 Chondrichthyan diversity

Chondrichthyan species richness ranged from 0 to 6 on a single BRUV (mean = 1.9), and overall was significantly higher on reef habitat and lowest in sand habitat (LRT, χ^2 = 9.7, df = 2, p=0.008) (Figures 3.3d, 3.4, Table B3). Chondrichthyan species richness was on average greatest in the Betty's Bay MPA compared to unprotected sites or the Walker Bay Whale Sanctuary, where species richness was the lowest (Figures 3.3c, 3.4). As such, the effects of protection on species richness also varied by region. Predicted richness increased by 6% with protection in Betty's Bay and decreased by 52% with protection in Walker Bay (LRT, χ^2 = 5.5, df = 1, p=0.019) (Table B3). Sites with high species richness were frequent in the Betty's Bay MPA, and the region in general, while a third of sites in Walker Bay, including those in its MPA (33%), had zero chondrichthyan species. Most chondrichthyan species richness in the Whale Sanctuary was concentrated on a few reef sites (Figure 3.4).

3.4.3 Chondrichthyan community composition

Habitat was the most important variable distinguishing chondrichthyan communities, whereas protection did not distinguish communities on the multivariate regression tree (Figure 3.5a). Reef and kelp chondrichthyan communities were distinct from those on sand; communities on sand also differed by region (Figure 3.5a). *Haploblepharus pictus, H. edwardsii, P. pantherinum*, and *P. africanum* were significant indicators of reef and kelp sites (DLI of 0.65, 0.17, 0.36, 0.46, respectively). In contrast, the tiger catshark *Halaelurus natalensis* and *M. mustelus* were significant indicators of sand sites (DLI of 0.14, 0.15, respectively); *Raja straeleni* was also a significant indicator, albeit with a smaller DLI (0.12) for sand habitats, particularly in Walker Bay (Figure 3.5a). The latent variable ordination confirmed the habitat classification of the multivariate regression tree, showing reef and kelp sites clustering apart from sand sites along the first axis (Figure 3.5b). The fitted latent variable coefficients placed different chondrichthyan species in each habitat cluster: *H. pictus*, *H. edwardsii*, *P. patherinum*, *P. africanum*, *T. megalopterus*, and *N. cepedianus* had small to negative coefficients for the first latent variable, indicating a higher relative abundance at reef and kelp sites, which were not strongly distinguished (Figure 3.5b). In contrast, *H. natalensis*, *M. mustelus*, the St. Joseph shark *Callorhinchus capensis*, the spearnose skate *Rostroraja alba*, *R. straeleni*, and the lesser guitarfish *Acroteriobatus annulatus* had positive coefficients for the first latent variable, reflective of their higher relative abundance and occurrence at sand sites (Figure 3.5b).

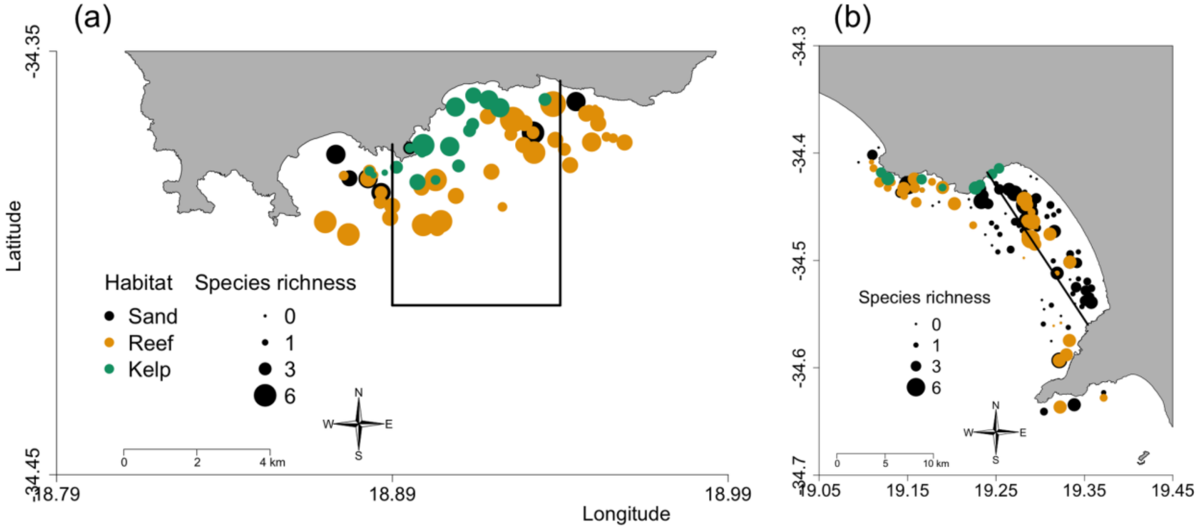

Figure 3.4 Maps of the study area showing BRUV sites categorized by habitat and species richness in (a) Betty's Bay and (b) Walker Bay.

3.4.4 Overlap of habitat and protection

The Walker Bay Whale Sanctuary had a significantly higher frequency of sand sites and a significantly lower frequency of reef sites, while the opposite was true in the Betty's Bay MPA (χ^2=47.185, p<0.001). The unprotected sites in each region had close to the overall average frequency of each habitat type. Kelp sites were rare across all protection levels, but still more frequent in the Betty's Bay MPA (Figure 3.4).

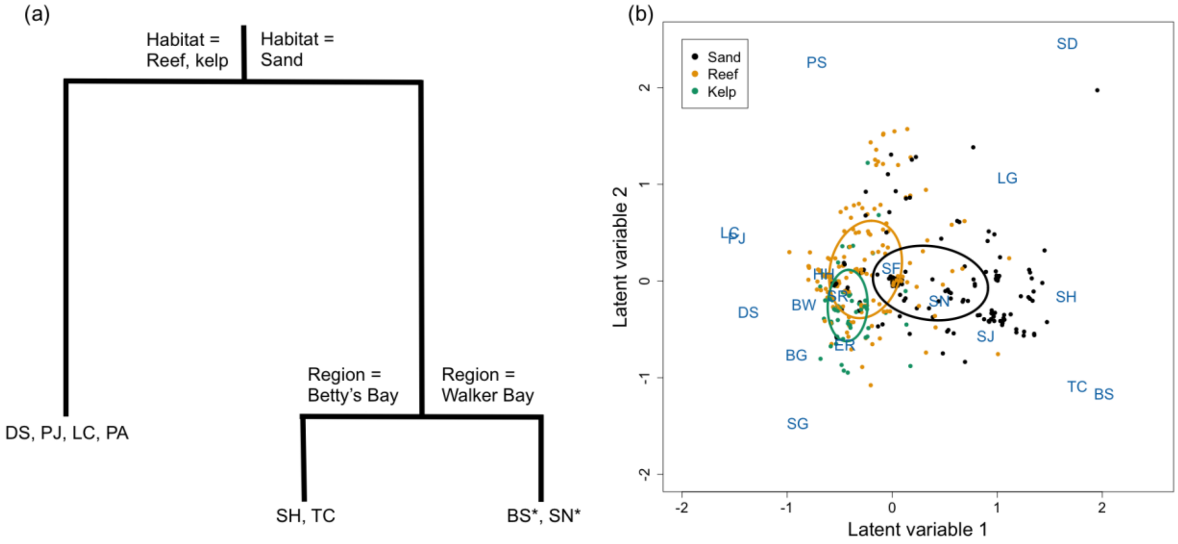

Figure 3.5 (a) Multivariate regression tree (MRT) and (b) boral latent variable ordination of the observed chondrichthyan community. Points are colour-coded by habitat. The ellipses represent 95% confidence intervals around the mean for sites from each habitat. Two-letter species' codes (explained in Table 3.1) (a) represent the species with DLI values > 0.15 (except those marked with *, the most important species for that cluster: DLI0.08-0.12), and (b) are positioned to show the relative values for the coefficient for that species on each latent variable axis.

3.5 Discussion

Our study found, as predicted, that the chondrichthyan community was dominated by small, endemic, mesopredatory catsharks, while larger shark species and batoids were considerably rarer. The high relative abundance and frequency of occurrence of the endemic catshark species suggests they may have been released from predation, as likely occurs for mesopredatory sharks at isolated, protected tropical reefs (Heupel et al. 2014, Roff et al. 2016), and that they are currently not heavily threatened by anthropogenic disturbances. However, the population trends of these catsharks are uncertain, and the rarity of other chondrichthyans suggest anthropogenic threats have impacted this region. In particular, the batoid species *R. alba* and *R. straeleni* are likely threatened along the Cape Whale Coast. Although the former species is not endemic to South Africa, it is endangered globally and its large size makes it vulnerable to extinction (Dulvy and Reynolds 2002). The endemic *R. straeleni* is data deficient, but taken by trawls in unknown quantities for human consumption and as bycatch (Smale 2009).

Larger shark species were seen only infrequently on our BRUVs, which could reflect the impact of fishing, as these sharks, particularly *C. brachyurus*, *G. galeorhinus* and *M. mustelus*, are targeted along the coast (da Silva et al. 2015). Fisheries pressure has recently increased on *C. brachyurus* and it is now being targeted inshore (M. McCord, pers. obs.). The low occurrence of large species is not likely an artifact of selectivity, as size selectivity is minimal for BRUVs (Brooks et al. 2011). In fact, BRUVs in the Stilbaai MPA ~300 km east of our sites, but with a similar ecosystem, captured a diversity of fishes, including a high relative abundance of larger sharks compared to mesopredators (De Vos et al. 2014). Notably, despite a great white shark *Carcharodon carcharias* hotspot at Gansbaai, an area near our sites in Walker Bay, we detected no individuals of this species, although sampling in False Bay, South Africa to the west, as well as in Australia suggests BRUVs can be effective at detecting them (De Vos et al. 2015, Harasti et al. 2016). The endemic *T. megalopterus* was also incredibly rare on our BRUVs despite being frequent in the limited catch data. This species has a limited bathymetric range, including a preference for the shallower waters where our BRUVs were deployed, suggesting a low relative abundance and possibly threatened status in the region (Compagno 2009). The catch data do provide hope for the abundance of some larger sharks, including *T. megalopterus* and *N. cepedianus*, in the region and corroborate the dominance of small mesopredators in the chondrichthyan community.

Habitat had the strongest influence on chondrichthyan frequency of occurrence, relative abundance, and species richness, all of which were significantly greater in rocky reef and kelp habitat than in sand habitat. The former, in particular, had the strongest effect on chondrichthyan community structure, likely due to its habitat complexity and higher prey biomass. However, both our multivariate analyses identified a distinct community of species found predominantly on the sand habitats, including two data deficient endemics (*R. straeleni* and *H. natalensis*) and the endemic *C. capensis*. These findings align with those of related BRUV studies: a study of tropical sharks on the Great Barrier Reef found proximity to reefs with high coral cover to be the most important factor structuring shark communities and a factor contributing to MPA success (Espinoza et al. 2014), while a previous analysis of the fish community in the Betty’s Bay MPA found habitat affected the diversity and species composition while protection had no effect (Roberson et al. 2015). However, in cases where fishing has had large impacts on populations of sharks and their prey, MPA presence can explain the most variation in shark abundance and community composition compared to environmental and habitat variables alone (Bond et al. 2012, Goetze et al. 2018). Our expanded analysis of chondrichthyan abundance and richness did find a limited positive effect of protection in Betty's Bay not previously detected (Roberson et al. 2015). Our results also confirm the differences in chondrichthyan community composition between reef and sand sites suggested in False Bay, where *H. pictus*, *H. edwardsii*, *P. patherinum*, and *P. africanum* were also found on reef sites and *M. mustelus*, *H. natalensis* and *G. galeus* on sand (De Vos et al. 2015).

We found that, independent of habitat, protection had limited, even negative effects on chondrichthyan relative abundance and species richness, and no effect on community composition. The apparent preference of the endemic catshark community for reef and kelp habitat explains the high diversity and abundance of chondrichthyans within the Betty's Bay MPA, and in the Betty's Bay region in general, with its concentration of high quality habitat. Because sand habitat, which had a distinct chondrichthyan community, dominated the Walker Bay Whale Sanctuary, its species richness, frequency of occurrence, and relative abundance of chondrichthyans was low even when compared to unprotected sites nearby. Thus, even though the Betty's Bay MPA is the smaller of the two protected areas, it has higher potential to protect endemic catshark diversity, should the limited threats they face worsen, especially given the recent re-proclamation of the MPA in South Africa, which outlaws shore angling within MPA boundaries (Department of Environmental Affairs, South Africa 2017). Additionally, the Betty's Bay MPA likely plays a role in protecting critical habitat from coastal development, considering Betty's Bay popularity as a vacation spot near the population centers of Cape Town and Hermanus. South Africa's endemic catsharks may not be currently threatened, but their abundance in the region is supported by the quality of habitat located in Betty's Bay, indicating even small MPAs could play a role in protecting coastal ecosystems and endemic species. Spatial protection has had strong effects on resident populations of more threatened sharks on tropical reefs (Bond et al. 2012, Goetze et a. 2018); thus, MPAs will likely play an important conservation role for endemic South African species should fishing pressure or habitat degradation intensify.

Protection had an even more limited effect on the larger shark species than the catsharks, as these species would likely have regular movements out of either MPA's boundaries (Knip et al. 2012, Speed et al. 2016). Although we observed a high frequency of *N. cepedianus* in the Betty's Bay MPA, the extent to which this MPA can protect this species depends on its currently unknown movement ecology in the region. The Walker Bay Whale Sanctuary might serve as nursery habitat for the vulnerable *M. mustelus*, the largest shark we frequently observed, since it appeared to be smaller in the MPA (G. Osgood, pers. obs.) and is known to show strong residency to shallow bays (da Silva et al. 2013). Larger, more mobile shark species often show higher residency as juveniles and can benefit from MPAs that protect nursery habitat (Heupel and Simpfendorfer 2005). Adult *M. mustelus* also frequent shallow sandbanks for foraging and predation avoidance (da Silva et al. 2013), and this could explain the relatively high abundance of larger shark species on sand in our study compared to other habitats. However, the overall rarity of large sharks on our BRUVs still suggests these MPAs, even when designed to protect whales, may be too small compared to the home ranges of these larger sharks to effectively curtail fisheries and anthropogenic effects (Knip et al. 2012). Ultimately, MPAs cannot replace effective fisheries management for these larger, more mobile species (Dulvy et al. 2017).

Marine protected areas, especially no-take zones, have shown preliminary success in other parts of the world in reducing the declines of shark species (Espinoza et al. 2014, Bond et al. 2017, Speed et al. 2018), but MPAs globally still do not effectively protect chondrichthyan diversity (Speed et al. 2018). There is some hope for effective chondrichthyan conservation in

South Africa if improved MPA design and enforcement can protect critical habitat, although the smaller, less mobile species that would benefit most are the most abundant in the region's coastal habitat. Protected areas could benefit more of the threatened species on the Cape Whale Coast if they were expanded to include more area around critical habitats and were enforced in tandem with improved fisheries regulations. Community led co-management initiatives to marine conservation that would engage people with regulations to ensure their enforcement and success would also be beneficial; combining spatial-based management with such community-based fisheries regulations will be an important way forward for marine conservation in developing countries (Sowman and Sunde 2018).

Ultimately, to succeed in conserving chondrichthyan evolutionary diversity globally, we must understand patterns of chondrichthyan endemism, and implement, enforce and monitor the success of conservation measures to protect it. Non-invasive techniques like BRUVs, which can capture the more elusive, endemic diversity that make developing countries important international targets for conservation, could play an important role in this regard, but to date few BRUV studies have been conducted in these countries. BRUV research carried out in Raja Ampat, Indonesia, similarly showed that the strength of regulations can be more important for shark conservation than MPA size alone (Jaiteh et al. 2016), but more focus is needed on imperiled endemic diversity. To help establish and monitor conservation measures, as well as improve knowledge of their endemic species, BRUVs programs should be expanded both in South Africa, as the country prepares to increase its MPA coverage to 5% of its exclusive economic zone (Department of Environmental Affairs, South Africa 2018), and in other developing countries (Osgood and Baum 2015). Even small MPAs protecting critical habitat could benefit unique endemic diversity, especially when placed in a network, but they need to be monitored (Floeter et al. 2006, Kerwath et al. 2013). By establishing a baseline, our study represents a step forward in establishing systematic BRUV monitoring of MPAs for endemic chondrichthyan diversity in the developing world.

Chapter 4 – Chondrichthyans as an umbrella-species complex for conserving South African biodiversity

Adapted from Geoffrey J. Osgood[1], Meaghen E. McCord[2], & Julia K. Baum[1]. 2020. *African Journal of Marine Science* 42(1): 81–93, DOI: 10.2989/1814232X.2020.1729859.

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Author contributions: G.J.O. and M.E.M conceived of and designed the study and collected the data. G.J.O. conducted the data analysis and wrote the manuscript with input from M.E.M. and J.K.B.

4.1 Abstract

Conservation surrogates, such as umbrella and flagship species, could help focus South Africa’s limited resources for research and management and enhance the conservation gains from marine protected areas (MPAs). Sharks, rays, and chimaeras (Chondrichthyes), which are charismatic and ecologically diverse, are potential umbrella candidates, but tests of the ecological suitability of putative marine umbrella species are lacking. Using baited remote underwater video in and around two MPAs in the Western Cape Province, we assessed the potential of chondrichthyans as an umbrella species complex by quantifying the relationships and co-occurrence patterns between chondrichthyan abundance and diversity and those of other taxa (primarily teleosts and crustaceans). Sites with abundant chondrichthyans, with catsharks or large sharks (>1 m total length), all had significantly greater abundance and diversity of these other taxa, and associations with species of commercial and conservation interest (e.g. roman *Chrysoblephus laticeps*). Endemic scyliorhinids (notably dark catshark *Haploblepharus pictus*) and the broadnose sevengill shark *Notorynchus cepedianus* also had many strong positive co-occurrences (28% and 21% of interactions, respectively). The puffadder catshark *H. edwardsii* had the highest centrality of any species, denoting its high connectedness to other taxa. Overall, chondrichthyans, especially the dark and puffadder catsharks and the broadnose sevengill shark, show strong potential as an umbrella-species complex in South Africa.

4.2 Introduction

South Africa’s marine ecosystems are biologically diverse and brimming with endemism, but are also heavily impacted by several threats, including exploitation and habitat destruction, particularly on the west coast (Lombard et al. 2004, Griffiths et al. 2010). Fisheries have severely reduced the biomass of many important linefish (hook-and-line) species, including the culturally and commercially important endemic sea bream, roman *Chrysoblephus laticeps* (Attwood and Farquhar 1999, Götz et al. 2008). Additionally, west coast rock lobster *Jasus lalandii*, one of South Africa's economically most valuable species, is estimated to have declined to less than 3% of its historical biomass (DAFF 2014). Marine protected areas (MPAs) have shown promise for conserving exploited species in South Africa (Götz et al. 2008, Kerwath et al. 2013, Mann et al. 2016), but currently comprise only 5% of the country's exclusive economic zone (Department of Environmental Affairs 2018). Additionally, few of South Africa's marine protected areas (MPAs) have a no-take component, resulting in sub-optimal protection (Currie et al. 2012), and many exclude habitat types that are important for species of conservation concern (Griffiths et al. 2010, Solano-Fernández et al. 2012, Sink 2016). Poaching of culturally and commercially important species like the west coast rock lobster is also widespread due to a poor capacity for enforcement and a failure to address social issues that could improve compliance (Brill and Raemaekers 2013, Sowman and Sunde 2018). South Africa's biodiversity would benefit from an expansion of its MPA network (Solano-Fernández et al. 2012), although improved monitoring and enforcement are required to ensure the effectiveness of MPAs (Marinesque et al. 2012). In a country where responses to MPA declarations can have large social repercussions (Faasen and Watts 2007), there is a need to ensure these MPAs at least achieve their ecological goals.

When resources are scarce, managers and conservation practitioners may focus efforts on select threatened species, termed surrogates, with the hopes of benefiting other species (Caro and O'Doherty 1999). One example is the 'umbrella species' concept, in which habitat protection focused on one or a few species aims to also conserve a multitude of co-occurring species of conservation concern (Caro and O'Doherty 1999). 'Flagships' are another form of surrogacy, where species with cultural appeal are used to raise public awareness and funds for broader conservation goals (Veríssimo et al. 2014, Jepson and Barua 2015). A species could serve as a combined flagship-umbrella if it is centred both in existing cultural norms and in networks of ecological interactions (Caro 2010, Jepson and Barua 2015).

The effectiveness of conservation surrogates is, however, equivocal and context-dependent, with many putative umbrella and flagship species failing to optimally protect diversity at local scales, by focusing resources on too few species or failing to account for the ecological needs of other threatened species (Roberge and Angelstam 2004, Caro 2010, 2015, Joseph et al. 2011). Traditionally, umbrella species have been chosen based on species-specific traits such as body size, home-range size, or trophic level and diet, without directly verifying ecological suitability or relationships to diversity and abundance of other species, resulting in reduced protection for other areas and species of high conservation priority (Branton and Richardson 2011, Stuber and Fontaine 2018). There have been calls to abandon the umbrella species concept (Roberge and Angelstam 2004), but when niche overlap and habitat associations between umbrella species and other species of conservation concern are explicitly considered, umbrella species can lead to conservation success (Maslo et al. 2016, Fourcade et al. 2017, Stuber and Fontaine 2018), even amongst unrelated taxa (Bichet et al. 2016). Testing co-occurrence of threatened species is an important first step in evaluating potential umbrella species (Cushman et al. 2010). Also, conservation outcomes could be improved using focal-species complexes, where multiple surrogate species with heterogeneous ecological needs and sensitivities to different potential threats generate wider appeal and a more diverse representation of habitats and landscape elements (Lambeck 1997, Roberge and Angelstam 2004, Veríssimo et al. 2014). The use of a flagship-umbrella species complex could be a way to increase funding for, and effectiveness of, both current and future conservation measures in South Africa.

Here, we propose the Chondrichthyes (sharks, skates, rays, and chimaeras) as a potential flagship-umbrella species complex for South Africa, because the country is a global hotspot for chondrichthyan diversity (Ebert and van Hees 2015). Many chondrichthyans are charismatic (Albert et al. 2018) and they support a thriving dive tourism industry in South Africa that creates economic opportunities out of conservation (Dicken and Hosking 2009, Gallagher and Hammerschlag 2011, Dicken 2014). The ecological and evolutionary diversity of chondrichthyans also widens their collective niche, making them good candidates for a flagship-umbrella taxon (Cortés 1999, Roff et al. 2016, Stein et al. 2018). Whereas some shark species are large, mobile apex predators, fitting the traditional definition of an umbrella species (Andelman and Fagan 2000, Sergio et al. 2008), chondrichthyans also include many smaller mesopredators, which might better reflect biodiversity at local scales. The Batoidea (skates and rays) exemplify the diversity of form within chondrichthyans, with their unique disc-like body shape, and also are ecologically diverse (Aschliman et al. 2012, Martinez et al. 2016). Many chondrichthyan populations are threatened (Stevens et al. 2000, Dulvy et al. 2014, 2017) and need enhanced protection (Dulvy et al. 2017). Severely threatened species do not always make the best umbrellas, as their rarity limits the extent of niche overlap with other species, but chondrichthyans are diverse in their conservation status (Dulvy et al. 2014, Macdonald et al. 2017). Despite these qualities, no study has rigorously examined the suitability of chondrichthyans as a flagship-umbrella taxon. Such suitability needs explicit testing to ensure long-term conservation goals can be met in the specific systems for which an umbrella is proposed (Cushman et al. 2010). Only a few studies have tested the umbrella-species concept in marine ecosystems (Zacharias and Roff 2001, Olds et al. 2014, Weng et al. 2015), including just one chondrichthyan, a ray species (Gilby et al. 2017). Unless co-occurrence is demonstrated, charismatic and wide-ranging surrogate species will not be useful in conserving biodiversity (Andelman and Fagan 2000).

