

Roles, risks and refugia: spatial ecology, ecosystem function and vulnerability of reef sharks in the central Indian Ocean.



THE UNIVERSITY OF
**WESTERN
AUSTRALIA**

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This thesis is presented for the degree of Doctor of Philosophy of Animal Science

of The University of Western Australia

School of Biological Sciences

The University of Western Australia

2021

Thesis declaration

I, David Tickler, certify that:

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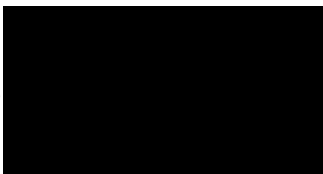
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The research involving animal data reported in this thesis was carried out in collaboration with the Hopkins Marine Station of Stanford University and assessed and approved by the Stanford University Administrative Panel on Laboratory Animal Care under permit APLAC-10765, held by the Block Laboratory at Hopkins Marine Station.

Fieldwork was carried out under a research permit from the United Kingdom Foreign and Commonwealth Office.

This thesis contains published work and work prepared for publication, some of which has been co-authored.

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Abstract

The vital services provided to humankind by the ocean depend in large part on the abundance and diversity of marine life, both of which have been impacted by anthropogenic forces. Of particular concern has been the widespread and unsustainable exploitation of high trophic-level predators like sharks. Large, mobile shark species are believed to exert wide-ranging influence over lower trophic-level species through direct predation and fear-based effects, structuring and stabilising marine community composition, and bolstering the resilience of ecosystems to external shocks. Mobile predators like sharks may also physically link ecosystems through the horizontal and vertical transfer of important nutrients, influencing primary productivity, and their movements may also influence their vulnerability to threats like fishing.

My thesis examined the threats faced by, and ecosystem role of, sharks on coral reefs, through the lens of their spatial ecology. My study focussed on two closely related sympatric species, the grey reef shark (*Carcharhinus amblyrhynchos*) and the silvertip shark (*Carcharchinus albimarginatus*) on reefs in the British Indian Ocean Territory (BIOT) Marine Protected Area (MPA), a large and largely-unexploited atoll system in the central Indian Ocean. I placed the space use of my focal species in the context of both the threat posed to them by shark fisheries and our current understanding of their ecology on Indo-Pacific coral reefs. Publicly available data on the spatial distribution of global fisheries catches from the *Sea Around Us* were used to quantify the increase and spatial expansion of shark catches from 1950 to 2014. I then used acoustic and archival tag data to examine the horizontal and vertical movements of my two focal species with respect to both environmental factors and their exposure to fishing pressure.

The reconstructed catch data showed consistent underreporting of shark catches – averaging 50% over a 65-year period - and a widespread lack of species-level reporting. Both factors degrade the data available to managers and inhibit science-based management of sharks in many fisheries. High catches and poor catch reporting in the Indian Ocean present a challenge to both fisheries management and shark conservation in my study region. Telemetry revealed significant inter- and intra-specific differences in the space use and detection cycles of grey reef and silvertip sharks, with residency patterns varying with species and size, and also with habitat type within the BIOT MPA. While some observed patterns were consistent with studies elsewhere, such as comparatively smaller home ranges, lower dispersal and a higher percentage of time spent near reefs for grey reef sharks, other observations, including diel detection cycles, differed from those made elsewhere in

the Indo-Pacific. This suggests that while commonalities exist, aspects of reef shark spatial ecology may vary with context. Spatial management, including protection from fishing, may need to be tailored to reef locations. The influence of spatial ecology on fisheries risk was illustrated by an illegal fishing event in BIOT which coincided with the disappearance of one third of the tagged sharks from the study site. Fishing vessel sightings were strongly correlated with tag 'losses' from the shark tracking project. Significantly more silvertip sharks were caught, which may be linked to their wider dispersal within BIOT and movements away from reefs into areas with higher exposure to fishing.

The lack of reliable and taxonomically-detailed data on shark catches, particularly for coastal countries in the Indo-Pacific region, suggests that effective science-based management is not currently possible for many shark fisheries. Given, widespread indications of declines in reef shark populations, precautionary management through well designed and enforced MPAs is needed to protect and restore reef shark populations in the Indian Ocean and elsewhere. Differences in spatial ecology between reef shark species, observed in BIOT and elsewhere, suggest varying needs with respect to spatial protection, but also different ecosystem roles resulting from the partitioning of space and resources. This latter point implies that reef sharks may play complimentary roles and assemblage-level protection is needed to maintain ecosystem services from these predators. However, the creation of appropriately located and sized MPAs alone will not be sufficient to ensure benefits for reef sharks. Effective protection is key, as even sporadic violations of shark fishing prohibitions can dramatically impact shark populations within MPAs. Integrating telemetry with other monitoring techniques will help better design and monitor MPAs for reef sharks.

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Acknowledgements

As a crossword enthusiast, it has always amused me that, alongside its more commonly-used definition, the dictionary defines the word *career* as ‘to move swiftly and in an uncontrolled way’. I have often looked at my resume and thought how apt that is. Just as Robert Brown’s smoke particles were directed hither and thither by their interactions with unseen water molecules, I am where I am thanks to a long series of fortuitous collisions with the people who have nudged me, mostly gently, along my trajectory.

In many ways this thesis had its genesis when this existential Brownian motion took me from an office job in Sydney, to dive boats in Cairns, to working as a deckhand in the yachting industry. The support of my then captain, Brendan O’Shannassy, and my employers, the Bertarelli family, landed me in April 2012 in Diego Garcia in the British Indian Ocean Territory, as the diving officer on a scientific expedition to survey the area’s newly-created marine protected area. It was on that research trip that I met Jessica Meeuwig, along with Heather Koldewey, Nick Graham and Charles Sheppard, the godfather of BIOT coral science. Having spent the previous eight years seeing the ocean as a diver I was becoming aware of what was at stake in places like BIOT, and was keen to put my shoulder to the wheel in marine conservation. I took advantage of captive audience on the research vessel to solicit advice as to how I might best get a foot in the door. While all advised me that I should get a grounding in marine ecology before trying to fix the ocean, it was Jessica who suggested that the shark and fish abundance data she and her team were collecting might be the perfect raw material for a master’s thesis. Six months later I was moving to Perth.

My masters with Jessica not only helped me more or less overcome a pathological fear of statistics, and possibly even gain a passable understanding of those dark arts, but also embedded me in the Marine Futures Lab – a group whose goal to use science to further the public understanding of, and support for, the need to protect wild places like BIOT I continue to share. As well as Jessica’s tutelage, I’ve benefitted from working alongside numerous lab members – students, staff and post-docs – and the opportunity to develop and hone research skills in support of the lab’s projects.

The journey that began in 2012 has continued to take its twists and turns. In 2013 I was fortunate to be back in the BIOT to help set up an exploratory acoustic tagging programme, also supported by the Bertarelli Foundation’s ongoing commitment to science in the BIOT. That introduced me to the team at Stanford University’s Hopkin’s Marine Station, and Barb Block, Taylor Chapple, Aaron Carlisle, John Dale and Robbie Schallert and Mike Castleton, among other Hopkin’s staff and

students, patiently showed me the ropes in the world of animal biotelemetry. The work also led to collaboration with the Zoological Society of London's (ZSL) Institute of Zoology, particularly Davids Curnick and Jacoby. In 2015 I launched into my PhD, collaborating with Stanford and ZSL over a series of four data collection expeditions and the resulting data analyses. In another fortuitous Brownian collision, also catalysed by Jessica, I had the opportunity to collaborate with the *Sea Around Us Project* team and Andrew and Nicola Forrest's Minderoo Foundation in drawing together the global data on fisheries and modern slavery. This collaboration gave me a strong taste for interdisciplinary work, and also gained me another expert supervisor, the *Sea Around Us* – Indian Ocean's Dirk Zeller, who has been indispensable in guiding the development of the PhD Thesis.

The others I need to thank for their assistance with my research are legion: the crews of the MY Vava, MY Vava II, and SV Tethys Supporter who went above and beyond the call of duty to help us get fieldwork done, the local fixers and agents in places like the Maldives and Singapore who have kept research trips on the rails. The team at ZSL handled much of the work required to get us research permits from the UK Foreign and Commonwealth Office. The MFL's former lab manager, James Hehre, shouldered the logistical burden of getting me to site. The University of Western Australia, and particularly the School of Animal Biology and its team of Graduate Research Coordinators, have provided direct support and patient and invaluable advice over the years. When Jessica suggested I apply to UWA to do a masters back in 2012, the one thing I knew was that it was a beautiful campus in a beautiful city. It's so much more than that, obviously, but it is also a lovely place to do science and I feel lucky to have spent much of the past few years there. To everyone there who's helped me along the road, a big thank you.

PhD's tend to expand into all corners of life, and, while thanking one's friends and family has been rendered hackneyed by a thousand Oscar acceptance speeches, I have to acknowledge the deep debt of gratitude I owe to the non-academic participants in my journey, willing or otherwise! My parents, Martin and Jane, instilled in me a deep curiosity about the world, a desire to travel and explore, itchy feet and a certain amount of stubbornness. They also pushed me to achieve the academic qualifications that have given me the freedom to experiment so widely along my career 'path'. Sadly, my mum can't see me reach the end of this chapter in my life, but imagining what she would have thought had I ever given up has kept me going through more than one tough patch. My dad has always been there, often to distract from the daily grind with a lengthy progress report on the family cottage's resident house martin (*Delichon urbicum*) colony, but always a steady source of support. It was with my brother Pete that I learned to scuba dive in a frigid clay pit in Lincolnshire

almost 25 years ago, picking up a skill and a passion that has reshaped my life. My partner Coraline has put up with a sometimes moody, often obsessive, and above all unavoidably English boyfriend with Gallic *sangfroid* and regular doses of *confit de canard*. Je t'aime, mon cœur. My friends have all, at various times, provided advice, patient listening, well-feigned interest, timely distractions, and votes of encouragement.

It's been a team effort.

This research was supported by an Australian Government Research Training Program (RTP) Scholarship and a UWA Top-Up Scholarship. Fieldwork in the British Indian Ocean Territory was funded by the Bertarelli Programme in Marine Science.

Authorship declaration

This thesis contains work that has been published or is being prepared for publication.

Details of the work:

Tickler D.M., Meeuwig J.M., Zeller D. You can't manage what you don't measure: global and regional trends in shark catch data, 1950-2014. PLOS One, in prep.

Location in thesis: Chapter 2

Student contribution to work:

DT overall contribution 75%. DZ suggested the topic and provided access to the data. DZ and JM helped develop manuscript narrative and advised on analysis and development of figures.

Dirk Zeller Jessica Meeuwig

29/11/2020 29/11/2020

Details of the work:

Tickler D.M., Meeuwig J.M., Carlisle A.B., Chapple T.K., Dale J.J., Ferretti F., White T.D., Castleton M., Curnick D.J., Jacoby D.M.P., Block B.A. Telemetry-derived space use patterns for two species of reef shark species in a large no-take MPA. PLOS One, in prep.

Location in thesis: Chapter 3

Student contribution to work:

DT overall contribution 75%. D.T., A.C., T.C., R.S., D.C., D.J., T.W., F.F. and J.D. collected the field data. M.C. managed the tagging database. A.C., D.J., D.C. and J.D. provided assistance with analyses. J.M. provided advice on circular regression and both J.M. and D.Z. advised on manuscript development and refinement. D.T analysed the data and drafted the manuscript, with reviews and editorial input from all co-authors.

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29/11/2020 21/11/2020 21/11/2020 21/11/2020

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25/11/2020 28/11/2020

Details of the work:

Tickler D.M., Carlisle A.B., Meeuwig J.M., Castleton M., Chapple T.K., Curnick D.J., Dale J.J., Schallert R.J., Block B.A. Environmental drivers of the vertical niche of the silvertip shark (*Carcharhinus albimarginatus*). Marine Ecological Progress Series, in prep.

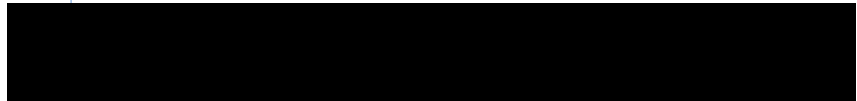
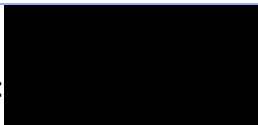
Location in thesis: Chapter 4

Student contribution to work:

DT overall contribution 75%. D.T., A.C., T.C., R.S., D.C. and J.D. collected the field data. A.C., T.C. and J.D. provided assistance with analyses. J.M. provided advice on statistics and manuscript refinement. D.Z. gave editorial advice on manuscript development. D.T analysed the data and drafted the manuscript, with reviews and editorial input from all co-authors.

Co-author signatures and dates (remaining co-authors provided written agreement):

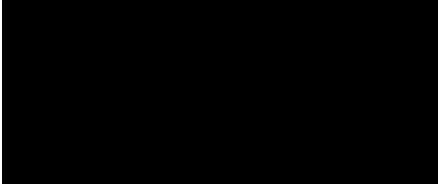
			
21/11/2020	21/11/2020	28/11/2020	29/11/2020

Details of the work:		
Tickler D.M., Carlisle A.B., Chapple T.K., Curnick D.J., Dale J.J., Schallert R.J., Block B.A. (2019) Potential detection of illegal fishing by passive acoustic telemetry. Animal Biotelemetry 7:1		
Location in thesis: Chapter 5		
Student contribution to work:		
DT overall contribution 75%. D.T., A.C., T.C., D.C and J.D. collected the field data. D.T. and A.C. conceived the manuscript. JM provided advice on framing and choice of analyses. D.T analysed the data and drafted the manuscript, with reviews and editorial input from all co-authors		
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I, Jessica Meeuwig, certify that the student's statements regarding their contribution to each of the works listed above are correct.

As all co-authors' signatures could not be obtained, I hereby authorise inclusion of the co-authored work in the thesis.

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Date: 30 November 2020

Chapter 1: Introduction

The ocean is the basis of life on earth. It incubated our planet's earliest lifeforms, initiating a chain of events that led to the evolution of *Homo sapiens*, and continues to support life on earth and human society in fundamental ways. At least half the oxygen in the earth's atmosphere comes from marine phytoplankton (Harris 1986), and millions of people rely on the ocean directly for food, livelihoods, or both (FAO 2020). Fish and shellfish are a vital source of micronutrients in food-insecure countries, playing an important role in public health (Hicks et al. 2019). Additionally, by cycling nutrients and organic matter between sunlit surface waters and buried sediments, the ocean's biological pump sequesters carbon in large quantities (Buesseler et al. 2020). In doing this, the ocean has contributed to stabilising global climate over the past centuries, absorbing both greenhouse gasses and the heat they have trapped (Siegenthaler & Sarmiento 1993, Cheng et al. 2019).

1.1 Marine biodiversity in the Anthropocene

Most of the services provided to humankind by the ocean depend on complex interactions between thousands of species of marine life (Worm et al. 2006). For centuries we have been removing vital cogs from the ocean's 'biological machinery', for food, fur, fuel or fun (Busch 1985, Scott Baker & Clapham 2004, Roberts 2010, Freire et al. 2020). Only in the last few decades, as marine science has begun to catch up with exploitation, have we begun to realise that the ocean might be under serious threat from us (Roberts 2010, IPBES 2019). This has prompted a growing recognition, enshrined in international commitments such as the Sustainable Development Goals (United Nations 2019), of the need for us to reduce our footprint on the ocean and to balance resource use with protection if we are to continue to benefit from the ocean's services (Worm et al. 2006).

In an age of ocean industrialisation, our impacts are now ubiquitous (McCauley et al. 2015). Marine traffic generates noise pollution and wildlife strikes (Putland et al. 2018, Crum et al. 2019), plastic waste and fishing gear choke and entangle marine life (Stelfox et al. 2016, Forrest et al. 2019), dredging and harmful fishing gears directly alter benthic habitats (Oberle et al. 2016, Wenger et al. 2018), and even recreational visitors to the ocean inadvertently poison the coral reefs they visit with their sunscreen (McCoshum et al. 2016). However, the most immediate, widespread and serious threat to marine life and biodiversity is unsustainable fishing (IPBES 2019). Overfishing has depleted the abundance and richness of fishes in coastal, pelagic and deep habitats, leading to trophic downgrading, a decline in the ocean's capacity to supply us with protein and nutrients, and a

defaunation of the oceans that undermines ecosystem function (Pauly & Palomares 2005, McCauley et al. 2015, Pauly & Zeller 2016). In particular, fisheries have caused widescale and steep declines in the abundances of predatory species, including those targeted for their desirable flesh, such as tunas, groupers and cods (Collette et al. 2011, Valdivia et al. 2017, Neuenhoff et al. 2018), and species like sharks, which have been killed as bycatch in fisheries targeting sympatric teleosts, to furnish demand for their highly valued fins, and increasingly for their meat (Dulvy et al. 2017, Sadovy de Mitcheson et al. 2018).

1.2 The importance of mobile marine predators

While all overfishing is a concern in an era when the ocean's resilience is being tested on multiple fronts (Sumaila & Tai 2020), over-exploitation of large predators is hardest to reverse due to their slower rates of reproduction (Smith et al. 1998), and may have disproportionately greater effects on ecosystem function (Ferretti et al. 2010). Predators in both terrestrial and marine ecosystems exert direct, i.e. predation mortality, and indirect, or fear-based, influences on prey species, the latter magnifying their influence beyond the direct consumption of prey (Zanette & Clinchy 2019). In the ocean, large mobile predators like sharks can create 'seascapes of fear' within which prey species modify their behaviour, and even growth, in response to predation risk, impacting their own fitness and creating cascading effects on lower trophic levels (Wirsing et al. 2008, Palacios & McCormick 2020). For example, the presence of tiger sharks (*Galeocerdo cuvier*) influences patterns of dolphin, turtle and dugong foraging in Shark Bay in Western Australia, in the latter case causing cascading effects on seagrass distribution (Heithaus & Dill 2002, Heithaus et al. 2007, Burkholder et al. 2013). On coral reefs, the diet and condition of mesopredatory fish are poorer when shark numbers are high (Barley et al. 2017a). Hammerschlag et al. (2018) even demonstrated that the presence of predation risk changes the morphology of prey. Predators also appear to promote the coexistence of species within ecosystems (Wallach et al. 2015), with fish species diversity lower on coral reefs where sharks have been removed by fishing (Barley et al. 2017b).

The role of large mobile predators in promoting the functional diversity of marine communities may be particularly important in highly biodiverse and ecologically valuable systems like coral reefs (Ruppert et al. 2013). Coral reefs provide direct benefits worth billions of dollars to coastal communities, including the provision of food, livelihoods from fisheries and tourism, and coastal protection (Moberg & Folke 1999). They are also hubs of biodiversity and genetic resources (Bruckner 2002, Arrieta et al. 2010), and may provide globally important regulatory functions such

as carbon sequestration (Atwood et al. 2018). While there is ongoing debate about the strength and direction of the causal links between reef sharks and the health of coral reefs (e.g., Roff et al. 2016), ‘natural experiments’ (Barley & Meeuwig 2016) comparing areas or periods of contrasting reef shark abundance have linked shark population declines to cascading ecosystem effects (Mumby 2006, Ruppert et al. 2013), the latter mediated by the release of other reef species from predation and competition (Barley et al. 2017b, Hammerschlag et al. 2018).

In addition to their ecological importance, reef sharks also provide direct economic benefits as a drawcard for tourism. Shark diving and related activities globally generate over US\$200 million per year and contribute significantly to the economies of coastal nations, often in developing regions (Vianna et al. 2011, Clua et al. 2011, Gallagher & Hammerschlag 2011, Haas et al. 2017, Huveneers et al. 2017). The importance of reefs and reef sharks to the communities immediately dependent on them, as well as coral reefs’ role as global hubs of marine biodiversity, means that effective conservation and rebuilding of reef shark populations is considered an urgent priority (MacNeil et al. 2020).

1.3 Roles, risks and refugia: the spatial dimensions of reef shark conservation

The study of marine spatial ecology, i.e. the patterns and drivers of animals’ horizontal and vertical movements in the ocean, has helped to elucidate and differentiate the ecosystem roles of individual shark species (Hussey et al. 2015), improving our understanding of the services they provide in marine ecosystems (Heupel et al. 2019). Similarly, understanding the spatial footprint of anthropogenic threats, particularly fisheries, alongside the space use of sharks helps understand the magnitude and extent of the threat’s they face (Queiroz et al. 2016). Combining the two helps identify and demarcate habitats within which sharks might most usefully and effectively be protected (Chapman et al. 2005, Dwyer et al. 2020) and prioritise species, geographical areas and jurisdictions for conservation actions (Lucifora et al. 2011).

1.3.1 Spatial dimensions of reef shark ecology

The movement of sharks helps define the area over which they exert influence and the horizontal and vertical connections they mediate between ecosystems (Hussey et al. 2015, Heupel et al. 2018, O’Leary & Roberts 2018). It also provides insights into species’ life histories and physiologies. Animal-borne telemetry, which simultaneously gathers spatial and environmental data from tagged animals and their surroundings, has provided information on the activity spaces (Schlaff et al. 2017), migrations (Ferreira et al. 2015), diving behaviour (Andrzejczek et al. 2019), and habitat

associations of sharks (Heithaus et al. 2002). These in turn have been used to infer ecologically important functions such as competitive exclusion and resource partitioning (Papastamatiou et al. 2018), nutrient transport (Williams et al. 2018) and gene flow (Bonnin et al. 2019). It has also allowed us to infer aspects of species biology, such as philopatry (Jorgensen et al. 2010, Howey-Jordan et al. 2013) and ontogenetic changes in behaviour (Afonso & Hazin 2015). Finally, it can give insights into important aspects of animal's physiology, such as thermoregulation (Campana et al. 2011) and hypoxia tolerance (Jorgensen et al. 2009).

On coral reefs, spatial ecology can help resolve outstanding questions on the ecological roles of individual reef shark species (Roff et al. 2016, Heupel et al. 2019). In the past decade, stable isotope and diet analyses have challenged the former blanket classification of reef sharks as apex predators (Heupel et al. 2014, Frisch et al. 2016, Roff et al. 2016). Hussey et al. (2014) found that the stable isotope profiles of grey reef sharks (*Carcharhinus amblyrhynchos*) placed them at the same trophic level as many large teleost predators, and Barley et al. (2020) recently suggested that an overlap in gape and prey size between smaller reef sharks and large teleosts might predict a degree of functional redundancy based on prey size consumed. The authors of the latter paper did, however, conclude that larger reef sharks likely play unique roles on reefs that are not easily compensated for by teleosts (Barley et al. 2020). Consistent with this hypothesis, telemetry studies have shown that not all reef predators are necessarily equal, particularly in terms of where and what they eat. Grey reef sharks on the Great Barrier Reef occupy activity spaces orders of magnitude larger than large teleost piscivores like coral trout (*Plectropomus leopardus*, Zeller 1997, Espinoza et al. 2015b) or giant trevally (*Caranx ignobilis*, Lédée et al. 2015). Comparatively larger-scale movements by reef sharks means they may play a key role in ecologically important functions such nutrient transfer, e.g. from pelagic to reef ecosystems (Williams et al. 2018). Stable isotope analysis of grey reef sharks at Palmyra has showed their diet to have a strong pelagic signature, likely making them a source of nutrient import to the reefs (McCauley et al. 2012). Sharks' longer-range movements, relative to reef fish, may also magnify the 'seascape of fear' they create (Wirsing et al. 2008). This means that sharks may exert indirect, fear-based, control over disproportionately large areas, relative to their abundance.

Telemetry also reveals interspecific differences within the reef shark guild, including spatial partitioning (Papastamatiou et al. 2018) and differences in the size of their activity spaces, range of movement and connectivity between reefs (Espinoza et al. 2015c). This may relate in part to resource partitioning and the energetic needs of different species, with Curnick et al. (2019)

reporting that silvertip sharks (*Carcharhinus albimarginatus*) in the British Indian Ocean Territory (BIOT) consumed a higher share of pelagic prey than grey reef sharks in the same location. The ecological function of reef shark species may also be context dependent, with grey reef sharks at Palmyra Atoll in the Pacific exploiting a higher share of pelagic prey in their diets (McCauley et al. 2012) and making longer excursions in epipelagic waters (White et al. 2017) than individuals studied on the Great Barrier Reef (Espinoza et al. 2015b, Frisch et al. 2016). This suggests that space use and ecologically important behaviours such as foraging vary both between and within species.

1.3.2 The footprint of anthropogenic threats to sharks

1.3.2.1 Fishing

Fishing has led to widespread declines in the abundance of sharks (Ferretti et al. 2010), and is thought to be the primary driver of extinction risk in this group (Dulvy et al. 2014, Dulvy et al. 2021). While many of the species recognised as threatened by extinction are iconic pelagic species like the great hammerhead (*Sphyrna mokarran*) and oceanic whitetip shark (*Carcharhinus longimanus*), fishing has also impacted the abundance and diversity of sharks on reefs (Graham et al. 2010, Nadon et al. 2012, Juhel et al. 2018, MacNeil et al. 2020). The spatial ecology of some pelagic shark species has been shown to influence their exposure to fishing (Queiroz et al. 2016). Similarly, interspecific differences in the space use of reef sharks may lead to some being at higher risk from fisheries than others. Silvertip sharks have declined more sharply in abundance on fished reefs in northwest Australia relative to grey reef sharks (Meekan et al. 2006), which may relate to increased exposure to fishing due to their greater space use and dispersal around coral reefs (Espinoza et al. 2015a). Similarly, silvertip sharks outnumber grey reef sharks in the catches taken by illegal fishing vessels targeting reefs in the BIOT (Martin et al. 2013, IOTC Secretariat 2015). Silvertip sharks' use of larger areas around coral reefs than grey reef sharks therefore appears to increase their relative exposure to fishing. Understanding both the footprint of fisheries catching sharks and the relative vulnerability of different species is urgent given the ubiquity of global fisheries, whose spatial expansion (Kroodsma et al. 2018, Tickler et al. 2018b) means that fisheries now impact both coastal and pelagic shark habitats throughout the ocean (Lucifora et al. 2011, Queiroz et al. 2016, Cinner et al. 2018), with few natural refugia remaining (Juhel et al. 2018, Letessier et al. 2019).

While sustainable shark fisheries have been identified, such as for the gummy shark (*Mustelus antarcticus*, Walker 1998) in Australia, these are generally limited to a handful of jurisdictions with well-resourced and sophisticated fisheries management, and consequently only a small fraction of the total global shark catch is currently estimated to be biologically sustainable (Simpfendorfer &

Dulvy 2017). Management of sharks in fisheries is complicated by the diversity of fisheries in which they are taken, from small-scale subsistence fishers using handlines to meet their immediate food security needs (Glaus et al. 2019) to industrial trawl, longline and gillnet operations (Dulvy et al. 2017, Sadovy de Mitcheson et al. 2018). Additionally, sharks are often classified as bycatch by fisheries managers and therefore may be subject to weaker management (Fowler 2016). This is despite incidental shark catches contributing over a third of the total catch of vessels targeting species like swordfish (*Xiphias gladius*), which makes the bycatch definition questionable (Mejuto et al. 2009). Effective management is further confounded by incomplete and imprecise data resulting from underreporting of shark catches (Jacquet et al. 2008, Temple et al. 2019) and a lack of taxonomic information needed for species-level stock assessment (Cashion et al. 2019).

While underreporting of catches is a systemic problem in fisheries (Pauly & Zeller 2016), the accuracy of official data regarding shark catches may be particularly poor. Estimates based on surveys of the shark fin trade suggest that data reported by fishing countries to the UN Food and Agriculture Organisation (FAO) capture only a quarter of total shark landings (Clarke et al. 2006), implying that 75% is unreported. For comparison, the *Sea Around Us* project estimated that around one third of the global fisheries catch was unreported between 1950 and 2010 (Pauly & Zeller 2016). In reconstructing the global fisheries catch, the *Sea Around Us* have also improved the spatial resolution of available catch data, restoring information lost in the coarse aggregation of official reports (Zeller et al. 2016). This facilitates analysis of both temporal and spatial patterns in shark catches and catch reporting which can help identify hotspots of fishing mortality and knowledge gaps, and prioritise regions and fishing entities for whom improved management of shark fisheries is most urgently needed.

1.3.2.2 Climate change

Fishing is the most acute threat to sharks (Dulvy et al. 2021), but increased water temperature and reduced oxygen in the oceans due to ocean warming may further stress shark populations. Ectothermic marine species, including most sharks, are physiologically adapted to a relatively narrow range of temperatures (Sunday et al. 2011). Poleward shift in species' ranges in response to increases in global ocean temperatures are already being observed, and are forecast to increase in the future (Cheung et al. 2012, Sunday et al. 2015). The sensitivity of individual shark species to ocean warming will be determined in part by their thermal niche, their capacity to expand their range into more suitable habitat as conditions change, and indirectly by the responses of their prey.

Thus, thermal physiology, spatial ecology, habitat dependence and diet may affect their capacity for adaptation (Chin et al. 2010, Donelson et al. 2019).

Climate change will also manifest itself vertically in the water column. Warming oceans will hold less oxygen and become more stratified, causing expansion and shoaling of oxygen minimum zones (Gilly et al. 2013, Breitburg et al. 2018) and compressing available habitat for fishes (Stramma et al. 2012). Oxygen availability is a key constraint on the metabolisms of gill-breathing animals (Pauly & Cheung 2017) and experiments on captive sharks show stress responses in the presence of low oxygen levels (Carlson and Parsons 2001, Crear et al. 2020), while telemetry studies indicate that the space use of many species is constrained by dissolved oxygen (DO) levels (Drymon et al. 2014, Banez 2019). Diving behaviour relative to ambient DO suggests that sixgill sharks (*Hexanchus griseus*) can tolerate DO levels below 1 ml l⁻¹ (Coffey & Holland 2015), whereas shortfin mako sharks (*Isurus oxyrinchus*) rarely dive below the 2 ml l⁻¹ threshold (Vetter et al. 2008). While few similar studies have been performed with reef sharks, it seems plausible that they are subject to similar physiological constraints and that future changes in DO levels in the rapidly warming tropics may reduce the availability of suitable habitat for these species.

1.3.3 Spatial management of reef sharks

Conservation researchers and managers recognise the threats that fishing pressure and environmental changes pose to sharks, particularly in tropical coastal regions where strong demographic and socio-economic pressures overlap with reef ecosystems (Cinner et al. 2018). While tackling climate change requires global changes in energy policy, fisheries mortality can be adjusted at local and regional scales through management measures (Simpfendorfer & Dulvy 2017, Bradshaw et al. 2018). However, competing pressures on the livelihoods of fishers may lead to patchy compliance with fishing regulations (Fulton et al. 2011, Collins et al. 2020). A lack of data for the scientific management of shark stocks may also limit the efficacy of management within fisheries, as does the taking of sharks as bycatch in mixed species fisheries.

A complementary strategy to restore and maintain shark populations is to create areas within which shark fishing is prohibited entirely. Shark sanctuaries and no-take marine protected areas (MPAs) have been designated in some areas of the tropical oceans to support population recovery in reef sharks and other key species (Dulvy 2006, Edgar et al. 2014, Ward-Paige & Worm 2017). Shark sanctuaries have been declared around the world, often covering countries' entire exclusive economic zone (EEZ) such as in the Marshall Islands the Maldives (Ward-Paige & Worm 2017).

Regulations vary by jurisdiction but all prohibit the direct targeting of sharks, although other species are still fished, and most also ban the possession and transshipment of sharks within the area (Ward-Paige & Worm 2017). No-take MPAs, when properly designed and enforced, protect not only sharks but also part or all of the ecosystems around them. Speed et al. (2018) reported a four-fold increase in observed reef shark numbers in a strictly enforced MPA in north west Australia. Similarly, shark density in no-entry areas on the Great Barrier Reef, where human disturbance is all but absent, is almost six times that in surrounding fished areas, and is believed to be approaching recovery to full carrying capacity (Frisch & Rizzari 2019). Importantly, Frisch and Rizzari (2019) also found that designated no-take areas, where fishing was prohibited but access allowed, had only half the density of sharks as no-entry areas, which underscores the need for full and effective protection of sharks if population rebuilding is to occur. Protecting and restoring reef shark populations may help reverse trophic cascades and shifts in reef communities that threaten reef ecosystem function. Ruppert et al. (2013) found that fish assemblages on reefs with sharks were more robust to disturbance from environmental shocks, than were reef communities where sharks have been removed. When abundant, reef sharks influence the diet, condition and behaviour of other trophic groups, particularly mesopredatory fishes (Barley et al. 2017a b, Hammerschlag et al. 2018). While protecting sharks helps reefs, protecting reefs and the biodiversity and biomass of reef fish is obviously important to predators like sharks. In an earlier study, colleagues and I found that the distribution of prey biomass was the strongest predictor of variations in reef shark abundance within a large MPA (Tickler et al. 2017). This ecosystem-level protection offers perhaps the best hope for buffering coral reef systems against climate change, by protecting both the reef and the biological assemblage of fishes and sharks that maintain the resilience of the system. However, not all protected areas are equally effective in protecting sharks, with size and the strictness and degree of enforcement of regulations key dimensions determining success (Edgar et al. 2014, Juhel et al. 2018, Dwyer et al. 2020).