We assessed the potential of chondrichthyans to serve as an umbrella-species complex in the Western Cape Province, South Africa, using an extensive dataset from baited remote underwater videos (BRUVs) (Osgood et al. 2019). The Western Cape is an important area for marine conservation in South Africa as it has experienced fisheries collapses (Attwood and Farquhar 1999) and is still impacted by heavy fishing pressure (Moloney et al. 2013, da Silva et al. 2015). There are multiple MPAs in the region, including two in our study area (Figure 4.1): the 113 km^2 Walker Bay Whale Sanctuary and the 20 km^2 Betty's Bay MPA. Both prohibit boat–based activity, although only seasonally (July–December) for the Walker Bay Whale Sanctuary, and shore angling occurs in both year-round. First, we related the abundance, diversity, and community composition of six other major taxonomic groups (teleosts, crustaceans, cephalopods, myxinidae, birds, and mammals) to the presence of chondrichthyans overall and to specific chondrichthyan groups: catsharks, large sharks (>1 m total length [TL]), or batoids. Second, we compared the co-occurrence patterns among chondrichthyans and these other taxa to assess the strength and centrality of chondrichthyans within the local ecological network. We also estimated the co-occurrence among chondrichthyans and species of conservation concern in the Western Cape, with a focus on two species of economic importance, roman and west coast rock lobster. To supplement our co-occurrence analysis, we calculated centrality measures for all species, which reflect the connectedness of a species with the network of its ecological community (Freeman 1978). Finally, in addition to statistical analyses of the BRUV data, we simulated small marine reserves based on our sampled sites to investigate whether designing reserves based upon knowledge of chondrichthyan occurrences would protect a greater abundance of species of conservation concern, as well as more overall community diversity, compared to designs in which sites were either selected at random or by habitat type.

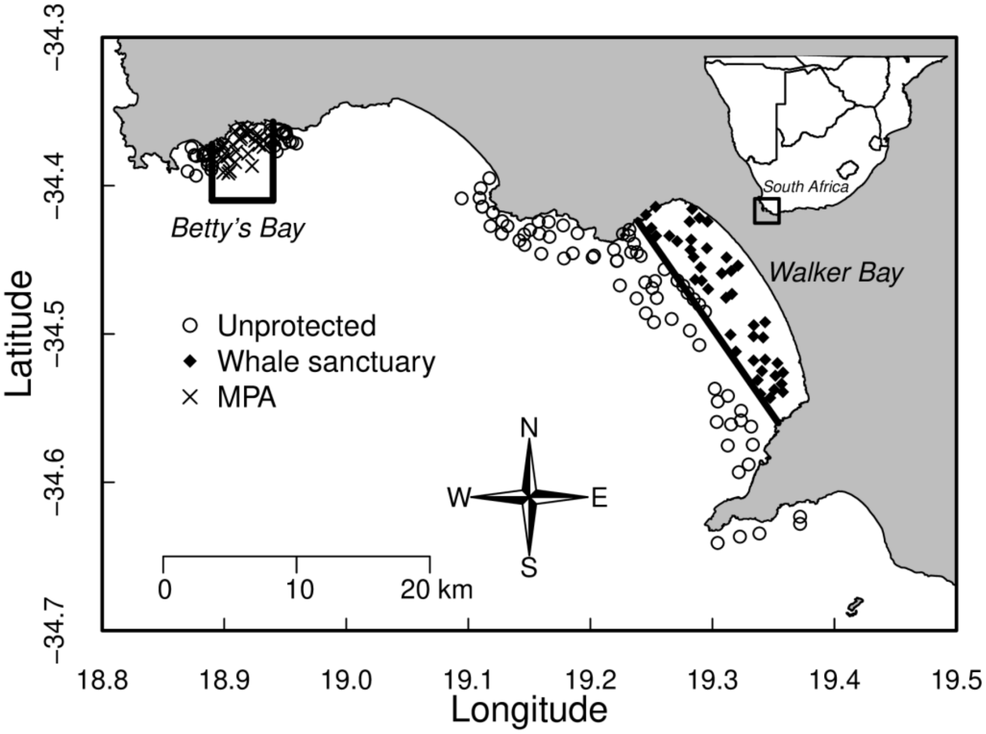

Figure 4.1 BRUV sampling sites along the coast of South Africa, categorized by protected status. Inset map shows the location of the study area within southern Africa (black square).

4.3 Methods and materials

4.3.1 Study site and BRUV data collection

At 167 sites along the South African coastline, we conducted a total of 419 BRUV deployments over multiple time-points between July 2016 and July 2018 (details in Osgood et al. 2019). Sites were randomly placed and stratified across two protected areas: inside (n = 40 sites, 109 deployments) and outside *(*n = 69 sites, 131 deployments) the Walker Bay Whale Sanctuary, and inside (n = 29 sites, 85 deployments) and outside (n = 29 sites, 94 deployments) the Betty's Bay MPA (Figure 4.1). When possible (i.e. barring weather and equipment constraints), deployments were conducted at each site in each season and each year. On average, a site received 2.5 replicate BRUV deployments over the study period. We selected sites to be 500 m apart from one another, other than within the Betty's Bay MPA where the smaller area dictated a 100–200 m minimum distance between sites; sites closer than 400 m apart were not sampled on the same day, if resources allowed. Sample size per habitat type (rocky reef, kelp forest, and sand) within each of the four sampled areas was dictated by habitat frequency within the area.

Each BRUV system was composed of a mild-steel cross-shaped base with a bait canister and camera set 111 cm apart from one another and raised 20-30 cm off the bottom of the system (details in Osgood et al. 2019). One kilogram of chopped, defrosted sardine *Sardinops sagax* was placed into the bait canister for each deployment. We used GoPro® cameras (Hero 1, Hero 2, Hero 3 Silver Edition, Hero+) set to 720p to prolong battery life and save memory card space. We deployed all BRUVs in daylight between 08:00 and 16:00. Mean deployment time was 62.7 min (SD 10.7; range 20.7–103.2).

For every chondrichthyan, teleost, cephalopod, crustacean, myxinid, bird, and mammal recorded during each BRUV deployment, we identified individuals to species level when possible. We then recorded the maximum number of individuals of a species observed at any one time on the entire video recording (MaxN) as a conservative measure of relative abundance (Cappo et al. 2004). We also recorded habitat type (sand, rocky reef, kelp) and visibility in broad categories (1 = <1 m; 2 = 1–5 m; 3 = 5–10 m; 4 = >10 m) for each BRUV video, using the distance to the bait canister as a reference. Visibility ranged from 0.5 m to approximately 20 m on the BRUV deployments. We recorded depth using an HDS-8m Gen2 Lowrance chartplotter for deployments in Betty's Bay and using one-meter markings on the BRUV rope in Walker Bay. Site depths ranged between 3 m and 55 m (mean 25.3 m [SD 12.2]). For reef and kelp sites, we also estimated the profile of the habitat, ranging between 0 for a flat profile and 4 for the steepest profile. We assigned a profile of 0 to all sand sites.

The University of Victoria Animal Care Committee authorised all observations of live animals (AUP 2016-032[1]). This study was conducted under the authority of a joint research permit issued by the South African Department of Agriculture, Forestry and Fisheries Branch Fisheries Management and Department of Environmental Affairs: Branch Oceans and Coasts (RES2017-31 and RES2018-59).

4.3.2 Data analysis

For each BRUV site, we first averaged the MaxN and species richness (total number of species) for all BRUV deployments replicated at the site. Then we assessed the relationship between the relative abundance (mean MaxN) and mean richness of all chondrichthyans to the mean MaxN and Shannon diversity index (calculated from mean MaxN) of species from all the other taxonomic groups pooled using Spearman rank correlations. Next, we assessed the associations between the MaxN of other taxa averaged per site and the presence of three chondrichthyan groups (catsharks, large sharks [>1 m TL], batoids) at a site using generalised linear models (GLMs) with a gamma distribution. We used *t*-tests to examine the relationships between the presence of these chondrichthyan groups and the mean Shannon diversity of the other taxa because they were normally distributed. We also used a gamma GLM and a *t*-test to assess whether sites with an above-average abundance in chondrichthyans (mean MaxN >3) had a greater total MaxN and Shannon diversity, respectively, of other taxa than sites with fewer chondrichthyans.

Next, we assessed whether the community composition of teleosts, cephalopods, crustaceans, myxinids, birds, and mammals differed between sites with and without catsharks, large sharks, batoids, and abundant chondrichthyans using a PERMANOVA. We determined which species of these other taxa were most responsible for any differences in community composition observed, based on significant Dufrêne-Legendre Indicator (DLI) values greater than 0.20 (Gilby et al. 2017).

To assess co-occurrence patterns between chondrichthyans and species from the other taxa, we used the package ‘co-occur’ in R (Griffith et al. 2016). We qualitatively compared the percent of positive and negative co-occurrences as well as the strength (effect size) of co-occurrences among chondrichthyan species as well as across specific groups: all chondrichthyans, catsharks, large sharks, and batoids. The effect size of a species pair’s co-occurrences is calculated as the observed number of co-occurrences minus the number of co-occurrences expected assuming random associations, standardised by number of sites, and ranges from -1 to +1. We also qualitatively compared the mean percent and strength of co-occurrences among chondrichthyans and, respectively, teleosts, cephalopods, and crustaceans, the taxa with the most observed species. We then determined which species had centrality within the network of these co-occurrences based on degree, betweenness, local bridging, closeness, and eigenvalue centrality. Centrality measures the importance of a node in a network (Freeman 1978), and in the case of ecological communities reflects the connectedness of a species to others through co-occurrence.

We examined the relationships between chondrichthyans and all species of conservation concern (red-listed by either the IUCN [www.iucn.org] or South African Sustainable Seafood Initiative [www.wwfsassi.co.za]), and also roman and west coast rock lobster, two species of local economic and conservation importance, based on habitat and co-occurrence. We ran a redundancy analysis (RDA) using habitat type, depth, habitat profile, and area as constraints to assess how the MaxN of chondrichthyans and species of conservation concern correlated based on habitat. We used non-averaged data (i.e. all 419 BRUV videos) due to small habitat heterogeneity at a site. We determined the strength of positive co-occurrences between chondrichthyans and these species of conservation concern, and we determined specifically which chondrichthyans had strong positive co-occurrences, both inside and outside the protected areas, with roman and west coast rock lobster. We also determined the mean strength of positive and negative co-occurrences between species of conservation concern and all other species to compare the connectivity of these threatened species, and their suitability as umbrella species, with that of chondrichthyans.

Finally, we simulated the creation of a small MPA (i.e. encompassing four sites) by randomly selecting a site of high chondrichthyan abundance and then joining it with its three closest sites. We repeated this procedure basing an MPA instead on sites with low chondrichthyan abundance, both over all habitats and over just reef and kelp habitats, to assess whether reef and kelp sites alone, even without high chondrichthyan abundance, would provide comparable conservation benefits. From this simulation, we calculated the percent increase in the Shannon diversity and species richness of all taxa, defining percent increase as the difference between the value for the MPA simulated based on abundant chondrichthyans and the value for the MPA based on fewer chondrichthyans, divided by the mean value for both MPAs. We also calculated the percent increase for the abundance of species of conservation concern along with the percent increase for both roman and west coast rock lobster abundance, specifically. We repeated the simulation 1000 times.

4.4 Results

In total, we observed on the BRUVs 18 chondrichthyan species and 52 other species; 39 teleosts, seven crustaceans, two cephalopods, two birds, one myxinid (the sixgill hagfish *Eptatretus hexatrema*) and one mammal (the Cape fur seal, *Arctocephalus pusillus*) (Table 4.1, Table C1). Two-thirds of these other species were only found at sites where we also observed chondrichthyans (*n*= 147 sites), including 29 teleosts, two crustaceans (Cape rock crab *Guinusia chabrus*, sandflat crab *Danielita edwardsii*), one cephalopod (chokka-squid, *Loligo reynaudii*), one bird (Cape cormorant, *Phalacrocorax capensis*), and the single myxinid species (Table C1). At least one chondrichthyan species occurred with every species of teleost, crustacean, and cephalopod at a minimum of one site. Both chondrichthyan total abundance (summed MaxN) and richness at a site were moderately correlated ($\rho = 0.42–0.53$) with each of the total abundance and Shannon diversity of the other taxa present, with stronger correlations occurring in the MPAs (Table 4.2).

There was also a significantly higher abundance of other taxa at sites with catsharks (likelihood ratio test (LRT), $\chi^2 = 37.84$, df = 1, $p < 0.001$) and large sharks (LRT, $\chi^2 = 4.82$, df = 1, $p = 0.00513$), but not batoids (LRT, $\chi^2 = 0.039$, df = 1, $p = 0.794$), compared to sites lacking these species (Figure 4.2a). Similarly, the Shannon diversity of other taxa was also significantly higher at sites with catsharks (two-sample *t*-test, t = 3.75, df = 165, $p < 0.001$) and large sharks (two-sample *t*-test, $t = 2.13$, df = 165, $p = 0.0342$) but not batoids (Figure 4.2b; two-sample *t*-test, *t* = 0.31, df = 165, *p* = 0.754). Sites with abundant chondrichthyans had both a significantly higher abundance (Figure 4.2a; LRT, $\chi^2 = 11.48$, df = 1, $p < 0.001$) and higher mean Shannon diversity (Figure 4.2b; two-sample *t*-test, $t = 7.94$, df = 165, $p < 0.001$) of other taxa, relative to sites with few chondrichthyans.

Table 4.1 Chondrichthyan species observed using baited remote underwater video in the Western Cape Province, South Africa and categorised by the major groupings used in the analysis of presence and co-occurrence. *Species endemic to southern Africa; †species with only one occurrence

Family	Species	Common name
Catsharks		
Scyliorhinidae	*Haploblepharus pictus**	Dark catshark
Scyliorhinidae	*Haploblepharus edwardsii**	Puffadder catshark
Scyliorhinidae	*Poroderma africanum**	Pyjama catshark
Scyliorhinidae	*Poroderma pantherinum**	Leopard catshark
Scyliorhinidae	*Halaelurus natalensis**	Tiger catshark
Large sharks (>1 m total length)		
Triakidae	*Mustelus mustelus*	Common smooth-hound shark
Hexanchidae	*Notorynchus cepedianus*	Broadnose sevengill shark
Triakidae	*Galeorhinus galeus*	Soupfin shark
Triakidae	*Triakis megalopterus**	Spotted gully shark
Carcharhinidae	*Carcharhinus brachyurus*†	Bronze whaler
Sphyrnidae	*Sphyrna zygaena*†	Smooth hammerhead shark
Batoids		
Rajidae	*Raja straeleni**	Biscuit skate
Rajidae	*Rostroraja alba*	Spearnose skate
Dasyatidae	*Bathytoshia brevicaudata*	Short-tail stingray
Rhinobatidae	*Acroteriobatos annulatus**	Lesser guitarfish
Myliobatidae	*Myliobatis aqulia*	Eagle ray
Other chondrichthyans		
Squalidae	*Squalus acutipinnis*†	Bluntnose spiny dogfish
Callorhinchidae	*Callorhinchus capensis**	St Joseph

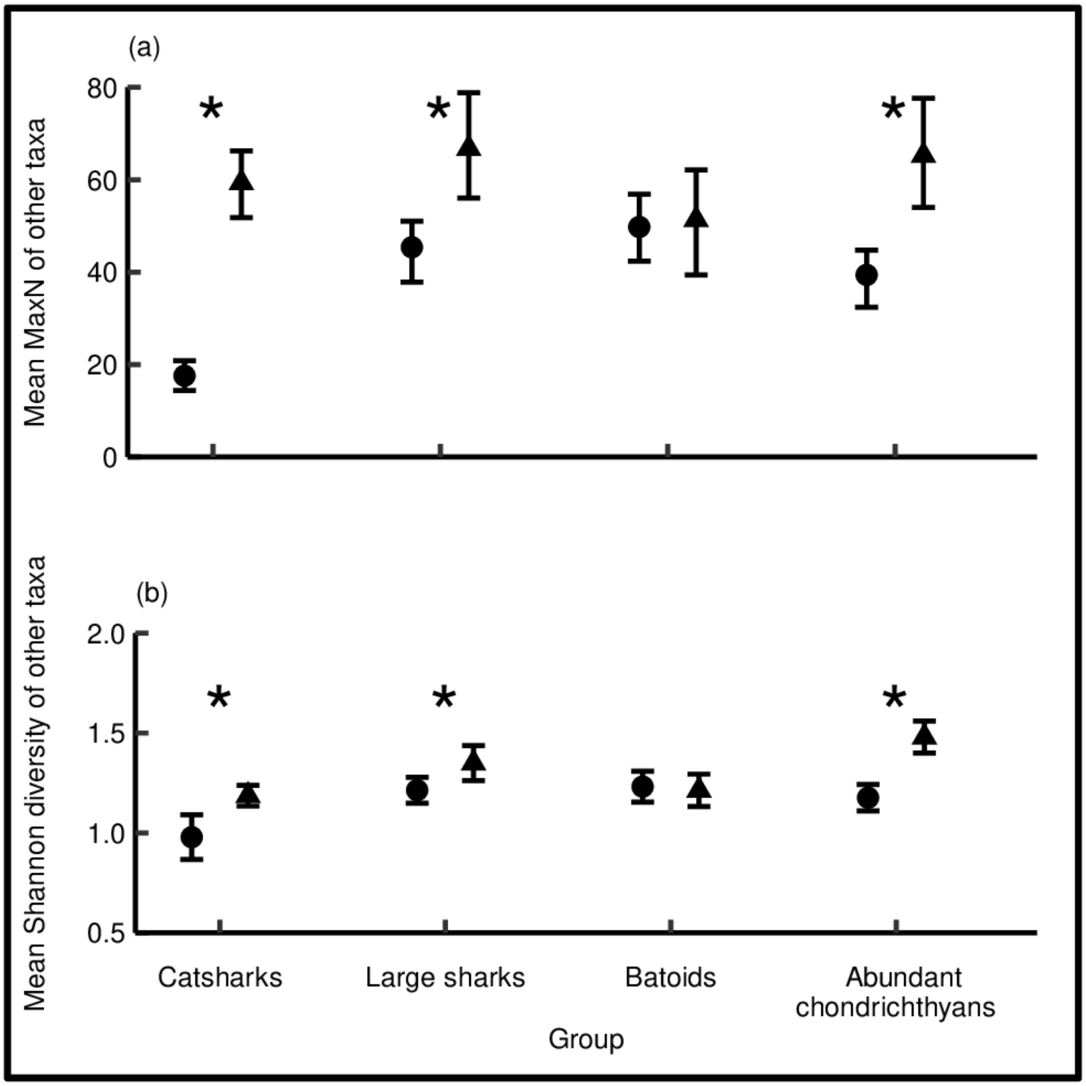

Figure 4.2 The difference in abundance and diversity between sites with and without chondrichthyan groups. (a) Mean relative abundance (MaxN; with 95% confidence interval based on the gamma distribution), and (b) mean Shannon diversity index (with 95% confidence interval based on the normal distribution) of the overall marine community of teleosts, cephalopods, crustaceans, birds, and mammals at sites without (circles) and with (triangles) catsharks, large sharks (>1 m total length), batoids, and abundant chondrichthyans (>3 mean MaxN). *significant differences ($p < 0.05$).

Table 4.2 The Spearman correlation coefficients between total relative abundance (MaxN) and species richness of chondrichthyans at a site, and the relative abundance and Shannon diversity indices of other taxa, in both protected and unprotected areas, observed using baited remote underwater video in the Western Cape Province, South Africa.

Chondrichthyes	Other taxa	
	Relative abundance	Shannon diversity
Relative abundance		
Overall	0.47	0.53
Protected	0.69	0.62
Unprotected	0.33	0.44
Richness		
Overall	0.42	0.48
Protected	0.62	0.61
Unprotected	0.33	0.46

Community composition differed significantly in the presence of catsharks (PERMANOVA, df = 1,165, Pseudo-F = 31.75, p = 0.001), large sharks (PERMANOVA, df = 1,165, Pseudo-F = 5.32, p = 0.002), batoids (PERMANOVA, df = 1,165, Pseudo-F = 3.59, p = 0.007), and abundant chondrichthyans (PERMANOVA, df = 1,165, Pseudo-F = 13.07, p = 0.001). Sixteen species were significantly more likely to occur at sites with catsharks or with abundant chondrichthyans, while 19 species were more likely to occur with large sharks. These both included three species of conservation interest; roman, red stumpnose *Chrysoblephus gibbiceps*, and west coast rock lobster. Only six species were more likely at sites with batoids, including bluefin gurnard *Chelidonichthys kumu* and the three-spotted swimming crab *Portunus sanguinolentus*, which were more likely to occur when catsharks and large sharks were absent.

Across all taxa, the number of positive and negative co-occurrences varied considerably by species (Figure 4.3). For chondrichthyans, the percentage of co-occurrences that were significantly positive, excluding species only observed once, ranged from 1.45% (with a mean strength of 0.0060) for lesser guitarfish *Acroteriobatus annulatus* to 36.23% (with a mean strength of 0.074) for the dark catshark *Haploblepharus pictus* (Figures 4.4a, 4.5a). Overall, 13.2% of chondrichthyan associations were significantly positive (Figure 4.4), with a mean strength of 0.048 (SD 0.037; 0.006–0.17) per positive co-occurrence (Figure 4.5b). In contrast, only 4.8% of chondrichthyan associations were negative (Figures 4.3, 4.4); these had a mean strength of -0.041 (SD 0.031; range -0.015 to -0.16) per negative co-occurrence (Figure 4.5b). Chondrichthyan negative co-occurrences ranged from 0.0% of associations for each of lesser guitarfish, short-tail stingray *Bathytoshia brevicaudata*, soupfin shark *Galeorhinus galeus*, and the common eagleray *Myliobatis aquila*, up to 20.3% for the biscuit skate *Raja straeleni*. The common smooth-hound shark *Mustelus mustelus*, tiger catshark *Halaelurus natalensis*, and dark catshark also had a high percentage of negative co-occurrences (11.6%, Figure 4.4a). The biscuit skate also had moderately strong mean positive and negative co-occurrences, at 0.035 and -0.033, respectively (Figure 4.5a). The catsharks had the highest percentage (overall 27.8%) and strength of both positive and negative co-occurrences on average amongst chondrichthyans, due largely to the many strong positive and negative co-occurrences of the dark catshark, pyjama catshark *Poroderma africanum*, and leopard catshark *P. pantherinum* (Figures 4.4, 4.5a,b). In fact, 13 of the 20 strongest interactions across the whole community involved one of these species. The dark catshark was one of the top three most-strongly co-occurring species for 15 species, followed by the pyjama catshark and the roman, with each being one of the top three co-occurring species for 12 other species. Large sharks and batoids co-occurred about half as strongly as the catsharks, almost tying for the smallest mean percentage of positive co-occurrences across all groups (Figure 4.5b). The broadnose sevengill shark (mean strength of 0.039) had the strongest positive co-occurrences among these species, with positive co-occurrences making up 20.9% of its associations (Figures 4.4a, 4.5a). These included an effect size of 0.053 with west coast rock lobster and 0.037 with roman.

Figure 4.3 Species co-occurrences in the BRUV data, categorized as positive, negative, or random. Species are ordered from most positive occurrences to most negative occurrences. Red font indicates chondrichthyan species.