Protected area size clearly matters for mobile species like sharks (Lea et al. 2016, Martín et al. 2020, Dwyer et al. 2020). Activity spaces for reef-attached but mobile species like grey reef sharks are of the order of 10-100 km², implying a protected area radius of at least 5 km (Espinoza et al. 2015b). Larger species, like silvertip sharks move over greater distances (Espinoza et al. 2015c, Martín et al. 2020) and therefore an MPA designed for one species may only confer partial protection on another; conversely, choosing to design MPAs around the spatial needs of a wider ranging umbrella species can confer benefits on more site-attached congeners (Osgood et al. 2020).

Marine protected area design, including for shark sanctuaries as 'taxon-specific' MPAs, also needs to account for the importance of different habitats to different shark species (Tickler et al. 2017, Letessier et al. 2019, Birkmanis et al. 2020). In particular, 'hidden' deep-water features such as submerged seamounts and canyons may be locations of enhanced productivity and predator abundance (Hosegood et al. 2019, Forrest et al. 2020, Leitner et al. 2020). Recognising the importance of vertical as well as horizontal space use in sharks and other taxa when designing individual or networked sanctuaries or MPAs may help ensure that protection better represents key habitats.

The effectiveness of spatial protection for sharks can be further influenced by both the socio-economic context and the strength of the protection measures themselves. Poverty, and the attendant lack of food security and alternative livelihoods, is commonly cited to explain fishers' failure to comply with shark conservation measures (Collins et al. 2020, MacKeracher et al. 2020). Effective shark conservation strategies clearly need to incorporate measures to mitigate any short-term economic consequences of area closures or shark fishing bans on fisheries-dependent communities, particularly in the developing world (Ali 2015, Smyth & Hanich 2019, MacKeracher et al. 2019). However, even when sharks are not actively targeted, their accidental capture continues to undermine conservation goals when species typically need decades to recover from over-exploitation (Russ & Alcala 2010). This implies that no-take areas will out-perform those with partial protection measures which do not exclude *all* fishing, such as shark sanctuaries or multiple use MPAs where some extractive activities (e.g., fishing with certain gears, or recreational fishing only) are still allowed (Costello & Ballantine 2015, Ward-Paige & Worm 2017, Zupan et al. 2018). Additionally, illegal fishing for sharks can persist in no-take areas, including in developed countries where the socio-economic defence is less credible, because legal activities in the MPA provide a cover for poaching (Bergseth & Roscher 2018, Frisch & Rizzari 2019). Taking the additional step of declaring MPAs as no-entry, not just no-take (McCook et al. 2010), appears to help address this problem by reducing the burden of proof required to identify illegal activity and thus simplifying the enforcement and prosecution process (Frisch & Rizzari 2019). As well as informing protected area design, spatial data, in the form of remote vessel position monitoring, can potentially be a powerful tool in helping enforcement in these cases (Bradley et al. 2019, Belhabib et al. 2020).

1.4 Using animal telemetry to investigate the role of space use in the ecology and protection of reef sharks at isolated coral reefs

My thesis uses animal telemetry to examine the spatial ecology of two common Indo-Pacific reef shark species, the grey reef (*Carcharhinus amblyrhynchos*) and the silvertip shark (*Carcharhinus albimarginatus*). The research is focused in the Chagos Archipelago in the BIOT, a large but isolated coral reef system in the central Indian Ocean (Figure 1.1). The goals were to describe their horizontal and vertical space use in the BIOT, contribute to refining our understanding of their ecosystem roles, and inform protected area design and management for the two species.

1.4.1 Study area: The British Indian Ocean Territory Marine Protected Area

The BIOT MPA, established in 2010, contains a large, isolated and largely unpopulated reef system, the Chagos Archipelago, set within 650,000 km² of open ocean in the central Indian Ocean. The Chagos Archipelago is part of the Chagos-Laccadive Ridge (CLR), a chain of volcanic features which includes the Maldives and the Laccadive Islands off the west coast of India (Ashalatha et al. 1991). While the Chagos Archipelago may have been connected to the northern parts of the CLR in the past (Ashalatha et al. 1991), it is now isolated from its closest neighbouring reef system by ~500 km of deep ocean.

The Chagos Archipelago is considered one of the most pristine coral reef systems in the world, and the BIOT MPA is the only MPA of comparable size in the Indian Ocean (Sheppard et al. 2012). The MPA contains diverse tropical marine habitats including coral atolls, islands and lagoons and numerous seamounts, some of which rise to within 80 m of the surface. The area is the focus of long-term studies of coral and reef fish communities, and is considered to be an important reference site for reef studies within the heavily impacted Indian Ocean (Sheppard 1999, Koldewey et al. 2010, Hays et al. 2020). An objective of the MPA was the recovery of reef shark populations, which had declined prior to protection, largely due to unlicensed fishing by vessels from southern India and Sri Lanka but also likely partly influenced by licensed fisheries targeting tunas offshore and reef fish around the atolls (Graham et al. 2010, Koldewey et al. 2010, Martin et al. 2013). Evidence from vessels arrested in the MPA since 2010 suggests that illegal fishing of reef sharks remains an ongoing issue (IOTC Secretariat 2015). Therefore, studying the spatial ecology of reef sharks in BIOT is of interest not only to test hypotheses about inter and intraspecific variation in space use with respect to results obtained in other locations, but also to understand the drivers of space use of sharks within BIOT and how this relates to illegal fishing risk and enforcement.

It must be noted that the Chagos Archipelago has a vexed political history. It was incorporated into the United Kingdom (UK) as an overseas territory in the late 1960s, when Britain's former colonies in the Indian Ocean were gaining independence. Until then, several of the larger islands were occupied by the descendants of indentured labourers who had been brought to the Archipelago to maintain coconut plantations. Their relocation by the UK government to Mauritius, the Seychelles and the UK, beginning in the early 1970s, is the subject of ongoing controversy and legal challenges (Vine 2004, Allen 2019). It was against this backdrop that the MPA was created by the British government in April 2010, and the UK's sovereignty over the area continues to be contested by the Mauritian government. However, although the United Nations International Court of Justice found in favour of Mauritius in its 2019 *Chagos Advisory Opinion* (Allen 2019), the UK continues to assert its sovereignty over the BIOT, and MPA continues to be managed as a no-take marine reserve.

1.4.2 Focal species

Grey reef and silvertip sharks are two widely occurring Indo-Pacific reef shark species (Compagno 1984). They are both of conservation concern and are assessed as Endangered and Vulnerable, respectively, by the IUCN (Dulvy et al. 2014, IUCN 2020, Dulvy et al. 2021), with the grey reef shark recently downgraded from Near-Threatened in the light of steep declines detected from several locations around the tropics (MacNeil et al. 2020, Dulvy et al. 2021). Surveys on reefs suggest that numbers of both have declined in response to fishing (Meekan et al. 2006, Graham et al. 2010, MacNeil et al. 2020). While the spatial ecology of grey reef sharks has been studied in a number of Indo-Pacific locations, the two species have only been studied together and concurrently on the Great Barrier Reef (Espinoza et al. 2015c) and at D'Arros Atoll in the Seychelles (Lea et al. 2016, Figure 1.1). Additionally, intra-specific differences between grey reef sharks monitored at Palmyra Atoll in the Pacific (White et al. 2017) and on the Great Barrier Reef (Espinoza et al. 2015b) suggest that their spatial ecology may vary with reef type (isolated atoll vs barrier reef) and in the context of competition from other species. Therefore, studying both species at an isolated reef system in the Indian Ocean allows questions of the role of context and competition in reef shark spatial ecology to be further explored.

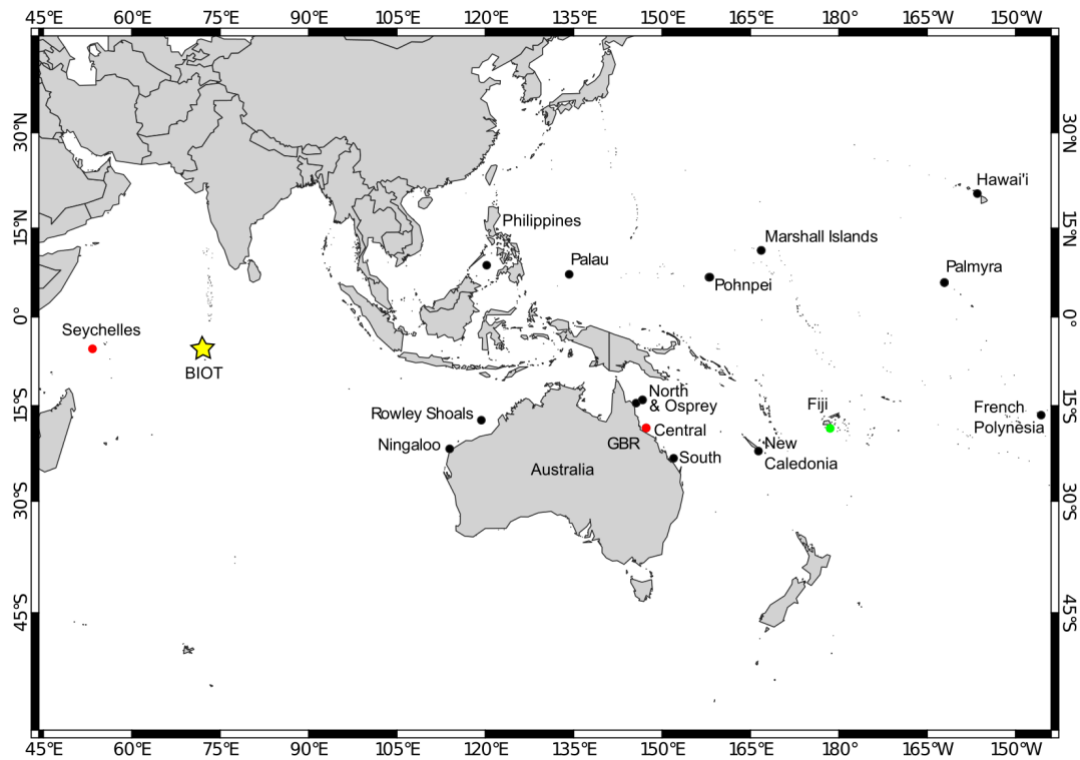


Figure 1.1: Map of the Indo-Pacific region highlighting sites where grey reef sharks (black), silvertip sharks (green) have been studied using telemetry. Red points are locations where both have been studied concurrently. The BIOT is marked with a yellow star.

1.4.3 Objective of the thesis

The objective of my thesis is to compare and contrast reef-associated sharks in the BIOT MPA in terms of their space use and habitat associations, in order to better understand the nature and extent of variations in spatial ecology between and within species and locations and inform broader questions on reef shark ecology. From a management perspective I hope to use the insights on reef shark spatial ecology generated from this study to improve our understanding of the risks they face from fisheries and other anthropogenic threats, and contribute to both species-specific management of reef sharks in BIOT. To do this, I use global fisheries data, vessel specific data on shark fishing in BIOT, and passive acoustic and satellite archival telemetry to examine both threats and ecology of reef sharks at multiple spatial and temporal scales. The specific questions addressed by my thesis are:

- 1) What are the key temporal and spatial trends in shark catches and their implications for shark conservation in general and for reef sharks in the Indian Ocean in particular?
- 2) What are the similarities and differences in the spatial ecologies of grey reef and silvertip sharks at shallow and deep reefs within BIOT, and between BIOT and the other locations where the two species have been studied?

- 3) What can the vertical ecology of reef sharks with respect to water column temperature and oxygen profiles tell us about their thermal and DO preferences and what does this imply for their vulnerability to climate change.

These questions are addressed across four data chapters:

- Chapter Two analyses spatial and temporal trends in catch volumes and catch reporting from global shark fisheries, using reconstructed catch data from the *Sea Around Us*. The data are used to identify key knowledge gaps and the geographies and jurisdictions with which to engage in improving the management of shark fisheries.
- Chapter Three analyses inter- and intraspecific variations in space use by grey reef and silvertip sharks at different reef habitats within BIOT using acoustic telemetry data, and looks at the similarities and differences to the results of studies conducted in other reef systems.
- Chapter Four examines the vertical and thermal niche and diving behaviour of silvertip sharks using high resolution depth and temperature data derived from miniature pop-up archival tags (mini-PATs). These data are used to identify drivers of the vertical movements of silvertips sharks, as well as infer thermal and oxygen-based constraints on their space use.
- Chapter Five reports a case of passive detection of illegal fishing activity through acoustic tagging, and discusses the potential of novel tag-based tools to improve the monitoring and enforcement of protected area for high value species like sharks.

1.5 Additional information

In addition to the core chapters of my thesis, I include, as appendices, related work undertaken during my PhD on fisheries and telemetry which connects to the core themes of reef shark space use and the threat of overfishing. Marine wilderness available to sharks and other marine taxa, has been increasingly constrained by the expansion of human activity in the ocean (Jones et al. 2018). Appendix 1 (Tickler et al. 2018b) looks at the spatial expansion of fisheries since the 1950s, in particular the boom-and-bust pattern of serial overexploitation by distant water fleets that now threatens the last remaining isolated refugia. An interdisciplinary investigation into the links between overfishing and labour abuses in fisheries (Tickler et al. 2018a), included as Appendix 2, found that labour abuses are most prevalent in unprofitable fisheries operating without adequate oversight, and concluded that addressing the underlying factors driving unsustainable fishing, including harmful subsidies and poor monitoring of fishing activity, benefits both fishers and the marine ecosystem. This latter work seeks to build on Kittinger et al. (2017) in making common cause

between those focussed on the conservation of species like sharks and those more concerned about equity and human rights issues. I also co-authored a high-level review of the efficacy of the BIOT MPA for taxa with varying spatial ecologies (Carlisle et al. 2019, included as Appendix 3). This compared the overall space use of pelagic sharks and tunas and reef sharks within the BIOT MPA, and also explored methodological questions related to the impact of acoustic array design on observed residency metrics for reef sharks.

1.6 Summary

Marine biodiversity is critical to the healthy function of the ocean (Worm et al. 2006) yet is threatened by defaunation (McCauley et al. 2015) and, in particular, by the removal of large, ecologically-important predators (Ferretti et al. 2010). As global fisheries have expanded (Tickler et al. 2018b) and anthropogenic climate change alters the physical properties of the marine environment (Breitburg et al. 2018, Cheng et al. 2019), the space use of marine predators like sharks is key to understanding their ecosystem roles, their vulnerabilities and their conservation.

Ensuring that the ecosystem function of sharks in economically important, biodiverse but threatened ecosystems like coral reefs is maintained in the Anthropocene requires us to understand both the space needs of sharks (Dwyer et al. 2020) and the nature and extent of the threats they face. Doing so will allow us to create areas free of direct anthropogenic disturbance, which are urgently needed to promote resilience to the longer-term threat of climate change, over which we may have limited, if any, effective control.

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Chapter 2: You can't manage what you don't measure: global and regional trends in shark catch data, 1950-2014.

2.1 Abstract

Populations of sharks and other large marine predators have declined globally as a result of exploitation, and improved management is urgently needed. Despite this, accurate catch data to inform management are absent for many fisheries. Analysis of reconstructed global fisheries catches from the *Sea Around Us* suggests that official data underestimate global shark catches by a factor of two. Catches more than doubled from 1950 to 2014 to 1.3 million tonnes per year, but average catch-per-unit-area declined by over two thirds over the same period. The fall in shark catch density, despite ever-increasing fishing effort, is further evidence of underlying population declines and unsustainable fishing levels. Catch growth has been strongest in tropical and subtropical waters, driven by large domestic shark fisheries in South and Southeast Asia, and a rapidly increasing catch by distant-water fleets on the High Seas and in the Exclusive Economic Zones of countries in Asia and Africa. Science-based management of sharks in these fisheries is impeded by a lack of transparency in catch data resulting from widespread under-reporting, particularly of discarded shark catches, and poor taxonomic resolution in the catch data that are reported. Better data collection will help close the knowledge gap in shark fisheries, but management of intrinsically vulnerable species will remain challenging. The complementary use of marine protected areas to provide refugia from fishing pressure would bolster management strategies against residual uncertainty, and help to safeguard shark populations and ecosystem integrity into the future.

2.2 Introduction

Sharks are among the most threatened marine vertebrate groups, with one in six species at risk of extinction compared with one in ten species for marine taxa as a whole (Dulvy et al. 2014, Dulvy et al. 2021). The key threat to sharks is fishing, which has greatly reduced populations of large marine predators (Myers & Worm 2005, Ferretti et al. 2008). The majority of shark catches are taken by commercial industrial and artisanal fisheries, which have historically been incentivised by high prices paid for fins in the luxury shark fin soup trade (Sadovy de Mitcheson et al. 2018). Increasing consumption of shark meat also contributes to their value as a fisheries target (Dulvy et al. 2017), although this may partly itself be a by-product of the fin trade as changing regulations motivate fishers to develop markets for previously discarded carcasses (Dent & Clarke 2015). The emergence of new markets for shark meat may also reflect global trends in increasing demand for marine protein and declining finfish stocks (FAO 2018, Glaus et al. 2019). Exploitation of sharks is therefore sustained both by ongoing demand for their fins and by broader trends in global fisheries, including rising population and per-capita seafood demand (FAO 2018), unsustainable increases in fishing effort (Rousseau et al. 2019), and the imperatives of food security and livelihoods in coastal regions (Teh & Sumaila 2011, Teh & Pauly 2018).

Fisheries-driven declines in shark populations have prompted concern over the impact on individual species and the wider marine ecosystem (Heithaus et al. 2008, Ferretti et al. 2010). As mobile high trophic-level predators, large sharks exert wide-ranging direct (i.e. predation) and indirect (e.g. behavioural) effects on competitors and prey species (Wirsing & Ripple 2011, Barley et al. 2017), and mediate ecological connections between ecosystems (Williams et al. 2018). These interactions impact the function and resilience of marine ecosystems, and ultimately the services they provide to humankind (Heithaus et al. 2014, Atwood et al. 2015). Sharks also provide direct, non-consumptive economic benefits through tourism, with the long-term value of sharks at popular diving destinations estimated to be several orders of magnitude higher than their one-off value as fisheries catch (Gallagher & Hammerschlag 2011, Vianna et al. 2012). In response to increasing evidence of the overexploitation threatening sharks and their ecological and socio-economic contributions, measures to halt population declines and promote recovery are a growing focal area for national and international policy (Fowler & Cavanagh 2005, Dulvy et al. 2017).

One approach to restoring shark populations is to set and enforce science-based sustainable limits for shark catches (Shiffman & Hammerschlag 2016). Sustainable shark fisheries are considered

possible for a subset of species, but require effective fisheries management and good data. (Simpfendorfer & Dulvy 2017). These criteria, particularly the last, are not currently met in most parts of the world, and fisheries for low-reliance species have only been identified in areas with well-resourced fisheries management (Simpfendorfer & Dulvy 2017). The reliability of shark catch data may be particularly influenced by their status as ‘bycatch’ in many, if not most, fisheries, leading to patchy and uninformative reporting of catches by both coastal states and Regional Fisheries Management Organisations (RFMOs, Oliver et al. 2015).

Complementary to the management of sharks within fisheries is the use of shark sanctuaries and no-take marine protected areas (MPAs) to provide sharks with spatial refugia from fishing effort (Davis 1989, Ward-Paige and Worm 2017, Dwyer et al. 2020). No-take MPAs in particular can play an important role in balancing economic and biodiversity conservation objectives in fisheries (Hoffmann & Pérez-Ruzafa 2009) and may be of particular value in data-poor situations requiring precautionary management, where they provide decision-makers with much-needed insurance against uncertainties (Lauck et al. 1998).

Identifying priority species and geographies for management reform and designing appropriate strategies to improve the management of sharks requires reliable, detailed and spatially explicit data on current and historical catches of sharks, and the fishing countries and jurisdictions involved in their management. Recognition of the uncertainties and knowledge gaps that persist is also needed to ensure that management takes an appropriately precautionary approach.

A key resource for assessing global fisheries catches is the data compiled by the United Nations’ Food and Agriculture Organisation (FAO), beginning in 1950 and updated annually (Garibaldi 2012). However, these data rely on country reports of fisheries landings, which vary in completeness and taxonomic resolution (Cashion et al. 2019), underestimating or excluding catches from small-scale fisheries, and excluding discarded catches (Pauly & Zeller 2016). The *Sea Around Us* (www.seaaroundus.org) has developed a detailed catch reconstruction process incorporating all available information on a country’s fisheries, including data not reported to FAO, estimates from country experts, scientific and grey literature, etc. (Pauly et al. 2020). These sources are used to infer gaps in the data reported by the FAO, estimate missing, unreported and discarded catches, and improve the taxonomic and spatial resolution of the data for every maritime country (Zeller et al. 2016).

I used the *Sea Around Us* reconstructed catch database to determine trends in total shark catches, catch reporting and the spatial distribution of catches from 1950 to 2014. I then examined variations in the operating areas, catch reporting and catch composition of the ten largest shark fishing countries to understand their differing roles in the global shark catch. Finally, I looked at the available data on shark catches on the High Seas, by RFMO management area, in terms of the major fishing countries involved, catch reporting and species composition. The results were used to identify key issues with available shark catch data, and focal regions and entities to target for improvements in data collection and catch management.

2.3 Materials and methods

2.3.1 Data sources

2.3.1.1 Reconstructed catch data

The *Sea Around Us* fisheries catch database (www.seaaroundus.org) contains over 270 Exclusive Economic Zone (EEZ)-level catch reconstructions, accounting for reported and unreported landed and discarded catches in all fishing sectors (Zeller et al. 2016), as well as harmonised catch data from the global, large pelagic fisheries ('tuna and billfish fisheries') reported by the RFMOs (Coulter et al. 2020). The *Sea Around Us* catch reconstructions are built on data reported by member states to the FAO, meaning that catches are assigned to the fishing country (i.e. flag state) identified in the original FAO reporting, rather than the country of beneficial ownership, if different. For example, catches by vessels flagged to Togo but owned by a South Korean company are assigned to Togo in both FAO data and the reconstructions. Reconstructed catch data are spatially allocated to ~150,000 0.5° x 0.5° grid cells covering the world's ice-free oceans. Spatial allocation of catches accounts for the political and historical accessibility of EEZ waters by the fleets of each fishing country (Zeller et al. 2016) and species' habitat affiliations and biological distributions (Palomares et al. 2016).

2.3.1.2 Data pre-processing

Grid cell-based catch data for all taxa for 1950 to 2014 were extracted from the *Sea Around Us* database. The data were summarised by year, cell ID (representing location), taxon ID, fishing country, fishing sector (industrial or small-scale: artisanal/subsistence/recreational combined), reporting status (reported or unreported) and catch status (retained or discarded). Each catch record's taxon ID was linked to a scientific name (i.e., species, genus or higher taxonomic rank) and a functional group (e.g., fish, shark, crustacean, mollusc, etc.) in the *Sea Around Us* taxonomic metadata. Catch records assigned to the two functional groups "Small to medium sharks (<90 cm)"

and “Large sharks (≥ 90 cm)” within the class Elasmobranchii were labelled as “sharks”; all other records were labelled as “fish”, meaning all other fishes and invertebrates in this case. The size split between functional groups is based on the ecological modelling parameters described in Christensen et al. (2009). The shark taxa included in the *Sea Around Us* data in the two functional groups above are listed in Supplementary Table 2.1, and include all major shark families, with the exception of the bullhead sharks, Heterodontidae. The shark groupings in the *Sea Around Us* data explicitly exclude the rays and sawfish (Myliobatiformes, Pristiformes, Rajiformes and Torpediniformes) and the chimaeras (Holocephali). This allowed the catch data to be filtered for subsequent analysis of shark catches only. Each catch record was also coded by the taxonomic rank to which it had been recorded – i.e. Species, Genus, Family, Order or Class. Where catch was identified to species level, the main ocean habitat classification of the species (Oceanic, Semipelagic, or Coastal) was determined based on the definitions in Appendix I of Camhi et al. (2009), with species not identified in that report considered Coastal for the purpose of my analysis.

2.3.1.3 Geographic metadata

Geographic metadata were appended to catches based on the cell ID and centroid (latitude/longitude) of each $0.5^\circ \times 0.5^\circ$ cell in the spatially allocated data, with cell centroids assumed to represent catch locations in subsequent analyses. Catches were assigned to EEZs or the High Seas (i.e. areas beyond national jurisdiction) based on *Sea Around Us* cell metadata. Major ocean regions (Atlantic, Pacific and Indian) were defined using the boundaries of the FAO Major Fishing Areas (FAO areas, <http://www.fao.org/fishery/area/search/en>). Climate zones in both hemispheres (Polar, Temperate, Subtropical and Tropical) were defined using the geographical bounds in Palomares et al. (2020), which largely reflect variations in surface water temperature (Supplementary Figure 2.1). Shapefiles of RFMO boundaries were obtained from the FAO GeoNetwork spatial data repository (<http://www.fao.org/geonetwork>). I used the function `over()` in the R package *sp* (Pebesma & Bivand 2005) to assign spatial catch cells in the *Sea Around Us* data to an ocean region, climate zone and RFMO based on their spatial overlap with the corresponding shapefile.

2.3.2 Analyses

2.3.2.1 Global trends in shark catch 1950-2014

Total shark catch was summed by year, divided into catches reported to species-level, catches reported at higher taxonomic levels, unreported but retained catches, and discarded catches. The trend in total shark catch was also disaggregated by fishing sector (Industrial or Small-scale) and

catch type (Retained or Discarded), jurisdiction (EEZ or High Seas), and species habitat (Oceanic, Semipelagic or Coastal). For the habitat analysis, catches of blue sharks (*Prionace glauca*) were shown separately from the other oceanic species due to their high prevalence in the catch data. Each cross-section of the catch time series was visualised as a stacked area chart. To compare catch reporting of sharks with that of other taxa, the share of catches reported, the share of reported catches identified to species, and discard rates were calculated for both sharks and fish.

2.3.2.2 Spatial expansion of global shark fisheries

I aggregated shark catches by year, ocean region and climate zone, and plotted catch time series by ocean region and by ocean/climate zone region. I calculated the average annual shark catch in each 0.5° x 0.5° cell in the spatially allocated data for each decade in the time series (1950 to 1959 = '1950s', etc.), pooling the years 2000 to 2014 as the '2000s'. I then calculated each cell's contribution to the global catch in each decade, and visualised changes in the geographical extent and concentration of shark catches by mapping the cells containing 50%, 75%, 95% and 99% of the global catch in each decade. To identify the cells falling within each threshold I ranked the cell catches in descending order and labelled the cells whose cumulative catch remained within the threshold percent of the global total.

2.3.2.3 Major shark fishing countries, catch areas, catch reporting and taxa caught

Shark catch data for the period 2005-2014 were aggregated by fishing country for the ten largest shark fishing countries, based on their total catches over that period. I calculated sharks catches for each country as a percentage of each country's total fisheries catch and as a percentage of the global shark catch, the percentage of shark catch reported and the percentage reported to species level. I calculated the average annual cell-based shark catch per unit area for each country. The resulting catch density rasters were mapped to visualise the distribution of each fishing country's catches. I assigned an 'area of operation' to each country's shark catches. Catch in a fishing country's own EEZ was "Domestic", that in the EEZs of other countries was "Other EEZ", and non-EEZ catches were labelled "High Seas". I calculated each fishing country's average annual catch in each area of operation and plotted the data as stacked bars with the countries ordered in descending order of their total average annual catches. Each country's catch reporting was analysed in a similar fashion, disaggregating total catch into catches reported to species, catches reported to genus or family, catches reported at higher taxonomic levels, unreported but retained catches, and discarded catches. Finally, I aggregated each country's average annual catch by shark family. Blue sharks were identified separately from other carcharhinid sharks, and the six largest categories were grouped

separately with the remainder grouped as “Other”. Unidentified shark catches were grouped as “Sharks nei” (not elsewhere included) as per FAO standards.

2.3.2.4 Catches in the top ten EEZs by fishing entity

Shark catch data for the period 2005-2014 were aggregated by EEZ for the ten EEZs with the largest total shark catches. I summed catches for the host nation and the six largest fishing countries catching sharks in those EEZs, with remaining catches assigned to the “Other” category.

2.3.2.5 High Seas catches in RFMO areas of competence

High Seas catches for the period 2005-2014 were aggregated by RFMO area for the four tuna RFMOs responsible for 95% of High Seas shark catches (www.seaaroundus.org, Coulter et al. 2020). The four RFMOs were the International Commission for the Conservation of Atlantic Tunas (ICCAT), the Inter-American Tropical Tuna Commission (IATTC), the Western and Central Pacific Fisheries Commission (WCPFC) and the Indian Ocean Tuna Commission (IOTC). Catches in the Commission for the Conservation of Southern Bluefin Tuna (CCSBT) were not analysed as they contributed only 5% of the tuna RFMO total. Catches in the area of overlap between the IATTC and WCPFC were assigned to the IATTC, since the majority of IATTC regulations now apply in this area (<https://www.federalregister.gov/d/2020-11981>). Each RFMO’s catch reporting was analysed in a similar fashion, disaggregated into catches reported to species, catches reported to genus or family, catches reported at higher taxonomic levels, unreported but retained catches, and discarded catches. Finally, I aggregated each RFMO’s average annual catch by shark family. Blue sharks were identified separately from other carcharhinid sharks, and the five next largest categories were presented separately with the remainder grouped as “Other”. Unidentified catches were grouped as “Sharks nei”.

2.4 Results

2.4.1 Overall trends in global shark catches

Total shark catches increased from around 550,000 tonnes per year in the early 1950s to 1.3 million tonnes per year by 2014. Only 50% of the total 67 million tonnes of sharks estimated to have been caught during this period were officially reported (Figure 2.1a). Catches peaked in 1999 at 1.4 million tonnes per year. The proportion of reported shark catches identified to species increased from ~20% in 1950 to ~40% in 2014 (Figure 2.1a, Supplementary Figure 2.2), although the improvement in catch identification appears largely due to increased reporting of catches of blue sharks (Supplementary Figure 2.2). The share of catches reported and the share of reported catches identified to species are both lower for sharks compared to the average for other exploited taxa (Supplementary Figure 2.2).

Increases in shark catches and discards have come mainly from industrial fisheries, whose share of the global total grew from 51% to 73% between 1950 and 2014, while catches from small-scale fisheries remained stable (Figure 2.1b). Industrial fisheries discarded 42% of shark catches between 1950 and 2014, while small-scale fisheries retained ~95% (Figure 2.1b). Discard rates of sharks in industrial fisheries have declined, however, from 47% in the 1950s to 30% at present. Overall, discarded catches make up 23% of the total reconstructed shark catch (Figure 2.1a).

With increased industrial fishing of sharks, the share of shark catches taken from the High Seas has also increased, from averaging 2.5% in the 1950s to an average of 20% between 2005 and 2014 (Figure 1c). This increase is particularly noticeable starting in the 1980s after the United Nations Convention of the Law of the Sea (UNCLOS) and the resultant growth in EEZ declarations (UN General Assembly 1982). There has been a concurrent increase in the proportion of oceanic species, in particular blue sharks, identified in the global shark catch, and a decline in the proportion of coastal shark species (Figure 2.1d).

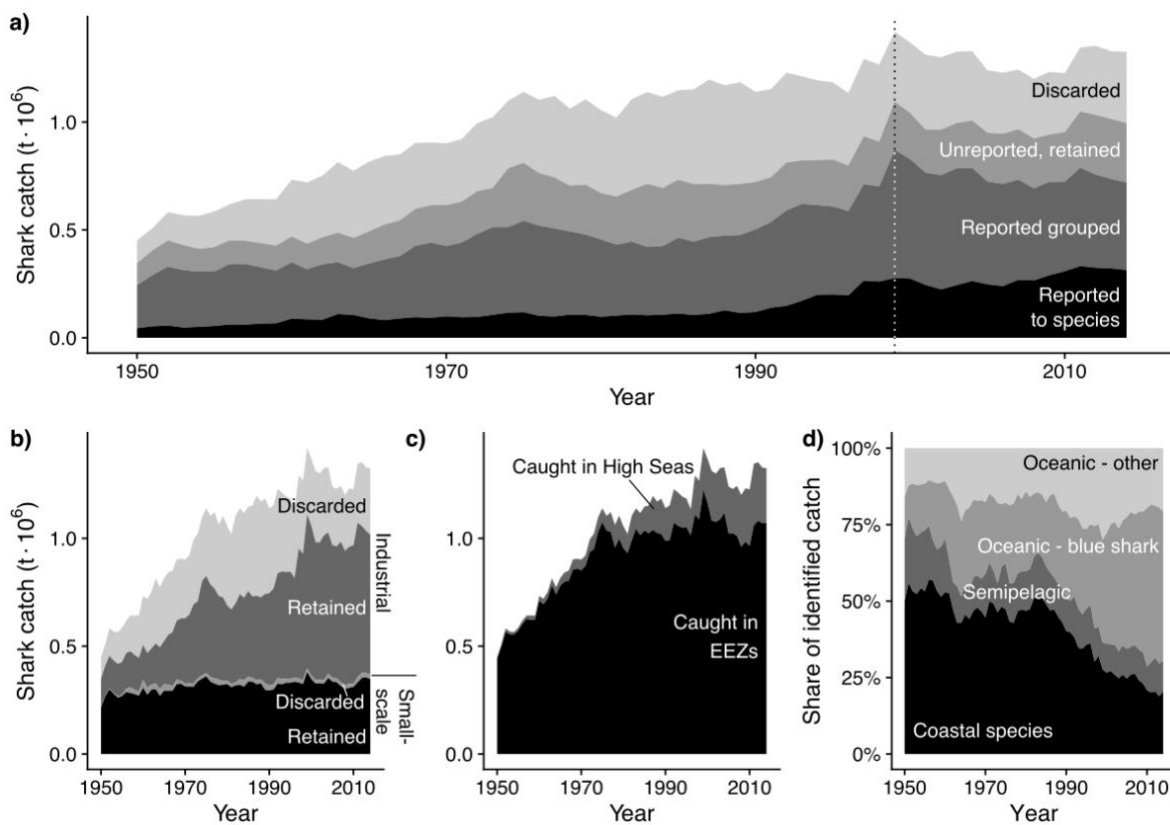


Figure 2.1: Global shark catch trends from 1950 to 2014. a) Shark catch by reporting status: reported to species, reported as a higher taxonomic group, unreported but retained, and discarded. Dotted line indicates year of peak shark catch. b) Retained and discarded shark catch by industrial and small-scale fishing sectors. c) Catch taken in EEZs vs High Seas. d) Breakdown of shark catch reported to species level by main habitat classifications (Coastal, Semipelagic and Oceanic). Blue sharks shown separately from other Oceanic species to illustrate their contribution to overall catch.

2.4.2 Temporal trends in shark catch by ocean and climate zone

Shark catch trends, disaggregated by ocean and climate zone, suggest sequential growth and senescence within regions (Figure 2.2a). Catch growth in the 1950s was strongest in the temperate north Atlantic, including the Mediterranean and Black seas, but catches in this area peaked in the 1960s, to be partly replaced by increased catches in subtropical and tropical regions of the Atlantic (Figure 2.2a,b). The Pacific Ocean became the largest source of the global shark catch in the 1970s, driven largely by catches in tropical waters (Figure 2.2a,b). Growth in catches in the Pacific began to slow in the 1990s, while catches in the Indian Ocean, which had begun to increase strongly in the 1970s, continue to rise. The tropical Indian Ocean is now the largest source of shark catches, with 31% of the global total (Figure 2.2a,b).

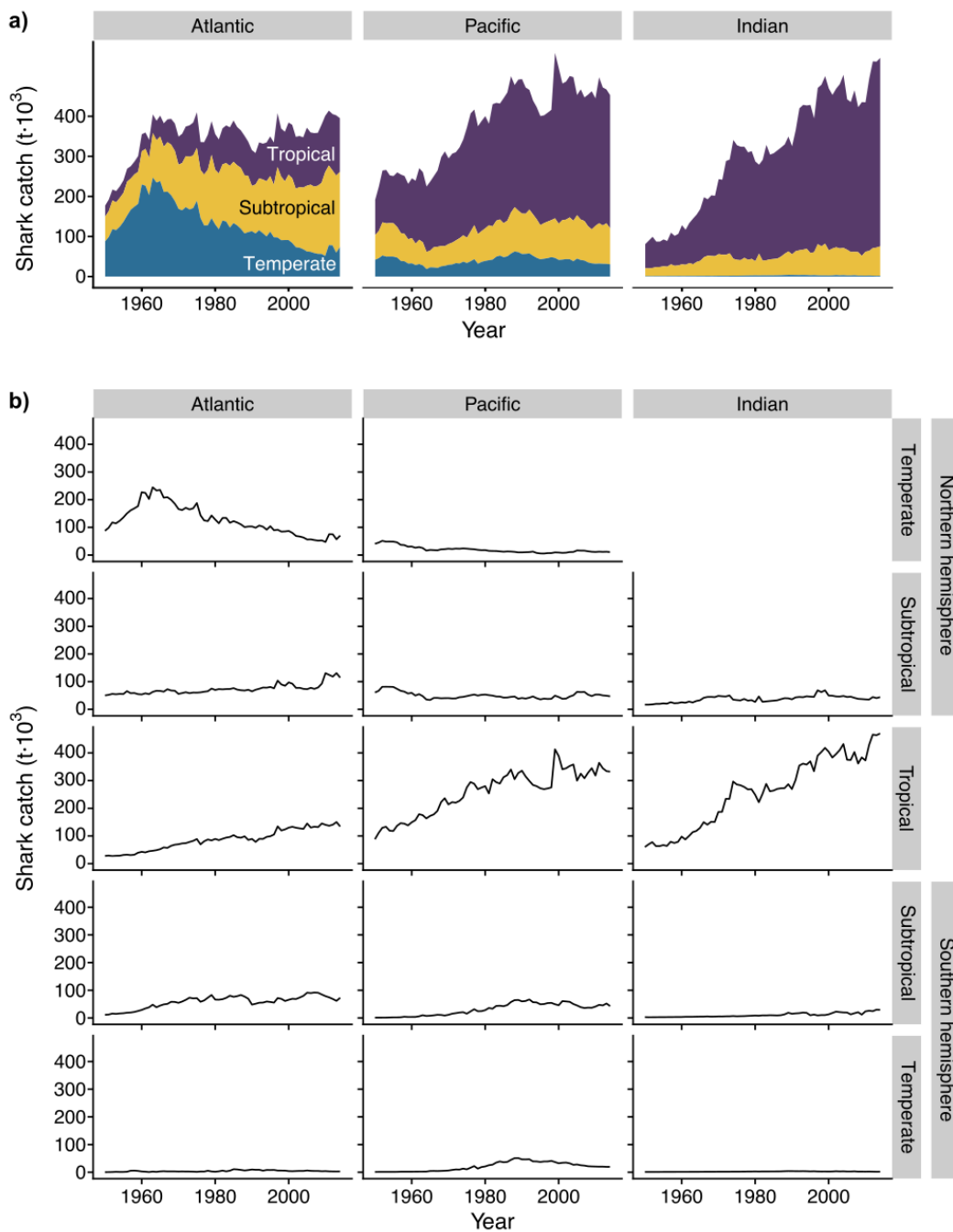


Figure 2.2: Global shark catch from 1950 to 2010 by major ocean region and climate zone. a) Total catch in each ocean by climate zone. b) Individual catch trends for ocean and climate zones in each hemisphere.

2.4.3 Spatial expansion of global shark fisheries

In the 1950s, shark catches were taken principally from European, North American and East Asian waters (Figure 2.3), the latter driven by catches by China and Japan (Supplementary Figure 2.3). At that time, less than 5% of the world's ocean generated 95% of the global catch, with catches concentrated in coastal waters and limited High Seas catches largely restricted to the Pacific Ocean. Shark catches are now concentrated in the northern Indian Ocean and in Southeast Asian waters,

along with smaller hotspots in West Africa, but High Seas catches have also expanded in the Indian Ocean and Atlantic Oceans, beginning in the 1970s (Figure 2.3). Growth in High Seas shark catches has been driven primarily by Spain and Taiwan, although Japan and Indonesia also contribute significantly to the total High Seas shark catch (Supplementary Figure 2.3, Supplementary Figure 2.4).

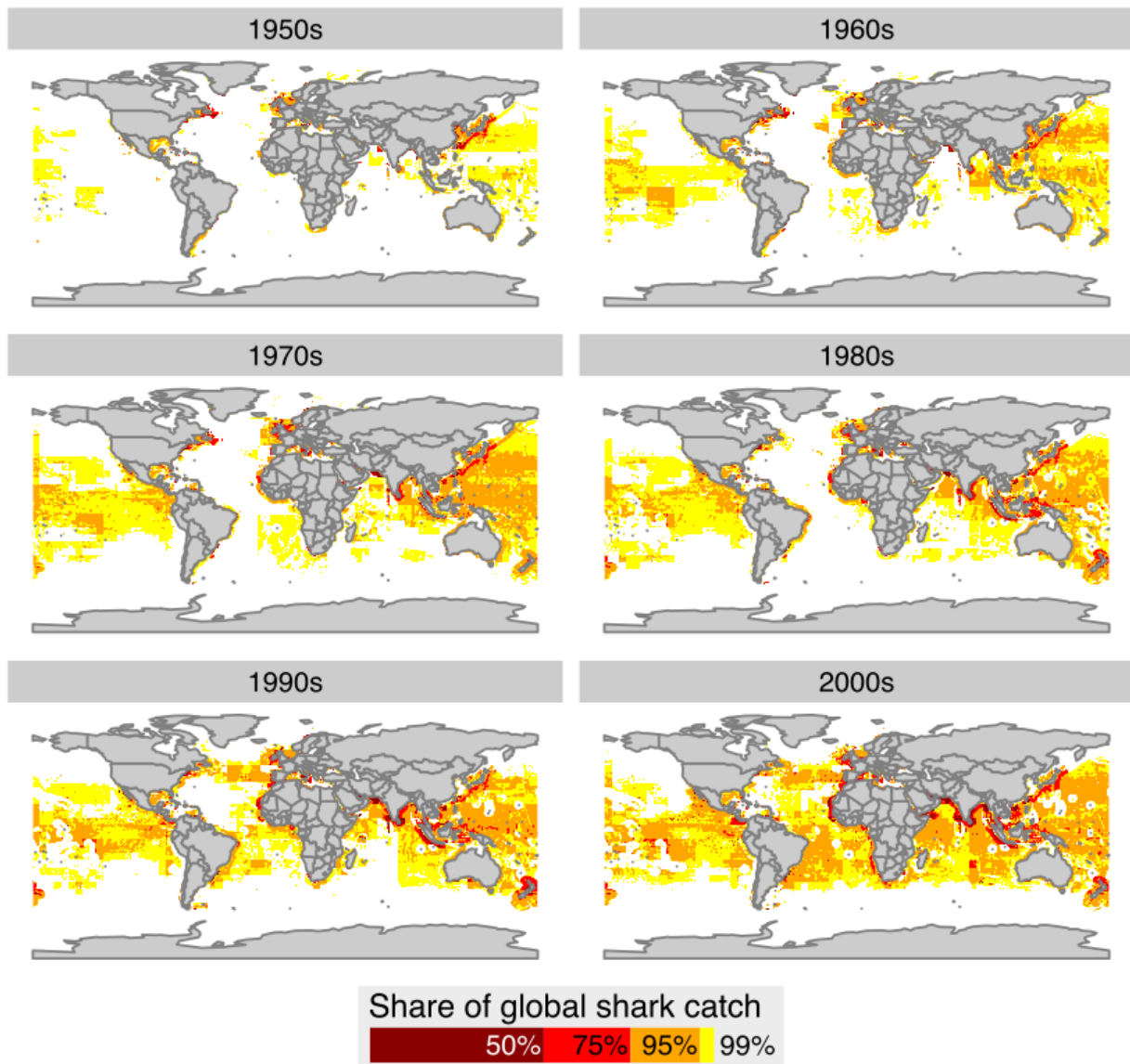


Figure 2.3: Spatial distribution of global shark catch, based on average annual catches in each decade. Cell shading denotes cells cumulatively contributing 50%, 75%, 95% and 99% of the global catch in each decade, i.e. cells shaded dark red, red, or orange collectively contributed 95% of the total global catch, with the dark red cells alone contributing 50% of the total catch.

The size of the core area exploited by shark fisheries, generating 95% of the global catch, has increased more than six-fold, from 17 million square kilometres in the 1950s to 110 million square kilometres today (Figure 2.3), while the global shark catch has increased 2.3 times (Figure 2.1a). Consequently, the average shark catch per unit area has fallen to around one third of its 1950s' value (Figure 2.4).

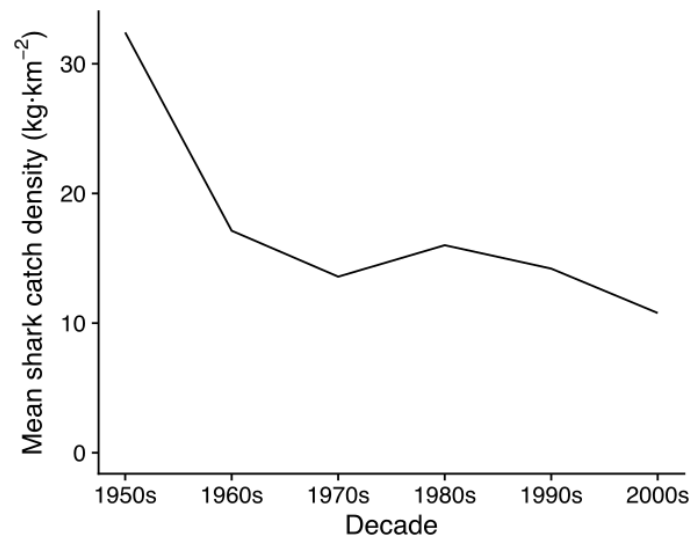


Figure 2.4: Global average spatial shark catch density, in kg per km², in each decade from 1950 to 2010. Catch density calculated by dividing the average annual global catch in each decade by the corresponding ocean area within which 95% of that catch was deemed to have been taken based on the Sea Around Us spatial catch allocation approach (Palomares et al. 2016, Zeller et al. 2016).

2.4.4 Major fishing countries and areas, catch reporting and taxa caught

Ten countries currently take over 50% of the global shark catch, based on average annual catches between 2005 and 2014, with one third of catches taken by just five countries: India, Spain, Indonesia, Taiwan and Pakistan (Table 2.1). The top ten countries take a larger proportion of sharks as a share of their total catch than do the rest of the world's fishing countries, with sharks making up an average of 1.8% of their catches, compared with less than 1% for the rest of the world (Table 2.1). Sharks contribute more than 5% of the total catches of Spain, Pakistan and Brazil and more than 10% of Yemen's total catch (Table 2.1).

Table 2.1: Summary catch and catch reporting statistics for the top ten shark fishing countries, plus the remaining 186 fishing countries grouped as 'Other'. Figures are based on annual average catches from 2005 to 2014.

Fishing country	Total catch (all taxa)	Shark catch	Sharks as share of country's total fisheries catch	Share of global shark catch	Share of shark catch reported	Share of reported shark catch identified to species
	tonnes	tonnes	percent	percent	percent	percent
India	4,643,833	104,666	2.3%	8.2%	52.1%	70.2%
Spain	1,702,224	96,554	5.7%	7.6%	95.9%	93.3%
Indonesia	5,459,597	80,555	1.5%	6.3%	58.6%	31.4%
Taiwan	1,249,147	70,578	5.7%	5.5%	62.2%	20.2%
Pakistan	870,099	62,845	7.2%	4.9%	19.2%	12.7%
Japan	4,978,994	61,223	1.2%	4.8%	49.1%	21.5%
China	15,959,587	58,579	0.4%	4.6%	79.1%	4.5%
Yemen	479,685	48,825	10.2%	3.8%	48.3%	0.0%
Brazil	906,593	46,656	5.2%	3.7%	27.7%	34.5%
Mexico	2,236,795	45,533	2.0%	3.6%	80.1%	15.9%
Other (n = 186)	73,425,972	596,512	0.8%	46.9%	55.6%	36.9%

In terms of where they take their shark catches, the top ten countries can be broadly divided into those with largely domestic shark fisheries operating within their own EEZs (India, Pakistan, Yemen, China, Brazil, Mexico, and Indonesia), and three distant water fishing countries (Spain, Taiwan, Japan) which take at least half their shark catches from the High Seas or the EEZs of other countries (Figure 2.5a, Figure 2.6). The presence of India, Pakistan, Yemen and Indonesia in the top ten underscores the emergence of the northern Indian Ocean and South East Asia as global shark fishing hotspots (Figure 2.3, Figure 2.5a). Notably, although Indonesia takes the majority of its shark catch within its own EEZ, its large total shark catch means it is also a significant fishing power on the High Seas, in terms of tonnes caught, although with less geographical reach than Spain, Taiwan and Japan (Figure 2.5a, Figure 2.6, Supplementary Figure 2.4).

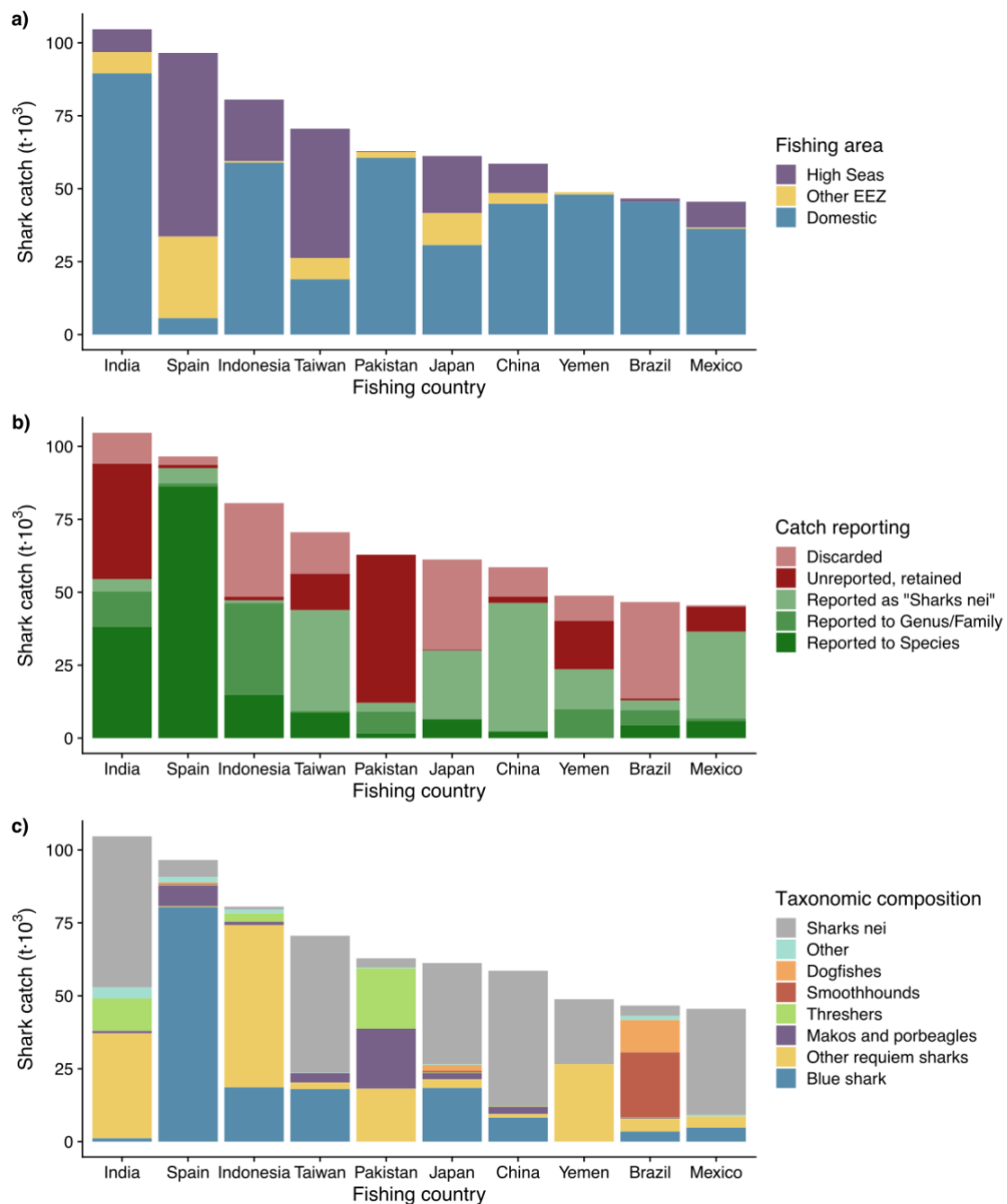


Figure 2.5: Fishing areas, catch reporting and shark taxon data for the top ten shark fishing countries. Stacked bars show average annual catch of each country between 2005 and 2014 broken down by a) main fishing area – Domestic (i.e. in that country’s own EEZ), in the EEZ of another country, or on the High Seas; b) catch reporting: reported catches by taxonomic resolution and unreported catches by catch status (retained or discarded); and c) taxonomic composition of shark catch.

Among the top ten shark fishing countries, Spain takes the largest share of shark catches from the EEZs of other countries, particularly in North and West Africa (Figure 2.5a, Figure 2.6, Supplementary Table 2.1). Surprisingly, China, a major distant water fishing country fishing far and wide around the world (Figure 2.6), appears to catch relatively few sharks outside its own EEZ (Figure 2.5a) based on currently available data.

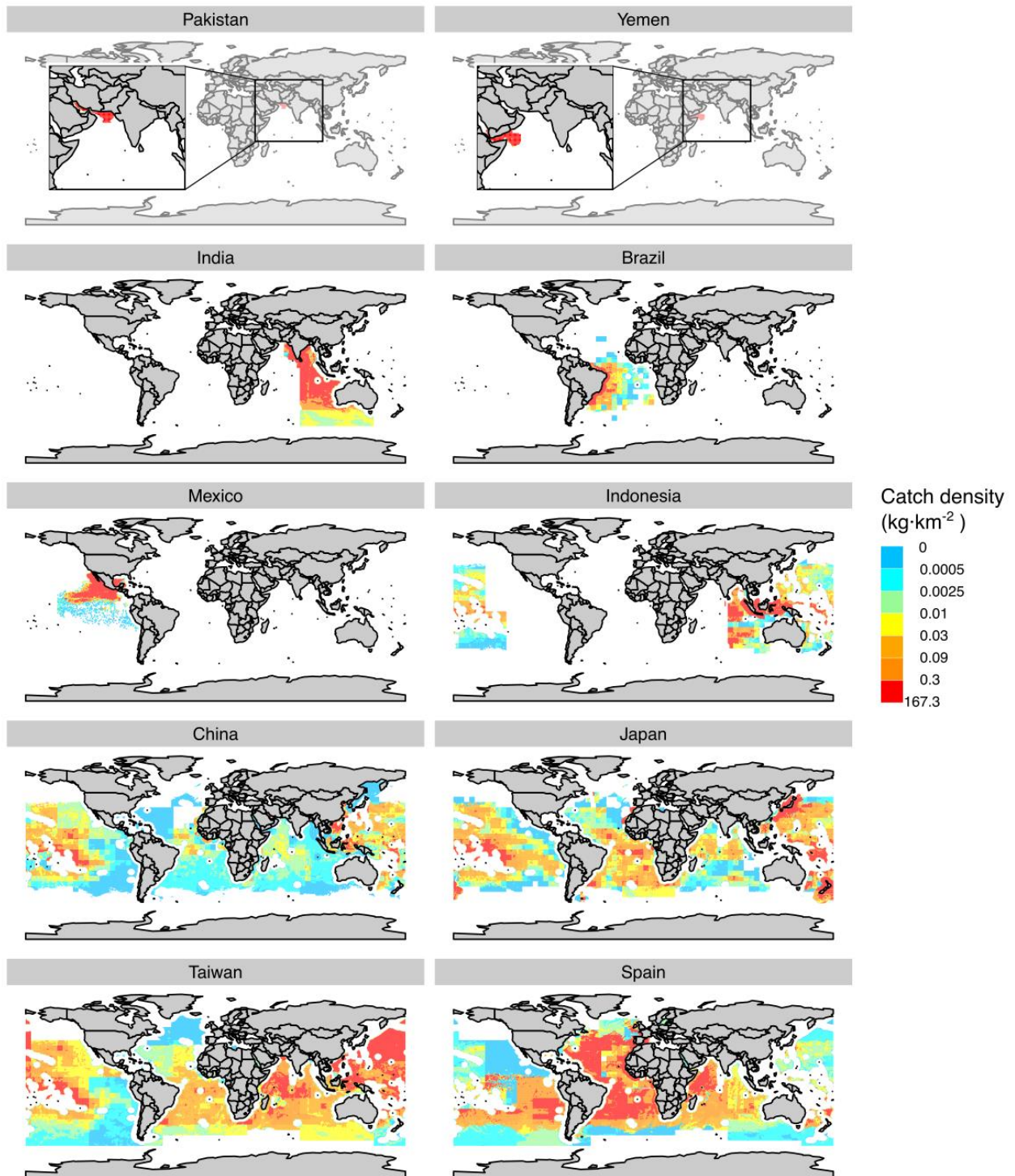


Figure 2.6: Global distribution of shark catches by the top ten shark fishing countries, based on average annual catches from 2005 to 2014. Cells are colour coded by catch density, divided into septiles across the full range of values. Catch density, in kg per km², is calculated at 0.5°x 0.5° grid cell resolution. See key for details of colour breaks. Pakistan and Yemen's fishing areas in the Indian Ocean are shown enlarged for clarity.

Consistent with the apparent high level of domestic shark fishing among the top ten fishing countries, eight of the ten national EEZs with the largest shark catches are those of major shark

fishing countries - India, Indonesia, Pakistan, Yemen, Brazil, China, Mexico and Japan - and catches in these areas are dominated by vessels flagged to the host country (Supplementary Figure 2.5). This overlap compounds the degree to which the top shark fishing countries have control over, and responsibility for, the global catch as both flag and coastal states. An exception is New Zealand's EEZ, where 50% of the shark catch is taken by foreign fishing vessels, primarily flagged to South Korea, Japan and Ukraine.

Catch reporting by the top ten fishing countries is highly variable in completeness and quality (Figure 2.5b). While some countries report their catch at high taxonomic resolution, in particular Spain, the majority either under-report or report catches in taxonomically uninformative groupings (Figure 2.5b). Under-reporting of shark landings is highest for India, Pakistan and Yemen (Figure 2.5b, Supplementary Figure 2.6). The volume of unreported catch is also driven by discarded shark catch for several major shark fishing countries including Japan, Indonesia and Brazil. This is also an issue for putatively well-managed fisheries in the USA and New Zealand (Supplementary Figure 2.7). Taiwan, Japan, China, Mexico and Yemen perform particularly poorly on the taxonomic resolution of their catch reporting, recording large proportions of their catches as "Sharks nei" (not elsewhere included).

Grouping catches by shark family, where identified, indicates differences in the catch composition of the top fishing countries, which broadly map to the area of operations of different countries' fleets (Figure 2.5c). Catches from the distant water fishing countries are chiefly comprised of blue sharks and pelagic species from the families Lamnidae (principally mako sharks [*Isurus* spp.] and porbeagle sharks [*Lamna nasus*]), Alopiidae (thresher sharks), and requiem sharks from the family Carcharhinidae (Figure 2.5c, Supplementary Table 2.2). Species identified in catches suggest that, for the distant water fishing countries, this latter group includes oceanic white tips (*Carcharhinus longimanus*) and silky sharks (*Carcharhinus falciformis*, Supplementary, Supplementary Table 2.2). Catches for India, in contrast, show a high proportion of coastal requiem sharks, including reef black tip (*Carcharhinus melanopterus*), black tip (*Carcharhinus limbatus*) and spot tail sharks (*Carcharhinus sorrah*) (Supplementary Table 2.2). India and Pakistan also catch relatively high proportions of thresher sharks (Figure 2.5c).

2.4.5 High Seas catches in RFMO areas of competence

Harmonised RFMO catch data indicate that shark catches on the High Seas are dominated by Spain and Taiwan, but the distribution of catches between the distant water fishing countries varies by

RFMO area (Figure 2.7a). In the Atlantic (ICCAT area) Spain and Portugal take the largest shares of total catches, although both Japan and Taiwan also have major impacts. Taiwan is the major High Seas shark fishing country the western Pacific (WCPFC area) while Spain, Japan and Mexico are dominant in the Eastern Pacific (IATTC area, Figure 2.7a). Indonesia takes the largest share of High Seas shark catches in the IOTC area, but Taiwan and Spain also make significant contributions to the total (Figure 2.7a). While focussed in the Atlantic Ocean and western Pacific Ocean respectively, the fleets of Spain, Taiwan and Japan have a significant global footprint in terms of their High Seas shark catches (Figure 2.6). Where shark catch is identified to species or genus, blue sharks are the dominant taxon identified in RFMO catches, alongside mako sharks. Thresher sharks also appear to be a significant component of High Seas catches in the IOTC area (Figure 2.7b).

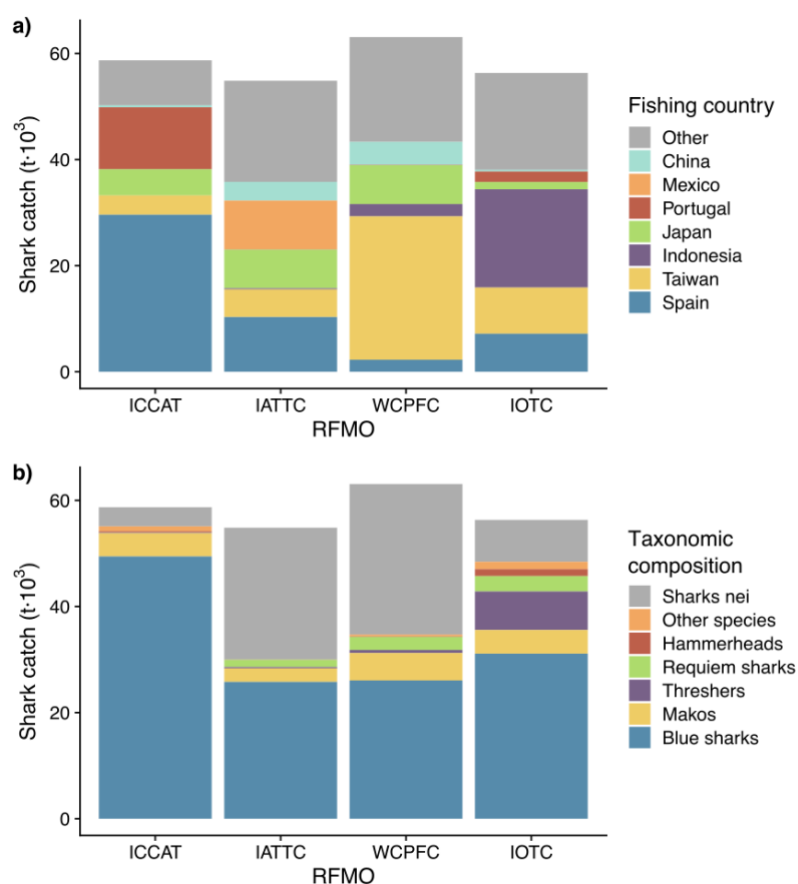


Figure 2.7: Fishing countries and shark taxon data for four tuna RFMOs covering the subtropical and tropical High Seas. Stacked bars show total shark catch in each RFMO area broken down by a) Catch by top seven High Seas shark fishing countries, and b) shark taxa identified in catches. RFMO abbreviations: ICCAT - International Commission for the Conservation of Atlantic Tunas, IATTC - Inter-American Tropical Tuna Commission (Eastern Pacific), WCPFC – Western and Central Pacific Fisheries Commission, IOTC – Indian Ocean Tuna Commission. The fifth tuna RFMO, the Commission for the Conservation of Southern Bluefin Tuna, was not included in the analysis since it accounts for only 5% of the global shark catch taken in tuna RFMO-managed waters (www.searoundus.org).

2.5 Discussion

Optimists envisage a future of sustainable shark fisheries, pointing to ‘bright spots’ in the well-managed coastal fisheries of countries like the USA and New Zealand and RFMO-managed stocks of blue and mako sharks in the Atlantic and Pacific Oceans as examples (Simpfendorfer & Dulvy 2017). However, recent reassessments of RFMO-managed sharks put their stock status in question (ICCAT Shark Species Group 2019, Sherley et al. 2020), and it is estimated that only 7-9% of the global shark catch is currently biologically sustainable and even less is actively managed for sustainability (Simpfendorfer & Dulvy 2017). My analysis of available shark catches suggests that a key barrier to expanding the scientific management of sharks is a widespread lack of accurate and informative catch data.