Both teleosts and cephalopods had a similar percentage of positive and negative co-occurrences to chondrichthyans on average, although catsharks still had the highest mean percentage of positive co-occurrences across all groups examined (Figures 4.3, 4.4). However, two teleosts, roman and the hottentot seabream *Pachymetopon blochii,* had the highest percentage of positive interactions across all taxa (Figure 4.3). Hottentot also had the strongest positive co-occurrences among all species (mean co-occurrence strength = 0.075), but the dark, pyjama, and leopard catshark species had interaction strengths nearly as strong (0.070–0.074). Despite having a lower mean percentage of positive co-occurrences to teleosts, cephalopods, and chondrichthyans (Figure 4.4b), crustaceans had strong positive co-occurrences on average, largely due to the west coast rock lobster (Figure 4.3). The strongest positive co-occurrences involving any species occurred between the dark catshark and each of the west cost rock lobster (0.17) and the hottentot seabream (0.16).

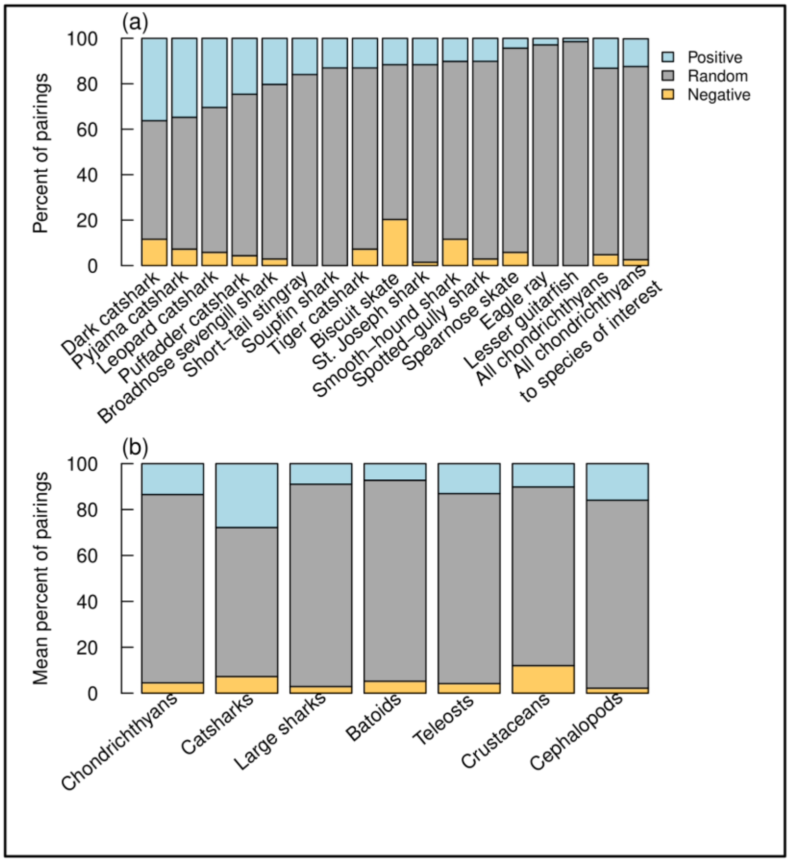

Figure 4.4 The percent of positive, random, and negative co-occurrences between groups. (a) The percent of positive, random, and negative co-occurrences between each chondrichthyan species and all other species, the total for all chondrichthyans, and the total for all chondrichthyans relative only to species of conservation concern. (b) The mean percent of positive, random, and negative co-occurrences for different groups of chondrichthyans, and for crustaceans and cephalopods.

The puffadder catshark had the highest centrality of any species of any taxa based on every measure except eigenvalue centrality, for which the teleost hottentot seabream was highest (Table C2). However, the pyjama catshark and the puffadder catshark had the second and fourth highest values of eigenvalue centrality, respectively. The pyjama catshark and hottentot seabream also tied with the puffadder catshark for the highest values for degree and closeness centrality.

Chondrichthyans had similar scores on the RDA to species of conservation concern, suggesting occurrences in similar habitats generally. The pyjama, leopard, and puffadder catsharks had similar scores on both axes of the RDA to roman, as well as red steenbras *Petrus rupestris,* with large scores on the first axis and negative scores on the second axis indicating a shared preference for deeper reef sites (Figure 4.6). The dark catshark had similar scores on both axes to the west coast rock lobster, due to similar abundance on shallow kelp sites in the Betty's Bay MPA (Figure 4.6).

Chondrichthyans co-occurred positively and significantly with seven species of conservation interest (Table 4.3). The strength of positive co-occurrences of chondrichthyans with species of conservation interest was mildly greater than the mean strength of their co-occurrences with other taxa in general (Figure 4.5b). The pyjama catshark (mean co-occurrence strength = 0.13) and dark catshark (0.11) were the second and third strongest species of any taxa co-occurring positively with the roman, behind hottentot seabream (0.14). The pyjama and dark catshark co-occurred more strongly with roman within the protected areas (0.18 and 0.13, respectively) than outside them (0.091 and 0.099). The dark catshark co-occurred most strongly (0.17), and the pyjama catshark third strongest (0.14), with the west coast rock lobster. These two catsharks also co-occurred more strongly with the west coast rock lobster in protected areas (0.20 and 0.17, respectively) than outside them (0.15 and 0.12, respectively). Only the west coast rock lobster and roman had co-occurrences stronger than chondrichthyans on average; most species of conservation concern did not have strong co-occurrences with other species (Figure 4.5c).

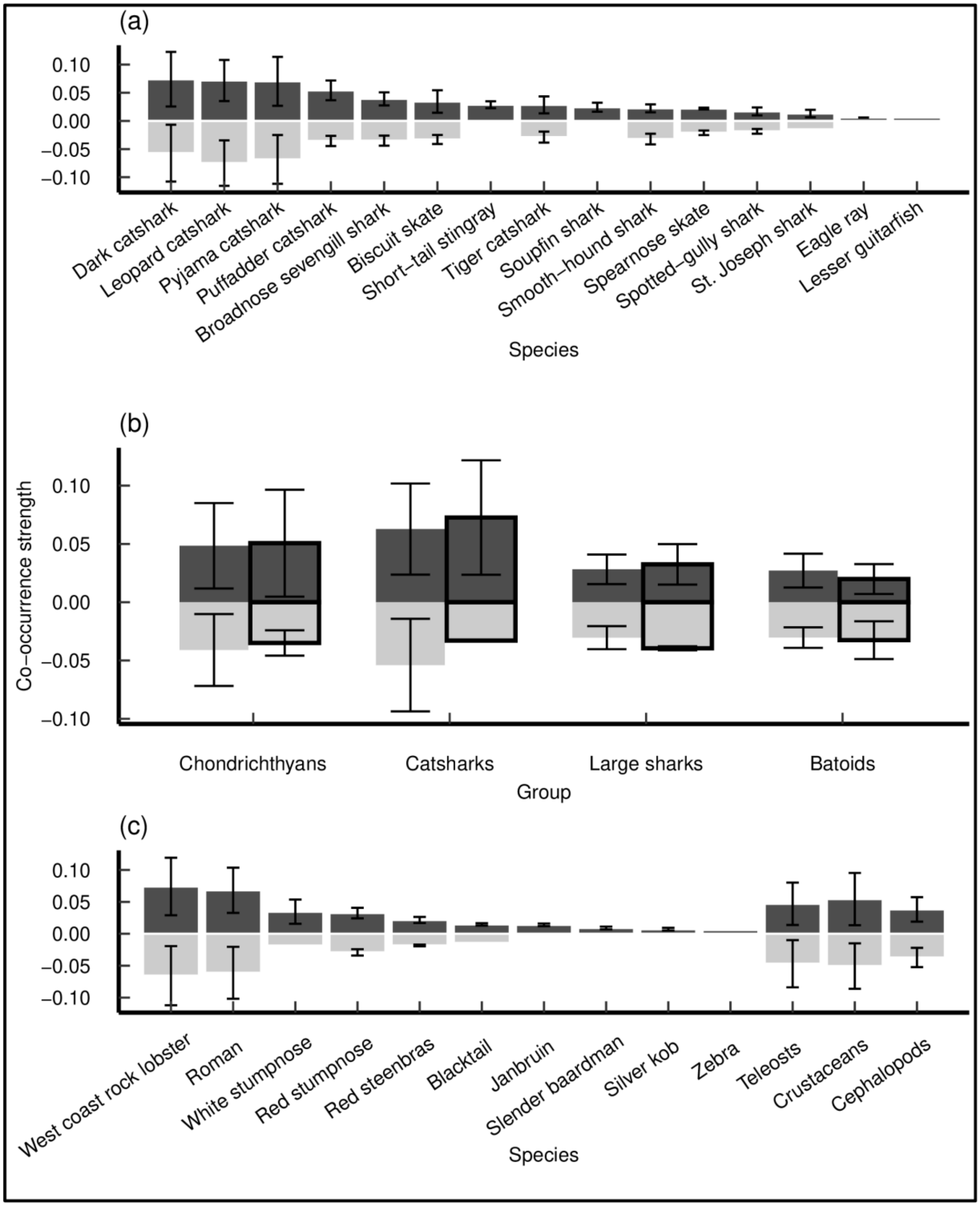

Figure 4.5 The mean strength of positive and negative co-occurrences with all other species for (a) each chondrichthyan species, (b) each chondrichthyan group (solid box relative only to species of conservation concern), and (c) each species of conservation concern, and teleosts, crustaceans, and cephalopods. Error bars represent ± standard deviation.

Table 4.3 The species of conservation concern observed at least twice in the baited remote underwater videos in the Western Cape Province, South Africa, ordered by taxon and the mean strength (effect size) of their positive co-occurrences with chondrichthyans. *Mean effect sizes derived from only significant positive co-occurrences; †species with only one occurrence. IUCN status (version 2019-2): LC = Least Concern; NT = Near Threatened; VU = Vulnerable; EN = Endangered; NA = not assessed. IUCN = International Union for the Conservation of Nature; SASSI = South African Sustainable Seafood Initiative.

Species	Common name	IUCN status	SASSI listing	Co-occurrence strength
Crustacea				
Jasus lalandii	West coast rock lobster	LC	Red	0.09*
Teleostei				
Chrysoblephus laticeps	Roman	NT	Orange	0.07*
Chrysoblephus gibbiceps	Red stumpnose	EN	Red	0.04*
Rhabdosargus globiceps	White stumpnose	VU	Red	0.03*
Petrus rupestris	Red steenbras	EN	Red	0.02*
Diplodus capensis	Blacktail	LC	Red	0.007
Pomatomus saltatrix†	Shad	VU	Red	0.006*
Atractoscion aequidens†	Geelbek	VU	Red	0.006*
Umbrina robinsoni	Slender baardman	NA	Red	0.006
Diplodus hottentotus	Zebra	LC	Red	0.004
Gymnocrotaphus curvidens	Janbruin	LC	Red	0.004
Argyrosomus inodorus	Silver kob	NA	Red	0.004
Dichistius capensis†	Galjoen	NA	Red	0.004
Epinephelus marginatus†	Yellowbelly rock cod	VU	Orange	0.003

Compared to selecting a random site of low chondrichthyan abundance, the mean Shannon diversity was 12.2% (95% CI 1.4) higher, species richness was 22.8% (2.3) higher, abundance of species of conservation concern was 33.5% (1.2) higher, and roman abundance was 97.6% (6.5) higher in simulations of MPAs based on sites of high chondrichthyan relative abundance. When compared to selecting a reef or kelp site of low chondrichthyan abundance, Shannon diversity was still 5.3% (1.1) higher, species richness 4.1% (1.5) higher, abundance of species of conservation concern 5.0% (3.1) higher, and roman abundance 20.2% (5.7) higher in simulations of MPAs based on sites of high chondrichthyan relative abundance. However, the abundance of the west coast rock lobster was 17.0% (8.6) lower in MPAs simulated based on high chondrichthyan abundance compared to those based on reef and kelp sites with few chondrichthyans. This species' abundance was, however, 58.8% (9.4) higher in the former simulated MPAs compared to sites of low chondrichthyan abundance over all habitats.

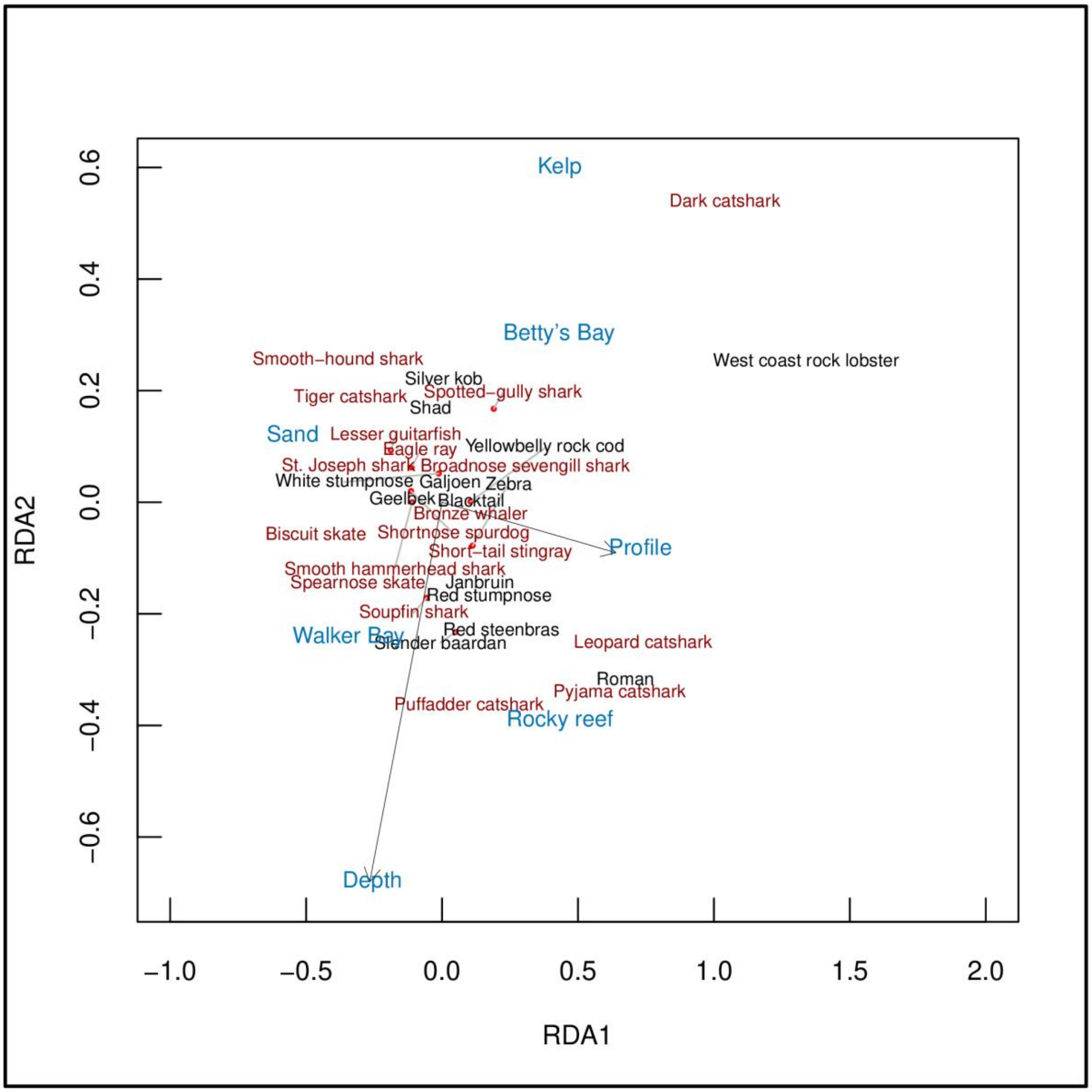

Figure 4.6 The scores of each chondrichthyan species (red) and each species of conservation concern (black) on the first two axes of a redundancy analysis (RDA) relative to habitat variables (overall type, profile, depth, and region) that were used as constraints (blue).

4.5 Discussion

Our analyses suggest that chondrichthyans could serve as an effective umbrella-species complex for marine conservation in South Africa. We found concordance in the abundance and species richness of this assemblage with that of other marine taxa, and they share habitat with many species of conservation concern in the Western Cape. Amongst chondrichthyans, the endemic catsharks showed the strongest umbrella species characteristics, and co-occurred with many species, including a strong association with reef species roman, the west coast rock lobster, and red stumpnose that are of economic and conservation importance. The umbrella potential of larger shark species was more equivocal due to their low abundance, but the more common broadnose sevengill shark had strong co-occurrence patterns with a range of taxa. This species has increased its habitat range due to the declining presence of white shark *Carcharodon carcharias* (Hammerschlag et al. 2019), an important predator and competitor, suggesting the broadnose sevengill shark has the wide range and high trophic level of a traditionally defined umbrella species coupled with demonstrated overlap in habitat with other species. A chondrichthyan umbrella-species complex including both catsharks and broadnose sevengill shark would cover biodiversity over multiple scales, optimizing their role as surrogate species (Stuber and Fontaine 2018). Some species (biscuit skate, common smooth-hound shark, and tiger catshark) did have high negative co-occurrences, likely reflecting their abundance on the sand habitat, for which other species did not have the same affinity.

Catsharks found in the Western Cape region of South Africa are small-bodied, locally resident, and abundant (Osgood et al. 2019), all qualities not traditionally associated with umbrella species (Roberge and Angelstam 2004, Caro 2010). However, tests of umbrella species that were selected based on large body- and home-range size, generalist diet, and high trophic level have shown that such qualities do not guarantee the protection of high abundance or species richness, even compared to a random selection of species (Andelman and Fagan 2000, Branton and Richardson 2011, Stuber and Fontaine 2018). In fact, in terrestrial systems, small avian species have stronger ecological associations with species richness and greater potential as umbrella species than large mammals (Branton and Richardson 2011). Smaller surrogates with strong associations to local biodiversity can be more useful than umbrella species with large home ranges, as hotspots of biodiversity on these larger scales have already been identified in many regions (Caro 2015). The abundance of catsharks and ease of capture in the Western Cape aids their use for more precisely identifying local sites of high diversity, and their lower mobility ensures close associations to habitats and local populations of interest. Rarer species are harder to record and study, limiting their use as a practical surrogate for selecting precise locations of conservation need (Fleishman et al. 2000). The use of smaller, localised, and endemic umbrella species also supports goals to protect traditionally overlooked biodiversity (Kalinkat et al. 2017).

Catsharks have other qualities besides habitat associations with species of conservation interest, including high centrality within the ecological community and complementarity in habitat use, that also imply they might serve as effective umbrella species (Lambeck 1997, Andelman and Fagan 2000). Most of the catsharks demonstrated centrality, and therefore high connectedness in the community. The puffadder catshark had high centrality on every metric, suggesting it is closely connected to many other species that do not necessarily co-occur with each other, and is therefore an ideal candidate to indicate site-level diversity (Pérez-García et al. 2016). The taxonomic and morphological similarity between the puffadder and dark catsharks encumbers conservation measures based on the former species alone, but both co-occurrence and centrality metrics indicate the dark catshark also had some of the strongest links in the community. The ‘friendship paradox’ borrowed from social-network theory, which postulates that species (the ‘friends’) linked to a species chosen at random are more central in the network than the originally chosen species, also provides evidence of the centrality of the dark catshark (Christakis and Fowler 2010, Pires et al. 2017). The co-occurrence patterns of the dark catshark, suggests it is the ‘friend’ of many species and thus central to the community. It was one of the strongest co-occuring species for each of 15 other species (i.e. it was one of the ‘best friends’ for these species). The species also associates with the habitat of the commercially important west coast rock lobster. Thus, together the puffadder and dark catsharks could form the basis of an umbrella-species complex, motivated further by the near-threatened status of the puffadder catshark. In addition to being highly central, the puffadder, pyjama, and leopard catsharks share habitat associations with species of conservation concern, including roman and red steenbras, species that are popular amongst anglers. The catsharks have some complementarity in habitat preference; although many are abundant on reefs and in kelp (Osgood et al. 2019), the tiger catshark associates strongly with sand, so that as an umbrella complex, they could protect diversity over a range of habitats.

Beyond chondrichthyans, our study also identified habitats and a few teleost species that could be used to select sites of conservation potential. Basing selection on habitat was almost as effective at forming speciose and abundant MPAs in our simulations as selecting sites based on chondrichthyan abundance, given that the quality of chondrichthyans as umbrella species comes from their association with productive reef and kelp habitats (Osgood et al. 2019). However, the small benefits observed in MPAs that were simulated based on chondrichthyan abundance suggests chondrichthyan abundance yields slightly more precise information on local diversity and abundance useful to MPA placement, other than MPAs that could benefit the west coast rock lobster, possibly due to their greater ubiquity in kelp habitats. Additionally, habitat quality is not well mapped along the Western Cape coastline, limiting its utility for targeting MPA placement. In contrast, the distribution of chondrichthyans, particularly catsharks, is accessible from substantial recreational and commercial fishing effort, and fishery independent surveys. Two teleost species, roman and hottentot seabream, are also potentially effective umbrella candidates since both co-occur with many species in the community. Roman was rarer on our BRUVs than chondrichthyans and not as prevalent across habitats; catsharks had higher co-occurrence and centrality. However, roman is charismatic in South Africa due to its popularity in recreational fisheries and as a food source, so the species could be used in tandem with a chondrichthyan umbrella species complex in local marketing and research campaigns. Ultimately, the close association of roman with chondrichthyans should help motivate the latter as an umbrella-species complex. Comparatively, hottentot seabream, found predominately on reefs, does not associate with the same breadth of habitat as chondrichthyans, and the species is not as charismatic, limiting its potential as an umbrella- or flagship species (Roberge and Angelstam 2004, Roberson et al. 2015).

We propose that chondrichthyans, especially a subset including catsharks and at least the broadnose sevengill shark, should be used as an umbrella-species complex in the Western Cape Province. Additional research on the relationship of these species to different habitats and seascape elements is required to assess their appropriateness for different conservation goals and target species, as co-occurrence can change with time and context (Cushman et al. 2010, Tulloch et al. 2016, Stuber and Fontaine 2018). More-detailed knowledge of multi-scale habitat associations that could be used in species distribution modeling would solidify the ecological suitability of chondrichthyans as umbrella species (MacPherson et al. 2018). Additionally, more data will be needed on the relationship of chondrichthyans to the less-frequently observed species. The bird, mammal, and squid species, as well as a few teleost species (e.g. pipefish *Syngnathus temminckii*, silver kob *Argyrosomus inodorus*, zebra *Diplodus hottentotus*), were observed only opportunistically on the BRUVs, likely due to a combination of rarity and BRUV selectivity. The results were not greatly affected by these sightings, and so more BRUV work, including sampling in the evening and night, combined with other methods of sampling besides BRUVs, could be done in the future to test chondrichthyan associations with these species.