The global shark catch data of the *Sea Around Us*, which combine reconstructed (i.e., reported plus unreported) domestic EEZ catches (Zeller et al. 2016) with globally harmonized foreign (Zeller et al. 2016) and high seas catches (Coulter et al. 2020), indicate three related areas that could facilitate improved and more effective management of sharks within fisheries: 1) more complete reporting of sharks catches, 2) better monitoring and collecting reporting of shark discarding, and 3) improving the taxonomic resolution of shark catch data. The importance of each of these varies with geography and the fishing and reporting entities involved, and prescriptions for improvement can be stratified accordingly. Actions might also be prioritised on the basis of identified hot-spots of both shark-fishing intensity and reporting deficiencies, with, for example, the major coastal shark fishing countries of the northern Indian Ocean targeted as a regional cluster for improvement. The urgency of achieving improvements in fisheries’ management of sharks is underscored both by the specific example of declines in shark abundance presented in the literature (Ferretti et al. 2010), and the decrease in overall shark catch per unit area density observed in the global catch data analysed here. The ~70% decline in shark catch per unit area is similar in magnitude to the global decline in catch per unit effort observed in fisheries in general as rapid increases in the number and power of fishing vessels have recently yielded only stagnating catch volumes, taken to suggest a general overexploitation of fish stocks (Rousseau et al. 2019).

Individual fishing countries vary widely in their treatment and reporting of shark catches, in part depending on where and how they operate and what they catch. Under-reporting of landings is a major issue for Pakistan, but also India and Yemen. These countries and their neighbours, including Iran and Sri Lanka, have very large industrial and artisanal fleets deploying a wide range of gears. Of

particular importance for sharks are the tens of thousands of gillnet and longline vessels operating in their EEZs and adjacent high seas waters (Ardill et al. 2013, Aranda 2017). Although nominally targeting tunas, the gears used and the timing and depth of sets leads to high shark bycatch, most of which is retained for local markets and to supply the fin trade (Aranda 2017, Karnad et al. 2019). The scale and diversity of the fleets involved confounds attempts to monitor catches and enforce regulations (Aranda 2017).

For other countries, including Indonesia, Japan and Brazil, shark discards appear to be a larger problem than unreported landings, leading to under-reporting of up to 50% of the total shark catch. Importantly, as discards for RFMO managed fisheries have only been subjected to preliminary estimates (Coulter et al. 2020) the current estimates of shark discards for countries with significant High Seas fisheries may be conservative. Ignoring discards in catch reporting, as is the norm in official statistics (Zeller et al. 2017), risks significantly underestimating total shark mortality, since a significant portion of animals are returned to the sea dead or dying and should therefore be counted in the total catch of a species. Studies suggest that combinations of at-haulback and post-release mortality result in the deaths of between 25% and 90% of sharks taken as bycatch, depending on species and condition upon release (Musyl & Gilman 2019, Matias Braccini & Waltrick 2019). If sharks are genuinely being caught 'by accident' with no intention by the vessel to retain them, then the high discard rates suggest that a greater focus on mitigation methods is required (Poisson et al. 2016). However, in addition to concerns that shark bycatch reduction measures might impact catch rates of target species, shark bycatch often represents significant additional revenue for a fishing vessel which has reduced support for bycatch mitigation measures in some fleets (Fowler 2016).

Shortfalls in total catch reporting, resulting from bycatch or under-reporting of landings, are compounded by a lack of species-level catch data in both coastal and high seas fisheries. While this appears to have improved since 1950, in fact the majority of the increase in species-level reporting of catch can be accounted for by reported catches of a single species, blue sharks, for which Spain is primarily responsible. Removing this effect suggests that the proportion of the global shark catch reported to species level has remained around 25%, meaning that important taxonomic details are missing for most of the world's shark catches. Among the top ten shark fishing countries, taxonomic resolution of shark catches is worst for China, Taiwan and Mexico, but also poor for India. Measures to address under-reporting of shark catches must also address taxonomic resolution if formal stock assessment methods, even those with modest data needs (e.g., Froese et al. 2017), are to be applied. Taxonomic information on discarded sharks, poorly reported by Japan, but also Taiwan, the

USA and New Zealand, is also required to better estimate total fishing mortality based on species-specific survival rates (Musyl & Gilman 2019). Increased use of fisheries observers and on-board electronic monitoring (Jaiteh et al. 2014, Emery et al. 2019), market surveys and genetic techniques post-harvest (Almerón-Souza et al. 2018, Karnad et al. 2019) could both help fill taxonomic gaps in the data.

Even if catch data can be improved, the widespread capture of sharks in fisheries which nominally target other species (Gilman et al. 2014, Oliver et al. 2015) has fundamental implications for shark management, beyond impacting data quality. Current rates of shark bycatch in gillnet and longline fisheries – in some cases exceeding 40% of the total catch (Garcia-Cortés & Mejuto 2005, Mejuto et al. 2009) – means that sharks will continue to suffer high fishing mortality even if targeted shark fisheries were to cease operating entirely. Since sharks are typically less resilient than the teleost species they are caught alongside (Schindler et al. 2002), ongoing bycatch mortality in fisheries targeting more resilient species will likely continue to exert unsustainable pressure on sharks. An approach taken for other sensitive species, including marine megafauna, such as sea turtles and cetaceans, but also certain fish species, such as rockfish (*Sebastes* spp.) in US and Canadian groundfish fisheries, is to set bycatch quotas for these species which limit total effort in the target fishery (Holland 2010, Holland & Martin 2019). Such quotas, and the incentives for fishers to remain within them, need to be carefully designed (Holland & Martin 2019), and they are obviously contingent on reliable bycatch data for their monitoring and enforcement, but may represent a means of incorporating vulnerable non-target shark species into the management plans of fisheries.

Dulvy et al. (2017) prescribe improved management *within* fisheries or complete protection *from* fisheries to address the conservation needs of sharks, depending on individual species' vulnerability to fishing. However, given the overall low levels of biological sustainability of global shark stocks (Simpfendorfer & Dulvy 2017), the lack of reliable data on actual fisheries mortality (e.g., Byrne et al. 2017), a global shortfall in effective fisheries management (Mora et al. 2009, Melnychuk et al. 2017), and the rapid spread of shark fisheries to every part of the global oceans, a more universal precautionary approach may be needed. Currently available catch data suggest the highest intensity of shark fishing likely occurs in the EEZs of coastal states, particularly in the northern Indian Ocean and Southeast Asia. However, these data also reveal intensifying High Seas catches in areas like the central Atlantic and eastern Pacific Oceans, which are key areas of overlap between High Seas fisheries and pelagic species (Queiroz et al. 2019). Strictly enforced no-take MPAs could provide shark populations in these regions with at least partial refugia from fishing (Dwyer et al. 2020),

particular if hypotheses about the selection effect of MPAs on the movements of pelagic species are correct (Mee et al. 2017). In doing so, they could help populations recover while investments in improving fisheries management take effect. Marine protection targets have broader goals than purely shark conservation, but MPAs designed to accommodate mobile predators like sharks will likely also confer “umbrella” protection on the wider ecosystem (Osgood et al. 2020). A focus on sharks and other large marine predators may therefore be useful in identifying opportunities for new marine protected areas under the UN Sustainable Development Goals (SDG 14.5) and the IUCN’s ‘30x30’ target (Zhao et al. 2020).

Much can certainly be done to improve our ability to scientifically manage sharks in fisheries, with core fundamentals requiring better reporting, management of discards and improving the taxonomic resolution of catches. Improvements in the data can be amplified by leveraging data-limited assessment methods (Froese et al. 2017, Free et al. 2017). However, even with these tools, addressing current management shortcomings will take time, and the evidence suggests that the need to reduce fishing pressure on sharks is urgent. Embracing MPAs as a key tool alongside conventional management may allow fisheries to more sustainably operate on ocean ecosystems that contain vulnerable, data-poor, but ecologically vital species like sharks, ensuring that both persist into the future (Hoffmann & Pérez-Ruzafa 2009).

2.6 Limitations of the study

Total shark catches in the *Sea Around Us* catch data are likely to be conservative for two main reasons. Firstly, the *Sea Around Us* reconstruction approach has so far only been applied to domestic fisheries within their home EEZs, and while some preliminary estimates of distant water fleet fishing in foreign EEZs and the High Seas have been made, total distant water and High Seas catches, including unreported landings, remain to be investigated (Coulter et al. 2020). Significant under- and mis-reporting of tunas and other species in RFMO catches (Souter et al. 2016) suggests that true High Seas shark catches will certainly be greater than presented here, particularly for countries such as China, Spain, Taiwan, South Korea and Japan which dominate distant water and High Seas fisheries (Sala et al. 2018). Secondly, this study only analysed catches taxonomically identified as sharks in the *Sea Around Us* data, thus excluding any unidentified shark catches currently hidden in higher data groupings, such as ‘Pelagic fishes nei’ or ‘Marine fishes nei’ in official FAO data and subsequently also in *Sea Around Us* data (Zeller et al. 2016). Catches labelled ‘Marine fishes nei’ in the *Sea Around Us* data are ten times those of sharks, by weight, so potentially reassigning even a

small percentage to shark taxa would have a large effect on the estimated shark catch. A smaller source of under- or over-estimation of shark catches reported in the analysis would be the assignment of unidentified elasmobranchs between the sharks and the rays. However, this error will be small relative to that caused by the “Marine fishes nei” category, and it also seems plausible, given the differences in morphology between sharks and rays, that where catches are identified as elasmobranchs they are assigned to the correct functional group in most cases.

A separate issue is the attribution of shark catches to individual fishing countries. Catches in both the underlying FAO data and the *Sea Around Us* reconstructions allocate catches to the reporting flag state. Countries whose fleets register vessels under flags other than their own (e.g., Open Registers, Flags of Convenience; Llácer 2003, Gianni & Simpson 2004) will potentially have their shark catches and/or areas of operation misrepresented. This is more likely an issue for distant water fishing countries like Taiwan which may have one fifth of their fleet registered under foreign flags (Tolvanen et al. 2010), and requires greater transparency and accountability in vessel registries.

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2.8 Supplementary material

2.8.1 Supplementary tables

Supplementary Table 2.1: Shark taxa included in classification of catches to taxon level in the *Sea Around Us* reconstructed catch database.

Functional group	Superclass	Class	Order	Family	Taxa
Small-medium sharks <90 cm	Chondrichthyes	Elasmobranchii	Carcharhiniformes	Carcharhinidae	2
	Chondrichthyes	Elasmobranchii	Carcharhiniformes	Leptochariidae	1
	Chondrichthyes	Elasmobranchii	Carcharhiniformes	Scyliorhinidae	8
	Chondrichthyes	Elasmobranchii	Carcharhiniformes	Triakidae	2
	Chondrichthyes	Elasmobranchii	Orectolobiformes	Hemiscylliidae	1
	Chondrichthyes	Elasmobranchii	Squaliformes	Centrophoridae	1
	Chondrichthyes	Elasmobranchii	Squaliformes	Dalatiidae	1
	Chondrichthyes	Elasmobranchii	Squaliformes	Etmopteridae	4
	Chondrichthyes	Elasmobranchii	Squaliformes	Somniosidae	1
	Chondrichthyes	Elasmobranchii	Squaliformes	Squalidae	1
Large sharks >=90 cm	Chondrichthyes				1
	Chondrichthyes	Elasmobranchii			1
	Chondrichthyes	Elasmobranchii	Carcharhiniformes		1
	Chondrichthyes	Elasmobranchii	Carcharhiniformes	Carcharhinidae	26
	Chondrichthyes	Elasmobranchii	Carcharhiniformes	Pseudotriakidae	1
	Chondrichthyes	Elasmobranchii	Carcharhiniformes	Scyliorhinidae	2
	Chondrichthyes	Elasmobranchii	Carcharhiniformes	Sphyrnidae	6
	Chondrichthyes	Elasmobranchii	Carcharhiniformes	Triakidae	10
	Chondrichthyes	Elasmobranchii	Hexanchiformes	Hexanchidae	3
	Chondrichthyes	Elasmobranchii	Lamniformes		1
	Chondrichthyes	Elasmobranchii	Lamniformes	Alopiidae	4
	Chondrichthyes	Elasmobranchii	Lamniformes	Cetorhinidae	1
	Chondrichthyes	Elasmobranchii	Lamniformes	Lamnidae	6
	Chondrichthyes	Elasmobranchii	Lamniformes	Odontaspidae	1
	Chondrichthyes	Elasmobranchii	Lamniformes	Pseudocarchariidae	1
	Chondrichthyes	Elasmobranchii	Orectolobiformes	Ginglymostomatidae	2

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Supplementary Table 2.2. Continued

Functional group	Superclass	Class	Order	Family	Taxa
Large sharks >=90 cm	Chondrichthyes	Elasmobranchii	Orectolobiformes	Rhincodontidae	1
	Chondrichthyes	Elasmobranchii	Orectolobiformes	Stegostomatidae	1
	Chondrichthyes	Elasmobranchii	Pristiophoriformes	Pristiophoridae	1
	Chondrichthyes	Elasmobranchii	Squaliformes		1
	Chondrichthyes	Elasmobranchii	Squaliformes	Centrophoridae	4
	Chondrichthyes	Elasmobranchii	Squaliformes	Dalatiidae	1
	Chondrichthyes	Elasmobranchii	Squaliformes	Echinorhinidae	1
	Chondrichthyes	Elasmobranchii	Squaliformes	Oxynotidae	2
	Chondrichthyes	Elasmobranchii	Squaliformes	Somniosidae	7
	Chondrichthyes	Elasmobranchii	Squaliformes	Squalidae	3
	Chondrichthyes	Elasmobranchii	Squatiformes	Squatidae	5

Supplementary Table 2.3: Catches taken by Spain's distant water fleet in the EEZs of other countries. The EEZs contributing 80% of the total catch by Spain in foreign EEZs listed are individually, ranked by average annual catches from 2005 to 2014.

EEZ	Average annual shark catch 2005-2014 tonnes	Share	Cumulative share
Morocco	7,910	28%	28%
Guinea	4,129	15%	43%
Algeria	2,195	8%	51%
Senegal	1,325	5%	56%
Canada	1,117	4%	60%
Azores Isl. (Portugal)	1,092	4%	64%
France	1,082	4%	67%
Gabon	1,056	4%	71%
Guinea-Bissau	975	3%	75%
Seychelles	830	3%	78%
Mauritania	773	3%	80%
Other	5,473	20%	100%

Supplementary Table 2.4: Shark catches by taxon for the top ten shark fishing countries. Top seven taxa (species or higher grouping) identified in the catches for each of the major shark fishing countries listed separately, with remaining taxa grouped as 'Other'.

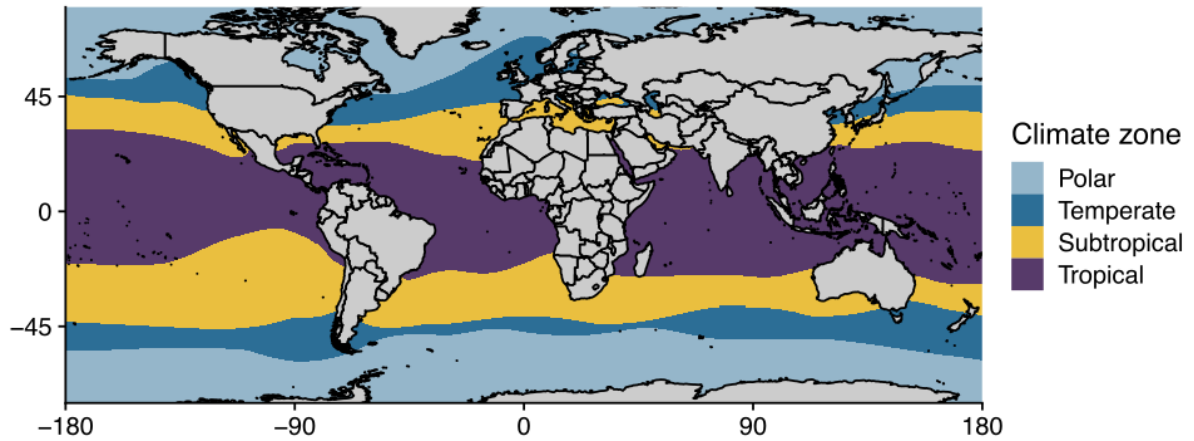
Fishing country	Taxon	Average annual catch 2005-2014
		tonnes
Brazil	<i>Mustelus schmitti</i>	11,082
	<i>Squalus</i> spp.	11,077
	<i>Mustelus</i> spp.	11,067
	Carcharhinidae	3,940
	<i>Prionace glauca</i>	3,466
	Elasmobranchii	2,814
	<i>Sphyrna</i> spp.	1,317
	Other	1,894
China	Elasmobranchii	45,918
	<i>Prionace glauca</i>	8,225
	<i>Isurus</i> spp.	1,972
	<i>Carcharhinus longimanus</i>	525
	<i>Isurus oxyrinchus</i>	505
	Squaliformes	459
	<i>Carcharhinus falciformis</i>	364
	Other	611
India	Elasmobranchii	51,777
	<i>Carcharhinus melanopterus</i>	12,279
	<i>Carcharhinus limbatus</i>	8,573
	<i>Alopias</i> spp.	7,355
	<i>Carcharhinus sorrah</i>	4,607
	Carcharhinidae	3,638
	<i>Alopias vulpinus</i>	2,551
	Other	13,886
Indonesia	<i>Carcharhinus</i> spp.	44,625
	<i>Prionace glauca</i>	18,600
	Carcharhinidae	10,349
	<i>Alopias</i> spp.	2,896
	<i>Sphyrna</i> spp.	1,340
	<i>Isurus</i> spp.	1,144
	Elasmobranchii	961
	Other	641

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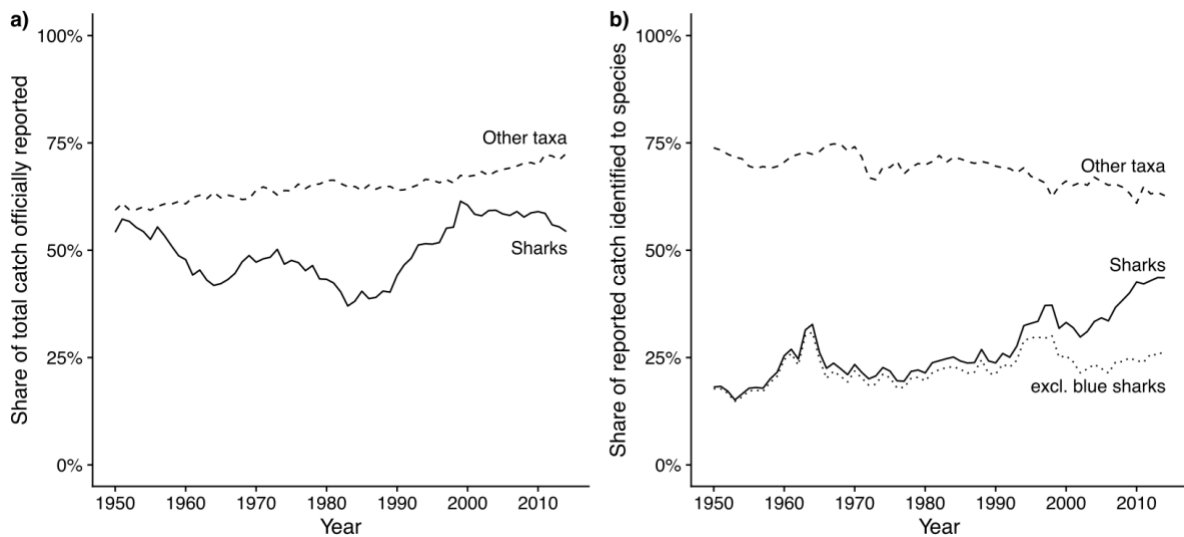
Supplementary Table 2.2 Continued

Fishing country	Taxon	Average annual catch 2005-2014
		tonnes
Japan	Elasmobranchii	33,605
	<i>Prionace glauca</i>	18,405
	Carcharhinidae	1,568
	<i>Isurus</i> spp.	1,359
	Squalidae	1,295
	Squaliformes	1,045
	<i>Carcharhinus longimanus</i>	745
	Other	3,200
Mexico	Elasmobranchii	36,413
	<i>Prionace glauca</i>	4,809
	<i>Carcharhinus falciformis</i>	2,018
	<i>Carcharhinus</i> spp.	1,267
	<i>Sphyrna</i> spp.	485
	<i>Carcharhinus limbatus</i>	289
	<i>Rhizoprionodon terraenovae</i>	185
	Other	68
Pakistan	<i>Alopias superciliosus</i>	20,453
	<i>Isurus oxyrinchus</i>	20,093
	Carcharhinidae	18,113
	Elasmobranchii	3,093
	<i>Isurus paucus</i>	516
	<i>Alopias</i> spp.	237
	<i>Sphyrna</i> spp.	178
	Other	163
Spain	<i>Prionace glauca</i>	80,433
	<i>Isurus oxyrinchus</i>	6,740
	Elasmobranchii	5,828
	<i>Scyliorhinus canicula</i>	480
	<i>Dalatias licha</i>	363
	Scyliorhinidae	362
	<i>Galeorhinus galeus</i>	283
	Other	2,066
Taiwan	Elasmobranchii	46,963
	<i>Prionace glauca</i>	18,001
	<i>Isurus</i> spp.	2,277
	<i>Carcharhinus falciformis</i>	1,216
	<i>Isurus oxyrinchus</i>	908
	<i>Carcharhinus longimanus</i>	513
	Carcharhinidae	407
	Other	293
Yemen	Carcharhinidae	26,574
	Elasmobranchii	22,251

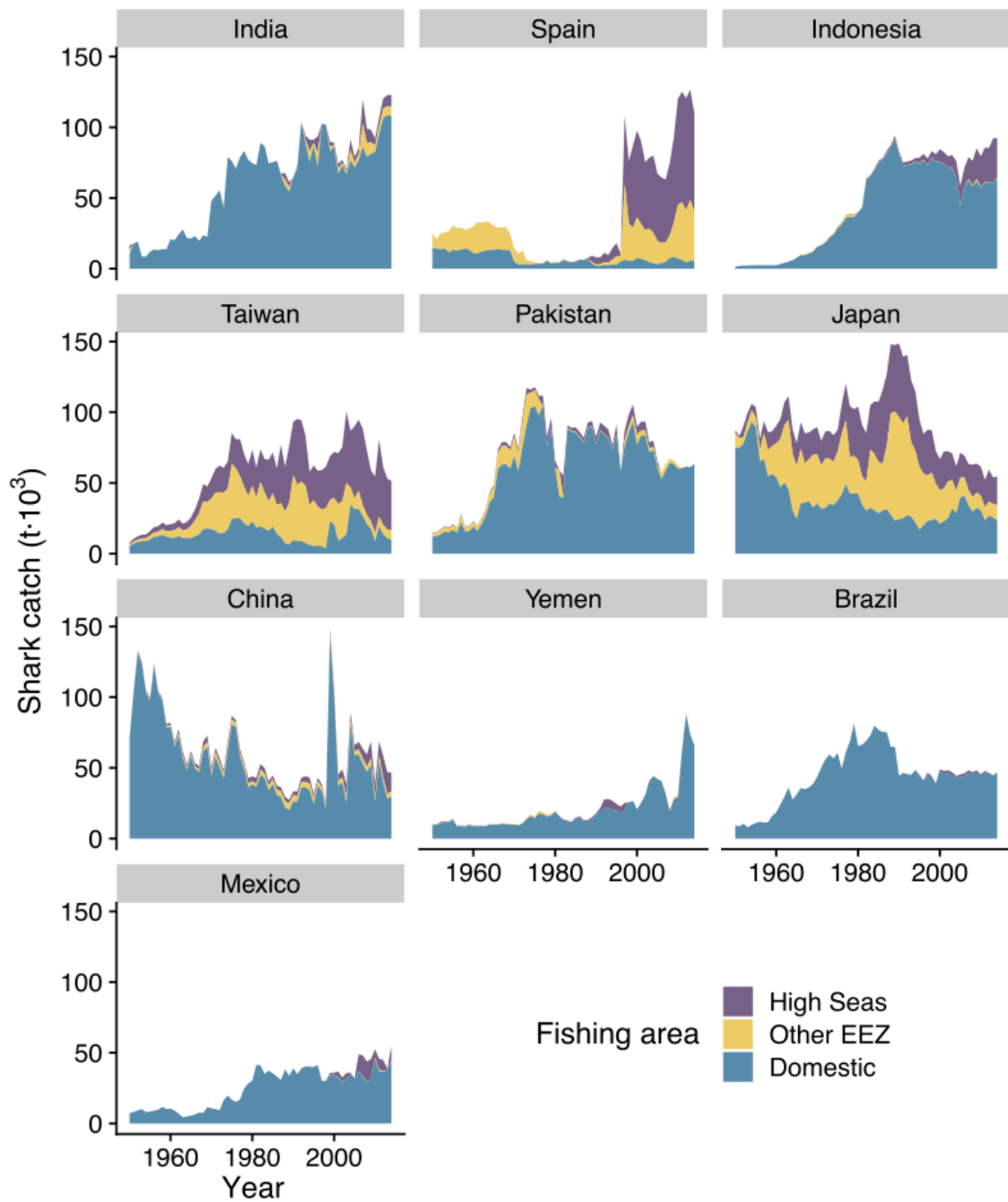
2.8.2 Supplementary figures



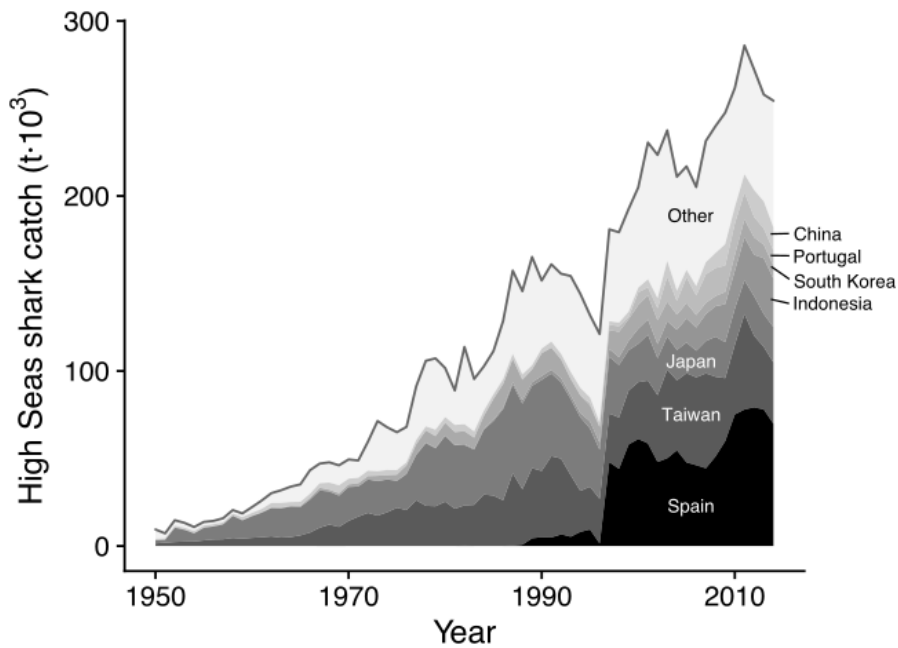
Supplementary Figure 2.1: Climate zones used for regional analysis. Definitions taken from Palomares et al. (2020).



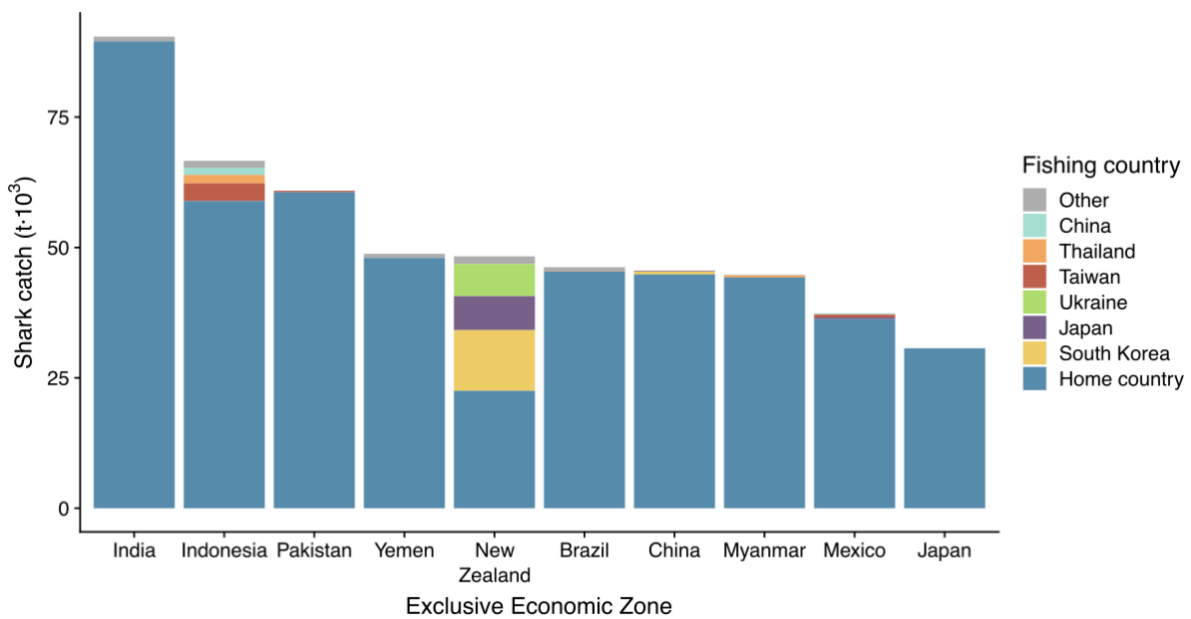
Supplementary Figure 2.2: Shark catch reporting (solid lines) compared to that of other marine taxa (dashed lines): a) Proportion of total global catch reported to official bodies and b) the share of the reported catch that is identified to species. Dotted line in panel b) shows the share of shark catch reported to species if blue sharks (*Prionace glauca*) are excluded.



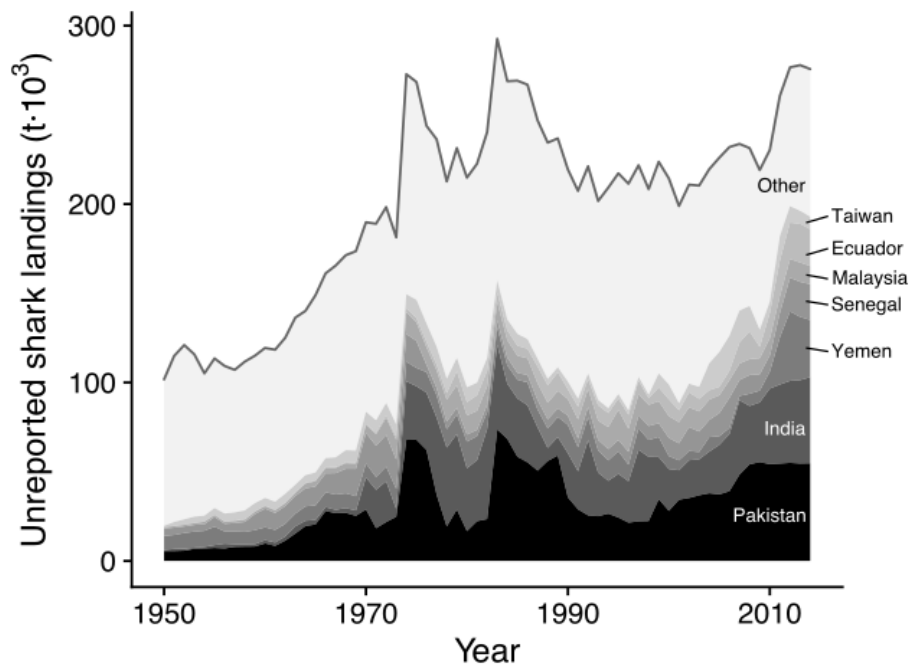
Supplementary Figure 2.3: Shark catches of the ten largest fishing countries, from 1950 to 2014, by the areas where their shark catch is taken: their own EEZ (Domestic), in the waters of other countries (Other EEZ), and the High Seas.