Chondrichthyans could also serve as a flagship-umbrella-species complex, as they have a cultural presence both internationally and locally in South Africa, and, given the high charisma of sharks in general, attitudes could be shifted for the less charismatic species with targeted marketing and educational programs (Albert et al. 2018, Curtin and Papworth 2018). Because of their endemism, catsharks are ideal for raising awareness of South Africa's unique, evolutionarily distinct chondrichthyan biota (Ebert and van Hees 2015). Marketing could also raise the potential of chondrichthyans for the conservation of species like roman. Conservation initiatives are already starting to turn to smaller species when large charismatic species are absent (Kalinkat et al. 2017), and this might be an effective approach in the highly impacted coastal ocean of the Western Cape. However, the spread of the broadnose sevengill shark into former white shark hotspots foreshadows a future for this larger, charismatic species as a flagship in the lucrative shark-related tourism industry of the country (Gallagher and Hammerschlag 2011, Hammerschlag et al. 2019). Chondrichthyans are charismatic, highly connected, and abundant in South Africa, creating promise for them as a flagship-umbrella-species complex. Since successful flagship species on the international stage do not always translate to charisma at the local level, the cultural suitability for different marine species to serve as flagships in South Africa needs to be investigated (Caro 2015, Jepson and Barua 2015). If research into how communities engage with chondrichthyans both in South Africa and abroad is incorporated into effective conservation marketing, they could attract conservation attention and funds on both the local and international level (Jepson and Barua 2015, Macdonald et al. 2017). When resources are scarce and diversity is threatened, chondrichthyans can be an ecologically, as well culturally, suitable set of surrogate species to optimise conservation in South Africa.

Chapter 5 – Temperature and El Niño events couple with ongoing population declines to alter the shark and ray community within a remote MPA in the Eastern Tropical Pacific

In prep as Geoffrey J. Osgood[1], Easton R. White[2], & Julia K. Baum[1]. *Journal of Animal Ecology*.

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Author contributions: G.J.O., E.R.W., and J.K.B conceived of the study. G.J.O. and E.R.W collated and cleaned the data. G.J.O. designed the study, conducted the data analysis, and wrote the manuscript with input from E.R.W and J.K.B.

5.1 Abstract

Marine protected areas (MPAs) have the potential to protect critical habitat for even mobile species of elasmobranchs—sharks, rays, and skates—as fishing impacts their populations. However, many MPAs suffer from poor planning and enforcement, and these insufficiencies may worsen as climate change alters the distribution of marine species in relation to environmental gradients. Additionally, fundamental knowledge of how elasmobranchs respond on a species-by-species basis to changes in temperature and productivity impedes predictions of how effective these MPAs will be under climate change. We used sightings collected by the dive company Undersea Hunter within an MPA at Cocos Island, Costa Rica to construct a 27-year long time series of relative abundance for seven species of elasmobranch differing in mobility and ecology. We used generalized linear mixed models to estimate the effect of sea surface temperature (SST) and the El Niño–Southern Oscillation (ENSO) on the counts and occurrence of each species, finding species-specific differences in their responses. Large, mobile species responded strongly but inconsistently to temperature (SST): *Sphyrna lewini* counts and *Mobula* ray occurrence both declined substantially with a few degrees rise in SST, while *Galeocerdo cuvier* occurrence sharply increased. For *S. lewini*, a 1°C rise in SST reduced counts by over 14%, and dropped the occurrence of their large schools by almost one quarter (24.2%). Similarly diverse responses occurred to the ENSO: *Mobula* rays responded weakly, but *S. lewini* and *G. cuvier* were sighted with greater frequency during the La Niña, and their abundance dropped considerably during El Niño conditions—over a 2-fold decline between a strong La Niña and strong El Niño for *S. lewini*. The smaller and sedentary *Triaenodon obesus* responded weakest of all species to both SST and the ENSO, likely reflecting its lower metabolic rates and mobility. Surprisingly, *Taeniurops meyeni*, a ray with limited mobility declined

significantly in response to both rising SST and the El Niño, suggesting climate change will impact the distribution and protection of even these more localized species within MPAs. Our results compel further work on the diversity of elasmobranch responses to environmental change and how their dynamic habitat associations will influence the ability of current MPAs to conserve their populations into the future.

5.2 Introduction

Marine predators are critical components of ocean food webs, connecting resources across seascapes (McCauley et al. 2012b, Williams et al. 2018), and yet they are experiencing rapid and severe declines across world oceans (Myers and Worm 2003, Heithaus et al. 2008, Britten et al. 2014). Fisheries exploitation poses a heightened risk to the population growth and stability of elasmobranch—shark, ray, and skate—populations due to their low fecundity and small intrinsic rate of increase (Dulvy et al. 2008a, Ferretti et al. 2010). As such, massive reductions in fisheries mortality on elasmobranch populations are needed if populations of depleted species are to recover and maintain their ecological role (Worm et al. 2013). Marine protected areas (MPAs) should play an important role in elasmobranch conservation by protecting critical habitat and limiting exposure to fisheries (Acuña-Marrero et al. 2017, White et al. 2017), especially if migratory and movement ecology is considered (Ketchum et al. 2014a, Speed et al. 2016, Yates et al. 2016).

Rising ocean temperatures, and the associated intensification of the El Niño Southern Oscillation's (ENSO) strength and frequency (Cai et al. 2014, Wang et al. 2017), however, could alter movement patterns due to an elasmobranch's need to thermoregulate (Bernal et al. 2012). Thus, climate change will likely shift populations into different jurisdictions and expose them to new fisheries, and reducing the effectiveness of current MPAs and further complicating conservation (Cheung et al. 2010, Bruno et al. 2018). In general, tropical fish maintain metabolic rates and body temperatures close to their upper physiological limits (Stuart-Smith et al. 2015) since many physiological and metabolic processes associated with foraging performance increase with temperature until near this upper critical limit (Hight and Lowe 2007, Whitney et al. 2016). High metabolic rates even within their optimal range, are costly and can be difficult to maintain in tropical ecosystems due to sparse prey distributions (Bernal et al. 2012, Whitney et al. 2016). So, to be efficient foragers, tropical elasmobranchs must thermoregulate to avoid even small deviations above their thermal limits where physiological performance drops precipitously (Martin and Huey 2008, Meekan et al. 2015, Andrzejaczek et al. 2018).

Despite spatial and temporal variability in ocean temperatures, elasmobranchs achieve optimal body temperatures for foraging, digestion, growth, and reproduction through regular movements across habitats and depths with differing thermal regimes (Sims et al. 2006, Bernal et al. 2012, Schlaff et al. 2014). For instance, tiger sharks *Galeocerdo cuvier* in Australia move both horizontally and vertically in the water column to stay in water 22°C despite both seasonal and diurnal fluctuations in temperature (Payne et al. 2018), and oceanic whitetips (*Carcharhinus longimanus*) increase dive frequency, duration, and depth during the summer to maintain optimal body temperatures (Musyl et al. 2011, Andrzejaczek et al. 2018). If current thermal habitat becomes too extreme, exceeding thermal limits, ectothermic elasmobranchs must move into new habitats to thermoregulate (Angilletta et al. 2002, Stebbing et al. 2002).

The distributions of marine fish species have already shifted poleward and into deeper waters in response to changes in thermal habitat and primary productivity induced by climate change and the ENSO (Perry et al. 2005, Brander 2007, Dulvy et al. 2008b, Pinsky et al. 2013).

Range expansions of whitetip reef sharks (*Triaendon obesus*) into Rapa Nui (Morales et al. 2019) and of manta rays into Raja Ambat (Beale et al. 2019) have already occurred, and are likely associated with rising temperatures and El Niño events. In addition to tracking changes in temperature, top predators also track prey distributions shifting in response to ENSO altered nutrient cycling, plankton and forage fish productivity (Marinovic et al. 2002, Yoder and Kennelly 2003, Lehodey et al. 2006, Su et al. 2011, Wolff et al. 2012). For instance, the strong 1997/1998 El Niño caused a northward shift into California of many marine species of the Eastern Tropical Pacific, including some elasmobranchs (Lea and Rosenblatt 2000). Therefore, as the ENSO cycles between warm El Niño phases and cold La Niña phases, the observations of many elasmobranch populations also fluctuate (Wilson et al. 2001, Bromhead et al. 2012, Adams et al. 2016, Lee et al. 2018, Beale et al. 2019). However, little is still known about how elasmobranchs respond to ENSO events and their intensification, especially outside the Indo-Pacific.

This lack of understanding is compounded by response variation related to species, size, and sex (Chin et al. 2010, Musyl et al. 2011, Towner et al. 2013). Since they are highly mobile, many elasmobranchs will likely shift distributions as temperatures rise (Perry et al. 2005, Sunday et al. 2015). The degree to which they shift, however, will depend on their ecology, lifestyle, body size, range size, and habitat needs (Chin et al. 2010, Lear et al. 2019). In the Marshall Islands, longline catch of blue sharks (*Prionace glauca*) and bigeye thresher sharks (*Alopias superciliosus*) increased during El Niño conditions while the catch of other species like silky shark (*Carcharhinus falciformis*) did not change, reflecting variation in responses even in the same system, potentially related to different physiological needs (Bromhead et al. 2012). Sedentary benthic sharks have lower metabolic rates and a higher cost of activity compared to ram ventilating pelagic species, leading to both a reduced capacity and reduced need to re-distribute with changing environmental conditions (Killen et al. 2010, Whitney et al. 2016). Species that actively hunt in the pelagic zone also have metabolic rates more greatly constrained by gill surface area and its effects on oxygen and waste transport, and by the need to swim fast enough to supply sufficient oxygen over the gills to meet any elevations to metabolic demand (Killen et al. 2010, Jacoby et al. 2015). Thus, more active species should be more sensitive to temperature and its metabolic effects, but more research is needed on how rising temperatures and the ENSO affect specific species if predictions about climate change impacts, and their effect on MPA effectiveness, are to be made.

Fluctuations in distribution and abundance associated with climate change and ENSO variability complicate our understanding of elasmobranch ecology and conservation in one further way: adding stochasticity to time series. Environmental stochasticity reduces statistical power by increasing noise around a trend (Humbert et al. 2009, McCain et al. 2016). The variability associated with ENSO events could also reduce the accuracy of detected trends because local changes in abundance may reflect distributional shifts rather than a real trend (Forney 2000). Explicitly modelling species-environment relationships can improve estimation and inference of trends (Forney 2000), but it is unclear if such benefits will occur regardless of times series length, given that longer time series are often needed for sufficient power to disentangle short-term variability from longer time changes (McCain et al. 2016, White 2019).

To best understand elasmobranch conservation and ecology in the face of climate change, we need to assess long-term data on how temperature changes and the ENSO affect elasmobranchs across species of differing ecology and movement characteristics. We especially need data on species impacted by fishing, and putatively protected within MPAs, to understand how climate change could interact with fishing threats. Here, we investigate the elasmobranch community at Cocos Island, Costa Rica, an MPA in the Eastern Tropical Pacific since 1978 (Alvarado et al. 2012), with protection extended to 22.2 km around the island in 2002 (Sibaja-Cordero 2008). Cocos Island is a hotspot of elasmobranch diversity due to its productive reef and seamount habitats situated at the nexus of multiple currents (Friedlander et al. 2012, White et al. 2015). Together with Malpelo Island in Colombia and the Galapagos Islands in Ecuador, Cocos Island forms an important link in a migration corridor for scalloped hammerhead sharks (*Sphyrna lewini*); large schools, potentially for mating, form at seamounts at the Island, drawing sharks from around the Eastern Tropical Pacific (Salinas-de-León et al. 2017, Nalesso et al. 2019). However, these elasmobranchs are impacted by fishing and habitat degradation in Costa Rica (Arias-Godínez et al. 2019), even within the MPA (White et al. 2015, Arias et al. 2016). The Island is also affected by ENSO events that occur at least every four to nine years (Lavín et al. 2006, Sibaja-Cordero 2008).

We assessed the effects of sea surface temperature (SST) and the Ocean Niño Index (ONI), a measure of SST anomaly indicating ENSO conditions, on the counts of four species of shark (*Sphyrna lewini*, whitetip reef shark *Triaenodon obesus*, blacktip shark *Carcharhinus limbatus*, tiger shark *Galeocerdo cuvier*) and three species of ray (mobula rays *Mobula spp.*, marble ray *Taeniurops meyeni*, spotted eagle ray *Aetobatus narinari*) during dives by the dive tourism company Undersea Hunter at Cocos Island, Costa Rica from 1993 to 2019. These species are the most abundant and frequently observed at Cocos Island and represent a range of variation in mobility, habitat use, ecology, and physiology that could affect their responses to SST and the ENSO. These dives have been used before to analyze trends in elasmobranchs at Cocos, discovering widespread declines for all these species save for *C. limbatus* and *G. cuvier*, which showed exponential increases (White et al. 2015). Since fishing has not strongly abated in the region, we predict these declines have continued, and have likely occurred for *C. limbatus* and *G. cuvier* in the last six years as well. Thus, it is a good time series to investigate how fisheries-impacted populations are affected by environmental change. If thermal sensitivity stimulates movements off island or into deeper waters to track preferred thermal habitat, we predict counts for all species to decline at higher temperatures and ONI values. Declines in productivity, scaling up to shifts in prey, should also reduce elasmobranch abundance at higher ONI values. We expect the strongest effects for the more migratory and active pelagic species, *S. lewini*, *G. cuvier,* and *Mobula* spp. Due to their migratory behaviour, we also expect the schooling frequency of *S. lewini* to decline at higher temperatures and during stronger El Niño events. We expect the weakest responses for the benthic species *T. obesus* and *T. meyeni*, which do not rely on ram ventilation and should be less mobile with less aerobic scope for activity. To address if variability associated with changes to SST and the ENSO complicate trend estimation, we also assessed the effect of explicitly modelling SST and ONI on the estimated year trend and how this effect, if any, varied based on time series length and sample size. We predict including ONI in our models will increase power and accuracy for detection of population trends, especially for shorter time intervals and smaller sample sizes.

5.3 Methods and materials

5.3.1 Data

From March 1993 to December 2019 (n = 27 years), experienced dive guides at Undersea Hunter (http://underseahunter.com/; n=46), a privately owned and operated dive operation, conducted a total of 34,342 dives on 5,664 total days at seventeen sites around Cocos Island, Costa Rica (Figure 5.1). At the end of each dive, the dive guide recorded the number of sharks or rays, or an estimate when counts were high (e.g. exceeded 100), using standardized data sheets. For three species (*C. limbatus, G. cuvier*, and *Mobula* spp.) only presence or absence was recorded. Dive guides recorded the presence of manta rays (*Mobula birostris*) and other *Mobula* species separately, but we combined them to bolster sample size and because of recent taxonomic revisions of *Manta* into the synonymy of *Mobula* (White et al. 2018). Although these dives lacked strict scientific protocol, they had consistent effort (~60 min), dive procedures, and depths at each site, which covered the range of shallow water habitat at Cocos Island. Data from all dives were previously transcribed into a single data base (White et al. 2015) and these, plus new data since 2015 already electronically recorded, were checked for errors.

5.3.2 Statistical analysis

To assess the influence of SST and ONI on the sightings of these species, and update their long-term trends, we modelled the abundance or presence-absence of each species using negative binomial generalized linear mixed models (GLMMs) or binomial GLMMs, respectively. We ran an additional model on *S. lewini* data, modelling the probability of observing a school (≥50 sharks) during a dive using a binomial GLMM. Since *A. narinari* abundance was recorded, but their frequency of occurrence was rare, we used zero-inflated negative binomial GLMMs for this species (Martin et al. 2005). Fixed effects included SST, ONI, year, and sine and cosine functions of Julian date to account for seasonality (Baum and Blanchard 2010). We scaled SST and visibility to a mean of zero and a standard deviation of one. We included year in the models to update trends from White et al. (2015). Visibility and current strength (categorical from 0 to 5) as recorded by the dive guides were also included in our models. We retrieved daily mean SST and the ONI data from NOAA (https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.highres.html, https://www.cpc.ncep.noaa.gov/data/indices/oni.ascii.txt). The ONI represents the running three month mean of SST anomalies in the Niño-3.4 region of the east-central Pacific (NOAA 2020). We included both SST and ONI in the same model to best account for the different scales over which each of SST and ONI operate to create variation of the sightings. The ONI index represents longer term changes to SST anomalies that correlate with other oceanographic changes in the Eastern Tropical Pacific, while daily mean SST represents more immediate impacts on the physiology and daily movement of these species. They were not strongly correlated (rho = 0.34) and so were modelled together. We determined the significance of the SST and the ONI coefficients using likelihood ratio tests. We also used likelihood ratio tests to determine if a significant quadratic relationship existed with SST or ONI for each species, but kept quadratic terms in a model only if they significantly improved fit. Random effects accounted for correlations due to unequal sampling effort across different dive guides and sites.

For each species, we used the SST coefficients to calculate the percent change in abundance or odds of occurrence as SST increased one standard deviation above the mean and from 25 to 30°C. We also used the ONI coefficient to calculate percent change from a neutral ENSO (ONI = 0) to moderate La Niña (ONI = -1) and El Niño (ONI = 1) conditions and also the percent change between strong La Niña (ONI = -1.5) and strong El Niño events (ONI = 1.5).

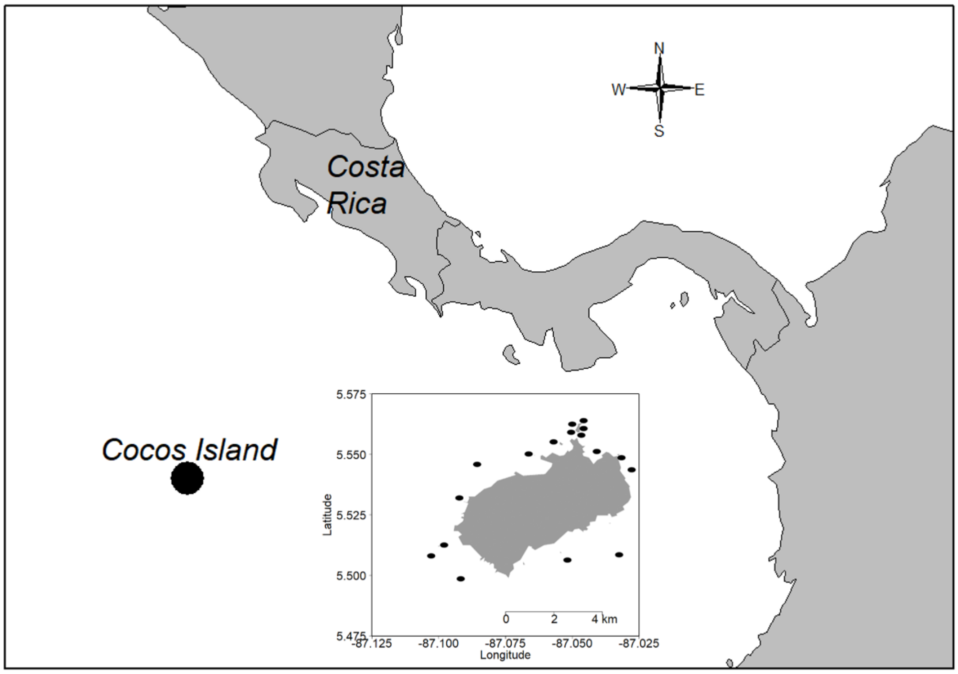

Figure 5.1 Map of Cocos Island in Costa Rica. Inset shows approximate location of dive sites.

Finally, to assess if explicitly modelling the effects of SST and ONI on the counts and occurrence of each species affect the estimation of the long-term population change important for understanding conservation status, we ran each model without either SST and ONI using the full data set. In addition, to assess if the effect of modelling SST and ONI on the estimated trend estimate mattered more when time series and sample size are limited and short, we also ran models with and without SST and ONI on subsets of the data for *S. lewini*, one of the most abundant and reliably observed species at the Island. We ran the same GLMMs on every possible five, ten, fifteen, and twenty-year continuous time series on our *S. lewini* count data. We then ran GLMs (removing random effects to reduce computing time) on a random selection of 10%, 25%, 50%, 75%, and 90% of the data, repeating each process 1000 times. The difference in effect size and p-value (from Wald's z-test) between models with and without both SST and ONI was compared for each subset.

5.4 Results

Sphyrna lewini and *T. obesus* were the most frequently observed sharks, counted on 77.7% and 97.2% of dives, respectively, while *Carcharhinus limbatus* was much less frequently observed (Table 5.1). *Taeniurops meyeni* was the most frequently observed ray species, with *Mobula* spp. and *A. narinari* observed less frequently (Table 5.1).

Table 5.1 The frequency of occurrence (FO), mean count per dive when the species was seen, maximum count observed, and temperature preferences from the literature for each studied species, ordered by general mobility.

Species	FO	Mean count (excluding zeros)	Max. count	Literature temperature preference	Reference
Galeocerdo cuvier	6.2%	–	–	22, >30°C	Payne et al. 2018, Lear et al. 2019
Sphyrna lewini	77.7%	42.1	1000	23–26°C	Ketchum et al. 2014a
Carcharhinus limbatus	4.8%	–	–	25–33°C	Wiley and Simpfendorfer 2007, Froeschke et al. 2010
Triaenodon obesus	97.2%	24.2	500	>26°C	Nadon et al. 2012, Richards et al. 2012
Mobula spp.	9.0%	–	–	20–26°C	Couturier et al. 2012
Aetobatus narinari	22.7%	2.2	60	23–31°C	Bassos-Hull et al. 2014
Taeniurops meyeni	78.9%	8.5	100	?	

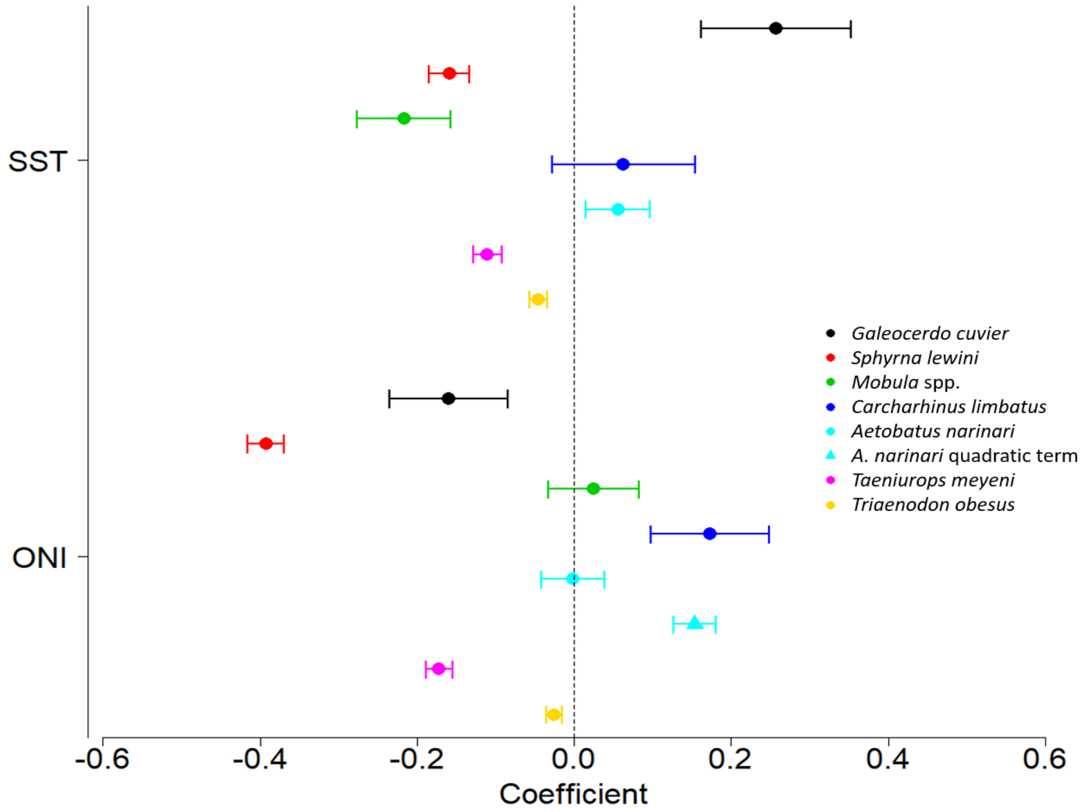

Figure 5.2 Coefficients and 95% confidence intervals for sea surface temperature (SST) and Oceanic Niño Index (ONI) terms from the generalized linear mixed models for each species ordered by mobility. The models for *Aetobatus narinari* had a quadratic term for ONI.