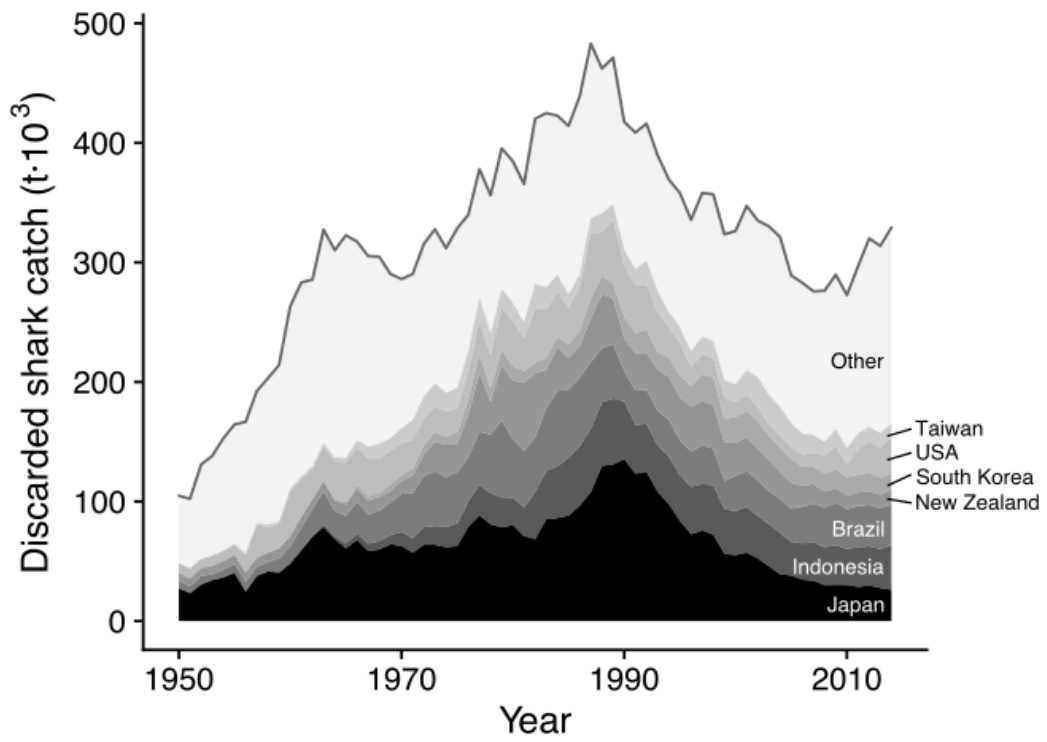
Supplementary Figure 2.4: Annual shark catch taken on the High Seas from 1950 to 2014. Catches of the seven fishing countries with the largest High Seas catches are shown separately, with the 196 remaining countries grouped as 'Other'.



Supplementary Figure 2.5: Contribution of individual fishing countries to shark catches in the top ten EEZs. EEZs ranked by their average annual shark catch from 2005 to 2014. Contribution of the home country's fleet, plus the six largest foreign operating in those EEZs, shown separately. Remaining fishing countries grouped as 'Other'.



Supplementary Figure 2.6: Unreported annual shark catch from 1950 to 2014. Catches of the seven fishing countries with the largest unreported catches are shown separately, with the remaining 189 countries grouped as 'Other'.



Supplementary Figure 2.7: Annual shark catch discarded from 1950 to 2014. Discarded catches of the seven fishing countries with the largest discards are shown separately, with the remaining 196 countries grouped as 'Other'.

Chapter 3: Telemetry-derived space use patterns for two species of reef shark species in a large no-take MPA

3.1 Abstract

Sharks play key roles in coral reef ecosystems, where they regulate competitors and prey species, promote species and functional diversity, and enhance the resilience of reefs to external stressors. However, sharks are increasingly threatened by overfishing and other anthropogenic threats. No-take marine protected areas (MPAs) can provide critical refugia for reef shark populations, but to be effective they must consider the space use of species of interest in the context of habitat type. To explore inter- and intra-specific variations in reef shark movements and space use within a large, remote reef system, I used acoustic telemetry to monitor grey reef (*Carcharhinus amblyrhynchos*) and silvertip sharks (*Carcharhinus albimarginatus*) in the British Indian Ocean Territory MPA over a three-year period. While overall residency to the study area was similar for both species, grey reef sharks had smaller movement ranges and 80% smaller activity spaces than silvertip sharks, which roamed widely and traversed distances of over 200 km during the study. Temporal variation in attendance was correlated with time of day, with both species less likely to be detected around shallow reefs at night and a stronger effect seen for silvertip sharks and larger individuals of both species. In contrast to their conspecifics at shallow reef sites, silvertip sharks showed round-the-clock presence near a group of deep seamounts. Interspecific differences in detection patterns near shallow reef sites are consistent with resource partitioning, whereas the intra-specific variation in silvertip shark attendance between shallow and deep sites may reflect differences in the availability and/or accessibility of prey resources. Spatial management must be adapted to species' movement patterns and habitat preferences. Large no-take MPAs which encompass a wide range of feature types and depths will better accommodate inter- and intraspecific variation in the space use of reef sharks.

3.2 Introduction

Reef sharks are thought to play important roles in coral reef ecosystems (Ruppert et al. 2013; Heupel et al. 2019), including regulating reef fish community structure through direct (i.e. predation) and indirect, i.e. competition or fear-based, effects (Barley et al. 2017a; Hammerschlag et al. 2018; Zanette and Clinchy 2019), and providing nutrient subsidies (Williams et al. 2018). However, temporal and spatial analyses of abundance suggest that steep declines and even local extirpations may have occurred throughout their ranges (Graham et al. 2010; Nadon et al. 2012; MacNeil et al. 2020). Protection and restoration of reef shark populations is therefore seen as important to sustain reef ecosystem function and safeguard the ecosystem services we receive from reefs (Cesar 2000; Worm et al. 2006; Ruppert et al. 2013).

Recent studies have shone light on the mechanisms by which reef sharks may influence trophic structure and ecosystem function on reefs (Barley et al. 2017a; Rasher et al. 2017; Hammerschlag et al. 2018). For example, Hammerschlag et al. (2018) found that reef fish had larger caudal fins and eyes on reefs with sharks. Barley et al. (2017a) reported increased species diversity, abundance and biomass of reef fishes on reefs where sharks were relatively abundant. A separate study found evidence that reef sharks impact the diet and growth of meso-predatory fishes (Barley et al. 2017b), a key mechanism underpinning the trophic cascade hypothesis (Terborgh and Estes 2010). Questions remain, however, as to the ecological roles of reef sharks and the protection needs of individual species (Roff et al. 2016, Heupel et al. 2019; Dwyer et al. 2020). Diet studies and gape analysis have been used to suggest that the diets and trophic roles of reef sharks overlap those of large piscivorous teleosts (Roff et al. 2016; Barley et al. 2020), implying that the loss of reef sharks may be compensated for by other members of the mesopredator guild. Resolving these questions is given urgency by the spatial overlap between hotspots of shark diversity and human activity along coastlines in the tropics (Stewart et al. 2010; Lucifora et al. 2012), and the strong and negative correlation between predator abundance on reefs and increasing human population density and proximity to markets (Cinner et al. 2018; Juhel et al. 2018).

The study of spatial ecology can provide insights into the ecological roles of sharks, based on their movements in relation to different habitats and to each other (Heupel et al. 2018; Lea et al. 2020), and inform the design of spatio-temporal measures to protect species of conservation concern (Simpfendorfer et al. 2010; Carlisle et al. 2019). Acoustic telemetry is frequently used to collect fine-scale movement data on site-resident species, generating information on their environmental

niches, habitat associations and activity spaces (Vianna et al. 2013; Espinoza et al. 2015a). Previous studies using acoustic telemetry and stable isotope analyses suggest spatial partitioning of sympatric reef shark species (Espinoza et al. 2015c; Heupel et al. 2018) which appears linked to resource partitioning (McCauley et al. 2012; Frisch et al. 2016; Curnick et al. 2019). Some common patterns emerge from these studies, with activity space typically increasing with shark size both within and among species (Speed et al. 2010), and ontogenetic and sex-based differences in movement patterns and residency (Muntaner López 2016; Bonnin et al. 2019). However, results reported to date also suggest that both the ecological roles and spatial ecologies of reef sharks are context dependent to some extent, varying with reef connectivity, habitat type and inter-specific competition (Field et al. 2010; Heupel et al. 2010; Papastamatiou et al. 2018).

Grey reef (*Carcharhinus amblyrhynchos*) and silvertip sharks (*Carcharhinus albimarginatus*) are two closely related and relatively common reef sharks species with overlapping Indo-Pacific distributions (Compagno 1984; Froese and Pauly 2010) and spatial niches within reef systems (Graham et al. 2010; Espinoza et al. 2015c). Where the spatial ecology of both species has been studied concurrently on the Great Barrier Reef, silvertip sharks, on average, showed lower residency to individual reefs and higher dispersal from tagging sites than grey reef sharks (Espinoza et al. 2015c). Stomach content and stable isotope analyses also suggest that the two species exploit overlapping but distinct prey resources, with silvertip sharks exploiting a higher proportion of pelagic prey species than grey reef sharks (Stevens 1984; Curnick et al. 2019). In addition to foraging needs, movement patterns of both species may also be coupled to environmental drivers. Vianna et al. (2013) found a strong influence of diel and lunar cycles, as well as season on the vertical movements of grey reef sharks in Palau, while Espinoza et al. (2015b) found both diel and seasonal variations in the detection of acoustically-tagged silvertip sharks on the Great Barrier Reef.

In the current study, I used acoustic telemetry to investigate long-term residency and space use of grey reef and silvertip sharks within the British Indian Ocean Territory Marine Protected Area (BIOT MPA), a remote archipelago of atolls and submerged reef features in the central Indian Ocean. I compared overall residency, daily attendance patterns and activity space between grey reef and silvertip sharks using acoustic telemetry data collected from 132 individuals over a three-year period. Intraspecific variation in spatial ecology was also examined based on the sex and size of individuals, and at both shallow and deep habitats in the study site. Temporal and spatial patterns in residency are discussed in the context of previous movement studies in other coastal and oceanic

reef systems, with the hypothesis that the spatial ecology of reef sharks is location as well as species dependent.

3.3 Methods

3.3.1 Study site

The BIOT MPA is a large no-take marine reserve in the central Indian Ocean, centred on approximately 6.5° south latitude, 72° east longitude (Figure 1). The MPA was established in April 2010 and covers over 600,000 km² of ocean, including over 60 atolls and islands, comprising the Chagos Archipelago, and around 80 seamounts (Sheppard et al. 2012; Yesson et al. 2020). Aside from a military base on the atoll of Diego Garcia in the south east of the archipelago (Figure 3.1) the area has been uninhabited since the 1970s and subject to very little direct anthropogenic disturbance. As such it is considered a key location at which to study both coral reef and pelagic ecology under near-natural conditions, in an otherwise heavily impacted region. The Chagos Archipelago is also relatively remote and isolated from neighbouring reefs. It is 450 km from its nearest neighbour, Addu Atoll in the southern Maldives, and separated from those neighbouring reef systems by waters at least 1000 m deep. The current study focussed on shallow reefs (20-30 m depth) around two of the northern atolls, Peros Banhos and Salomon Atolls, as well as an area of deeper seamounts (~80 m on summits) in the south of the archipelago (Figure 3.1).

3.3.2 Acoustic receiver array

An array of acoustic receivers (VR2W, VR4UWM, VR4G; Vemco Inc., Nova Scotia, Canada) has been maintained around atoll reefs and seamounts in BIOT since February 2013 (Figure 1). Receivers are serviced annually during regular site visits between February and May each year, during which existing units are retrieved and serviced, and additional units are added. Since the number of receivers has changed in each project year due to additions and, sometimes, losses, the current study uses data from 29 receiver located around the shallow atolls of Peros Banhos and Salomon, in the north of BIOT, which were continuously monitored from April 2014 to May 2017 providing consistent coverage of the study area. I also use data from four locations on seamounts in the south of the study area (Figure 3.1).

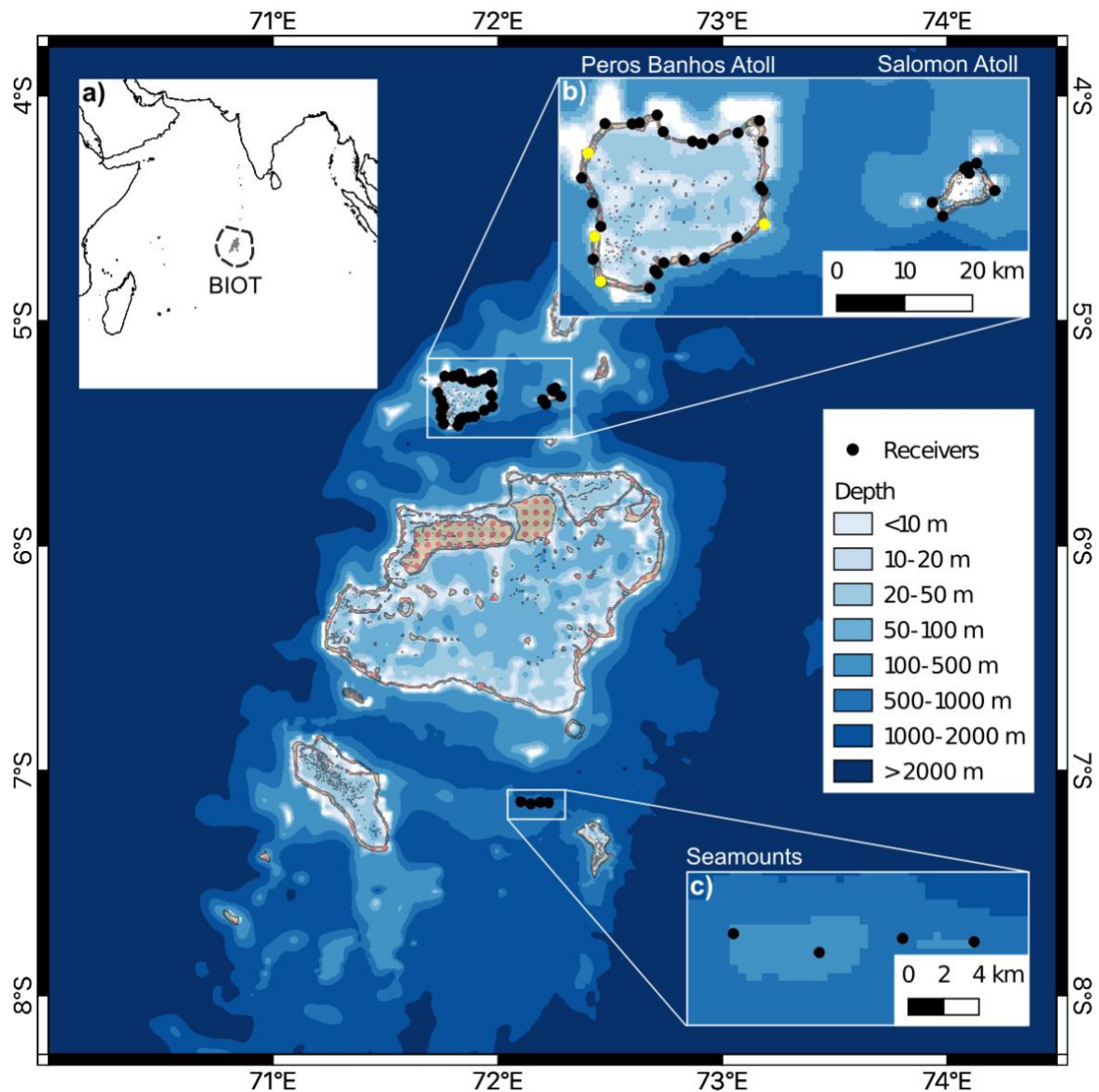


Figure 3.1: Map of the BIOT showing location of receivers for which data were analysed in the current study. Insets show (a) the BIOT's location in the Indian Ocean, with the MPA's outer boundary indicated with a dashed border; (b) the shallow atoll reef locations, monitored continuously from April 2014 to April 2017. Receiver locations with control tags used to estimate detection efficiency are indicated in yellow; (c) the seamount locations monitored from April 2016 to April 2017. Map shading indicates depth as per legend; depth data from GEBCO 15 arc-second global bathymetry dataset.

The seamounts were first biologically surveyed in 2012, and there are known to be at least two main peaks, Sandes and Swartz, rising to around 80 m (Hosegood et al. 2019). The area around these two seamounts was monitored from April 2016 to May 2017, providing a year of overlapping coverage between the shallow reef and deep seamount sites. (Supplementary Figure 3.2). Full details of the receiver array development and installation methods are included in the supplementary material. Briefly, receivers around the northern atolls were moored at depths between 20 m and 30 m on the outer reef or in the entrances of channels using cement blocks, rope risers and submersible plastic floats. Moorings were installed by scuba divers, using a liftbag to avoid damaging live benthos with

the heavy block. Receivers were protected with insulating tape to prevent direct attachment of fouling organisms, and were attached directly to the mooring risers using a large hose clamp and heavy-duty cable ties (Supplementary Figure 3.1). Receivers were positioned with the receiver tip oriented towards the surface. During annual servicing trips, divers retrieved the receivers which were cleaned and had their data downloaded before being replaced in the array. Mooring ropes were replaced every two years to prevent losses from wear. Receivers on the seamounts were sited in deep water (80-200 m) and fitted with acoustic release mechanisms allowing them to float free of the mooring block for retrieval.

3.3.3 Acoustic tag deployment

3.1.1.1 Acoustic tags

A total of 222 acoustic tags (VR16 coded tags, 69 kHz, transmission interval 30-90 s or 60-180 s, Vemco, Halifax, Nova Scotia, Canada) were deployed on grey reef and silvertip sharks during regular site visits conducted between February 2013 and May 2016. The tags had a nominal battery life of 9.3 years. Acoustic tags transmit a unique pulse sequence which identifies the tag when detected by a compatible acoustic receiver (Kessel et al. 2014). Twenty-nine of the tags were also equipped with depth and/or temperature sensors, which transmitted *in situ* measurements along with the tag identity. Nine tags transmitted depth and temperature measurements, seven transmitted depth only and 13 transmitted temperature only.

The interval between an acoustic tag's transmissions varies quasi-randomly with its programmed transmission interval. This reduces the chance of simultaneous transmissions by two or more tags which might result in signal interference and corrupted or false detections (Simpfendorfer et al. 2015). Tag detection can also be impacted by acoustic interference from environmental and biogenic noise, and even echoes of a tag's own transmissions under certain conditions (Mathies et al. 2014; Kessel et al. 2015). Maximum detection range can be up to 1000 m from a receiver, but this is typically reduced by environmental conditions (Kessel et al. 2014), especially in shallow reef environments (Welsh et al. 2012).

3.1.1.2 Tag deployment

Sharks were captured on handlines using barbless circle hooks on wire leaders, baited with imported frozen squid. Once hooked, sharks were brought alongside the tagging vessel and restrained using a soft tail rope. Animals less than approximately 150 cm total length were lifted onto a padded tagging mat. Their gills were irrigated with sea water via a perforated pipe placed in the mouth and

connected to a hose with a submersible pump immersed alongside the vessel. Eyes were covered with a cloth soaked in sea water to further reduce stress stimuli (Stehfest et al. 2014). Larger individuals were left in the water and rolled ventral side up to induce tonic immobility (Henningsen 1994). An additional soft fabric strap was looped under the mid-section of these animals, just behind the pectoral fins, to support the shark's body during the tagging operation. Most tags deployed in 2013 were attached externally, using a titanium dart and nylon leader, with the dart inserted into the musculature below the dorsal fin (Bradford et al. 2009). A small number of tags deployed in 2013 and all tags from 2014 onwards were surgically implanted (Wagner et al. 2011). Tags were inserted into the abdominal cavity of the shark via a small incision, made posterior to the pectoral fins and just off the ventral midline (Haulsee et al. 2016), and closed with a single non-absorbable nylon suture (3-0, 24 mm) using a reverse cutting needle (Ethion, US). Tissue samples were taken for separate genetic and stable isotope analyses (Matich et al. 2011; Momigliano et al. 2017). I recorded each shark's tagging location and time, its species, total length (TL), fork length (FL) and pre-caudal length (PCL), and its sex, where apparent. The tagging operation was kept to no more than five minutes. Animal handling procedures were approved by the Stanford University Administrative Panel on Laboratory Animal Care under permit APLAC-10765, held by the Block Laboratory at Hopkins Marine Station, and fieldwork was carried out under a research permit from the UK Foreign and Commonwealth Office.

3.1.1.3 Control tags

To test for detection range and variations in the probability of a tag being detected in the array while in range of a receiver, fixed control tags (Payne et al. 2010) were deployed at four locations within the array (Figure 1, Supplementary Table 3.2). Control tags (V16, 300-900s nominal delay, Vemco, Nova Scotia) were deployed 290 m to 500 m from receivers (Supplementary Table 3.2). Tags were suspended in the water column ~2 m above the reef substrate using a simple sub-surface mooring made from a dive weight, 2.5 m of 5 mm polypropylene line and a small polystyrene float. Control tags were only deployed on the reefs around the shallow atoll sites; no testing of receiver detection range or efficiency was performed at the seamounts due to logistical constraints. However, Scherrer et al. (2018) found that VRW2 receivers moored at 300 m depth in Hawaii had a detection range of ~840 m, compared with ~290 m for receivers moored at 25 m. Therefore, a detection range effect at the seamounts was anticipated and considered when interpreting the detection data, in the context of the known distribution and aggregation behaviour of sharks in BIOT (e.g., Tickler et al. 2017; Hosegood et al. 2019)

3.3.4 Data preparation

Data were filtered to include only those detections recorded between April 2014 and May 2017 at 29 locations in the northern atolls and four locations on the southern seamounts (Figure 3.1). Since research projects in BIOT had deployed acoustic tags on species other than grey reef and silvertip sharks (e.g. red bass, *Lutjanus bohar*), raw detection data were filtered to remove data from acoustic tag IDs which did not belong to this study. Detection times recorded by the receivers were converted from the default Coordinated Universal Time (UTC) to the study site's local time zone (UTC +5 h). Data recorded during annual receiver servicing and shark tagging fieldwork were removed from the data set, since both receiver and tag numbers fluctuated during these periods. Animal metadata recorded during tagging operations (tagging date, tagging location, species, sex and length) were appended to the resulting dataset based on the tag ID. Receiver latitude and longitude were appended from receiver deployment records, based on location ID. Detection records were classified as belonging to the shallow atoll reef sections of the array or the deep seamount sites, based on their location ID.

Detections were aggregated by date, hour of day (0 – 23), tag ID and location code. A shark was deemed present in the array if two or more detections were logged on a single day (Vianna et al. 2013; Espinoza et al. 2015a). Monitoring period for each shark was defined as the number of days between its tagging date and the date of its last detection in the data series. On days when a shark was deemed present, an hourly detection event was defined as one or more detections in a given hour of the day. This prevents variations in tag transmission rates from biasing the comparison of detection patterns from individual tags (Vianna et al. 2013).

3.3.5 Analyses

3.3.5.1 Data exploration and detection controls

Patterns in the detection of the control tags were compared with those of sharks detected at the same receivers to assess whether diel variations in detection probability existed and the extent to which they might bias the shark detection data. Detection events were summed by hour of day for each control tag and for any shark tags detected at the same location, and I calculated detection density by hour as the share of all detections received from each tag that were recorded in each hour of the day (0-23). Since I was modelling detection density around a 24-cycle, circular regression (deBruyn and Meeuwig 2001) was used to test for the effects of hour angle (circular: hour transformed to radians by dividing by 24 and multiplying by 2π) and tag 'type' (factor: control, grey

reef or silvertip), and their interaction, on detection density. I included both sine(hour angle) and cosine(hour angle) as cyclical predictors (deBruyn and Meeuwig 2001).

3.3.5.2 Inter- and intraspecific differences in shark residency

Comparisons between grey reef and silvertip sharks were restricted to data recorded on the northern atoll reef section of the array where both species were monitored together. I calculated the residency index of each shark as the number of days it was present within the array, divided by its total monitoring period (Vianna et al. 2013; Espinoza et al. 2015a). Daily attendance for each shark was calculated as the number hours a shark was detected on each day it was present in the array. I used multiple regression to test for the effect of species (factor: grey reef or silvertip), sex (factor: Male or Female) and total length (continuous: centimetres), and their interactions, on the residency, attendance and dispersal (movement range and activity space) metrics of individual sharks. Model selection was performed using the function dredge() in the R package *MuMIn* (multimodel inference (multi-model inference, Bartoń 2018)). The function takes a full model (all terms and interactions) and then builds alternate models using subsets of predictors. Alternate models are ranked by the Aikike Information Criterion, corrected for sample size, AICc (Burnham and Anderson 2002). I inspected the top ranked models to determine which terms were significant. In the event that a single categorical variable was the only predictor in the model, I calculated the mean and confidence interval of the variable in question at the two factor levels, and tested for a significant difference with a t-test (Zar 1996). Confidence intervals (CI) were calculated as 1.96 standard errors of the mean (Fisher 1934).

I also tested for intra-specific differences in residency index and daily attendance between silvertip sharks tagged around the atoll reef-based acoustic receivers described above, and the four receivers deployed and recovered on the deep seamounts. Only detection data for 2016 were used for this comparison as that was the year the seamount acoustic receivers were active (Supplementary Figure 3.2). I used multiple regression to test for the effect of location (factor: atoll or seamount), sex (factor: male or female) and total length (continuous: centimetres), and their interactions, on residency and attendance metrics.

3.3.5.3 Dispersal from tagging sites

I calculated the distance between each shark's tagging location and each of the receiver locations it visited using the function geoDist() in the R package *geosphere* (Hijmans 2017). The number of unique individual receivers visited and the maximum displacement from the tagging site was

determined for each shark. After visually inspecting histograms of distance and receiver count data, these were log-transformed to make them approximately normal. I used multiple regression to test for the effect of location, sex and length, and their interactions, on the log transformed dispersal metrics. Where only a single factor was found to have significant effect the mean \pm 95% CI of each measure was calculated for the two species. Means and CIs were calculated on the log-transformed data, then back-transformed into the original units for ease of interpretation.

3.3.5.4 Activity space

I estimated the activity space of each shark as the core 95% of a utilisation distribution (UD) generated by a Brownian Bridge Movement Model (BBMM, Horne et al. 2007). A BBMM estimates potential space use between consecutive detections of an animal by simulating likely paths between origin and destination using directed random walks. The UD combines random walks from a set of detections to represent the probability of an animal being located at each point in a study area over a given period. I used the `kernelbb()` function in the package *adehabitathr* to generate BBMM UDs (Calenge 2006). So that distances and areas would be calculated in metres and hectares, respectively, receiver locations were converted from latitude and longitude in decimal degrees to northings and eastings in metres, using a Lambert conformic conic projection centred on 6.5° S, 72° E. The `kernelbb()` function's 'sig1' parameter, relating to the rate of movement between locations, was estimated from the detection data using the maximum likelihood function `liker()` in the *adehabitathr* package. The 'sig2' parameter, relating to location accuracy, was set to 400 m, which was the assumed detection radius of the receivers based on control tags' performance as well as typical detection ranges reported in the literature (Kessel et al. 2014; Mathies et al. 2014). The 'grid' parameter, which controls the spatial resolution of the utilisation estimates generated by the algorithms, was set to 400, resulting in a UD cell size of approximately 50 m x 50 m. The activity space (i.e. 95% utilisation area) of each shark was determined using the function `getverticeshr()`. The function returned an activity space in hectares, which I converted into square kilometres. The distribution of activity space areas for all sharks was right-skewed, so activity space data were log-transformed before analysis. I used a multiple regression model of log-transformed activity space against species and tag monitoring time to test whether activity space estimates may have been influenced by the length of time I had monitored individual sharks. I calculated the mean \pm CI for the activity space of grey reef and silvertip sharks around the atoll reefs, and for silvertip sharks at atoll reefs and seamounts. The effect of species, sex and length on activity space was tested with multiple regression.

3.3.5.5 Detection cycles

I calculated average diel variation in shark attendance within the receiver array by summing detection events for each tag by hour of day and calculating the proportion of total detection events occurring in each hour. Detection density by species and hour was averaged across all tags and plotted on a circular plot representing the 24-hour cycle. Diel periods were defined based on the sharks' average detection cycles: dawn, 05:00 to 07:00; day, 07:00 to 17:00; dusk, 17:00 to 19:00; and night, 19:00 to 05:00. To test for the effects of hour of day, species and total length on detection, I used circular regression, with hour transformed into a circular predictor. Model selection began with the most complex model, including both $\cos/\sin(\theta)$ and $\cos/\sin(2\theta)$ terms, and removed insignificant terms until all remaining terms, or their interactions, were significant.

3.3.5.6 Depth and ambient temperature

I aggregated depth and temperature sensor data from 29 sharks (11 grey reef sharks and 18 silvertip sharks) by species and hour of detection, and calculated means and confidence intervals for each hour and species to examine diel variations. Temperature analyses were restricted to tags attached externally to ensure that water temperature was measured, and not the internal body temperature of the shark, which was slower to respond to environmental changes (Supplementary Figure 3.3). I used circular regression to test for the effects of shark species and hour of day on tag depth and ambient temperature, separately.

3.4 Results

3.4.1 Detection efficiency

Control tags were reliably detected up to 380 m from receiver locations (Supplementary Table 3.2). The control tags deployed generated ~4,000 detections in total (Supplementary Table 3.2), with two receiver locations on outer reef sites in the southeast and southwest of Peros Banhos atoll (Figure 3.1) receiving enough control tag detections to allow diel patterns in detections to be analysed. The number of control tag transmissions detected varied by time of day, with apparent detection efficiency higher during daylight (Supplementary Figure 3.4). However, shark tag detections by the same receivers showed both diurnal and nocturnal peaks in detection events for different individuals (Supplementary Figure 3.4). Variation in detection density by tags was best predicted by a circular regression model containing both hour of day (expressed in radians) and the factor tag type (control, grey reef shark or silvertip shark) and their interaction ($R^2_{\text{adj}} = 0.52$, $p < 0.001$; Supplementary Table 3.1). There were significant effects of the interaction of both shark species

with the sinusoidal terms modelling hour of day, indicating that patterns of diel variation in detections for the tagged sharks differed from those of the control tags (Supplementary Table 3.1). This was interpreted as meaning that shark behaviour, and not just detection efficiency, was influencing diel variation in detection probability.

3.4.2 Summary tag detection statistics

Between April 2014 and April 2017, 132 tags were active in the study site. The dataset included 42 grey reef sharks (33 female, 9 male) and 50 silvertip sharks (30 female, 20 male) tagged on the shallow atoll reef sites, and 40 silvertip sharks (23 females and 17 males) tagged on the deep seamount sites. In total, there were 20,408 days of detection data over 49,639 days of monitoring (Table 3.1, Supplementary Figure 3.2). Median monitoring time was 376 days for grey reef sharks (range 4 to 922 days) and 338 days for silvertip sharks (range 10 to 1092 days; Supplementary Tables 3.3 and 3.4).

Table 3.1: Summary of the acoustic tag deployments on reef sharks in the BIOT which were used in the current study, by habitat (atoll or seamount), species and sex.

Habitat	Species	Sex	n	Total length (\pm 95% CI) cm	Total days monitored	Total days detected	Total hours detected
Atoll reef	Grey reef	F	33	130.7 \pm 6.1	13,729	4,441	21,117
Atoll reef	Grey reef	M	9	122.3 \pm 6.5	4,123	2,027	11,427
Atoll reef	Silvertip	F	30	124.8 \pm 7.4	10,477	4,346	15,181
Atoll reef	Silvertip	M	20	130.2 \pm 12.7	9,535	4,508	22,052
Seamount	Silvertip	F	23	147.5 \pm 8.6	6,872	2,437	17,184
Seamount	Silvertip	M	17	150.4 \pm 10.5	4,903	2,649	18,837

3.4.3 Residency, attendance, dispersal and activity space for grey reef and silvertip sharks

There was no significant difference in residency index or daily attendance between grey reef and silvertip sharks on shallow reef sites. Grey reef and silvertip sharks were detected on $41.1 \pm 10.5\%$ and $45.0 \pm 7.3\%$ of monitored days around the shallow reefs, respectively. On days when they were present, grey reef sharks were detected for 4.2 ± 0.6 hours and silvertip sharks for 3.5 ± 0.5 hours. There were no significant effects of species, sex or total length on either residency or attendance.

Significant differences were evident between grey reef and silvertip sharks for the number of receiver locations visited, their dispersal distance and their total activity space within the study site. Grey reef sharks visited 2.9 sites on average (CI: 2.4-3.4 sites) compared with 5.2 sites for silvertip sharks (CI: 4.5-6.1 sites, $t = -4.7707$, $p < 0.001$). Both species and total length had significant effects

on the number of receivers visited by sharks, with the model predicting that silvertip sharks would visit 80% more sites than grey reef sharks but that larger sharks of both species would visit fewer sites than smaller sharks, with the number of individual receivers visited declining by one third for each 50cm increase in total length (Figure 3.2a). Grey reef sharks moved significantly shorter distances away from their tagging sites than silvertip sharks ($t = -3.54$, $p < 0.001$, Figure 3.2b). Grey reef sharks were detected, on average, 6.6 km (CI: 5.0-8.7 km) from their tagging site, with a maximum of 76 km. Average dispersal distance for silvertip sharks was 13.1km (CI: 10.5-16.3 km, $t = -3.5422$, $p < 0.001$) with the maximum recorded displacement being 87 km. Grey reef sharks also had smaller activity spaces than silvertip sharks, utilising an average area of 29 km² (CI: 13 to 66 km²) compared with 116 km² (CI: 81 to 164 km², $t = -2.36$, $p = 0.03$, Figure 3.2c). There were no significant sex or sized-based differences in dispersal or activity space.