Sea surface temperature varied from 24.6°C to 31.4°C, with a mean of 27.8°C, while ONI varied from -1.70 to 2.64 with a mean of -0.023. Both SST and El Niño strength affected the observations of the four shark species, albeit in different ways for each, and SST was not significant for *C. limbatus* (Figures 5.2, 5.3, Table D1). *Sphyrna lewini* responded the strongest, with predicted counts declining by 14.7% with an increase from 27.8°C (mean SST over all dives) to 28.8°C (one SD above mean SST) and by 52.8% with an increase from 25°C to 30°C. Additionally, *S. lewini* predicted counts were 48.1% higher during moderate La Niña (ONI = 1) and 32.5% lower during moderate El Niño conditions compared to when each event was absent

(ONI = 0) (Figure 5.3b). Predicted counts were also 224.7% higher during strong La Niña (ONI < - 1.5) compared to strong El Niño (ONI > 1.5) conditions. In contrast, *T. obesus* declined only by 4.4% when SST increased by one standard deviation above the mean and by 19.3% when SST increased from 25°C to 30°C. Similarly, *T. obesus* predicted counts were only 7.9% higher during a strong La Niña compared to a strong El Niño, and they increased by only 2.5% during a moderate La Niña and decreased by only 2.5% during a moderate El Niño (Figure 5.3d). In contrast to all other sharks, the probability of observing *C. limbatus* was not significantly affected by SST and it shrank by 15.7% during moderate La Niña and grew by 18.6% during moderate El Niño conditions compared to when the ONI was weaker (Figure 5.3c). It was also 40.1% higher during strong El Niño compared to strong La Niña conditions. Observations of *G. cuvier* had the opposite trend to SST compared to all other sharks, being 29.0% more likely one standard deviation above the mean and 234.1% more likely at 30°C than at 25°C. However, like most of the other shark species, the probability of observing *G. cuvier* rose during La Niña conditions, by 17.2% during moderate La Niña conditions compared to weaker ENSO conditions and by 61.1% during strong La Niña compared to strong El Niño conditions (Figure 5.3a). Its probability of occurrence also declined by 14.7% during moderate El Niño conditions.

The probability of observing *S. lewini* schools (>50 individuals) also declined significantly with increasing SST and ONI (Table D1). Schooling was 19.8% more likely at the mean SST than even one standard deviation above it, and it was 64.5% more likely at 25°C than at 30°C. When the ONI value was indicative of a moderate El Niño, the predicted probability of observing a hammerhead school dropped by 38.2% compared to weaker conditions, but it increased by 60.6% when the ONI indicated moderate La Niña conditions. Schooling was also 317.9% more likely during strong La Niña conditions than during strong El Niño conditions.

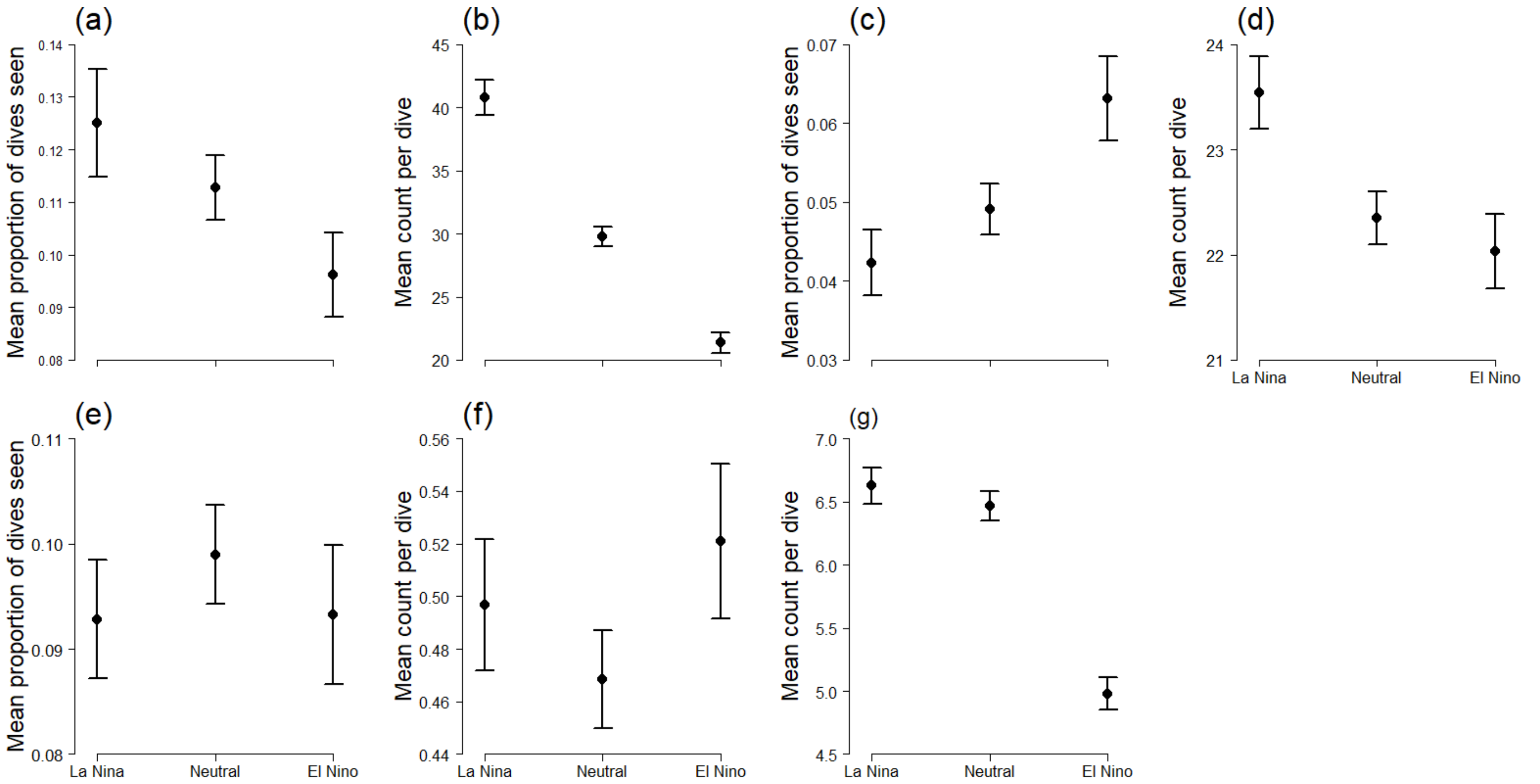

Figure 5.3 The mean count (or mean proportion) of each species observed per dive. (a) tiger shark *Galeocerdo cuvier*, (b) scalloped hammerhead shark *Sphyrna lewini*, (c) blacktip shark *Carcharhinus limbatus*, (d) whitetip reef shark *Triaenodon obesus*, (e) *Mobula* spp., (f) spotted eagle rays *Aetobatus narinari*, and (g) marble rays *Taeniurops meyeni* observed when the ONI indicated an ENSO event was present (> 0.5 for El Niño, < - 0.5 for La Niña) or absent (-0.5 < ONI < 0.5). Means were calculated accounting for the interannual trend, with the 95% confidence intervals (error bars) calculated using the year for which the yearly mean per species was most precisely estimated.

All rays were also significantly affected by SST, but ONI only affected the counts of *T. meyeni* and *A. narinari* (Figures 5.2, 5.3, Table D1). The probability of spotting *Mobula* spp. decreased by 18.3% as SST increased from 27.8°C to 28.8°C and by 60.9% as SST increased from 25°C to 30°C. The predicted counts of *T. mayeni* also declined, by 10.4% and 40.6% over the same respective ranges. As ONI shifted from 0 to a moderate La Niña or moderate El Niño, predicted counts of *T. meyeni* increased by 18.8% or declined by 15.8%, respectively (Figure 5.3g). Its predicted counts were also 67.5% higher during strong La Niña compared to strong El Niño conditions. In contrast, the predicted counts of *A. narinari* grew with increasing SST, by 5.7% from 27.8°C to 28.8°C and 30.2% from 25°C to 30°C. The counts of *A. narinari* had a significant quadratic relationship to ONI (Figure 5.2, Table D1); predicted counts were higher during both La Niña and El Niño conditions compared to years with weaker ONI values (Figure 5.3f).

Declines continued for all species since the analysis of data up to 2013 by White et al. (2015) (Figure 5.4, Table D2). However, the increases observed by White et al. (2015) for both *C. limbatus* and *G. cuvier* have since reversed (Figure 5.4a,c, Table D2). Overall, *C. limbatus* has shown no net change over the 27-year time series and the increase of the *G. cuvier* population has declined to 33% per year from 79% per year. Additionally, the declines of *A. narinari* have grown increasingly severe: from a 34% decline to a 93% decline (Table D2).

Removing both SST and ONI as explanatory variables only affected the year coefficient for *S. lewini*, reducing its effect size (Table 5.2). For *S. lewini*, year coefficients estimated from subsets of continuous five-year time series had the greatest differences from those estimated using the entire data set, but including SST and ONI as explanatory variables was irrelevant to the detected trend (Figure 5.5a). However, modelling the explicit effect of SST and ONI drew estimates closer to those from the full data set when continuous time series of ten or more years were subsetted from the data (Figure 5.5b-d). Ultimately, regardless of time series length, starting the time series during the strong La Niña of 1998 biased estimation, increasing the magnitude of estimated declines. Independent of time series length, sample size did not influence the trend estimate, as including ONI reduced the year coefficient of each GLM from a mean of -0.049 to a mean of -0.036 regardless of sample size. Power was neither affected by time series length nor sample size; all year coefficients for *S. lewini* were highly significant ($p<0.001$).

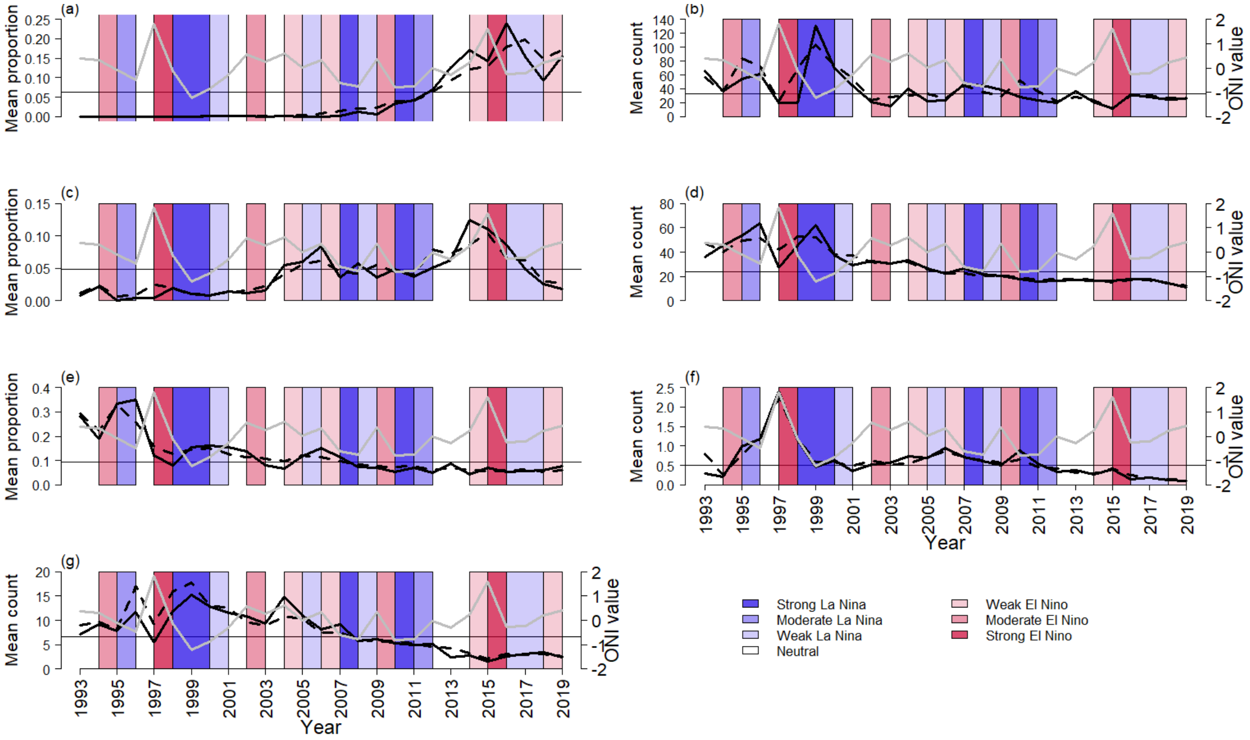

Figure 5.4 The mean (solid black line) count or frequency of occurrence, mean (dotted black line) predicted value from a GLMM, and mean ONI value (solid grey line) by year for each species. Solid black line is the mean over all years. (a) tiger shark *Galeocerdo cuvier*, (b) scalloped hammerhead shark *Sphyrna lewini*, (c) blacktip shark *Carcharhinus limbatus*, (d) whitetip reef shark *Triaenodon obesus*, (e) *Mobula* spp., (f) spotted eagle rays *Aetobatus narinari*, and (g) marble rays *Taeniurops meyeni*.

Table 5.2 The year coefficient from GLMMs without SST and ONI and with SST and ONI included in as predictors for each species. The 95% confidence intervals are in brackets.

Species	No SST and ONI	SST and ONI
Galeocerdo cuvier	0.28 (0.26 – 0.30)	0.28 (0.26 – 0.31)
Sphyrna lewini	-0.047 (-0.053 – -0.041)	-0.025 (-0.031 – -0.018)
Carcharhinus limbatus	0.0094 (-0.01 – 0.031)	0.00033 (-0.022 – 0.023)
Triaenodon obesus	-0.041 (-0.044 – -0.038)	-0.038 (-0.041 – -0.035)
Mobula spp.	-0.054 (-0.066 – -0.042)	-0.048 (-0.060 – -0.036)
Aetobatus narinari	-0.10 (-0.12 – -0.092)	-0.10 (-0.11 – -0.088)
Taeniura meyeni	-0.090 (-0.095 – -0.085)	-0.078 (-0.083 – -0.073)

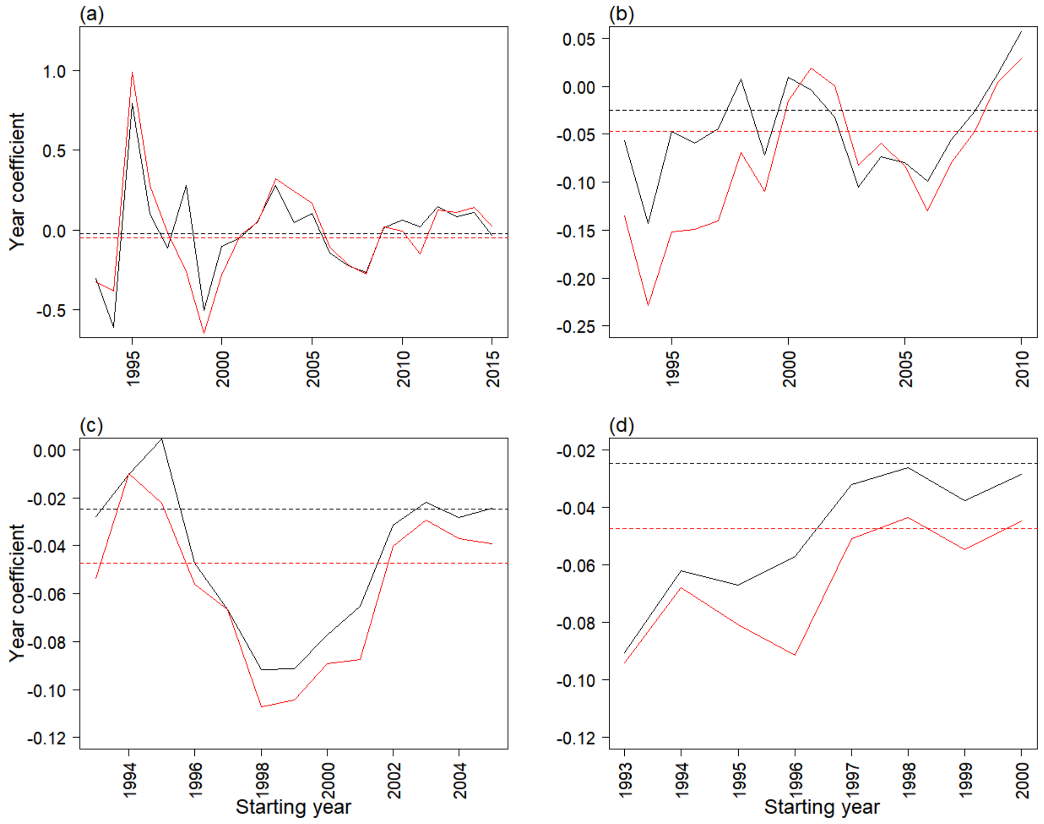

Figure 5.5 The coefficient for year for negative binomial GLMMs on *Sphyrna lewini* abundance at Cocos for all possible (a) five year, (b) ten year, (c) fifteen year, and (d) twenty year time series based on starting year. Black represents coefficients from models with ONI and SST and red coefficients from models without ONI or SST. The horizonal dotted lines represent the year coefficients from models run on all the data.

5.5 Discussion

Sea surface temperature and the ENSO both had large impacts on elasmobranch abundance at Cocos Island and, as predicted, the severity of this impact varied by species. The more mobile species—*S. lewini, G. cuvier,* and the *Mobula* rays—had the strongest response to SST, while the less mobile *T. obesus* had the weakest. The benthic ray *T. meyeni* also had a smaller response to SST compared to *Mobula* rays, but it was higher than the response of *A. narinari, T. obesus* or *C. limbatus* despite the higher mobility of these species. *Taeniurops meyeni* also had a strong response to the ENSO, although the strongest effects were again by the more mobile species, save for *Mobula* rays, which did not respond. Drastic changes in local abundance with even a few degrees change in temperature, reflective of shifts in location and depth to avoid untenably high oxygen consumption and decreases in aerobic scope, have occurred for other coral reef fish species as well (Nilsson et al. 2010, Magel et al. 2020), and our results suggest large changes in community structure can be expected at Cocos, if not other parts of the Pacific, with the rise in global SST expected under current carbon dioxide emission scenarios (Collins et al. 2013; Kirtman et al. 2013).

A decline in abundance with rising SST—the general pattern we observed—is expected for ectothermic fish given that metabolic performance declines faster with increases above the thermal optimum than with similar decreases below it (Martin and Huey 2008). Since these elasmobranchs likely have thermal optima near their upper thermal limit—tropical waters have SSTs near the limit of most elasmobranch species (Bernal et al. 2012)—even small increases in SST would impair physiological functions—an untenable situation for species needing peak performance to hunt in tropical ecosystems. Thus, these species should move both horizontally and vertically in the water column for thermoregulation (McMahon and Hays 2006, Andrzejaczek et al. 2018), thereby decreasing their sightings at the accessible dive sites with rising SST.

Similarly, the general decline in relative abundance and occurrence observed during El Niño conditions, and conversely, the increase in abundance during La Niña conditions, was expected given the rise in primary and secondary productivity during La Niña events in the Eastern Tropical Pacific (Lavín et al. 2006, Pennington et al. 2006). In contrast, even weak El Niño events reduce chlorophyll-a concentrations, phytoplankton size, and zooplankton biomass as the thermocline deepens and nutrient poor water is advected (Sanchez et al. 2000, Ambriz-Arreola et al. 2018, Conde et al. 2018, Coria-Monter et al. 2019). Since prey availability is one of the most important determinants of elasmobranch habitat selection (Hearn et al. 2010, Couturier et al. 2012, Ketchum et al. 2014b), the elasmobranchs at Cocos are likely shifting their horizontal and vertical distribution to track spatial changes in productivity associated with both positive and negative phases of the ENSO (Fiedler 2002, Lavín et al. 2006).

Although the trends associated with temperature and the ENSO likely reflect distributional change rather than real population decline, the decadal declines continued for most species and the previously observed increases of *C. limbatus* and *G. cuvier* have since dampened (White et al. 2015). Since 2015 both these species have started declining, although continued monitoring is required to assess if these declines are real or if they represent natural variability or population movement. Ongoing fisheries exploitation likely affects the elasmobranch community at Cocos, especially the larger and more pelagic *S. lewini*, *G. cuvier,* and *C. limbatus*, which are more likely to be caught in the pelagic longlines dominating the region’s fishing (Friedlander et al. 2012, Arias et al. 2016). A climate change-induced gradual rise in SST and ENSO strength during the time series may have contributed to these declines by forcing permanent distributional shifts or reducing the fitness of the less mobile species. For instance, *Triaenodon obesus* exhibited large declines despite its lower mobility and less catchability in longlines, and so the small negative effects of SST may have impacted its population fitness. However, the sharp declines in *A. narinari* relative abundance, and its positive relationship to SST, suggest fishing could be impacting their populations despite a generally high residency and site fidelity (Ajemian & Powers, 2014). Ultimately, more fisheries data from across the Eastern Tropical Pacific is needed to assess how much of these trends are due to distributional shifts versus real population declines, and how much climate change will influence fisheries exploitation through changing interactions with MPAs (Bruno et al., 2018).

5.5.1 Interspecific variability in response to SST and ENSO

Differences in size and mobility should create variation around these general patterns by influencing physiological tolerance to temperature changes, energetic requirements, and the ability for behavioural thermoregulation and migration (Bernal et al. 2012, Papastamatiou et al. 2013, Lea et al. 2018). Both *S. lewini* and *G. cuvier* are large, active hunters that make regular diel and annual migrations for foraging, occasionally over large spatial scales (Heithaus et al. 2007, Bessudo et al. 2011, Ketchum et al. 2014b, 2014a, Acuña-Marrero et al. 2017), and *G. cuvier* maintains home ranges on the order of 1000s of square kilometers (Holland et al. 1999, Meyer et al. 2009a, Ferreira et al. 2015). Both sharks had some of the strongest responses to SST and the ENSO among our studied species. Similarly, *Mobula* rays had the strongest negative response to SST and share with *S. lewini* and *G. cuvier* a pelagic, obligate ram-ventilating lifestyle. For instance, the giant manta *M. birostris*, which is common at Cocos, occupies large home ranges and can migrate over 1000s of kilometers in a few months (Croll et al. 2012, Hearn et al. 2014). This pelagic lifestyle requires both high standard and maximum metabolic rates that are easily pushed past physiological upper limits, with even a few degrees of warming rapidly reducing aerobic scope for activies like foraging, reproduction, and growth (Martin and Huey 2008, Killen et al. 2010, Bernal et al. 2012). Since these elasmobranchs ram ventilate, and thus acquire oxygen through active movement, oxygen demand at high temperatures can become impossible to meet through modulation of swim speed (Pörtner and Knust 2007, Jacoby et al. 2015). While little is known about the metabolism or thermal physiology of *Mobula* rays, *S. lewini* has one of the highest known metabolic rates among elasmobranchs—higher than even some endothermic sharks—and needs to consume large rations relative to body weight (Lowe 2001, 2002, Duncan 2006). Similarly, *G. cuvier* closely tracks changes in thermal habitat to maintain tight control on body temperature and optimize swimming performance (Meyer et al. 2009a, Payne et al. 2018). Additionally, the hammerhead sharks at Cocos are likely mostly female, at least during some parts of the year due to sexual segregation in habitat related to different energetic needs between the sexes (Klimley 1987, Sibaja-Cordero 2008, Nalesso et al. 2019); female sharks generally maintain higher metabolic rates due to the energetic demands of reproductive functions, and therefore can be more sensitive to changes in temperature (Schlaff et al. 2014). *Mobula* rays do have cranial rete mirabilia, implying some endothermic capacity that would raise their metabolic rates and tolerance to lower temperatures, but no work has solidified how their thermal preferences are affected by these heat exchangers (Alexander 1996).