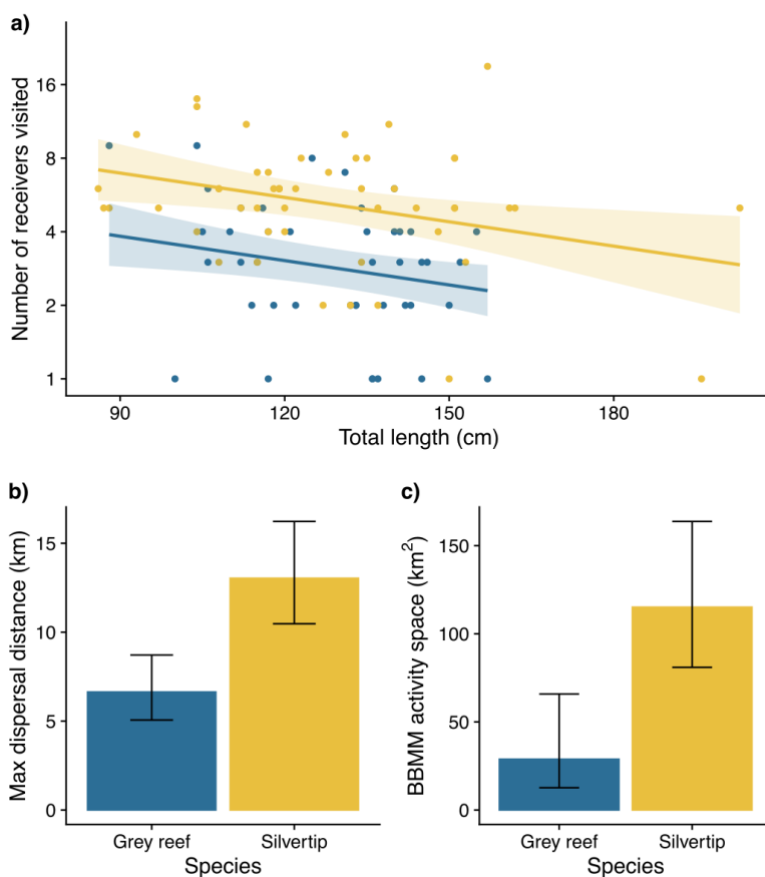


Figure 3.2: Average residency and space use metrics for grey reef (blue) and silvertip sharks (gold): a) number of receivers visited by shark species and length. Line and ribbon indicate slope (\pm 95% CI) for each species from a multiple linear regression model with species and total length as independent predictors of receivers visited ($R^2_{adj} = 0.26$, $F_{[4, 88]} = 9.226$, $p = < 0.001$); b) Mean (\pm CI) maximum dispersal distance from tagging location by species; and c) mean (\pm CI) Dynamic Brownian Bridge Movement Model (BBMM)-based activity. Activity space is defined as the modelled 2-D region within which there is a 95% probability of a shark's movement occurring. Note: Values for dispersal distance and BBMM activity space were log-transformed before calculating the mean \pm CI, and the statistics were back-transformed for plotting.

Table 3.2: Parameters of the multiple linear regression model used to predict the number of acoustic receivers (log-transformed) visited by sharks. Estimated effect size for each parameter is shown along with its standard error (SE) T statistic (T) and p-value (p). Significant predictors indicated in bold.

Predictors	Estimate	SE	T	p
(Intercept)	2.032	0.381	5.33	<0.001
Species (Silvertip)	0.595	0.121	4.92	<0.001
Total length	-0.008	0.003	-2.66	0.01
Model statistics: $R^2 = 0.29$, $R^2_{adj} = 0.26$; $F_{[4, 88]} = 9.226$, $p = < 0.001$				

3.4.4 Diel detection cycles of grey reef and silvertip sharks

Grey reef sharks, on average, spent a greater proportion of their time around the atoll reef sites at night compared with silvertip sharks (Figure 3a, Supplementary Figure 3.5). Detections density was predicted by the hour, and the species and size of the shark. The concentration of detections during daylight increased with size for both species, but the model predicted lower detections by silvertip sharks in the middle of the night (Figure 3.3). Whereas smaller grey reef sharks showed little diel variation in detection density, smaller silvertip sharks had a distinct crepuscular pattern in their detections, with clear dawn and dusk peaks (Figure 3.3). There was a significant interaction between the Species(Silvertip) and $\cos(2 \times \text{hour})$ terms in the model, corresponding to this double peak in activity for silvertip sharks.

Table 3.3: *Parameters of the circular regression model used to predict the proportion of shark activity (i.e. detections) in each hour of the day. Estimated effect size for each parameter is shown along with its standard error (SE) T statistic (T) and p-value (p). Significant predictors indicated in bold.*

Predictors	Estimate	SE	T	p
(Intercept)	4.17e ⁻⁰²	5.16E ⁻⁰³	8.08	<0.001
$\sin(\text{hour})$	-4.07e ⁻⁰³	1.15E ⁻⁰³	-3.54	<0.001
$\cos(\text{hour})$	2.64e ⁻⁰²	7.12E ⁻⁰³	3.71	<0.001
$\sin(2 \times \text{hour})$	9.80e ⁻⁰⁵	1.70E ⁻⁰³	0.06	0.95
$\cos(2 \times \text{hour})$	2.01e ⁻⁰³	1.70E ⁻⁰³	1.18	0.24
Species(Silvertip)	-7.90e ⁻¹⁸	1.63E ⁻⁰³	0.00	1
Total length	-4.59e ⁻¹⁹	3.89E ⁻⁰⁵	0.00	1
$\sin(2 \times \text{hour}) \text{Species(Silvertip)}$	8.27e ⁻⁰³	2.31E ⁻⁰³	3.58	<0.001
$\cos(2 \times \text{hour}) \text{Species(Silvertip)}$	-1.26e ⁻⁰²	2.31E ⁻⁰³	-5.45	<0.001
$\cos(\text{hour}) \text{Total length}$	-4.08e ⁻⁰⁴	5.49E ⁻⁰⁵	-7.43	<0.001
Model statistics: $R^2 = 0.23$, $R^2_{adj} = 0.22$; $F_{[9, 2198]} = 71.76$, $p = < 0.001$				

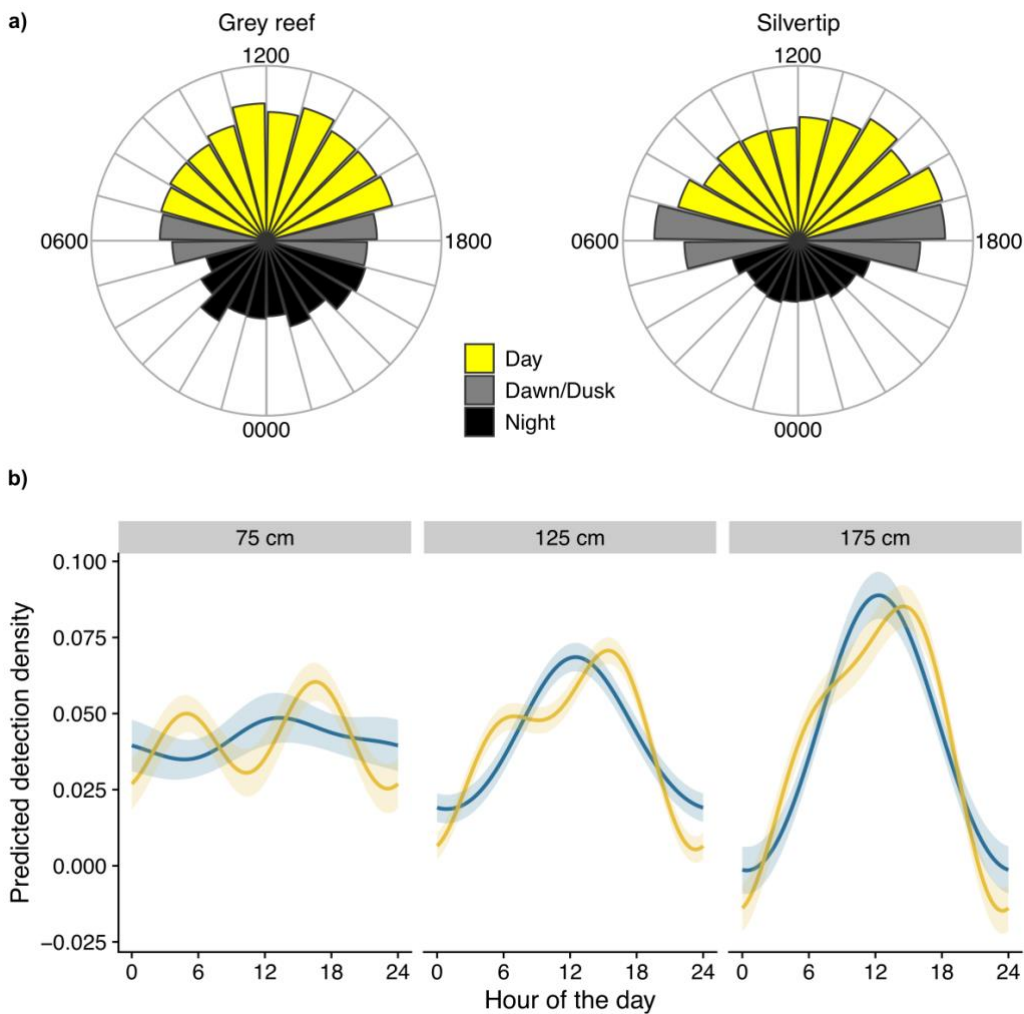


Figure 3.3: Detection cycles for grey reef and silvertip sharks, at atoll sites only. a) Mean distribution of detections by time of day. Segment areas are proportional to the percentage of detections occurring in each hour. Segments colour coded for dawn (0500 to 0700, grey), day (0700 to 1700, yellow), dusk (1700 to 1900, grey) and night (1900 to 0500, black). b) Predicted detection density (with 95% confidence ribbons) from a circular regression model with hour as a circular predictor, along with its interactions with species and total length, respectively (Table 3.3). Predicted detection density, by species and hour, shown for a 75 cm, 125 cm and 175 cm shark.

3.4.5 Depths and ambient temperatures occupied by sharks

Grey reef sharks occupied shallower depths (13.0 ± 0.1 m vs 38.0 ± 0.4 m, $t = -142.71$, $p < 0.001$, Figure 3.4a) and warmer water ($28.3 \pm 0.1^\circ\text{C}$ vs $27.0 \pm 0.04^\circ\text{C}$, $t = 90.96$, $p < 0.001$, Figure 3.4b) than silvertip sharks. Grey reef sharks occupied fairly constant depth and water temperature regimes throughout the day, whereas silvertip sharks occupied significantly deeper, cooler water during daytime (Figure 3.4). On average, silvertip sharks were 31.4 m deeper and occupied water 1.3°C cooler than grey reef sharks (Tables 3.4 and 3.5).

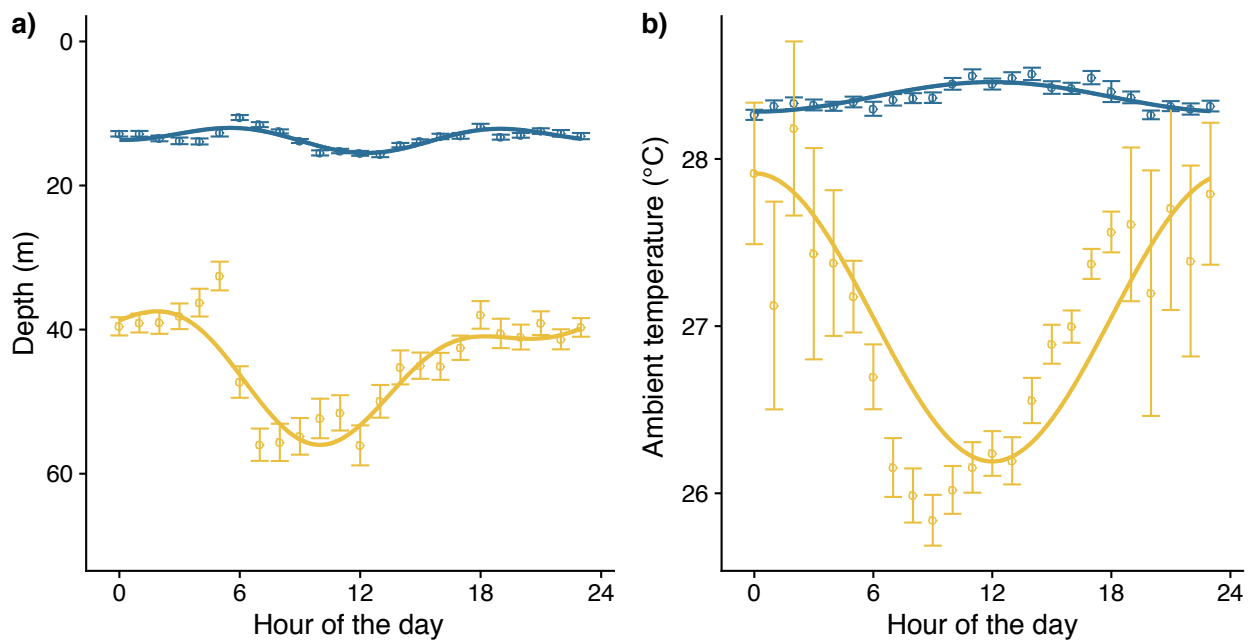


Figure 3.4: In situ depth and temperature data for a subsample of tagged sharks. a) Average depth, in metres, and b) average ambient water temperature, in degrees centigrade, against hour of day for grey reef (blue) and silvertip sharks (yellow). Error bars show 95% confidence interval of the mean values in each hour. Sample sizes: six depth and five temperature sensors for grey reef sharks, ten depth and eight temperature sensors for silvertip sharks. Curves and ribbons show predicted values (\pm 95% confidence interval) of circular regression models of depth and temperature, respectively, against hour (circular predictor) and species, and their interactions (Tables 3.4 and 3.5)

Table 3.4: Parameters of the circular regression model used to predict the depth of grey reef and silvertip sharks in each hour of the day. Estimated effect size for each parameter is shown along with its standard error (SE) T statistic (T) and p-value (p). Significant predictors indicated in bold.

Predictors	Estimate	SE	T	p
(Intercept)	13.37	0.10	136.9	<0.001
sin(hour)	-0.12	0.14	-0.8	0.404
cos(hour)	-0.90	0.13	-6.8	<0.001
Species(Silvertip)	31.44	0.16	195.5	<0.001
sin(2xhour)	0.15	0.13	1.1	0.257
cos(2xhour)	1.21	0.11	11.0	<0.001
sin(hour) Species(Silvertip)	2.78	0.23	11.9	<0.001
cos(hour) Species(Silvertip)	-6.37	0.22	-28.4	<0.001
sin(2x hour) Species(Silvertip)	-3.58	0.23	-15.8	<0.001
Model statistics: $R^2 = 0.56$, $R^2_{adj} = 0.54$; $F_{[8, 30931]} = 4955$, $p = < 0.001$				

Table 3.5: Parameters of the circular regression model used to predict the ambient temperature of the water occupied by grey reef and silvertip sharks in each hour of the day. Estimated effect size for each parameter is shown along with its standard error (SE) T statistic (T) and p-value (p). Significant predictors indicated in bold.

Predictors	Estimate	SE	T	p
(Intercept)	28.37	0.01	3062.1	<0.001
cos(hour)	-0.09	0.01	-6.9	<0.001
Species(Silvertip)	-1.32	0.02	-60.6	<0.001
cos(hour) Species(Silvertip)	0.95	0.03	30.2	<0.001
Model statistics: $R^2 = 0.36$, $R^2_{adj} = 0.34$; $F_{[3, 27805]} = 4794$, $p = < 0.001$				

3.4.6 Residency and detection cycles of silvertip sharks in atoll reef and seamount habitats

During 2016, 30 silvertip sharks (18 females, 12 males) were monitored on shallow atoll reef sites, and 40 silvertip sharks (23 females, 17 males) were monitored on the seamounts. Two individuals which spent most of their time at the seamounts, one 151 cm male and one 150 cm female, were also briefly detected on receivers in the northern atolls. The share of silvertip shark detections occurring at night on the seamounts was double that on the atoll reefs ($57.0 \pm 7.5\%$ vs $29.0 \pm 7.6\%$, $t = -5.15$, $p < 0.001$, Figure 3.5a). There was no difference in the residency index of silvertip sharks between shallow and deep sites, but measured daily attendance of animals tagged near the seamounts was twice that of their conspecifics on the atoll reefs ($5.93 \pm 1.06 \text{ hr d}^{-1}$ vs $2.97 \pm 0.551 \text{ hr d}^{-1}$, $t = -4.84$, $p < 0.001$, Figure 3.5b). Mean activity space of silvertip sharks on the seamounts (23 km^2 ; CI 13 to 39 km^2) was 80% smaller than the activity space of conspecifics on the atoll reefs (115 km^2 ; CI 81 to 164 km^2 , $t = 4.92$, $p < 0.001$, Figure 3.5c). There were no size or sex-based trends evident.

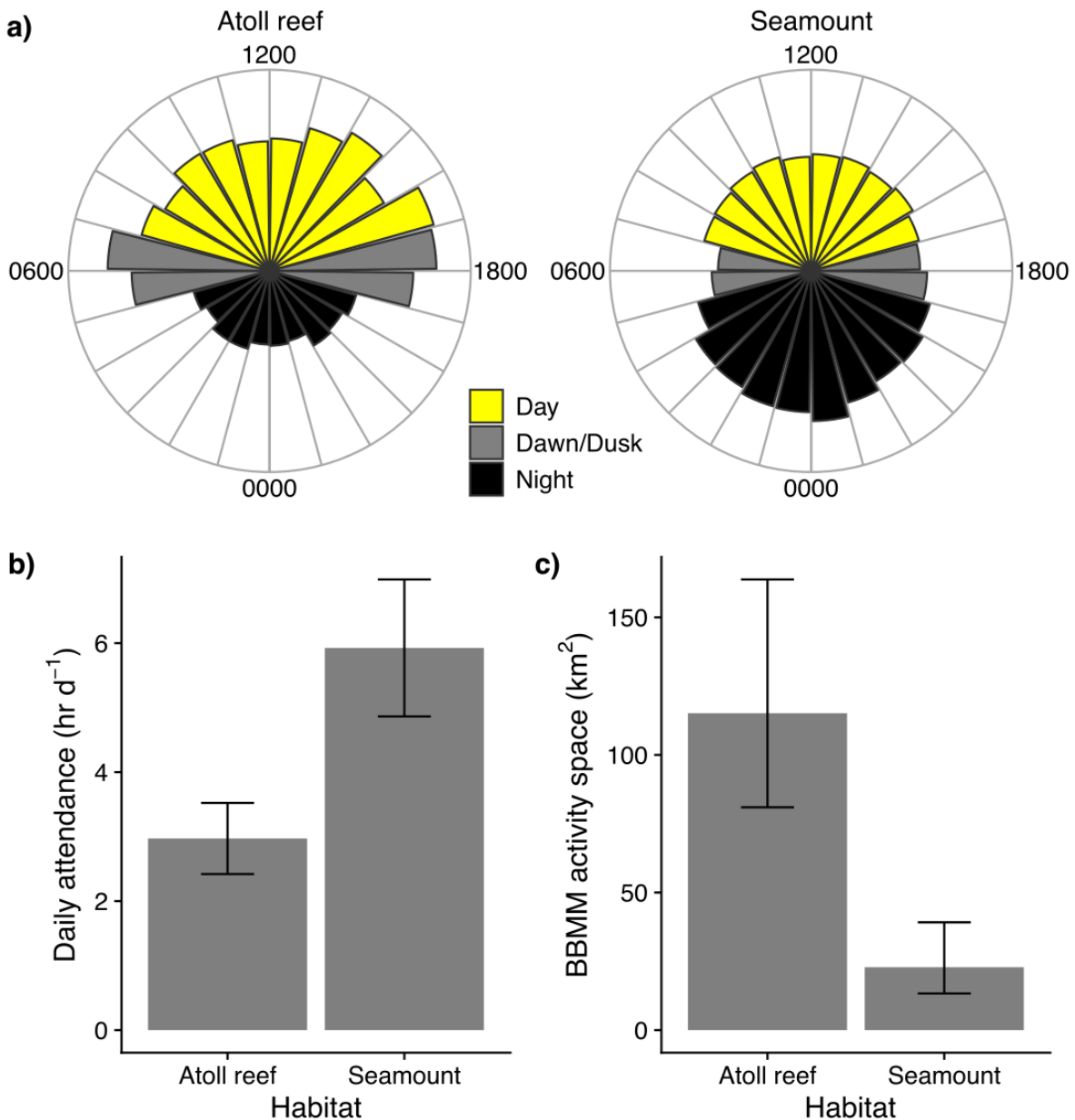


Figure 3.5: Intraspecific variation between silvertip sharks tagged near shallow atoll reefs and deep seamount habitats. *a)* Mean distribution of detections by time of day in each habitat. Segment areas are proportional to the percentage of detections occurring in each hour. Segments colour coded for dawn (0500 to 0700, grey), day (0700 to 1700, yellow), dusk (1700 to 1900, grey) and night (1900 to 0500, black); *b)* daily attendance (hours detected on days present); and *c)* Dynamic Brownian Bridge Movement Model (dBBMM)-based activity space (activity space defined as the modelled 2-D region within which there is a 95% probability of movement occurring). Error bars indicate 95% confidence interval (CI) of the mean of each metric. Activity space was log-transformed to calculate mean \pm CI, and the statistics back-transformed for plotting.

3.5 Discussion

Grey reef and silvertip sharks exhibit distinct spatial ecologies around reefs in BIOT in terms of temporal patterns in their presence around reef sites, activity spaces, the distances over which they connect reef elements, and the depth and thermal niches they occupy. The spatial ecology of grey reef and silvertip sharks has only been studied concurrently at a few locations, including the central Great Barrier Reef (GBR, Espinoza et al. 2015c) and D'Arros Atoll in the Seychelles (Lea et al. 2016), although the spatial ecology of grey reef sharks has been studied more widely (e.g., Vianna et al. 2013; White et al. 2017). My study both confirms and contradicts some of the findings from these studies. Consistent with the results of Espinoza et al. (2015c), I found that silvertip sharks occupy larger areas and disperse further than grey reef sharks around reefs where they co-occur, implying that they provide a higher degree of ecological connectivity across reef systems but may also be more vulnerable to fishing activity. However, while silvertip sharks were detected more frequently at night on the GBR (Espinoza et al. 2015b), I found the opposite pattern, suggesting that aspects of their spatial ecology may vary with location or reef type. While grey reef sharks exhibited small activity spaces and limited movements within BIOT, White et al. (2017) recorded pelagic excursions by multiple individuals at Palmyra Atoll in the Pacific. Such apparent variation in spatial ecology between and within species supports the conclusion of Dwyer et al. (2020) that spatial management of reef sharks, including the design and enforcement of MPAs, needs to be tailored to both inter- and intra-specific differences in reef use. These differences may relate to overall residency to reef systems, activity space and dispersal within reefs, and temporal variation in reef use.

3.5.1 Variation in reef shark residency

Espinoza et al. (2015c) found that grey reef sharks had higher overall residency indices than silvertip sharks within their study site on the GBR, with grey reef sharks being detected on more monitored days through the study, but I found no evidence of such a difference in BIOT with both species detected on a similar proportion of days. Lea et al. (2016) reported similar residency index values for both species at D'Arros Atoll in the Seychelles, but reef shark residency at their study site was half that observed in this study. Variations in reef shark residency observed in these different studies might be due to the degree of isolation of each study site. Espinoza et al. used an extensive receiver array to monitor a section of well-connected patch reef habitat in the central GBR (Espinoza et al. 2015c). In this continuous reef habitat, silvertip sharks, with a larger activity space and wider dispersal, may still move outside a study area, whereas grey reef sharks may be more likely to remain within the range of receivers, leading to higher residency index values. In BIOT, while

silvertip sharks move greater distances, they are still restricted to the isolated atoll complex, which may lead to a similar overall residency index as measured for grey reef sharks. In study by Lea et al. (2016), array layout may have influenced observed residency metrics. Their receiver array monitored a very small portion of larger shallow and isolated feature (the Amirantes Plateau, Lea et al. 2016). This may have meant while reef sharks of both species were restricted, by depth, to the area surrounding the focal reefs, leading to similar residency values, they were detected on a smaller fraction of monitoring days due to lower relative receiver coverage. Comparing these studies suggests that residency to study sites by reef sharks may be context-dependent to some extent, with reef isolation potentially a key factor.

3.5.2 Reef shark movements within study areas

Average dispersal ranges and activity spaces were smaller for grey reef sharks than silvertip sharks, and broadly consistent with previous studies. My activity space estimate for grey reef sharks is of a similar order of magnitude to that reported for this species on Western Australia's Ningaloo Reef (~20 km², Speed et al. 2016), and similar to an upper estimate generated for grey reef sharks on the GBR (~13-38 km², Espinoza et al. 2015a). Similarly, my average dispersal distances of around 7 km were within the range reported in a meta-analysis of reef shark movement patterns (4-14 km, Dwyer et al. 2020). I recorded maximum dispersals of 78 km and 87 km for grey reef and silvertip sharks, respectively, in the northern atoll array, but also recorded two silvertip sharks, one of each sex, moving over 200 km between the seamounts and atoll reef studied in BIOT. Espinoza et al. (2015c) reported maximum movements of 45 km and 50 km for grey reef sharks and silvertip sharks, respectively, although the majority of individuals remained within 10-15 km of their tagging site. Single movements of over 130 km have been recorded for a male grey reef shark moving back and forth between Osprey Reef in the Coral Sea and the GBR (Heupel et al. 2010), and Bonnin et al. (2019) reported long round-trip migrations by multiple male grey reef sharks in New Caledonia. My results support both the overall definition of grey reef sharks as the more site-attached species (Heupel et al. 2014; Espinoza et al. 2015c) and suggests that, in spatial terms, silvertip sharks may act as an umbrella species for more resident reef sharks in MPA planning. The evidence of long-range movements also reinforces the importance of accounting for individual variations in movement in predicting the efficacy of different scales of spatial protection (Dwyer et al. 2020), and the potential benefits of networks of smaller MPAs to at least partially account for the protection needs of both resident and more transient individuals within a population (McCook et al. 2010; Martín et al. 2020).

3.5.3 Detection cycles

Silvertip sharks in BIOT were detected less at night on the shallow receivers around the atolls than were grey reef sharks, and larger individuals of both species were also detected less at night time than smaller conspecifics. Larger sharks also appeared to visit fewer of the reef locations, which may be a consequence of them spending less time overall near the reefs, although silvertip sharks visited more locations than grey reef sharks of the same size. Smaller silvertip sharks appeared to have activity peaks, in terms of their detection near reefs, at dawn and dusk, which may correspond to crepuscular foraging activity. Vianna et al. (2013) reported a similar crepuscular cycle among grey reef sharks monitored in Palau, which was assumed to be linked to hunting on the reefs. Cyclical variations in detection patterns between shark species have also been hypothesised to correspond to habitat and resource partitioning (Papastamatiou et al. 2018). In BIOT, assuming that lower detection rate means genuine absence from the reefs, this may correlate with species-based and ontogenetic differences in reef- and pelagic-based foraging. Diet studies have shown that both species may exploit pelagic prey sources, and suggest that diets change, and trophic level increases, as individuals become larger (McCauley et al. 2012; Frisch et al. 2016; Roff et al. 2016; Curnick et al. 2019). The relationship between increased shark size and absence at night (and inferred offshore foraging) may relate both to the increasing energy needs of larger bodies and ontogenetic dietary shifts (Lowe et al. 1996; Newman et al. 2012), and conversely the increased predation risk that would be experienced by smaller sharks venturing away from reefs (Ahrens et al. 2012; Guttridge et al. 2012; Heupel et al. 2014).

3.5.4 Depth and temperature

Diel cycles in detection activity may also be linked to patterns in depth use and thermoregulation. The observed pattern in grey reef shark detections - more during the day than at night - was consistent with observations by Vianna et al. in Palau (2013) and Speed et al. (2016) at the Ningaloo Reef. However, diel variation in the detection of silvertip sharks in BIOT was the inverse to that observed for silvertip sharks on the GBR, where higher detections on reefs occurred at night (Espinoza et al. 2015b). This may be explained in part by thermoregulation. In both BIOT and the GBR (Espinoza et al. 2015b), but also in Fiji (Bond et al. 2015), silvertip sharks appear to use deeper, cooler water during daylight hours. Espinoza et al. (2015b) hypothesised that silvertip sharks' diel depth and temperature variations might represent a "hunt warm, rest cool" strategy (Sims et al. 2006). On the GBR, silvertip sharks appear to find thermal refuge in deep channels during the day, and hunt on the reefs, where they are more likely to be detected, at night (Espinoza et al. 2015b).

In contrast, silvertip sharks in the BIOT can find deeper, cooler water by moving a short vertical distance down the reef wall during the day, while remaining within detection distance of the reef-based receivers, but may move up and away into warm surface waters to hunt pelagic prey at night.

Grey reef sharks did not exhibit any apparent diel variation in depth in my study, which contrasts with results from Palau showing a significant diel variation in depth, from ~20-30 m at night to 30-40 m during the day (Vianna et al. 2013), as well as studies on the GBR (Heupel and Simpfendorfer 2014) and in Palmyra (Papastamatiou et al. 2018). While it is possible that my limited set of sensor tags missed detecting this behaviour, it is also possible that grey reef sharks in BIOT are responding to different environmental drivers. Vianna et al. (2013) observed that the grey reef sharks in Palau appeared to adjust their depth range according to the depth of the 29°C isotherm, and only went deeper when the water warmed at depth. The mean ambient temperature reported by the sensor tags on grey reef sharks in BIOT was also consistently between 28°C and 29°C, and it may therefore be that the shallows in BIOT represent their thermal niche. An alternative hypothesis is that grey reef sharks remain at relative shallow depths in the BIOT as a means of segregating vertically from silvertip sharks, and possibly other larger species. Depth partitioning by the two species would be consistent with previous assessments of relative reef shark abundance in BIOT, which found grey reef sharks far more abundant than silvertip sharks on shallow reef sites, but silvertip sharks the main species observed on deeper sites (Tickler et al. 2017).

3.5.5 Intraspecific variation in space use and activity space of silvertip sharks

Silvertip sharks appear to exhibit different spatial ecologies at the atoll reef and seamount sites within the BIOT atoll system, which suggests that deeper habitats like the seamounts may play an important role for the species. Silvertip sharks showed higher attendance and had smaller home ranges around the 80 m deep seamounts surveyed in my study. Compared with their conspecifics directly associated with the shallow atoll reef, they appear to exhibit a higher degree of site attachment to the seamounts, with higher daily attendance and less diel variation in detections. Differences in detection efficiency and, in particular, range may be the most parsimonious explanation, with the deeper receivers near the seamounts 'seeing' more of the silvertip sharks' movements both day and night. However, silvertip sharks' affinity to the seamounts is also consistent with both dietary evidence (Curnick et al. 2019), which indicates a dependence by silvertip sharks on pelagic prey in the BIOT, and the seamounts' role in aggregating pelagic biomass (Letessier et al. 2016; Hosegood et al. 2019). Echosounder transects over the seamounts combined with current and tidal modelling suggest that the seamounts interact with prevailing currents to

entrain plankton, in turn concentrating fish biomass around and above the seamount peaks (Hosegood et al. 2019). One possibility is that rather than radiating away from reefs to forage at night, silvertip sharks at the seamounts exploit localised spikes in prey biomass, remaining in range of the receivers. Such variations in space use within species in response to concentrations of prey has been observed with reef sharks and fish aggregations in Micronesia (Rhodes et al. 2019). Residence to the seamount is clearly not permanent, as shown by the movement of one male and one female to the northern atolls. Such connectivity suggests that the seamounts, and other similar areas yet to be investigated, may be important to the wider population of silvertip sharks in BIOT. Deep habitats may also be a key niche for other shark species not investigated in this study, including scalloped hammerheads (*Sphyrna lewini*) which were observed schooling over one seamount during baited remote underwater video surveys (Tickler et al. 2017). Combined with other studies of the seamounts in BIOT, these telemetry results suggest that the seamounts may be a hotspot for larger shark species within the MPA.

3.5.6 Limitations of the study

Several caveats must be considered in interpreting the telemetry data, both at the shallow and deep sites. First is the bias that comes from the siting and spacing of receivers and the location of shark tagging effort, particularly for more site attached species. Carlisle et al. (2019) modelled sub-samples of the full data set described here to show that array density (i.e. the distance between adjacent receivers) impacted measured values of residency, and that additional metrics such as dispersal or home range estimation were also sensitive to array design (Carlisle et al. 2019). To reduce bias in the current study, I restricted analysis to receiver locations that were monitored continuously throughout a three-year period, meaning array size and density were held constant. However, differences in array layout between this and other studies may have confounded direct comparison of these results for individual species to those obtained elsewhere. Simulating shark movements within different arrays, as was explored in Carlisle et al. (2019), may help develop better account for the influence of array design in comparing across studies.

A second issue is that of detection efficiency and detection range by the receivers themselves. Background reef noise and reef topography are both known to impact the likelihood of a tag being detected, and this may vary cyclically, thus affecting not only overall detections but their apparent temporal variation (Kessel et al. 2014; Mathies et al. 2014). Additionally, receiver detection range can vary with mooring depth (Scherrer et al. 2018). The control tags provided only limited samples of detection efficiency within my study site, and are unlikely to fully represent spatial and temporal

variation. To lessen the impact of this, analyses were focussed on broad patterns in residency and other long-term metrics that are less sensitive to fluctuations in detection efficiency. An apparent reduction in night time detections of a control tag did not prevent individual sharks from being detected at night at the same location, and modelling found significant effect of shark species on detection patterns, compared with control tag detections. These results suggest that control tag-based estimated of detection efficiency may depend on the exact location of the tag, potentially including the surrounding reef structures, and not necessarily be representative of the detectability of mobile sharks at the same location. In the BIOT case more comprehensive measurement of detection range and efficiency within the array should help better address this question in the future. In the case of the seamount results, enhanced detection efficiency may be an issue due to both receiver siting and detection range. Assuming receivers are oriented towards the surface, as was the case in my study, deeper receivers will theoretically 'see' a larger volume of the water column and so may have a greater chance of detecting animals as they swim over, relative to receivers located on reef wall. Therefore, the apparent higher attendance on the seamount sites may be an artefact of a larger sampling unit, in terms of water volume, and the detection efficiency and range of deep receivers used in BIOT requires further investigation (Scherrer et al. 2018). However, the results obtained in this study are consistent with hypotheses about the ecology of silvertip sharks from dietary studies (i.e. higher energy demands and greater dependence on pelagic prey; Curnick et al. 2019), evidence of higher pelagic fish biomass around the seamounts (Hosegood et al. 2019), and independently observed abundance patterns within BIOT (Tickler et al. 2017).

3.6 Conclusion

Spatial ecology and the tools of telemetry are increasingly used to investigate the space use of reef sharks, with the goal of understanding their ecological roles, vulnerabilities and the conservation actions needed to protect populations (Heupel et al. 2019). For results to be generalisable, or, conversely, to determine what research is needed to fill remaining gaps, we need to understand the extent to which the behaviour of my study species may vary with reef typology (oceanic atoll, fringing reef, continental barrier reef, etc.) and the biological context - in particular the presence or absence of particular competitors or prey species. My study suggests that the spatial ecologies of grey reef and silvertip sharks do have some general features that may hold wherever they are encountered, with silvertip sharks in general the more mobile and wide-ranging species in reef habitats. However, it appears that variations in these patterns may occur in the context of different reef types, including the depth of the reef and its surrounds. Some results that are common across

studies, such as the greater depth of silvertip sharks, may relate to fundamental physiological constraints, such as thermal tolerance. Other aspects, such as habitat used for foraging, may vary with prey availability and competition, with species adapting behavioural strategies to the local context. Integrating results and datasets across current and future spatial ecology studies may help build a better understanding of the perhaps underappreciated complexity of reef sharks. While very large MPAs like the BIOT are likely sufficient to provide total protection to reef-associated species like grey reef and silvertip sharks (Carlisle et al. 2019), most MPAs are much smaller (www.mpatlas.org/), implying that not all species will be equally well protected (Dwyer et al. 2020). Taking account of inter- and intraspecific variations in reef shark spatial ecology can help better tailor MPAs around the space needs of species in a particular context and, importantly, ensure that MPAs for shark conservation are not just large enough, but also include the diversity of habitats required to support them.

3.7 References

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3.8 Supplementary material

3.8.1 Supplementary tables

Supplementary Table 3.1: Candidate models to predict hourly detection density at receivers with control tags. Predictors tested were the sine and cosine of the hour (0-23, converted to an angular variable in radians from 0 to 2π) and tag type (i.e. control tag, deployed on grey reef shark, deployed on silvertip shark). Control tag was the reference level for the factor tag type. Three models were tested: sine and cosine of hour; sine and cosine of hour plus tag type; sine and cosine of hour plus their interactions with tag type. Coefficients, standard errors and corresponding p-values are reported for each individual predictor, and their interactions where modelled; Each models coefficient of determination (R^2) and adjusted R^2 are reported under each model.

Response variable:	Model 1:			Model 2:			Model 3:		
Mean hourly detection density	sin(hour) + cos(hour)			sin(hour) + cos(hour) + tag type			sin(hour) + cos(hour) plus interactions with tag type		
Predictors	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p
(Intercept)	0.052	0.005	<0.001	0.043	0.007	<0.001	0.042	0.005	<0.001
sin(hour)	0.007	0.006	0.255	0.007	0.006	0.278	-0.009	0.007	0.193
cos(hour)	-0.012	0.006	0.057	-0.013	0.006	0.035	-0.051	0.007	<0.001
tag type: grey reef shark				0.020	0.011	0.076	0.007	0.008	0.391
tag type: silvertip shark				0.010	0.011	0.334	0.010	0.008	0.183
sin(hour) x tag type: grey reef shark							0.024	0.011	0.036
sin(hour) x tag type: silvertip shark							0.027	0.011	0.012
cos(hour) x tag type: grey reef shark							0.109	0.011	<0.001
cos(hour) x tag type: silvertip shark							0.021	0.011	0.055
Observations	116			116			116		
R^2 / adjusted R^2	0.042 / 0.025			0.069 / 0.036			0.550 / 0.516		

Supplementary Table 3.2: Details of control tags deployed within the BIOT acoustic array, including tag location, distance to nearest receiver, and the number of times it was detected.

Atoll	Receiver	Tag_ID	Latitude degrees	Longitude degrees	Distance to receiver m	Detections
Peros Banhos	PB01	65138	-5.2851	71.7334	390	19
Peros Banhos	PB27	65137	-5.3990	71.7487	390	3052
Peros Banhos	PB18	65136	-5.4584	71.7625	500	5
Peros Banhos	PB12	65139	-5.3807	71.9727	290	388

Supplementary Table 3.3: Summary of shark details (species, sex, length) and detection metrics for tags deployed and monitored at Peros Banhos and Salomon atolls and monitored between April 2014 and May 2017

Habitat	Tag ID	Species	Sex	Total length cm	Days monitored	Days detected	Residency index	Hours detected	Hours detected per days detected (hr d ⁻¹)	Unique receivers visited
Reef	25537	Grey reef shark	F	88	824	197	0.24	1289	6.54	9
Reef	54883	Grey reef shark	F	100	376	17	0.05	27	1.59	1
Reef	54959	Grey reef shark	F	104	168	135	0.80	573	4.24	9
Reef	59969	Grey reef shark	F	105	636	3	0.00	8	2.67	4
Reef	25541	Grey reef shark	F	106	839	585	0.70	2224	3.80	3
Reef	19318	Grey reef shark	F	110	106	4	0.04	13	3.25	4
Reef	59964	Grey reef shark	F	112	737	553	0.75	2816	5.09	5
Reef	59988	Grey reef shark	F	112	737	275	0.37	1368	4.97	3
Reef	54914	Grey reef shark	F	117	375	268	0.71	1087	4.06	1
Reef	54962	Grey reef shark	F	117	376	250	0.66	1032	4.13	4
Reef	54904	Grey reef shark	F	122	376	177	0.47	473	2.67	2
Reef	54892	Grey reef shark	F	132	376	22	0.06	41	1.86	2
Reef	59957	Grey reef shark	F	133	417	37	0.09	59	1.59	2
Reef	59959	Grey reef shark	F	133	737	31	0.04	110	3.55	2
Reef	54846	Grey reef shark	F	135	376	321	0.85	2898	9.03	4
Reef	54860	Grey reef shark	F	136	4	2	0.50	3	1.50	1
Reef	59962	Grey reef shark	F	136	528	28	0.05	188	6.71	1
Reef	25540	Grey reef shark	F	137	13	4	0.31	13	3.25	1
Reef	54958	Grey reef shark	F	138	376	224	0.60	1059	4.73	2
Reef	25543	Grey reef shark	F	140	922	120	0.13	711	5.93	6
Reef	25552	Grey reef shark	F	140	248	217	0.88	1182	5.45	4

Supplementary Table 3.3: Continued

Habitat	Tag ID	Species	Sex	Total length cm	Days monitored	Days detected	Residency index	Hours detected	Hours detected per days detected (hr d ⁻¹)	Unique receivers visited
Reef	54866	Grey reef shark	F	141	376	25	0.07	70	2.80	4
Reef	59958	Grey reef shark	F	141	737	5	0.01	14	2.80	3
Reef	54955	Grey reef shark	F	142	376	197	0.52	568	2.88	2
Reef	19524	Grey reef shark	F	143	375	244	0.65	1036	4.25	4
Reef	54877	Grey reef shark	F	143	202	10	0.05	25	2.50	2
Reef	54954	Grey reef shark	F	145	376	267	0.71	1286	4.82	3
Reef	59961	Grey reef shark	F	145	287	6	0.02	7	1.17	1
Reef	54952	Grey reef shark	F	146	376	10	0.03	51	5.10	3
Reef	59960	Grey reef shark	F	150	187	4	0.02	8	2.00	2
Reef	54901	Grey reef shark	F	152	376	84	0.22	206	2.45	3
Reef	54884	Grey reef shark	F	155	138	116	0.84	663	5.72	4
Reef	54896	Grey reef shark	F	157	376	3	0.01	9	3.00	1
Reef	54895	Grey reef shark	M	106	376	240	0.64	759	3.16	6
Reef	54852	Grey reef shark	M	114	376	367	0.98	3337	9.09	2
Reef	25549	Grey reef shark	M	116	732	29	0.04	52	1.79	5
Reef	2390	Grey reef shark	M	118	157	96	0.61	396	4.13	2
Reef	54931	Grey reef shark	M	121	376	328	0.87	1651	5.03	4
Reef	25546	Grey reef shark	M	125	827	459	0.56	3222	7.02	8
Reef	25553	Grey reef shark	M	131	766	110	0.14	440	4.00	7
Reef	54882	Grey reef shark	M	134	138	105	0.76	537	5.11	5
Reef	54890	Grey reef shark	M	136	375	293	0.78	1033	3.53	3
Reef	27591	Grey reef shark	U	125	30	25	0.83	155	6.20	3
Reef	54880	Silvertip shark	F	87	376	146	0.39	304	2.08	5

Supplementary Table 3.3: Continued

Habitat	Tag ID	Species	Sex	Total length	Days monitored	Days detected	Residency index	Hours detected	Hours detected per days detected	Unique receivers visited
				cm					(hr d ⁻¹)	
Reef	54889	Silvertip shark	F	88	376	171	0.45	397	2.32	5
Reef	54957	Silvertip shark	F	93	376	139	0.37	298	2.14	10
Reef	12964	Silvertip shark	F	104	938	341	0.36	951	2.79	14
Reef	54911	Silvertip shark	F	104	376	51	0.14	153	3.00	4
Reef	25545	Silvertip shark	F	108	925	420	0.45	1150	2.74	3
Reef	27584	Silvertip shark	F	108	247	156	0.63	448	2.87	6
Reef	2388	Silvertip shark	F	112	163	15	0.09	24	1.60	5
Reef	25534	Silvertip shark	F	113	715	213	0.30	754	3.54	11
Reef	25542	Silvertip shark	F	115	248	151	0.61	463	3.07	3
Reef	27611	Silvertip shark	F	115	256	255	1.00	2671	10.47	3
Reef	25548	Silvertip shark	F	117	713	448	0.63	1371	3.06	7
Reef	25547	Silvertip shark	F	118	108	61	0.56	155	2.54	6
Reef	12950	Silvertip shark	F	119	248	168	0.68	502	2.99	6
Reef	54905	Silvertip shark	F	120	66	47	0.71	160	3.40	5
Reef	59963	Silvertip shark	F	120	737	108	0.15	280	2.59	4
Reef	25550	Silvertip shark	F	122	50	44	0.88	194	4.41	6
Reef	59991	Silvertip shark	F	132	737	294	0.40	1390	4.73	2
Reef	12960	Silvertip shark	F	133	106	86	0.81	553	6.43	8
Reef	54817	Silvertip shark	F	134	10	2	0.20	5	2.50	3
Reef	54822	Silvertip shark	F	135	183	81	0.44	258	3.19	8
Reef	54915	Silvertip shark	F	139	375	230	0.61	755	3.28	11
Reef	34176	Silvertip shark	F	140	237	77	0.32	218	2.83	6
Reef	54947	Silvertip shark	F	144	376	177	0.47	466	2.63	5
Reef	54933	Silvertip shark	F	148	376	231	0.61	641	2.77	4

Supplementary Table 3.3: Continued

Habitat	Tag ID	Species	Sex	Total length cm	Days monitored	Days detected	Residency index	Hours detected	Hours detected per days detected (hr d ⁻¹)	Unique receivers visited
Reef	12956	Silvertip shark	F	150	81	2	0.02	3	1.50	1
Reef	54845	Silvertip shark	F	151	169	4	0.02	15	3.75	11
Reef	59994	Silvertip shark	F	153	335	8	0.02	18	2.25	3
Reef	54887	Silvertip shark	F	161	198	55	0.28	153	2.78	5
Reef	54893	Silvertip shark	F	162	376	165	0.44	431	2.61	5
Reef	54961	Silvertip shark	M	86	376	198	0.53	648	3.27	6
Reef	12952	Silvertip shark	M	97	255	176	0.69	608	3.45	5
Reef	25539	Silvertip shark	M	104	841	385	0.46	1743	4.53	13
Reef	25535	Silvertip shark	M	108	29	6	0.21	25	4.17	6
Reef	12968	Silvertip shark	M	115	251	128	0.51	422	3.30	7
Reef	34177	Silvertip shark	M	115	254	3	0.01	19	6.33	5
Reef	12966	Silvertip shark	M	117	1092	499	0.46	1363	2.73	4
Reef	13577	Silvertip shark	M	119	996	651	0.65	2451	3.76	6
Reef	27603	Silvertip shark	M	119	253	150	0.59	746	4.97	6
Reef	52975	Silvertip shark	M	123	247	45	0.18	104	2.31	8
Reef	12962	Silvertip shark	M	127	1092	842	0.77	9039	10.74	2
Reef	25536	Silvertip shark	M	128	249	169	0.68	563	3.33	7
Reef	59992	Silvertip shark	M	131	737	58	0.08	125	2.16	10
Reef	25544	Silvertip shark	M	134	247	197	0.80	695	3.53	6
Reef	19523	Silvertip shark	M	137	375	309	0.82	1493	4.83	2
Reef	54849	Silvertip shark	M	137	376	185	0.49	574	3.10	5
Reef	54898	Silvertip shark	M	151	376	74	0.20	172	2.32	9
Reef	59993	Silvertip shark	M	157	737	201	0.27	552	2.75	19
Reef	54912	Silvertip shark	M	196	376	1	0.00	2	2.00	1

Supplementary Table 3.4: Summary of shark details (species, sex, length) and detection metrics for tags deployed and monitored at the BIOT seamounts and monitored between April 2016 and May 2017

Habitat	Tag ID	Species	Sex	Total length (cm)	Days monitored	Days detected	Residency index	Hours detected	Hours detected per day detected (hr d ⁻¹)	Unique receivers visited
Seamount	54837	Silvertip shark	F	105	368	59	0.16	95	1.61	3
Seamount	54814	Silvertip shark	F	111	372	38	0.10	89	2.34	3
Seamount	54848	Silvertip shark	F	115	334	45	0.13	89	1.98	1
Seamount	54906	Silvertip shark	F	123	367	107	0.29	567	5.30	3
Seamount	19517	Silvertip shark	F	129	365	300	0.82	4504	15.01	4
Seamount	54937	Silvertip shark	F	136	262	125	0.48	1176	9.41	3
Seamount	54903	Silvertip shark	F	137	370	166	0.45	1260	7.59	2
Seamount	54878	Silvertip shark	F	140	241	136	0.56	1014	7.46	4
Seamount	54946	Silvertip shark	F	146	373	302	0.81	2284	7.56	4
Seamount	54944	Silvertip shark	F	149	375	147	0.39	657	4.47	2
Seamount	54845	Silvertip shark	F	151	131	19	0.15	91	4.79	11
Seamount	54816	Silvertip shark	F	152	165	7	0.04	9	1.29	2
Seamount	54843	Silvertip shark	F	154	360	57	0.16	142	2.49	3
Seamount	54841	Silvertip shark	F	155	340	84	0.25	217	2.58	3
Seamount	54842	Silvertip shark	F	155	318	30	0.09	141	4.70	3
Seamount	54847	Silvertip shark	F	157	68	22	0.32	69	3.14	4
Seamount	54844	Silvertip shark	F	159	255	69	0.27	423	6.13	3
Seamount	54856	Silvertip shark	F	160	375	263	0.70	1320	5.02	3
Seamount	19515	Silvertip shark	F	161	146	41	0.28	139	3.39	1
Seamount	54943	Silvertip shark	F	165	348	175	0.50	1598	9.13	4

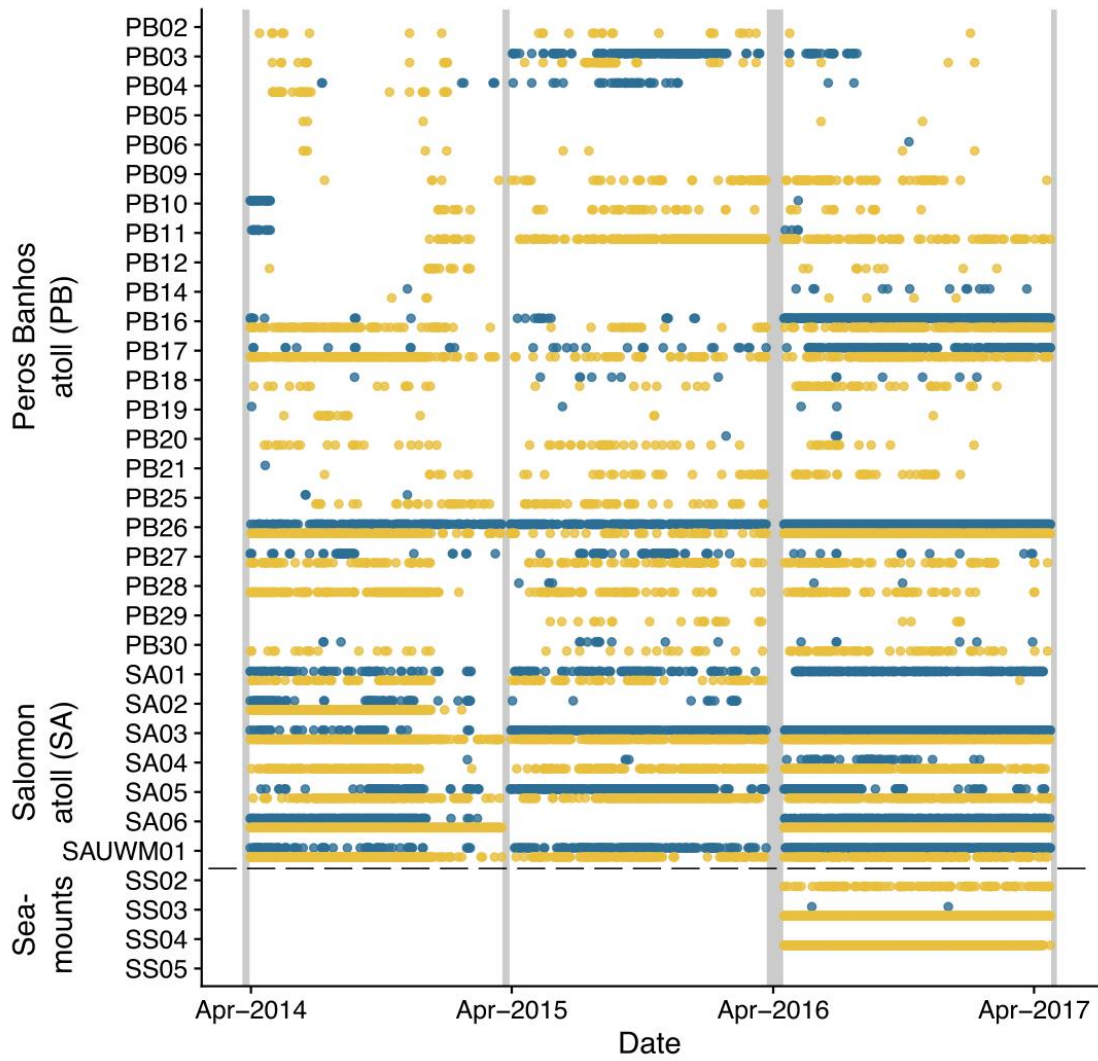
Supplementary Table 3.4: Continued

Habitat	Tag ID	Species	Sex	Total length (cm)	Days monitored	Days detected	Residency index	Hours detected	Hours detected per day detected (hr d ⁻¹)	Unique receivers visited
Seamount	54859	Silvertip shark	F	166	243	89	0.37	497	5.58	3
Seamount	54835	Silvertip shark	F	168	321	16	0.05	47	2.94	3
Seamount	54940	Silvertip shark	F	198	375	140	0.37	756	5.40	3
Seamount	54939	Silvertip shark	M	113	373	48	0.13	108	2.25	3
Seamount	54942	Silvertip shark	M	122	336	61	0.18	169	2.77	2
Seamount	54934	Silvertip shark	M	125	375	339	0.90	4359	12.86	4
Seamount	54876	Silvertip shark	M	136	365	202	0.55	1068	5.29	3
Seamount	54935	Silvertip shark	M	136	19	12	0.63	54	4.50	4
Seamount	54853	Silvertip shark	M	142	374	223	0.60	1490	6.68	4
Seamount	54873	Silvertip shark	M	144	201	171	0.85	1739	10.17	4
Seamount	54950	Silvertip shark	M	149	296	160	0.54	843	5.27	4
Seamount	54898	Silvertip shark	M	151	131	113	0.86	980	8.67	9
Seamount	54875	Silvertip shark	M	152	375	291	0.78	2103	7.23	4
Seamount	54948	Silvertip shark	M	156	283	83	0.29	334	4.02	4
Seamount	54838	Silvertip shark	M	160	374	188	0.50	837	4.45	4
Seamount	54941	Silvertip shark	M	160	291	161	0.55	1088	6.76	4
Seamount	54824	Silvertip shark	M	163	321	54	0.17	128	2.37	4
Seamount	54823	Silvertip shark	M	168	215	25	0.12	46	1.84	3
Seamount	54840	Silvertip shark	M	171	209	176	0.84	1066	6.06	4
Seamount	54900	Silvertip shark	M	208	365	342	0.94	2425	7.09	4

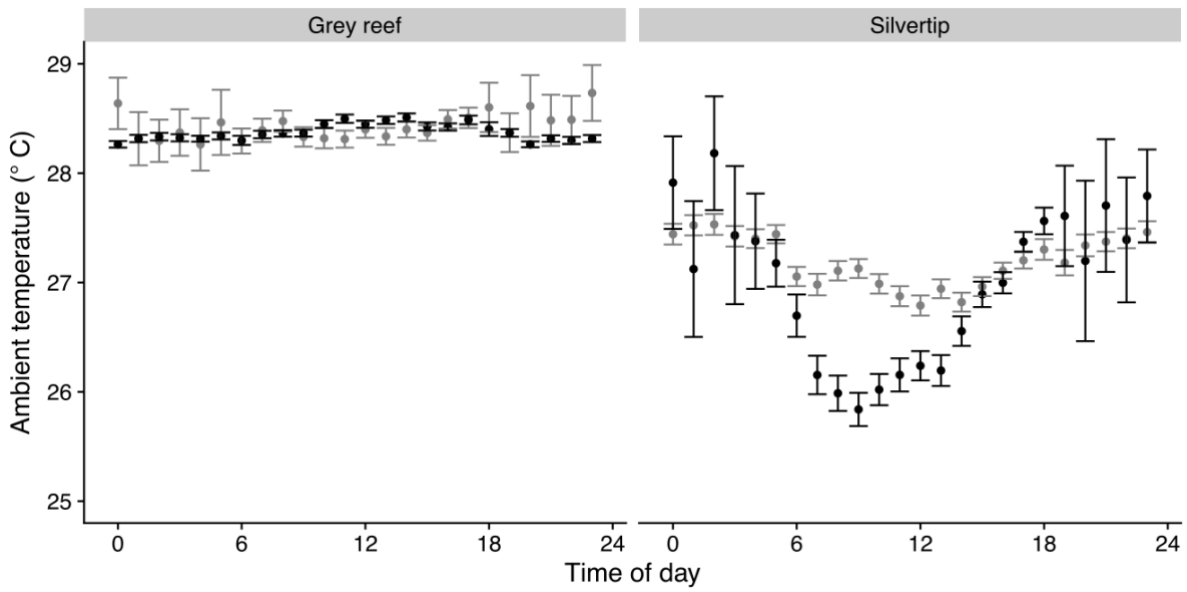
3.8.2 Supplementary figures



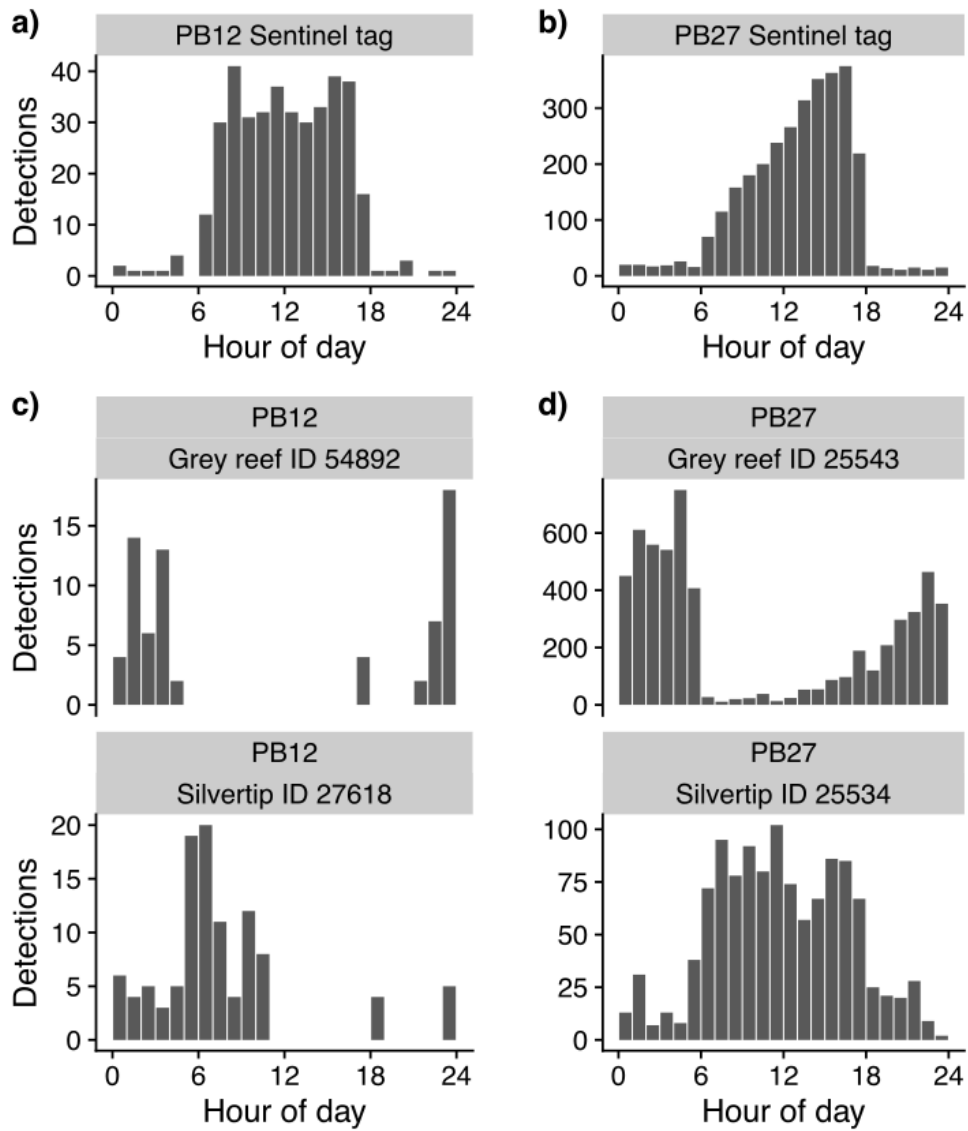
Supplementary Figure 3.1: Attaching a VR2W receiver to a mooring line in the BIOT acoustic array. Grooves in the receiver body used to secure a hose clamp (top groove) and two or more heavy duty cable ties.



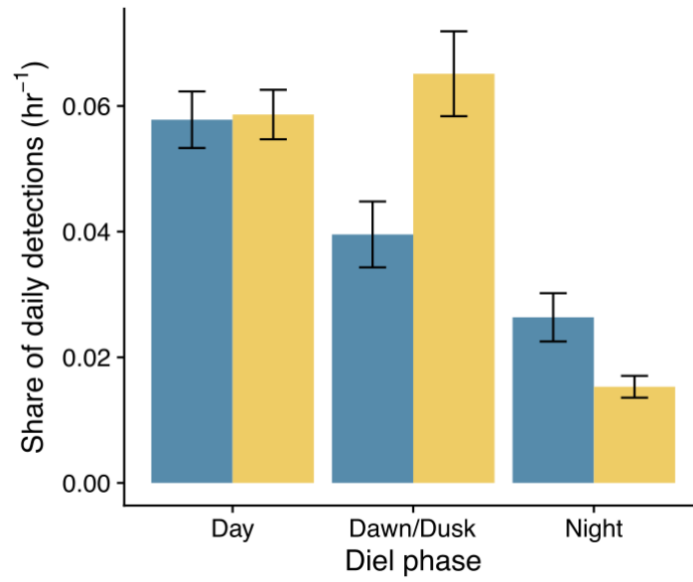
Supplementary Figure 3.2: Presence plot of tag detections for grey reef sharks (blue) and silvertip sharks (yellow) for the acoustic receivers in this study. Receivers at Peros Banhos and Salomon atolls (coded PB-- and SA--, respectively) were active from April 2014 to May 2017; receivers at the seamounts (coded SS--) were active from April 2016 to May 2017.



Supplementary Figure 3.3: Average hourly temperature data (\pm CI) recorded by tag temperature sensors by tag placement position: external (black) or internal (grey). Data are shown separately for grey reef and silvertip sharks.



Supplementary Figure 3.4: Detection patterns of control tags (panels a, b) deployed at two reef sites monitored by acoustic receivers on Peros Banhos Atoll, and corresponding detection patterns of individual grey reef and silvertip sharks (c, d) detected at the same locations.