As expected, sightings of both *S. lewini* and *Mobula* rays declined with rises in SST, but, in contrast, the occurrence of *G. cuvier* increased despite their similar mobility. The thermal preference of the former two species is in the lower range of what was encountered at Cocos (Couturier et al. 2012, Croll et al. 2012, Ketchum et al. 2014a) and so corroborates the negative relationship we observed between *S. lewini* and *Mobula* rays and SST. The optimal temperature of *G. cuvier* is over 30°C in the Gulf of Mexico (Lear et al. 2019), reflecting the response at Cocos, but does vary by location, being closer to 22°C in Hawaii (Payne et al. 2018), possibly through acclimatization or adaptation. Thus, *G. cuvier* thermal tolerance seems adaptable and broad on a global level (Ferreira et al. 2015), possibly related to its large size. *Galeocerdo cuvier* is one of the largest shark species, and such a large body size would reduce its mass-specific metabolic rate, raise its thermal inertia, and let it achieve more efficient lift and momentum while swimming (Iosilevskii and Papastamatiou 2016, Killen et al. 2010, Ryan et al. 2015). By reducing its energetic cost of movement, the size of *G. cuvier* could relax its thermal constraints. The strong response of *G. cuvier* to SST in our study suggests most of the sharks at Cocos are large, since temperature sensitivity and mobility are highly size dependent in the species (Lea et al. 2018). Additionally, *G. cuvier* differs ecologically from *S. lewini* and *Mobula* rays, not schooling nor filter feeding, which could affect how it uses habitat on the Island.

The size and mobility of *S. lewini* and *G. cuvier*, and their need for high consumption rates to meet their energetic requirements, also likely explain why counts of both species increased during strong La Niña conditions—over 2-fold for *S. lewini*. Both species likely shifted distributions in response to changing distributions of their prey and long-term changes in SST (Lavín et al. 2006, Chapman et al. 2012, Lea et al. 2018). Prey availability is one of the most important determinants of habitat selection for each of *S. lewini* (Hearn et al. 2010, Ketchum et al. 2014b, 2014a), *G. cuvier* (Wirsing et al. 2007, Acuña-Marrero et al. 2017, Lea et al. 2018), and *Mobula* spp. (Luiz et al. 2009, Croll et al. 2012, Hacohen-Domené et al. 2017). In fact, in Brazil, productivity had the strongest influence on *M. tarapacana* abundance, another of the Cocos *Mobula* rays, while SST had no effect (Mendonça et al. 2018). Yet, the occurrence of mobile *Mobula* rays changed little during ENSO events at Cocos even though the El Niño alters the distribution of their mesopelagic zooplankton and larval fish prey (Sánchez-Velasco et al. 2017, Kozak et al. 2018). *Mobula* rays may be responding to shifts in prey availability by changing diving behaviour rather than latitudinal distribution (Thorrold et al. 2014, Stewart et al. 2016b), and even large *M. birostris* are spatially restricted in their movements; populations in the Indo-Pacific and Mexico have high site-fidelity, and possibly also high residency, with no long-distance migratory movements observed over multiple years, which suggests that these species do not migrate as much as their pelagic lifestyle would imply (Graham et al. 2012, Stewart et al. 2016a). Ultimately, the absence of *Mobula* aggregations at Cocos suggests that the lack of an ENSO response at the Island stems from it serving more as a migration stopover and cleaning station than foraging habitat (Mejía-Falla et al. 2014). However, new sightings of *M. birostris* at cleaning stations in Raja Ampat associated with El Niño events suggest that our lack of significance lies in a lack of importance of Cocos for their ecology or their rarity from their recent and ongoing populations declines (White et al. 2015, Beale et al. 2019).

These changes in abundance for the mobile species likely reflect both vertical and horizontal changes in distribution. Both *S. lewini* and *G. cuvier* use depth to thermoregulate (Ketchum et al. 2014a, Payne et al. 2018), and at the El Bajo Espiritu Santo Seamount in the Gulf of California, *S. lewini* abundance at 30 m increased with temperature while abundance at the surface decreased with temperature (Jorgensen et al. 2016). However, *S. lewini* does make long distance movements to other islands within the Galapagos and Eastern Tropical Pacific, up to 1186 km during warmer seasons (Ketchum et al. 2014b), and their appearance off California during the 1997-1998 El Niño suggests that at least some latitudinal shifts occur (Lea and Rosenblatt 2000).

Contrasting with most of the other elasmobranchs we examined, *C. limbatus* and *A. narinari*, both showed increases with SST and El Niño conditions; in fact, *A. narinari* counts were highest during ENSO events, regardless of whether it was a La Niña or El Niño. Both *C. limbatus* and *A. narinari* are generally smaller and more resident species than the larger sharks and rays, with smaller home ranges and movements typically restrained to local reefs or sandflats (Ajemian and Powers 2014, Bassos-Hull et al. 2014, Yates et al. 2016). *Carcharhinus limbatus* does make occasional long-distance migrations (Yates et al. 2016) and has a relatively high metabolic rate and swimming speed compared to benthic species, which suggest both sensitivity to temperature changes and an ability to respond (Bernal et al. 2012, Lear et al. 2017). In fact, *C. limbatus* generally avoids cooler water, preferring temperatures between 25–33°C (Wiley and Simpfendorfer 2007, Froeschke et al. 2010, Bangley et al. 2018), including in the Galapagos (Llerena-Martillo et al. 2018). Cooler temperatures likely impair the metabolic rate it needs for an active lifestyle, while its generally lower activity compared to other ram ventilating species may explain its lower sensitivity to higher SSTs. However, at Cocos, the positive effect of SST on its occurrence was weak, although its lack of significance was likely due to the rarity of *C. limbatus* observations. *Aetobatus narinari* also prefers higher temperatures (Bassos-Hull et al. 2014), the common trend for small myliobatid rays (Matern et al. 2000, Yamaguchi et al. 2005, Ajemian and Powers 2014), reflecting the increased ability and drive to hunt when warmer (Matern et al. 2000, Pistevos et al. 2015).

Both *C. limbatus* and *A. narinari* track shifts in prey availability like the larger sharks and mobulid rays (Heupel and Hueter 2002, Ajemian et al. 2012, Drymon et al. 2013), yet both showed increases at Cocos during the El Niño. The mollusk prey of *A. narinari* may benefit from changing currents and warmer temperatures during El Niño events (Tarazona et al. 1996, Montagne and Cadien 2001), and *A. narinari* may also be shifting to avoid predation by large sharks (Heithaus et al. 2008, Bond et al. 2019), although *T. meyeni*, similar ecologically, responded oppositely. Research on *A. narinari* in the Pacific is lacking so these explanations are difficult to disentangle. Research is also scarce for *C. limbatus*, but since it is not as common at Cocos as other elasmobranchs, perhaps its increase during El Niño conditions represents a latitudinal shift from hotspots elsewhere in the Pacific as it tracks preferred temperatures or reduced competition from the larger sharks. More research is needed on the thermal preference of both species, particularly adult *C. limbatus* in oceanic habitat, and on changes to fish and invertebrate communities at Cocos during ENSO events, to draw definite conclusions on how temperature and the ENSO affect the physiology and migration of these two species.

In contrast to all other sharks at Cocos, *T. obseus* is relatively small and inactive, spending approximately 30% of its time resting while ventilating through buccal pumping (Whitney et al. 2007, Barnett et al. 2012). Although long-range dispersal does happen on occasion, *T. obesus* spends most of its life resident within a few kilometers of specific aggregation sites, including at Cocos, reflecting its reduced mobility and activity rate (Barnett et al. 2012, Whitney et al. 2012a, Zanella et al. 2012). These traits would lower the metabolic rate of *T. obesus* while increasing its metabolic cost of activity, limiting both the ability and need for *T. obesus* to shift habitats in response to thermal changes (Whitney et al. 2007, 2016). Abundance on other Pacific reefs also did not vary greatly with temperature (Nadon et al. 2012, Mejía-Falla et al. 2014). As expected, *T. obesus* counts also barely changed in response to the ENSO, reflecting its poorer ability to disperse (Barnett et al. 2012, Whitney et al. 2012a).

Although having the weakest response to SST besides *T. obesus*, the benthic—and much less mobile—ray *T. meyeni* responded to the ENSO surprisingly similarly to *G. cuvier*. Its strong negative response to the ENSO is puzzling, since it shares a similar niche to *A. narinari*, but perhaps is potentially tracking long-term cycles in temperature during the ENSO. Despite a low metabolic rate compared to sharks, its stronger response to SST than *T. obesus* likely reflects the genus' narrow thermal niche, limited ability to acclimatize, and preference for cooler water (Chin et al. 2010, Dabruzzi et al. 2013).

5.5.2 Ecological implications of climate change

These varied environmental effects on the elasmobranchs at Cocos Island suggest climate change—through gradual rises in SST and more intense and frequent ENSO events—will have consequences for the ecology, conservation, and tourism of the MPA. Changing temperature regimes have altered migration patterns, including both timing and location, in many taxa (Sims et al. 2001, Juanes et al. 2004, Shaw 2016), and our results indicate similar effects will occur at Cocos Island. The MPA is an important landmark for sharks navigating from the islands of the Eastern Tropical Pacific to the coasts of Central and South American during seasonal migrations (Bessudo et al. 2011, Ketchum et al. 2014b, Nalesso et al. 2019). Our results suggest that changes in temperature and productivity associated with climate change could alter these migration patterns and weaken the connectivity these elasmobranchs provide to the ecosystems of the eastern Pacific by reducing the suitability of Cocos, and likely other nearby islands, as stopover during these migrations (Bauer and Hoye 2014). Thus, beyond affecting the behaviour of individual species, rising temperatures and the intensification of El Niño events complicate the conservation of migration as a phenomenon, limiting the ecological connectivity it provides to these islands (Wilcove and Wikelski 2008).

As climate change and El Niño events alter thermal habitat, ocean currents, and primary productivity in the region, range expansions and distributional shifts are likely for most of these elasmobranchs, even for species considered less mobile. In fact, El Niño events, by expanding thermal habitat and changing currents serving as barriers to dispersal, are likely causes of recent range expansions of *T. obesus* into Rapa Nui in Chile and the Raoul and Meyer Islands, Kermadec Islands of New Zealand (Duffy et al. 2017, Morales et al. 2019). A high biomass of predators dominate the current marine community at Cocos (Fourriére et al. 2019), and so climate change has the potential to radically alter the ecological dynamics within the MPA as larger species re-distribute faster than smaller ones (Perry et al. 2005). These distributional changes will reduce overlap between these predators and their prey (Sadykova et al. 2020), further altering ecological relationships and community structure at the Island by reducing predation pressure on the smaller, less mobile species while potentially stressing larger predators to search for new prey and to travel longer distances between foraging grounds and other key habitats like cleaning stations (Péron et al. 2012).

In our own time series, the highly migratory and mobile *G. cuvier* exhibited a range expansion potentially associated with the La Niña events in 2005/2006 and 2007/2008 that certainly would have altered the predation landscape at Cocos. Since *G. cuvier* has mostly increased at Cocos since its establishment in the early 2000s, the La Niña events may have afforded an opportunity, through reduced barriers to dispersal, to discover new foraging habitat. A similar expansion may have occurred for *C. limbatus* during the El Niño events of 2002–2005, explaining its increasing presence at the Island. However, the influence of the ENSO on *G. cuvier* and *C. limbatus* abundance and their potential range expansion at Cocos are merely hypotheses. More work is needed to understand the proximate and ultimate causes of migration and dispersal in these species if we are to precisely predict climate change's effects on their migration and understand the influence of the ENSO on their movement ecology (Shaw 2016).

5.5.3 Conservation implications of a changing climate for MPAs

Migrating, mobile species are considered generally adaptable to climate change (Robinson et al. 2009), but changing migration patterns and distributional shifts could also exacerbate fishing effects on their populations by reducing the time spent in current MPAs (Bruno et al. 2018). Illegal fishing already undermines the role of Cocos as a conservation refuge in the Eastern Tropical Pacific (Arias et al. 2016), exemplified by the ongoing and, in some cases, increasingly severe declines we observed for the elasmobranchs, but our results suggest climate change will further reduce its MPA functionality. The exposure these elasmobranchs face will depend on whether distributional shifts occur horizontally or vertically, but changes in *S. lewini* and *G. cuvier* counts likely reflect both types of movements (Ketchum et al. 2014b, 2014a, Lea et al. 2018, Payne et al. 2018). Marine protected areas like Cocos generally cover only small portions of shark home ranges (Graham et al. 2016, Yates et al. 2016). As such, climate change induced distributional changes will interact with fisheries exploitation to either exacerbate or ameliorate ongoing declines depending on how the species response to rises in SST changes how they interact with the MPA (Lea et al. 2018).

We lack the information for informed conservation for most species, and the strong species-environment relationships we identified suggest the knowledge we currently have will become less valid without detailed modelling of movement, temperature, and habitat changes with time. The species-specific effects of environmental change will make designing MPAs for these elasmobranchs a challenge, but we hope our work will motivate searches for generalities based on size and mobility that will help scientists adapt conservation plans and predict the conservation consequences of climate change. Marine protected area design will need to address the dynamic habitat associations and biotic relationships that occur for migratory species and their ever-changing range (Game et al. 2009, Hobday 2011). Modelling predicted changes to a species' habitat and distribution in response to environmental change can help MPAs remain effective longer (Hobday 2011). However, this will require more fundamental research on elasmobranch metabolism and temperature sensitivity, as most research currently focuses on Carcharhinidae and charismatic species (Bernal et al. 2012, Shiffman et al. 2020).

5.5.4 Citizen science implications

If shifting distributions and migration patterns are responsible for the effects we observed, climate change and ENSO intensification will have consequences for both citizen science and dive tourism at Cocos. Schools of *S. lewini*, an important draw for the dive industry at Cocos (Friedlander et al. 2012), declined in frequency with only a few degree changes in SST as well as during strong El Niño events, likely reflecting a shift in where schooling happens and in the role of Cocos as a foraging refuge for the species. Such changes in the location of "hotspots" of high abundance also threaten to mask real trends with distributional shifts (Fournier et al. 2019) and could reduce the reliability of dive tourism at Cocos. Citizen shark science relies on the popularity of shark diving for consistent data, but if diving hotspots change and effort is shifted among dive spots or islands, time series length and sampling intervals at particular sites will be reduced, hindering statistical power (White 2019). Climate change could also cause increased frequency and amplitude of swings in the ENSO cycle (Cai et al. 2014, Wang et al. 2017), heightening environmental variability in abundance data. Considering El

Niño events explicitly in modelling, as we did at Cocos, helps reduce uncertainty when studying citizen science data, although, contrary to our predictions, this improvement only happens for data sets long enough to infer accurate trends, regardless of total sample size. Explicitly modelling bias between dive guides and sites is also critical to improving precision in the estimates (Bird et al. 2014), but we cannot statistically account for long-term shifts in effort that climate change may bring to the Island.

5.5.5 Conclusion

Elasmobranchs respond strongly to both temperature and ENSO events, likely due to metabolic constraints and effects on prey availability. As both SST and ENSO events are predicted to intensify during the coming century, the local abundance of elasmobranchs will change within static MPAs in accordance to their thermal tolerance and capacity to move. We observed ongoing declines in the relative abundance of many species of elasmobranch at Cocos Island, although with species-specific differences. These declines, likely fisheries-induced, have the potential to interact with future environmental changes to drastically alter the elasmobranch community at Cocos and across the Eastern Tropical Pacific. This highlights the need to research the causes and consequences of species-environment relationships, and how they interact with fisheries impacts, especially in important marine corridors within MPAs like Cocos to predict the consequences of ongoing threats to marine communities and design effective conservation.

Chapter 6 – Discussion

Basic studies of chondrichthyan diversity are paramount to understanding their natural history, ecology, and conservation (Espinoza et al. 2014, Huveneers et al. 2015) to gain insight into the environmental drivers of diversity patterns (Espinoza et al. 2014, Yates et al. 2015) and how their worldwide declines will impact ecosystem functioning (Heithaus et al. 2008, Roff et al. 2016). Marine protected areas effectively conserve some chondrichthyan populations by protecting critical foraging or reproductive habitats from fishing and other anthropogenic impacts, and MPAs could help protect many others if knowledge of their habitat use and ecology was not lacking (White et al. 2017, Dwyer et al. 2020). Therefore, elucidating species-habitat associations is critical to planning and evaluating conservation measures (Yates et al. 2015, 2016, Lea et al. 2018). Despite the importance of chondrichthyans to both ecosystems and cultures worldwide, we lack knowledge of the basic biology and ecology of many species, and without such data informing their design and monitoring, MPAs will fail, especially in data-poor developing countries (Griffiths and Dos Santos 2012, Huveneers et al. 2015). This thesis first discusses knowledge gaps in chondrichthyan biological, ecological, and conservation research and then proceeds to fill some of those gaps, presenting case studies from MPAs in two developing countries using non-invasive techniques to survey chondrichthyan diversity, discovering important associations to habitat and their marine community that must be considered for these MPAs to succeed.

My second chapter revealed that considerable advances have been made in shark science this century, especially in the study of shark spatial ecology and movement. Even more advances in reef shark movement and population structure have occurred since the review was published in 2015 (e.g. Graham et al. 2016, White et al. 2017, Dwyer et al. 2020). In particular, crucial advances made in our understanding of Indo-Pacific population structure and life history traits for the silvertip shark *Carcharhinus albimaginatus,* which my review deemed understudied (Smart et al. 2017, Green et al. 2019). The abundance of many species had been studied through a variety of methods, from fishing surveys to baited remote underwater video (BRUVs) to mark-recapture (Dudgeon et al. 2008, Heupel et al. 2009, Bond et al. 2012). However, information useful to the update of IUCN status was still scarce for all but the three best studied reef shark species. Technological advances, such as the increasing use of stereo-BRUVs, since the review has enhanced our understanding of reef sharks by allowing more accurate and precise estimates of biomass and abundance (Kilfoil et al. 2017, Goetze et al. 2018), but focus has remained on the genus *Carcharhinus* despite the taxonomic and functional diversity of reef sharks I identified. It is unlikely knowledge of carcharhinids will carry over well to other species due to differences in behaviour and ecology. The review did not include coral reef rays and skates, but they likely suffer similar—if not larger—research gaps (Dulvy et al. 2017). Carcharhinid chondrichthyans may be charismatic and attract intensive research effort (Huveneers et al. 2015, Shiffman et al. 2020), but some of the most vulnerable chondrichthyan species in some of the most threatened places remain grossly understudied (Figures 2.3, 2.4). This is particularly true for large stretches of reefs in the Indo-Pacific, which need monitoring through a combination of techniques, incluidng BRUVs, to reduce the uncertainty surrounding their marine fish biodiversity (Figure 2.4), and for small benthic shark species like the catsharks of Hemiscylliidae and Scyliorhinidae (Figure 2.3).

In South Africa, an incredible diversity of chondrichthyan species exists, including an abundance of endemic catshark species (Figure 3.2). Endemic diversity in developing nations is poorly understood regardless of this general deficiency in studying catshark taxa, and my third chapter provided a first glimpse into the strong habitat associations of these species within and around two small South African MPAs (Figures 3.3, 3.4). Five catshark species were some of the numerically most dominant fishes in their ecosystem, likely serving important, albeit poorly understood, mesopredatory roles. In ecosystems impacted by fisheries exploitation, mesopredators often become the most abundant predators through trophic cascades (Prugh et al. 2009). Larger shark species were generally absent across all my sites, regardless of protection status, likely reflecting the intense fisheries in the region, although this is difficult to assess without historical baselines (Figure 3.2). Thus, the abundance of these mesopredators could be a mark of the long history of fisheries exploitation along South Africa’s coast (Attwood and Farquhar 1999, da Silva et al. 2015). The small MPAs of the region are ineffective for most larger sharks, however, letting their mesopredatory prey reach high abundance within the borders of both MPAs (Figure 3.3) (Heupel et al. 2014). A wider variety of sampling techniques, including other forms of BRUVs and fishing surveys, is required to quantify more precisely the abundance of more mobile shark species, especially for those species which are nocturnal. An accurate baseline of historical abundance is needed to draw definite conclusions about the effects of fisheries exploitation; although none currently exist, our work is a start.

My BRUV data revealed strong habitat associations, sharply dividing the South African chondrichthyan community even among the related catsharks (Figures 3.1, 3.5). Marine protected areas designated without consideration to these associations will be setup for failure with low diversity. The rush to proclaim MPAs is rising with recent scrambles to meet Aichi targets (Toonen et al. 2013, Jones and De Santo 2016), but knowledge gaps on what quality habitat means for different species and where it is located will hinder their effectiveness (Dulvy

2013, Briscoe et al. 2016). Fortunately, the smaller Betty's Bay MPA was established based on the quality of its habitat, albeit for commercially important fish and abalone species, and my BRUVs in and around that MPA showed some of the highest frequency of occurrence for chondrichthyans on BRUVs anywhere in the world outside of remote atolls. Thus, small MPAs do have conservation potential when enforced to protect habitat, even when minor fishing is allowed. However, the larger MPA designed to protect breeding southern right whales, and thus operating only seasonally, had poor quality habitat with a low diversity of associated species. Contrary to most theory on umbrella species (Zacharias and Roff 2001), we show large, migratory species are not always the best indicators of biodiversity.

My fourth chapter found the South African endemic catsharks have traits indicative of good umbrella species that could aid conservation planning in South Africa. Chondrichthyans had strong spatial relationships to other marine taxa (Figures 4.2, 4.3, 4.4), and with diverse habitat preferences would serve as indicators of diversity for the variety of ecosystems found along South Africa's coast. The endemic catsharks had strong connections to teleost fishes, cephalopods, and crustaceans (Figures 4.4, 4.5). The catsharks also had high connectance within their ecological networks, and, in particular, the puffadder catshark *Haploblepharus edwardsii*—a threatened species itself—distinguished sites of high diversity. Thus, South African MPAs could use catsharks, which are easy to catch and locate, as indicators to maximize the abundance and diversity of threatened and commercially important taxa using limited resources. Chondrichthyes also contains many charismatic species, and thus, chondrichthyans would idealy serve as both flagship and umbrella species (Caro 2010, Kalinkat et al. 2017). Charismatic species can serve as flagships for the conservation of more threatened taxa if the marketing of required conservation action is informed by social research (MacDonald et al. 2017). Therefore more research on the cultural relevance of chondrichthyans is needed, especially understanding how the charisma of Chondrichthyes' more publically appealing members could extend to other species, like catsharks, to generate public support for South African conservation both locally and globally (Bowen-Jones and Entwistle 2002, Jepson and Barua 2015). The conclusions would also benefit from detailed species-environmental modelling, relating catshark abundance to various fine-scale environmental variables like habitat complexity and mean temperature.

Finally, in my fifth chapter I found evidence of species-specific relationships between sightings of seven chondrichthyans and temperature and the El Niño–Southern Oscillation (ENSO) within the Cocos Island MPA off Costa Rica. The occurrence of mobile sharks and rays responded strongly to environmental change, with just a few degrees rise in SST drastically altering their relative abundance at the seamount, likely through shifts in distribution vertically and horizontally in the water column. The ENSO, an intensification of which can be expected under climate change (Cai et al. 2014), reduced the occurrence of most species during El Niño events while La Niña events likely optimized thermal habitat and productivity for most species within the MPA. In particular, *Sphyrna lewini* showed drastic declines with rising SST and intense El Niño events, suggesting changes to their ecology in the Eastern Tropical Pacific should SST rise and the ENSO cycles grow in frequency and intensity. Surprisingly, the marbled ray *Taeniurops meyeni* also showed strong responses to both SST and the ENSO despite its lower mobility. This species is not well studied in the ecological literature, but must have similar metabolic demands as sharks, driving an imperative to move with a changing environment. Surprises like this—holding keys to general patterns—await those who study fundamental aspects of the ecology and biology of the less charismatic species. The effectiveness of Cocos' MPA, already weakened by illegal fishing (Arias et al. 2016), is poised to grow weaker with climate change (Bruno et al. 2018), as is the thriving dive industry at the island—SST and the ENSO had the largest impacts on the most sharks most popular with divers.

6.1 Caveats and limitations

Despite a high sampling effort in both South Africa and Cocos Island—the latter with over 30 000 observations over 27 years—statistical analyses of both data sets were limited by the nature of our non-invasive techniques. Baited remote underwater videos are sensitive to variation in visibility, light, and undetected changes to currents that can alter bait plume size and direction (Taylor et al. 2013, Whitmarsh et al. 2016, 2019). Measuring current will be critical for future BRUV monitoring projects to produce more accurate estimates of temporal variability in community structure (Taylor et al. 2013). The use of MaxN as a relative abundance measure is also overly conservative, underestimating abundance at high densities due to saturation of the screen and the camera's restricted field of view (Kilfoil et al. 2017). In areas with more localized abundance than I observed in South Africa, counting the total number of times an animal enters the screen is less conservative, but at the risk of extreme overestimates. Spherical cameras can help researchers track fish movement around the bait by expanding the field of view, but they also incur greater financial costs and effort to deploy and analyze (Kilfoil et al. 2017). Using unique patterns to identify individuals is also an effective alternative to MaxN, but only when such identifying patterns exist (Sherman et al. 2018). We only used benthic BRUVs, limiting our ability to detect larger pelagic species. However, pelagic BRUVs, which suspend cameras in the water column, are becoming increasingly popular to monitor pelagic species, and combining them with benthic BRUVs should be the next step in monitoring MPAs, including in South Africa (Clarke et al. 2019). Additionally, we could only draw conclusions about species identity, but given the importance of body size in structuring marine food webs and habitat use patterns

(Trebilco et al. 2013, Lea et al. 2018), stereo-BRUVs—the use of two cameras to estimate fish size—are critical next steps to disentangle how size-selective fishing has affected local food webs and how MPAs may impact the habitat for different size-classes and life history stages (Santana-Garcon et al. 2014, Harasti et al. 2016). Stereo-BRUVs also have the potential to measure swim speeds, and thus relative activity levels, across a range of species in the field, letting researchers answer both fundamental and applied questions on shark ecology simultaneously and at a relatively low cost (Ryan et al. 2015). Utlimately, combining BRUVs with methods with different selectivity, for instance methods that can sample at night, will provide the best overall picture of diversity in an area.

Citizen science is also controversial: when legions from the public collect data, issues of data reliability, consistency, and bias arise (Bird et al. 2014, Bonney et al. 2014). Generalized linear mixed models—as used in chapter 5—contend with most variability introduced by multiple observers of varying skill (Bird et al. 2014, Kosmala et al. 2016). Additionally, I only used a small number of experienced dive masters, not thousands of volunteers of varying skill-level, which reduced my identification issues. Given sharks and rays are popular species to locate and identify, and are easily distinguishable with repeated experience, these dive masters likely had identification expertise as skilled as many shark scientists. However, the dive masters were not formally trained scientists, and thus effort was not consistent nor reliably recorded, and abundance was not precisely estimated when high, common issues for citizen science data (Dickinson et al. 2010). Additionally, citizen scientists have biases toward populated hotspots of abundance or diversity and do not collect data outside popular dives sites like protected areas (Tulloch et al. 2013, Lin et al. 2015), and such site selection bias could create spurious long-term trends (Fournier et al. 2019). Regardless, the long-term datasets afforded by citizen science cannot be ignored, especially when one of the main limitations to effective conservation is a lack of data (Dissanayake et al. 2019, Gouraguine et al. 2019).

6.2 Future directions

My research underscores the need for more fundamental research in the field of shark science. The mechanistic underpinnings of habitat use, the basics of metabolic and physiological variation across taxonomic groups, and the natural history of predator-prey interactions are lacking for most major orders and families (Huveneers et al. 2015, Shiffman et al. 2020). Fundamental research will not only make shark science more predictive, but it will help conservation in data-poor situations learn from more data-rich contexts (Bland et al. 2015). Species distribution modelling—trained using detailed knowledge of species-environment relationships—allows for better predictions of habitat use across broad geographic ranges (Sequeira et al. 2012, Phillips et al. 2017), which aids MPA planning (Sundblad et al. 2011), and helps us evaluate chondrichthyans as umbrella species (Ozaki et al. 2006). Most recent pushes in research have continued to focus on local habitat use; although much needed, shark science needs greater coupling between local patterns and mechanistic theory applicable across systems.

Climate change is a burgeoning threat for many marine taxa and compels fundamental research on species-habitat associations. Although fisheries exploitation and habitat destruction remain the largest threats for most chondrichthyans, climate change, by increasing temporal and spatial variability in preferred habitat, will invalidate many of the management measures used to guard against these threats today. For instance, current MPAs may soon be protecting the wrong habitat as marine envrionments continue to change (Hobday 2011). Dynamic marine protected areas, shifting in space over time, can increase protection over time when spatial habitat use varies across years due to fluxes in environmental variables like temperature (Game et al. 2009), assuming these dynamic habitat associations are modelled, understood, and predictable (Hobday and Hartmann 2006, Hobday 2011). Static MPAs are appropriate for key habitats, such as seamounts, but if climate change alters the use of these habitats with time, it is unclear how management should adapt; a combination of tactics will likely be needed (Hobday 2011).

The most severe hindrance to successful chondrichthyan conservation, in MPAs or otherwise, is a lack of research on the social dimensions of conservation initiatives and the potential for co-management from both local and national stakeholders (Oldekop et al. 2016, MacKeracher et al. 2018). The study of MPA size must consider the social consequences of larger MPAs compared to smaller ones and the potential of stakeholder engagement in both. To deploy our BRUVs, we worked with the local fishing community of the Kodelberg area around Betty's Bay in South Africa and saw firsthand the benefits of engaging with the local fishing community to share passions for science and promote compliance. Conservation efforts will fail if they create feelings of disenfranchisement within local communities and continue to ignore issues of poverty and food security, as legislation will appear illegitimate and increase social conflict (Isaacs 2006, De Santo 2013, Bennett and Dearden 2014). This is particularly the case in post-apartheid South Africa (Sowman et al. 2011). It is imperative that developing countries develop a "sustainable coastal livelihoods approach" (Glavovic 2006) including community engagement and social and economic perspectives into its tradition of managing from centralized, natural science-based perspectives (Sowman and Sunde 2018). The use of a network of small MPAs is one solution to facilitate community support and participation in enforcement (Aswani and Hamilton 2004, Mills et al. 2010, De Santo 2013), as well as promoting the local-scale management that works most effectively with localized populations, such as most of the endemic chondrichthyans of South Africa (Prince 2003). Ultimately, more work is needed on the social impacts of MPAs and how they affect local economies (Mascia and Claus 2009).

The strongest imperative for shark scientists is the need to start and maintain monitoring of chondrichthyan populations around the world. If I continue in chondrichthyan science and conservation, I would work to increase monitoring and research in Canadian chondrichthyan species, particularly on the west coast. Baited remote underwater video programs could help survey and monitor Canadian marine biodiversity and better understand the distributions and habitat use of that diversity. More data on Canadian chondrichthyans would help assess their conservation status and inform management, including MPAs. Canada was recently identified as a priority area to conserve marine biodiversity, potentially within MPAs, because of its unique biodiversity (Zhao et al. 2020). However, without data on chondrichthyan abundance, diversity, and ecology within Canada, prioritizing management around this component of Canadian biodiversity will be impossible.

Marine protected areas are an effective solution to certain problems and for some species, but the incredible diversity of chondrichthyans necessitates integration of diverse management efforts, each incurring different benefits and costs (Hilborn et al. 2004, Agardy et al. 2011, MacKeracher et al. 2018). However, management efforts cannot be tailored and tested for specific contexts without knowledge of spatial and temporal patterns of chondrichthyan diversity. The BRUVs of the Global Finprint project (https://globalfinprint.org/) aim to estimate the abundance of coral reef sharks and rays from across all tropical ecosystems and inform conservation, and they have succeeded on many reefs (e.g. Goetze et al. 2018). An equivalent program is needed for ecosystems at other latitudes. Environmental DNA (eDNA), when combined with metabarcoding, may also become an efficient complement to BRUVs and citizen science for detecting and monitoring biodiversity (Thomsen and Willerslev 2015, Valentini et al. 2016). Largetooth sawfish *Pristis pristis*, for example, are critically endangered and extremely rare in traditional surveys, including BRUVs, but are easily detected using eDNA (Simpfendorfer et al. 2016). Monitoring will let scientists identify patterns of diversity for multiple taxa, track relationships to environmental variables, and detect long-term changes in abundance, including potential range shifts. Most importantly, intense and consistent vigilance will ensure rare and elusive species are discovered and studied. Continued BRUV monitoring of the Saint Peter and Saint Paul Archipelago recently rediscovered the presence of Galapagos sharks *Carcharhinus galapagensis* at the islands (Pimentel et al. 2020), thought extirpated from that part of the Atlantic when my review in chapter 2 was written (Luiz and Edwards 2011). Successes happen when committed efforts are made to understand, conserve, and monitor.

6.3 Conclusion

Chondrichthyans are some of the most imperiled species in the ocean (Dulvy and Reynolds 2002, Worm et al. 2013, Dulvy et al. 2014). Despite their diversity, the largest threat to most species is overfishing; even with this generality, diverse measures will be needed to conserve them (Davidson et al. 2016, Shiffman and Hammerschlag 2016). This thesis provides basic data on chondrichthyan relationships to their biotic and abiotic environments to gain a better understanding of chondrichthyan diversity, and the potential of MPAs to conserve that diversity, in developing countries. For instance, my research builds on the limited research on the effects of ENSO events on chondrichthyans globally (Sequeira et al. 2012, Beale et al. 2019), with a start to examining general patterns in the species-specific responses that will inform MPAs in a dynamic future (Hobday 2011). Therefore, species associations to their environment and marine community must be addressed, especially for understudied taxa and countries, and non-invasive monitoring pushed forward, if MPAs are to play any role under climate change. If designed and managed effectively, even small MPAs can protect chondrichthyans and their habitat, providing hope to the often neglected diversity lurking unstudied in the ecosystems of the developing world.

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Appendices

Appendix A: Supplemental Material for Chapter 2

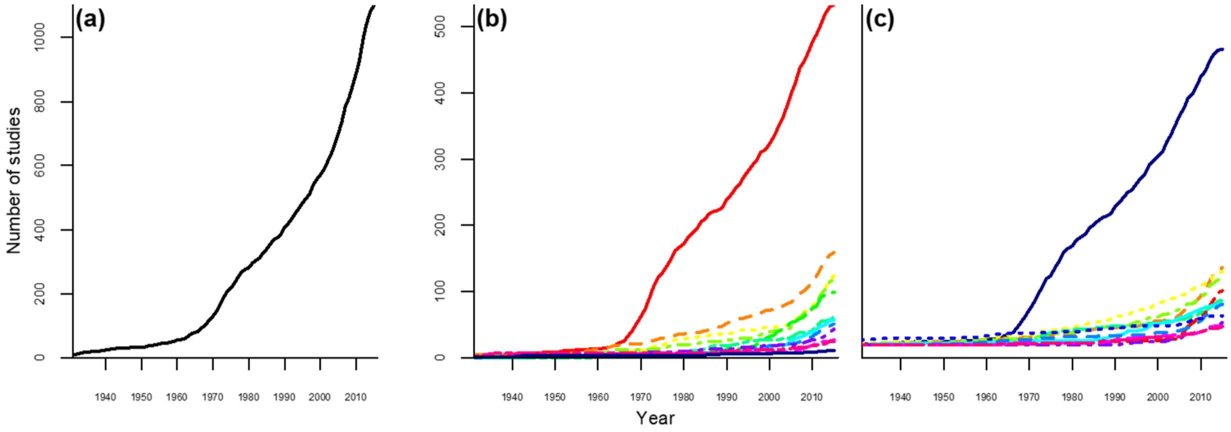

Figure A1 The cumulative number of studies (including physiology studies) on reef sharks published in peer-reviewed journals by year (a) for all species and topics combined, (b) by species (or Family), and (c) topic. Other Ginglymostomatidae includes *Nebrius ferrugineus* and *Pseudoginglymostoma brevicaudatum*. For (a), (b), and (c), the x-axis starts at 1931 although nine early taxonomic studies occurred earlier, from 1867. *Ginglymostoma cirratum* (—), *C. melanopterus* (- - -), *C. amblyrhynchos* (····), *T. obesus* (–·), Hemiscylliidae (– –), *C. galapagensis* (—·), *C. perezi* (—), *S. fasciatum* (- - -), other Ginglymostomatidae (····), *C. albimarginatus* (–·), Orectolobidae (– –), Scyliorhinidae (—·), and Heterodontidae (—). Physiology (—), habitat use (- - -), basic biology (····), other (–·), abundance (– –), behaviour (—·), parasites (—), socio-economics conservation (- - -), taxonomy (····), genetics (–·), captive (– –), and diet (—·).

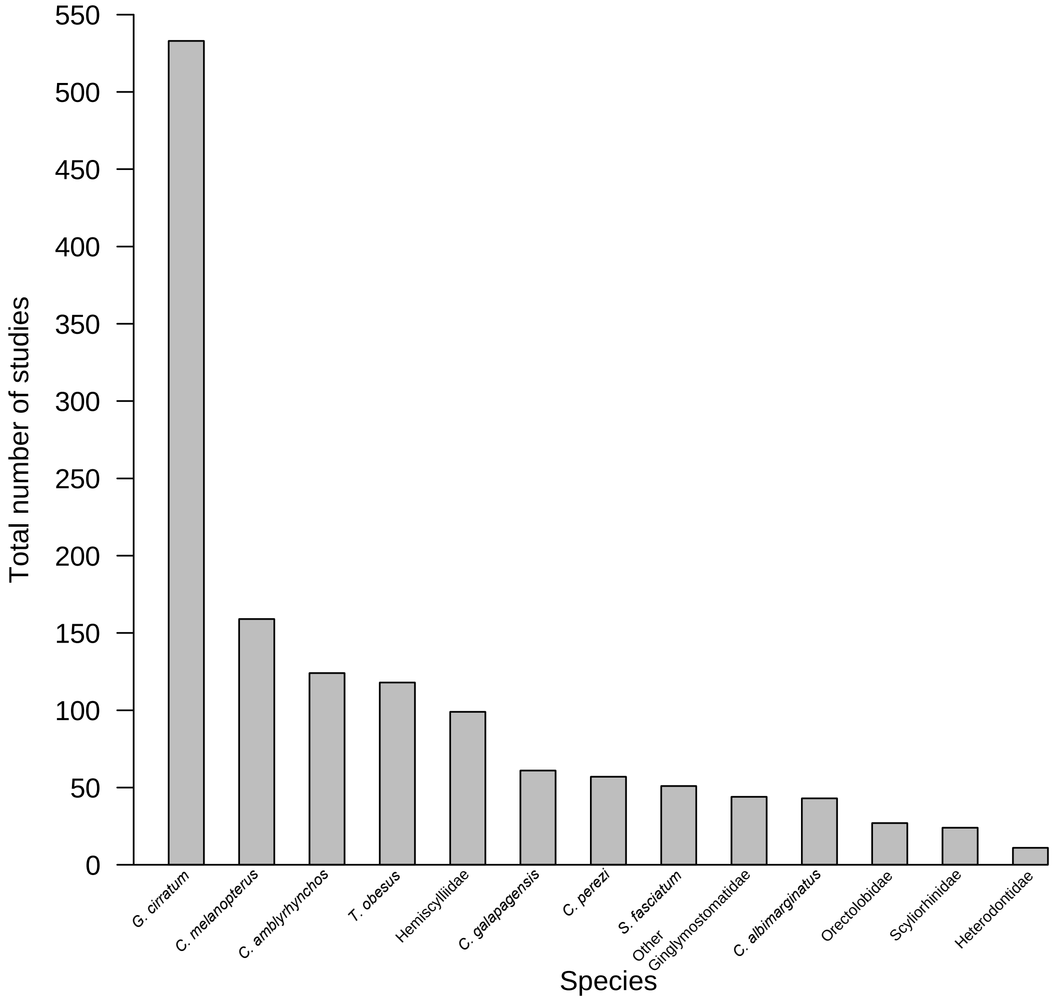

Figure A2. Frequency distribution of peer-reviewed reef shark studies by species (or group), with physiology studies included. Other Ginglymostomatidae includes *Nebrius ferrugineus* and *Pseudoginglymostoma brevicaudatum.*

Appendix B: Supplemental Material for Chapter 3

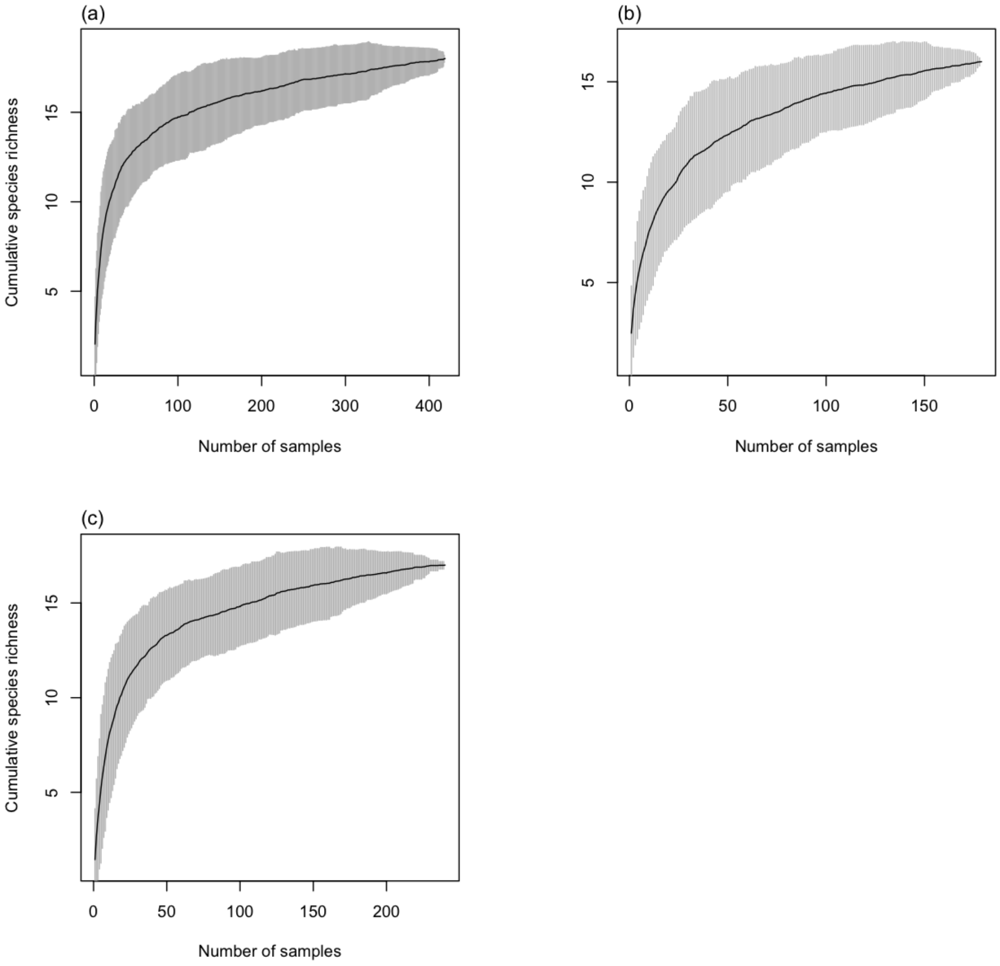

Figure B1. Species accumulation curve for (a) all BRUVs in Walker Bay and Betty's Bay, (b) BRUVs in Betty's Bay, and (c) BRUVs in Walker Bay.

Table B1. Number of samples in each region and protection level each year in each season (winter: June-November; summer: December-May).

		2016		2017		2018		Total
Region	Protection	Winter	Summer	Winter	Summer	Winter	Summer	
Walker Bay	Unprotected	56	0	18	33	2	22	131
	Protected	0	0	9	63	12	25	109
Betty's Bay	Unprotected	0	0	25	29	21	19	94
	Protected	0	0	25	27	18	15	85

Table B2. Chondrichthyan records in Rock and Surf Super Pro League (2008-2018) and Ocean Research Institute of South Africa tagging databases (2012-2018) from Betty's Bay and from the South African Shark Conservancy shore and boat fishing databases (2010-2018) in Walker Bay, South Africa.

Species	RASSPL	ORI	SASC	
			Shore-based	Total
Scyliorhinidae				
Haploblepharus pictus			650	851
H. edwardsii			65	209
H. fuscus			12	23
Poroderma africanum	13		200	373
P. pantherinum			203	267
total*	239		1130	1723
Triakidae				
Triakis megalopterus	24	166	6	12
Mustelus mustelus	4	9	1	28
Galeorhinus galeus				28
total*	70	177**	7	68
Other sharks				
Notorynchus cepedianus		64		29
Carcharias taurus		1		2
Sphyrna zygaena				2
S. lewini				2
Carcharhinus brachyurus				7
Batoidea				
Raja straeleni		1	1	13
Rostroraja alba				2
Acroteriobatus annulatus				1
total		1		16
Holocephali				
Callorhinchus capensis	1			1
Overall total chondrichthyans	310	243	1138	1850

*Includes individuals not identified beyond family, if present

**Two records were identified as Hardnosed Smooth-hound (*Mustelus mosis*) despite this species' distribution not including Betty's Bay, South Africa and so are treated as unidentified Triakidae here

Table B3. Relative abundance, species richness, frequency of occurrence (FO) model coefficients, with p-values based on Wald's test shown in brackets, for each fixed effect in generalized linear mixed models (GLMMs), with a baseline of protected, Walker Bay, sand, winter, 2016, and low visibility.

	Protection: Unprotected	**Region: Betty's Bay**	**Protection-Region interaction**	**Habitat: Reef**	**Habitat: Kelp**	**Depth**	**Water temp.**	**Year: 2017**	**Year: 2018**	**Sine time**	**Cosine time**	**Visibility (low vs high)**
FO												
total	0.39 (0.59)	1.35 (0.034)*	NA	1.21 (0.013)*	12.2 (0.91)	-0.024 (0.31)	-0.02 (0.86)	0.97 (0.21)	0.77 (0.37)	-0.24 (0.56)	1.06 (0.003)*	0.98 (0.02)*
catsharks	-0.53 (0.44)	2.35 (<0.001)*	NA	2.16 (<0.001)*	3.63 (0.003)*	0.004 (0.86)	-0.016 (0.87)	0.52 (0.45)	0.83 (0.30)	0.065 (0.87)	0.52 (0.080)	1.05 (0.011)*
large sharks	-0.47 (0.23)	1.01 (0.016)	NA	-0.67 (0.067)	-1.23 (0.020)*	-0.026 (0.14)	-0.11 (0.21)	-1.60 (0.011)*	-2.21 (0.0016)*	-0.72 (0.017)*	0.42 (0.058)	0.79 (0.05)
batoids	-0.07 (0.86)	-0.23 (0.60)	NA	-0.44 (0.25)	-1.39 (0.032)*	-0.005 (0.76)	0.11 (0.23)	0.11 (0.85)	-0.22 (0.75)	-0.40 (0.18)	0.66 (0.0037)*	0.82 (0.032)
Relative abundance												
total	0.70 (0.035)*	0.81 (<0.001)*	-0.83 (0.023)*	0.46 (<0.001)*	0.49 (0.001)*	0.005 (0.31)	-0.033 (0.14)	0.029 (0.85)	0.15 (0.37)	-0.18 (0.008)*	0.13 (0.012)*	0.35 (0.002)*
catsharks	-0.023 (0.87)	0.68 (<0.001)*	NA	0.71 (<0.001)*	0.82 (<0.001)*	0.009 (0.10)	-0.028 (0.25)	0.011 (0.95)	0.21 (0.25)	-0.14 (0.056)	0.099 (0.081)	0.31 (0.017)*
large sharks	-0.096 (0.75)	0.86 (0.012)*	NA	-0.56 (0.046)*	-1.01 (0.015)*	-0.024 (0.090)	-0.10 (0.16)	-1.22 (0.015)*	-1.73 (0.0016)*	-0.56 (0.024)*	0.29 (0.085)	0.56 (0.062)
Species richness	0.73 (0.023)*	0.83 (<0.001)*	-0.80 (0.019)*	0.32 (0.002)*	0.22 (0.13)	0.0015 (0.75)	-0.017 (0.50)	0.035 (0.84)	0.084 (0.67)	-0.21 (0.008)*	0.13 (0.028)*	0.31 (0.009)*

*Statistically significant coefficients

Table B4. Coordinates in decimal degrees of sampling sites from Betty's Bay (BB) and from Walker Bay (A-G, Y), South Africa.

Area	Station	Latitude	Longitude
A	A2	-34.39493	19.11724
A	A3	-34.4017	19.11019
A	A4	-34.4086	19.09452
A	A5	-34.40832	19.10923
A	A6	-34.41415	19.11148
A	A8	-34.43242	19.1275
A	A9B	-34.4272	19.1321
A	A10B	-34.4142	19.1115
A	A11	-34.4399	19.1461
A	A12	-34.43691	19.1419
A	A13	-34.43293	19.14573
A	A14	-34.429873	19.15054
A	A15	-34.43239	19.15821
A	A16	-34.42443	19.16587
A	A17	-34.42417	19.15755
A	A18	-34.4324	19.1275
A	A19	-34.42394	19.12781
A	A20	-34.41812	19.12012
A	A21	-34.4272	19.1182
B	B1	-34.4268	19.17771
B	B2	-34.4345	19.16653
B	B4	-34.4459	19.15983
B	B7	-34.44906	19.17839
B	B8	-34.43208	19.18955
B	B12A	-34.44311	19.21939
B	B13	-34.44716	19.20303
B	B16	-34.44481	19.2334
B	B17	-34.43367	19.23161
B	B18	-34.43914	19.23576
B	B19	-34.44735	19.24121
C	C1	-34.4652	19.24499
C	C1A	-34.4508	19.2217
C	C2	-34.476	19.2379
C	C3	-34.46727	19.22419
C	C4	-34.46905	19.25068
C	C4A	-34.4483	19.2019
C	C6A	-34.4456	19.1856
C	C7	-34.47578	19.25442
C	C11	-34.486	19.2455
C	C12	-34.4921	19.2521
D	D1	-34.4977	19.2815
D	D9	-34.54555	19.304416
D	D10	-34.55933	19.30357
D	D11	-34.57521	19.3126
D	D12	-34.59321	19.32164
D	D13	-34.57463	19.3331
D	D14	-34.58799	19.32969
D	D15	-34.56244	19.33177
D	D16	-34.5518	19.32353
D	D17	-34.54177	19.3127
D	D18	-34.55826	19.3234

Area	Station	Latitude	Longitude
D	D19	-34.56097	19.31528
D	D20	-34.53692	19.30196
E	E1	-34.50236008	19.34161501
E	E2	-34.492088	19.343179
E	E3	-34.517287	19.34328
E	E4	-34.494141	19.333903
E	E5	-34.47300985	19.31605562
E	E6	-34.531091	19.33705
E	E7	-34.524958	19.340608
E	E8	-34.54043	19.339306
E	E9	-34.543079	19.347299
E	E10	-34.537572	19.350699
E	E11	-34.539124	19.357785
E	E12	-34.47555567	19.31112971
E	E13	-34.51967	19.35329
E	E14	-34.526048	19.357881
E	E15	-34.528132	19.351615
E	E16	-34.53363	19.356721
E	E17	-34.5004897	19.31484098
E	E18	-34.5118795	19.31919772
E	E19	-34.517886	19.333751
E	E20	-34.50156	19.33372
F	F1	-34.42173	19.28935
F	F2	-34.43382	19.25385
F	F3	-34.43379	19.26473
F	F5	-34.43749	19.27114
F	F6	-34.4364	19.28265
F	F7	-34.4640556	19.29125521
F	F8	-34.44806	19.28461
F	F9	-34.46970016	19.29656082
F	F10	-34.45506082	19.29033436
F	F11	-34.45753	19.31536
F	F12	-34.453922	19.321057
F	F13	-34.4484	19.311602
F	F14	-34.44221	19.29547
F	F15	-34.42418	19.29604
F	F17	-34.4433	19.28204
F	F18	-34.45914	19.30769
F	F19	-34.42852	19.25
F	F20	-34.46332325	19.28584843
G	G1	-34.6409	19.3043
G	G2	-34.636668	19.322543
G	G3	-34.634512	19.338552
G	G5	-34.628033	19.371857
G	G6	-34.623233	19.371857
F	Kelp1	-34.414238	19.253473
F	Kelp2	-34.41966	19.245623
B	Kelp3	-34.429718	19.23203
B	Kelp4	-34.432568	19.226693
Y	Y1	-34.4888	19.2984
Y	Y2	-34.4849	19.2939
Y	Y3	-34.4802	19.2892
Y	Y4	-34.47661	19.2847
Y	Y5	-34.4723	19.2797
Y	Y6	-34.46748	19.27606

Area	Station	Latitude	Longitude
Y	Y7	-34.46399	19.27136
Y	Y8	-34.4899	19.2666
Y	Y9	-34.4564	19.2608
BB	BB10	-34.3725	18.90708
BB	BB12	-34.36045	18.91412
BB	BB16	-34.36417	18.94855
BB	BB17	-34.37393	18.9322
BB	BB18	-34.38651	18.88993
BB	BB24	-34.38337	18.88663
BB	BB28	-34.38935	18.88934
BB	BB29	-34.39327	18.87692
BB	BB3	-34.38089	18.89748
BB	BB36	-34.380017	18.8772
BB	BB38	-34.390166	18.9045
BB	BB39	-34.39027	18.90455
BB	BB40	-34.38676	18.92278
BB	BB43	-34.39031	18.87002
BB	BB46	-34.3783	18.88318
BB	BB48	-34.37707	18.90972
BB	BB49	-34.391767	18.90335
BB	BB5	-34.37286	18.89515
BB	BB50	-34.3804	18.90287
BB	BB51	-34.38567	18.8864
BB	BB52	-34.3794	18.875533
BB	BB55	-34.36696	18.92937
BB	BB56	-34.36334	18.92201
BB	BB57	-34.36148	18.91868
BB	BB58	-34.36725	18.913917
BB	BB59	-34.368731	18.913002
BB	BB6	-34.372186	18.899185
BB	BB60	-34.36536	18.91844
BB	BB61	-34.36965	18.92528
BB	BB62	-34.37092	18.93853
BB	BB63	-34.37254	18.9286
BB	BB64	-34.36139	18.93546
BB	BB65	-34.36492	18.95066
BB	BB66	-34.37021	18.95375
BB	BB67	-34.36473	18.94773
BB	BB68	-34.36248	18.93787
BB	BB69	-34.36189	18.94469
BB	BB70	-34.36338	18.95041
BB	BB71	-34.36705	18.9513
BB	BB72	-34.37144	18.94935
BB	BB73	-34.37154	18.95915
BB	BB75	-34.37689	18.94293
BB	BB76	-34.37053	18.95578
BB	BB77	-34.36616	18.92586
BB	BB78	-34.37215	18.92901
BB	BB79	-34.36923	18.93189
BB	BB8	-34.36316	18.90879
BB	BB80	-34.37845	18.9195
BB	BB81	-34.38416	18.90892
BB	BB82	-34.37739	18.89123
BB	BB83	-34.37867	18.88773
BB	BB84	-34.37927	18.88439

Area	Station	Latitude	Longitude
BB	BB85	-34.37436	18.87318
BB	BB86	-34.38008	18.88276
BB	BB87	-34.38219	18.89867
BB	BB88	-34.39102	18.89917
BB	BB9	-34.37398	18.89886
BB	BB90	-34.37318	18.94125

Appendix C: Supplemental Material for Chapter 4

Table C1. The species of teleosts, myxinids, crustaceans, cephalopods, birds, and mammals observed on the BRUVs and their frequency of occurrence (FO) over the 167 sites. Species found only at sites with chondrichthyans are denoted with (*).

Taxon	Species	Name	FO
Teleostei	Hottentot	*Pachymetopon blochii*	0.653
	Cape horse mackerel	*Trachurus capensis*	0.599
	Panga	*Pterogymnus laniarius*	0.599
	Carpenter	*Argyrozona argyrozona*	0.503
	White seacatfish	*Galeichthys feliceps*	0.443
	Bluefin gurnard	*Chelidonichthys kumu*	0.437
	Roman	*Chrysoblephus laticeps*	0.437
	Redfingers*	*Cheilodactylus fasciatus*	0.359
	Black seacatfish	*Galeichthys ater*	0.311
	Steentjie	*Spondyliosoma emarginatum*	0.240
	Super klipfish*	*Clinus superciliosus*	0.222
	White stumpnose	*Rhabdosargus globiceps*	0.198
	Blue hottentot*	*Pachymetopon aeneum*	0.168
	Fransmadam*	*Boopsoidea inornata*	0.138
	Red stumpnose*	*Chrysoblephus gibbiceps*	0.132
	Yellowback fusilier*	*Caesio xanthonota*	0.108
	Strepie*	*Sarpa salpa*	0.102
	Bank steenbras*	*Chirodactylus grandis*	0.072
	Red steenbras*	*Petrus rupestris*	0.054
	Twotone fingerfin*	*Chirodactylus brachydactylus*	0.054
	Barred fingerfin	*Cheilodactylus pixi*	0.048
	Barehead goby	*Caffrogobius nudiceps*	0.036
	Janbruin*	*Gymnocrotaphus curvidens*	0.030
	Blacktail*	*Diplodus capensis*	0.024
	Jutjaw*	*Parascorpis typus*	0.018
	Evileye blaasop*	*Amblyrhynchotes honckenii*	0.012
	Longsnout pipefish*	*Syngnathus temminckii*	0.012
	Silver kob*	*Argyrosomus inodorus*	0.012
	Slender baardman*	*Umbrina robinsoni*	0.012
	Spinynose horsefish*	*Congiopodis spinifer*	0.012
	Zebra*	*Diplodus hottentotus*	0.012
	Beaked sandfish*	*Cyprinus gonorynchus*	0.006
	Cape sole*	*Heteromycteris capensis*	0.006
	Galjoen*	*Dichistius capensis*	0.006
	Geelbek*	*Atractoscion aequidens*	0.006
	Giant yellowtail*	*Seriola lalandi*	0.006
	Shad*	*Pomatomus saltatrix*	0.006
	Snakelet*	*Halidesmus scapularis*	0.006
	Yellowbelly rock cod*	*Epinephelus marginatus*	0.006
Myxinidae	Sixgill hagfish	*Eptatretus hexatrema*	0.260
Crustacea	West coast rock lobster	*Jasus lalandii*	0.569
	Three-spotted swimming crab	*Portunus sanguinolentus*	0.353
	Hermit crab	Anomura	0.156
	Cape rock crab*	*Guinusia chabrus*	0.066
	Masked crab	*Nautilocorystes ocellata*	0.054
	Masked crab	*Mursia cristiata*	0.042
	Sandflat crab*	*Danielita edwardsii*	0.006
Cephalopoda	Common octopus	*Octopus vulgaris*	0.180
	Chokka squid*	*Loligo reynaudii*	0.048
Aves	African penguin	*Spheniscus demersus*	0.030
	Cape cormorant*	*Phalacrocorax capensis*	0.006
Mammalia	Cape fur seal	*Arctocephalus pusillus*	0.084

Table C2. The top five species in the marine community of chondrichthyans, teleosts, crustaceans, cephalopods, birds, and mammals observed on our baited remote underwater videos in Walker Bay and Betty's Bay by each measure of network centrality, ordered by their value for that index. Each measure of centrality is based on their number of positive, negative, and random co-occurrences with other species.

	Centrality
Degree centrality	
H. edwardsii	63
P. africanum	63
P. blochii	63
J. lalandii	62
H. pictus	61
Betweenness centrality	
H. edwardsii	78.8
T. capensis	68.1
P. africanum	62.9
J. lalandii	57.2
P. blochii	54.9
Local bridging centrality	
H. edwardsii	142.8
P. africanum	134.6
P. blochii	128.6
J. lalandii	124.8
T. capensis	120.5
Closeness centrality	
H. edwardsii	0.0133
P. africanum	0.0133
P. blochii	0.0133
J. lalandii	0.0132
H. pictus	0.0130
Eigenvalue centrality	
P. blochii	1.00
P. africanum	0.99
J. lalandii	0.98
H. edwardsii	0.98
H. pictus	0.97

Appendix D: Supplemental Material for Chapter 5

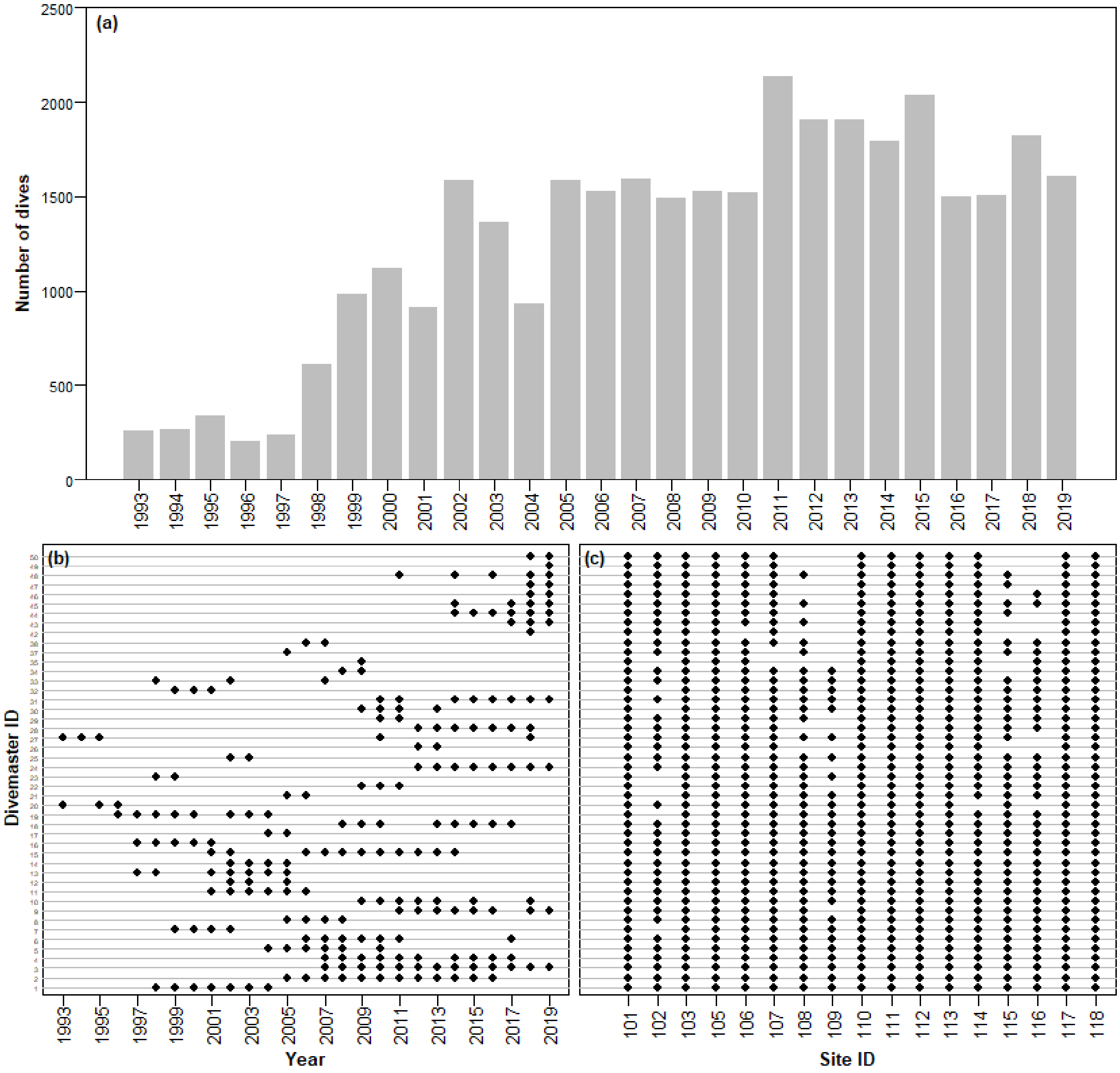

Figure D1. (a) The number of dives by year; and the dive guides that have dived each (b) year and (c) dive site at Cocos.

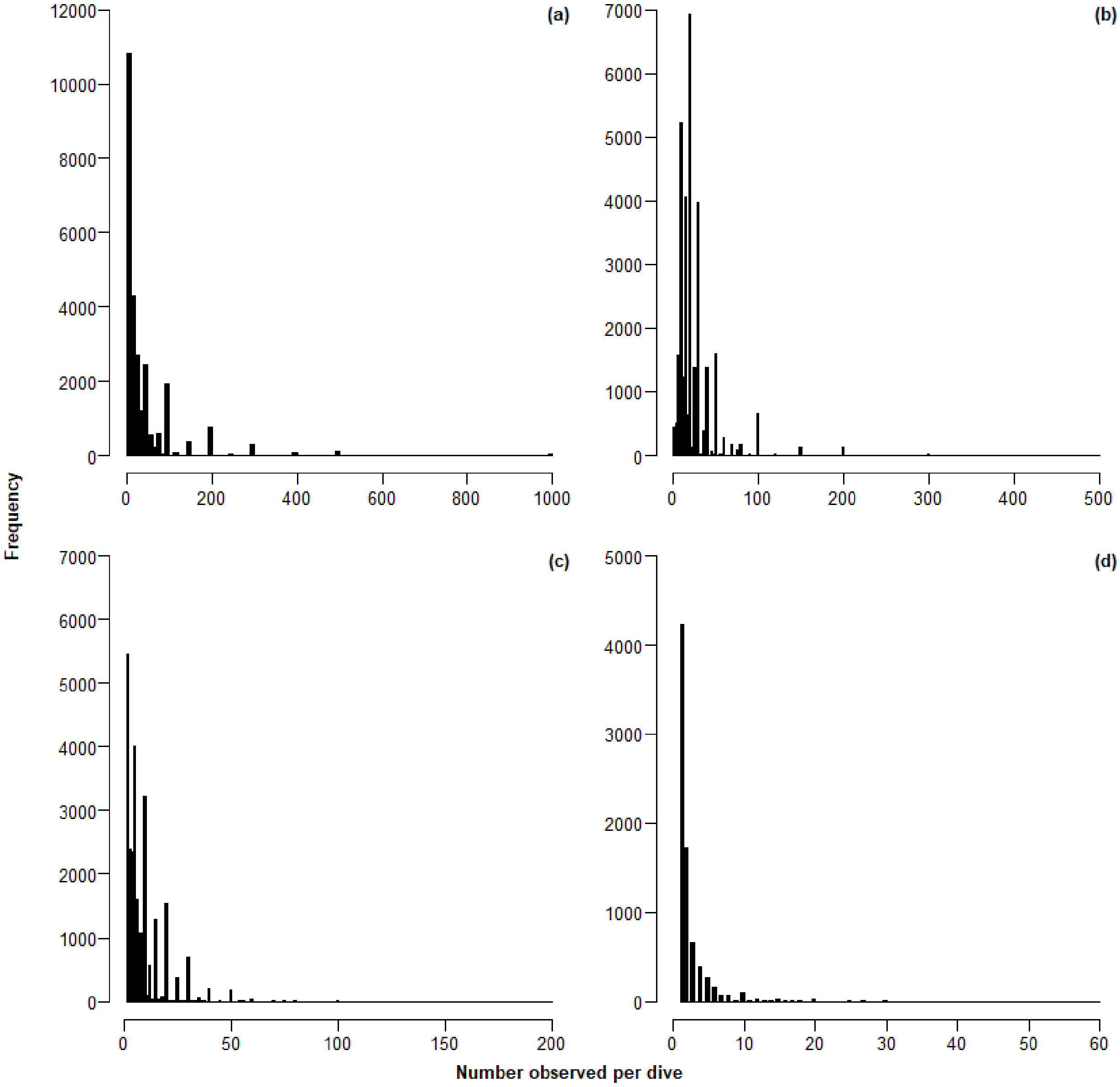

Figure D2. Histograms of counts of (a) *Sphyrna lewini*, (b) *Triaenodon obesus*, (c) *Taeniura meyeni*, and (d) *Aetobatus narinari* observed at Cocos Island with zeros removed.

Table D1. The χ^2 values (and p-values) from likelihood ratio tests for the SST and ONI variables in the models for each species. The ONI effect for *A. narinari* is the overall significance of both terms of the quadratic relationship.

Species	SST effect	ONI effect
Galeocerdo cuvier	28.2 (<0.001)	17.4 (<0.001)
Sphyrna lewini	149.9 (<0.001)	1063.0 (<0.001)
S. lewini schooling probability	77.5 (<0.001)	395.7 (<0.001)
Carcharhinus limbatus	1.86 (0.17)	20.2 (<0.001)
Triaenodon obesus	68.3 (<0.001)	24.8 (<0.001)
Mobula spp.	50.9 (<0.001)	0.68 (0.41)
Aetobatus narinari	7.2 (0.0073)	135.7 (<0.001)
Taeniura meyeni	139.0 (<0.001)	378.8 (<0.001)

Table D2. The percent change estimated in this study (over 27 years) and in White et al. 2015 (over 21 years) for the species included in this study. Red indicates percent declines and blue percent increases. The 95% confidence intervals are in brackets. Mobula rays and manta rays were treated separately in White et al. 2015.

Species	This study	White et al., 2015
Galeocerdo cuvier	33%/year (30% – 36%)	79%/year (69% – 89%)
Sphyrna lewini	48% (40% – 57%)	45% (39% – 50%)
Carcharhinus limbatus	0%/year (2% – 2%)	9%/year (8% – 10%)
Triaenodon obesus	64% (61% – 67%)	77% (76% – 78%)
Mobula spp.	69% (60% – 78%)	Mobula: 78% (72% – 84%) Manta: 89% (85% – 92%)
Aetobatus narinari	93% (91% – 95%)	34% (23% – 43%)
Taeniura meyeni	88% (86% – 89%)	73% (71% – 75%)