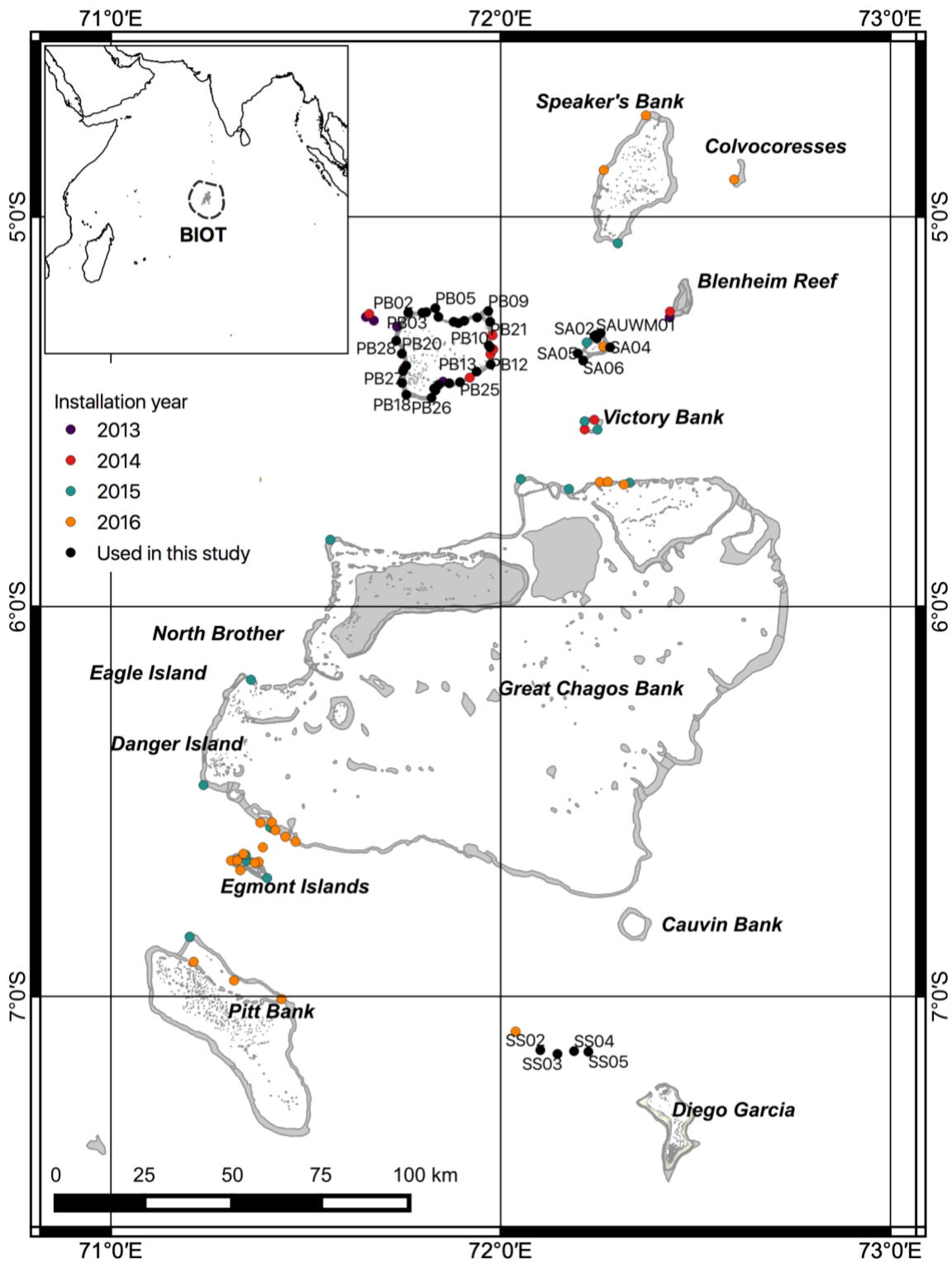


Supplementary Figure 3.5: Average share of daily detections, by species, occurring in each hour of the day, by diel periods: day (0700 to 1700), dawn/dusk (0500 to 0700 and 1700 to 1900), and night (1900 to 0500). Error bars indicate 95% confidence interval of the mean.

3.8.3 Supplementary methods

3.8.3.1 The BIOT acoustic receiver array

Acoustic receivers have been deployed around reefs in the BIOT MPA since February 2013 to monitor acoustically tagged sharks, rays and teleosts (Supplementary Figure 3.6, Carlisle et al. 2019). In 2013, 28 VR2W receivers (Vemco Inc., Nova Scotia, Canada), were deployed in the north of the Archipelago. 20 VR2W receivers were deployed around Peros Banhos, five around Salomon Atoll, two at Benares Shoals, and one at Blenheim Reef. Receivers at Peros Banhos and Salomon Atolls were placed on outer reef and reef channel sites which encircled those atolls. The remaining receivers were sited to detect potential movements of tagged animals away from the core reef areas. In 2014, 18 receivers were added to infill the Peros Banhos and Salomon sub-arrays, and to extend coverage to the submerged atoll of Victory Bank southeast of Salomon Atoll (Supplementary Figure 3.6). In 2015, 15 additional VR2W units were added to include locations in the central and southern parts of the Archipelago: the north western and western rim of the Great Chagos Bank, Egmont Atoll, and Speakers Bank. In 2016 29 additional receivers were deployed at Nelson Island, Egmont Atoll, along the western edge of the Great Chagos Bank and on and near Sandes an Swartz seamounts in the south of the Archipelago (Supplementary Figure 3.6). These included 16 VR2Ws fitted with remotely-operated acoustic releases (VR2W-AR), allowing them to be sited in depths beyond diver range and retrieved from the surface. In addition, two VR4 Global (VR4G) units, capable of transmitting live detection data via the Iridium satellite network, were deployed in 2013, and four VR4 Underwater Monitors (VR4-UWM), whose data can be downloaded from the surface using an acoustic modem, were deployed in 2014. The receiver array as at April 2016 consisted of 92 units in total (Supplementary Figure 3.6). As the array expanded, each new location was assigned a unique location code within the array, e.g. 'SA01' for the first receiver deployed at Salomon Atoll (Supplementary Figure 3.6).



Supplementary Figure 3.6: Map of the Chagos Archipelago in the British Indian Ocean showing names islands and atolls, and locations of current acoustic receiver network.

3.8.3.2 Receiver deployment

Receiver deployment and retrieval took place annually between February and May each year, typically a period of calm surface conditions in the BIOT. VR2W receivers were deployed on subsurface moorings consisting of an anchor, a mooring line made from three meters of 20 mm polypropylene line, and a 150 mm diameter orange plastic submersible fishing float (Plastech, depth-rated to 300m). Subsurface moorings avoid impeding vessel traffic and provide a degree of insulation from surface water movement. The anchor consisted of a loop of reinforcing steel bar embedded in a 40 kg cylindrical cement block. One end of the mooring line was spliced around the anchor loop using a short length of plastic hose as protection against chafing, and the other end was looped through the central hole in the float and spliced back onto itself. Receiver bodies were wrapped in electrical tape to prevent fouling organisms attaching directly. Only the receiver tip containing the acoustic detector was left uncovered. This was found to be more effective than using antifouling paints and resulted in minimal fouling of the receiver tips, as long as they were not scratched or otherwise damaged. Receivers were attached to the mooring ropes with a 70-90mm adjustable stainless-steel hose clamp and two heavy duty cable ties, positioned in the three grooves in the VR2W casing (Supplementary Figure 3.2). VR2W receivers were deployed using divers and placed on sand patches or dead coral between 15 and 25 m depth. We used a liftbag to manoeuvre the anchor underwater to avoid damage to coral and ensure a secure placement. Divers were supported by a surface team in a dive tender. Divers deployed a surface marker buoy while working and the receiver location was recorded by the surface team using a handheld GPS.

VR2W-AR receivers were anchored to moorings in a similar manner, with two floats used to ensure that the receiver detached and floated free when the release was triggered, and an extra cement anchor was used to compensate for the additional float. To deploy the VR2W-AR units in deep water the mooring and receiver assembly was dropped from the surface, with a hand-held GPS used to record the location. VR4G and VR4-UWM units were moored to purpose-built steel anchors using Nilspin cable (Union Wire Rope, Kansa City, Missouri) and high-volume submersible (VR4-UWM) or surface (VR4G) floats. The VR4G surface floats were also equipped with a navigation marker light and an Iridium satellite antenna. In all cases the location code within the array, latitude, longitude, six-digit Vemco receiver ID and depth were recorded for subsequent receiver servicing and data management.

3.8.3.3 Receiver recovery and servicing

Receivers were retrieved annually by divers supported by a dive tender. Since moorings were not always visible from the surface, a drop line, made from a dive weight anchor, 40 m of 10 mm polypropylene line and a polystyrene surface float, was deployed at the recorded GPS location of a receiver to guide the divers. Mooring lines were inspected for wear and removed and replaced if the anchor attachment point was badly worn, but otherwise were left in place for up to two years at a time. If the mooring needed replacement, it was cut free and the mooring and receiver retrieved by the dive tender. If the mooring was to be left the receiver was detached from the mooring line by cutting the cable ties and loosening the hose clamp. On receiver recovery, any detection data was downloaded and receivers were cleaned, reset, fitted with a new battery and redeployed. The six-digit ID code identifying each receiver was logged against its new location in the array, since this typically changed between project years. Receivers equipped with acoustic release mechanisms were recovered annually by activating the acoustic release from the surface using an acoustic trigger and collecting the receiver and floats at the surface. They were serviced in the same way as standard VR2Ws with the additional step of replacing the acoustic release. VR4G and VR4-UWM units require battery changes only every four years and so required minimal annual servicing, beyond remotely downloading detection data from the VR4-UWMs from the surface with an acoustic modem.

Chapter 4: Environmental drivers of the vertical niche of the silvertip shark (*Carcharhinus albimarginatus*)

4.1 Abstract

Understanding the space use of reef-associated sharks is essential for their management. While the vertical distribution and movements of reef-associated sharks are less commonly investigated than species' horizontal movements, vertical spatial ecology can further improve our understanding of sharks ecosystem role, environmental preferences and susceptibility to threats. Here, I analyse depth and temperature data from pop-up archival tags deployed on seven silvertip sharks (*Carcharhinus albimarginatus*), around atoll reefs in the central Indian Ocean. Silvertip sharks occupied the lower third of the mixed layer as its depth varied seasonally, and moved deeper with increasing sea surface temperature. Variations in median depth by the sharks may relate to thermoregulation, maintaining their ambient water temperature at $\sim 27^{\circ}\text{C}$. Within the seasonal trend, shark depth varied cyclically with surface light levels, ~ 15 m deeper during daylight and ~ 6 m deeper on nights around full moon. These movements correlate with the diel and lunar movements of vertically migrating mesopelagic species, suggesting that foraging may be driver of this behaviour. Silvertip sharks spent the majority of their time shallower than 100 m, but short mesopelagic dives of 200-800 m depth were recorded on average every three days. Analysis of high-resolution depth-time data found that dives below 200 m showed a distinct 'dog-leg' ascent profile. Reconstructing the dissolved oxygen (DO) profile of the water column suggested that sharks ascended rapidly while in low-DO waters and promptly reduced their ascent rate by 50-80% once DO levels began to increase. Rapid ascents from low-DO waters may indicate a low tolerance to low-DO conditions by silvertip sharks. I suggest that silvertip sharks' predictable use of relatively shallow surface waters near reefs likely contributes to their sensitivity to fisheries targeting species with overlapping vertical niches, such as neritic tunas. Their narrow temperature preference and apparent sensitivity to low DO levels may exacerbate threats to this species as oceanic warming and shoaling of oxygen minimum zones modify habitat availability in the tropics.

4.2 Introduction

Sharks are an important group of marine predators, but both pelagic and reef-associated species are under threat (Baum & Myers 2004, Graham et al. 2010, Ferretti et al. 2010, Worm & Tittensor 2011, Nadon et al. 2012, MacNeil et al. 2020). Population declines of many species have been

observed in all oceans, with fisheries (Meekan et al. 2006, Vianna et al. 2016) and habitat degradation (Knip & Heupel 2010, Sguotti et al. 2016) key drivers. Furthermore, sharks are likely to be increasingly impacted by ocean warming and reduction in dissolved oxygen resulting from climate change (Chin et al. 2010, Gilly et al. 2013, Rosa et al. 2017).

Knowledge of sharks' spatial ecology improves our understanding of their ecosystem roles (Williams et al. 2018), vulnerability to threats (Jacoby et al. 2020), and aids in designing conservation strategies (Chapman et al. 2005, Lea et al. 2016, Dwyer et al. 2020). While defining appropriate boundaries for a marine protected area (MPA) might require data on the horizontal movements of sharks, information on their vertical space use is required to fully describe the ecology of many mobile species (Andrzejczek et al. 2019). Species' vertical space use may be driven by, *inter alia*, thermoregulation (Sims et al. 2006, Campana et al. 2011), prey distribution and behaviour, including diel vertical migration (Bost et al. 2002, Baumgartner et al. 2011), and dissolved oxygen (DO) levels (Carlson 2003, Carlisle et al. 2016). Characterizing species' vertical space provides insights into many aspects of their biology, including revealing cryptic behaviours, such as foraging or aggregating at depth (Cagua et al. 2015, Braun et al. 2019), and physiological constraints such as temperature and DO thresholds (Abascal et al. 2011, Carlisle et al. 2015). The vertical space use of taxa also provides insights into their role in connecting ecosystems and food webs, for example by mediating nutrient transfers between surface, meso- and bathypelagic layers (Roman & McCarthy 2010, Braun et al. 2014, Howey et al. 2016).

Highly mobile pelagic species are commonly studied with pop-up satellite archival tags (hereafter PATs), which collect data on both vertical and horizontal movements *in situ* and transmit back to the lab in summary form (Hammerschlag et al. 2011, Block et al. 2011, Hussey et al. 2015). Satellite tagging studies have been conducted on many oceanic or migratory shark species, including oceanic white tip (*Carcharhinus longimanus*, Howey-Jordan et al. 2013), blue (*Prionace glauca*, Campana et al. 2011), white (*Carcharodon carcharias*, Jorgensen et al. 2012), salmon (*Lamna ditropis*, Carlisle et al. 2011), porbeagle (*Lamna nasus*, Francis et al. 2015), basking (*Cetorhinus maximus*, Doherty et al. 2019), tiger (*Galeocerdo cuvier*, Heithaus et al. 2007), whale (*Rhincodon typus*, Araujo et al. 2019), and mako (*Isurus* spp.) and thresher sharks (*Alopias* spp., Block et al. 2011). Nominally resident species such as reef-associated sharks are more commonly studied with passive acoustic telemetry, which typically focuses on horizontal movements of animals based on the timing of visits by tagged animals to fixed acoustic receiver locations (e.g. Donaldson et al. 2014, Espinoza et al. 2015b, White et al. 2017, Jacoby et al. 2020). Much of this acoustic telemetry research has focussed on quantifying

aspects of horizontal space use such as habitat associations, movement networks and home ranges, although acoustic tagging can also provide data on depth and temperature. Vianna et al. (2013), for example, used tags equipped with depth and temperature sensors to investigate thermal preferences and depth use in grey reef sharks (*Carcharhinus amblyrhynchos*) in Palau, and Espinoza et al (2015a) applied a similar approach with silvertip sharks (*Carcharhinus albimarginatus*). However, collection of depth and temperature data via acoustic telemetry relies on animals being within coverage of a receiver array, meaning continuous high-resolution data may be difficult to acquire.

To date, few studies have used PAT tags to study the vertical space use of reef-associated sharks. Archival tags have been deployed on a single silvertip shark in Fiji (Bond et al. 2015), 16 grey reef sharks in the Marshall Islands (Bradley et al. 2019), and six Caribbean reef sharks (*Carcharhinus perezi*) in Belize (Chapman et al. 2007). These studies have generated insights beyond the capabilities of acoustic telemetry, including describing a much larger vertical and thermal niche than previously suspected for Caribbean reef sharks (Chapman et al. 2007), and providing direct evidence of offshore mesopelagic diving in silvertip sharks (Bond et al. 2015). Although limited to date, these studies' use of PATs may be of great value even on these nominally site-attached species by providing time series of *in situ* measurements of depth and environmental variables regardless of whether a tagged individual remains within the detection range of acoustic receivers within a defined study area.

To investigate the vertical space use of silvertip sharks, I deployed satellite archival tags on seven individuals in the British Indian Ocean Territory (BIOT) MPA as part of a larger telemetry study using both PATs and acoustic tags (Carlisle et al. 2019). Silvertip sharks are a large, mobile but reef-associated species with a wide but fragmented Indo-Pacific distribution (Compagno 1984). They are listed as Vulnerable by the IUCN (Espinoza et al. 2016) and populations have been seriously impacted by fishing in several parts of its range (Meekan et al. 2006, Graham et al. 2010). In BIOT, it is the most commonly identified species in the catches of illegal fishing vessels targeting sharks in the MPA (Martin et al. 2013, Tickler et al. 2019). Ferretti et al. (2018) attempted to reconstruct historical population trajectories for grey reef and silvertip sharks in the BIOT, and concluded that silvertip sharks were at very low abundance levels relative to their historical abundance and carrying capacity, and relative to grey reef shark numbers (Ferretti et al. 2018). However, results of this study may have been biased by the relative sparse data available to generate anchor point assumptions for the model, in particular the different depths targeted by the historical fishing activity used to

infer relative abundance of grey reef and silvertips sharks. A previous study using baited remote underwater video found that silvertip sharks are present across a broad depth range in BIOT, but with higher relative abundance on the peaks of seamounts at 80 m depth than on shallow reef sites (Tickler et al. 2017), and the species is reported to dive up to 800 m (Compagno 1984). As such their true abundance in BIOT may be hard to determine based on shallow visual surveys or fishing, and better knowledge of their spatial ecology can better inform abundance surveys and models. A short deployment of a satellite tag on a silvertip shark in Fiji found that the animal occupied a mean water temperature of 26.3°C and a depth range of 0-380 m, albeit with only brief excursions below 200 m (Bond et al. 2015). Compared with its smaller congener, the grey reef shark, the silvertip shark has been relatively under-studied and improved knowledge of its spatial ecology would better inform its conservation management.

Data from PATs deployed on silvertip sharks in BIOT in April 2013 (4 tags) and April 2014 (3 tags) were used to investigate the depth use and thermal niche of this species. I hypothesised that silvertip sharks would spend more time in relatively deeper, cooler water, based on the findings of Bond et al (2015). I examined temporal variation in the depth use of sharks in relation to sea surface temperature and the depth of the surface mixed layer, since both have been shown to drive vertical space use in other mobile ectothermic shark species (Campana et al. 2011, Howey et al. 2016). I also investigated the influence of diel and lunar cycles which have both been shown to predict depth use in multiple species including the grey reef shark (Vianna et al. 2013), blue shark (Queiroz et al. 2010) and blacktip reef shark (*Carcharhinus melanopterus*, Papastamatiou et al. 2018). Lastly, I investigated diving behaviour relative to water column stratification by temperature and DO, which are known to influence the diving behaviour of other species that make mesopelagic excursions (such as the oceanic whitetip shark; Howey et al. 2016). The goal of my study was to describe the vertical space use of silvertip sharks in relation to physical drivers including sea surface temperature, water column structure and solar and lunar illumination, to better predict temporal variations in its susceptibility to fishing gears (e.g. surface longlines), and to identify any thermal or other constraints that might provide insight into this species' vulnerability to ocean warming under climate change.

4.3 Methods

4.3.1 Study area

The BIOT comprises a group of atolls, islands and seamounts in the central Indian Ocean (Figure 4.1a), as well the surrounding oceanic exclusive economic zone (EEZ). The majority of the EEZ, an

area totalling over 640,000 km², is a no-take MPA, although a 3 nm zone around the military base at Diego Garcia is excluded. The area has been largely unpopulated since the 1970s, with the exception of Diego Garcia, and since the MPA's creation in 2010, all commercial fishing and other extractive activities have been prohibited. Only very limited subsistence fishing for finfish by visiting yachts remains permitted within the MPA. As such the BIOT MPA is a valuable location at which to investigate the ecology of both reef and pelagic sharks under conditions of very low anthropogenic disturbance.

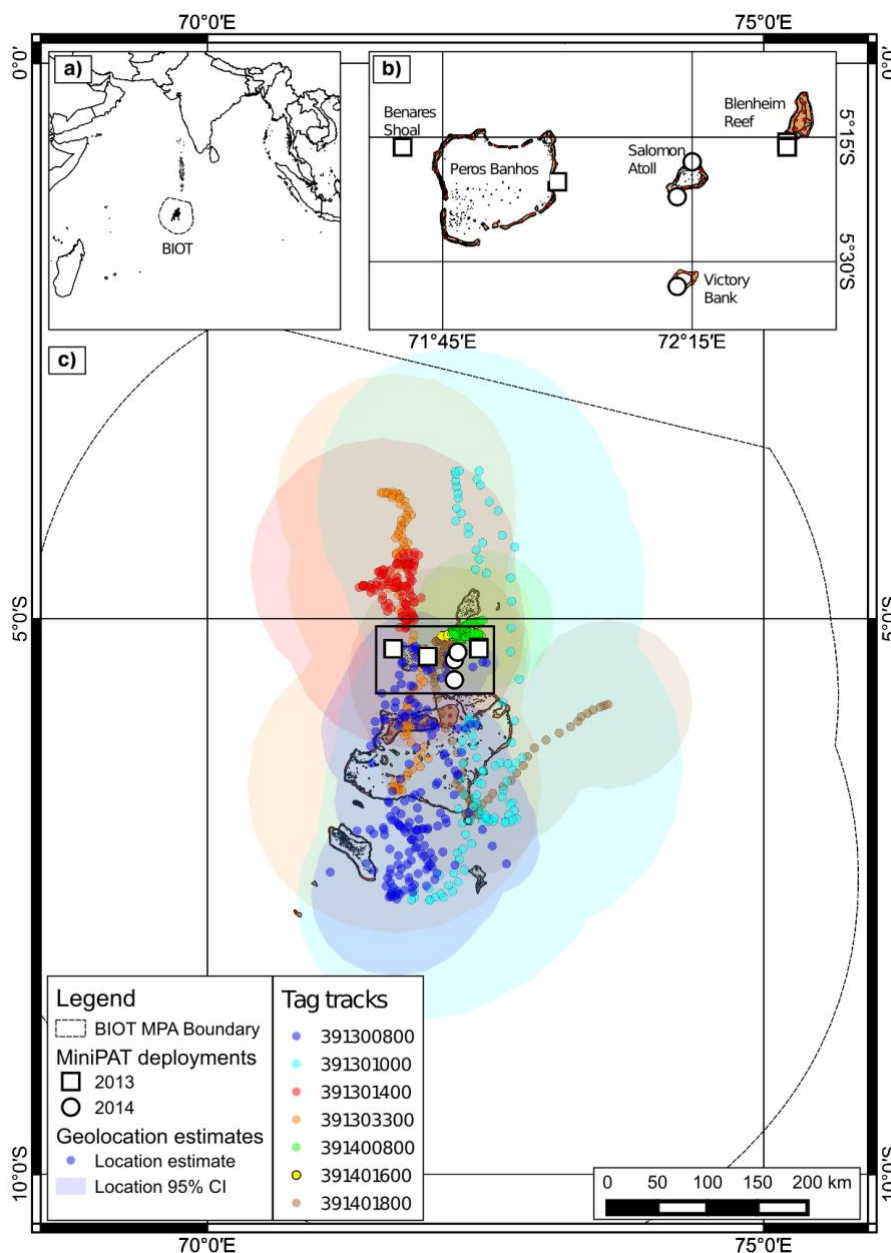


Figure 4.1: Map of study area showing a) location of the BIOT EEZ in the Indian Ocean; b) locations of seven PAT tag deployments on silvertip sharks in 2013 (squares, n=4) and 2014 (circles, n=3); and c) daily geolocation-based position estimates and their 95% confidence areas, for all seven tags colour coded by tag ID as per legend.

4.3.2 Miniature pop-up archival tags

Seven silvertip sharks were tagged in the BIOT MPA with PAT tags (MiniPAT-247 model tags, Wildlife Computers, Redmond WA) between February 2013 and March 2014. Tags were prepared with anti-fouling paint (Trilux 33; International Paint LLC, Union, NJ, USA), and attached to a custom-made titanium dart using 15 cm of 180 kg monofilament leader (Moimoi, Kobe, Japan). The leader material was protected from abrasion with a layer of Spectra (Honeywell Advanced Fibres and Composites, Colonial Heights, VA, USA) covered with a length of heatshrink tubing. Tags recorded ambient temperature, depth and light level at 15 s intervals and were programmed to detach after 120, 180 or 270 days (Table 1). PATs were programmed to transmit temperature and depth data summarized as time-at-depth (TAD) and time-at-temperature (TAT) ‘histograms’, in 6- or 24-hour intervals. The histogram data were reported as the proportion of time spent in each of 12 pre-defined depth or temperature bins during each 6- or 24-hour period (Supplementary Tables 4.1 and 4.2). A subset of tags was programmed to transmit time series of their depth and temperature data sampled at 5-minute or 7.5-minute intervals (Table 4.1). Tags also reported summarised light level data for geolocation purposes, daily temperature and depth profiles (PDT), minimum and maximum depth in each reporting period, and daily estimates of mixed layer depth (MLD).

4.3.3 Tag deployment

Animals were tagged at Peros Banhos and Salomon atolls and near the submerged features at Benares Shoals, Blenheim Reef and Victory Bank (Figure 4.1b). Seven PATs were attached to silvertip sharks in February and March 2013 (4 tags) and in April 2014 (3 tags). Sharks were captured using barbless 16/0 circle hooks, attached to a wire leader (1 m of 3 mm steel wire rope) joined to 2 m of 10-15 mm polypropylene line with a swivel, and terminated with a large longline branch hanger (‘tuna clip’). These hook sets were baited with pieces of squid and deployed either singly, clipped to a weighted polypropylene drop line, or in sets of up to 10 at a time clipped at 15 m intervals to a floating polypropylene surface line. Once a shark was hooked, it was brought alongside the tagging vessel and a soft tail rope was secured just anterior to the caudal fin. Animals larger than approximately 1.5 m were left in the water and turned ventral side up to induce tonic immobility (Kessel & Hussey 2015). Smaller individuals were lifted onto a large vinyl padded mat and restrained while irrigation of the gills was performed using a perforated plastic pipe attached to a seawater pump and hose. The shark’s eyes were covered with a wet cloth to further reduce stress. The PATs were attached externally by inserting the dart into the dorsal musculature just below the dorsal fin, using a short tagging pole whose tip fits into a socket in the rear of the dart. The dart was inserted

at a shallow angle relative to the axis of the shark's body, from the tail towards the head, to minimise drag from the tag once the animal was released. In all cases precaudal (PCL), fork (FL) and total (TL) lengths were measured to the nearest cm, a fin clip from a pectoral fin was taken for DNA analysis, a muscle punch taken for stable isotope analysis. One shark (Tag 6, ID 391401600) was tagged with both a PAT and an acoustic tag (V16 model tag, Vemco, Halifax, Nova Scotia; see Methods in Chapter 3 for details of the acoustic tagging procedure). So that previously tagged animals could be identified if recaptured, animals were tagged externally with a conventional identification tag, on the opposite side to the PAT to avoid entanglement. All sharks were tagged and released within five minutes. Animal handling procedures were approved by the Stanford University Administrative Panel on Laboratory Animal Care under permit APLAC-10765, held by the Block Laboratory at Hopkins Marine Station.

4.3.4 Tag recovery and data pre-processing

Six of the seven PATs were never recovered after releasing from their sharks, but successfully transmitted summary data back to Wildlife Computers via the Argos satellite network. The remaining tag was physically recovered, after drifting to the Kenyan coast, and provided a complete archival dataset of depth and temperature measurements recorded at 15 second intervals for six months. Raw data transmitted by the PATs were processed using Wildlife Computers' Data Analysis Program (DAP; Wildlife Computers, Redmond, WA, USA). The DAP software generates daily summaries of TAD, TAT, PDT, MLD, SST, minimum/maximum depth (MinMaxDepth) and light levels. Data times in UTC were converted to the local timezone (UTC+5).

Table 4.1: Summary of satellite archival tag (PAT) deployments on silvertip sharks in the BIOT MPA in 2013 and 2014.

Tag	Tag ID	Sex	Precaudal length (PCL, cm)	Fork length (FL, cm)	Total length (TL, cm)	Deployment date	Deployment latitude (degrees)	Deployment longitude(degrees)	Pop-off date	Pop-off latitude (degrees)	Pop-off longitude (degrees)	Days programmed	Days active	Share of programmed time completed	Histogram summary interval (hrs)	Maximum recorded depth (m) ¹	Days of data	Time series data available?
1	391300800 ²	-	141	155	185	12/02/13	-5.34	71.98	11/08/13	-5.32	72.00	180	180	100%	24	594±6	179	Y
2	391301000	-	122	134	160	16/03/13	-5.26	72.44	27/07/13	-5.91	71.35	270	133	49%	24	488±4	87	N
3	391301400	-	122	134	160	12/03/13	-5.27	72.44	06/07/13	-5.26	71.67	180	116	64%	6	760±4	104	N
4	391303300	-	113	124	148	22/03/13	-5.27	71.67	04/07/13	-5.24	71.66	180	105	58%	24	792±4	105	N
5	391400800 ³	F	129	139	161	24/03/14	-5.37	72.22	22/07/14	-5.04	73.02	120	120	100%	24	464±4	102	Y
6	391401600 ⁴	F	110	124	145	25/03/14	-5.30	72.25	30/07/14	-5.29	71.72	180	127	71%	6	400±4	107	N
7	391401800 ³	F	109	120	150	27/03/14	-5.55	72.22	06/07/14	-4.87	74.12	180	101	56%	24	328±4	86	Y

Notes:

¹ Max depth estimates obtained from daily temperature and depth summaries or directly from tag series data.

² Tag 391300800 was physically recovered, allowing the full on-board data archive to be downloaded (15 second-interval time series).

³ Tags 391400800 and 391401800 transmitted time series data, sampled from the on-board data archive at 5 minute and 7.5 minute intervals, respectively.

⁴ Tag 391401600 was tagged with both a PAT and a Vemco V16 acoustic tag.

Five tags generated data summaries at 24-hour intervals. Two of these tags also transmitted higher resolution time series data, at 5-minute and 7.5-minute sampling intervals, and a third was the one physically recovered with 15 s interval time series data (Table 1). The remaining two tags generated data summaries at six-hour intervals, at 0000, 0600, 1200 and 1800 UTC. Two tags did not report mixed layer depth estimates (Table 1). In these cases I used the method of Kara et al. (2000) to generate estimates of the isothermal layer depth (approximating the MLD) directly from tag data, by analysing temperature changes with depth to identify the bounds of the mixed layer. Briefly, the algorithm searches the depth-temperature profile from the surface downwards until it finds a point where the change in temperature with depth exceeds a defined threshold (Kara et al. 2000). The isothermal layer depth is defined as the depth at which the difference between the ambient temperature and the mixed layer temperature first exceeds this threshold (Kara et al. 2000). In this case 1.5°C was chosen as the temperature change threshold after calibrating the Kara algorithm against MLD estimates from the tags.

Geolocation estimates were generated based on light level data and SST using the method of Teo et al. (2004). The algorithm uses changing ambient light levels to identify local times of dawn and dusk and calculate day length, related to latitude, and time of local noon, related to longitude (Hill & Braun 2001). Light-based geolocation position estimates were then validated by comparing *in situ* SST measurements from the tag with remote-sensed SST distributions (Teo et al. 2004). The resulting position estimates were refined using a state-space model which takes into account additional data on local cloud cover and bathymetry (Block et al. 2011, Winship et al. 2011). Daily estimated positions and associated errors (95% confidence intervals) were generated for each tag track.

4.3.5 Data analysis

4.3.5.1 Shark horizontal movements

Shark tracks, and associated error ellipses based on 95% confidence intervals of estimated longitude and latitude, were overlaid on a map of the BIOT MPA to visualise shark movements with respect to their tagging locations, the atolls of BIOT and the MPA boundary. To further investigate the accuracy of geolocation-based positions I analysed data from a silvertip shark tagged with both a PAT and an acoustic tag. Each day's geolocation-based position estimate from the PAT data was compared with the location of any acoustic detections recorded during the same period. The locations of all acoustic detections on a given day were averaged, weighting locations by the

absolute difference between the local time of each acoustic detection and the time of local noon corresponding to that day's geolocation estimate. I calculated the difference, in degrees latitude and longitude, between the mean acoustic detection location and the geolocation-based position estimate for each day. I then used these values to calculate the great circle distance, in kilometres, between the mean daily acoustic detection positions and the corresponding geolocation estimates using the function `distGeo()` in the R package *geosphere* (Hijmans 2017). This 'error' distance was plotted against the mean absolute time difference between daily acoustic detections and geolocation estimates to determine if the shark could have reasonably travelled between the two locations in the time available. A mean swim speed of 0.7 ms^{-1} was assumed for this purpose, based on Ryan et al. (2015).

4.3.5.2 Exploration of tag depth and temperature and water column profiles

To compare data across all tags, I aggregated all TAD and TAT histogram data to 24-hour periods, by averaging across shorter 6-hour summaries where necessary. For each tag, I calculated the median, interquartile range (IQR) and 95% range for depth and temperature for each daily summary by linearly interpolating within the depth and temperature bin ranges to estimate the depth or temperature value for each quantile. Where upper bin boundaries for depth and temperature were open (i.e., $> 500 \text{ m}$ or $> 32^\circ\text{C}$, respectively; Supplementary Tables 1 and 2) they were set to 1000 m and 34°C , respectively.

I reconstructed water column thermal profiles, or bathythermographs, over time from each tag's daily depth and temperature profiles. I created the bathythermograph data from each tag's PDT records by interpolating temperature linearly between depth steps to produce a depth/temperature raster with 2 m vertical resolution for each tag and date. In the case of the tag with a full data archive, the raster was obtained by aggregating the 15 s resolution depth and temperature data to the $2 \text{ m} / 24\text{-hour}$ resolution, with each raster cell recording the mean temperature value for that depth band and day. I calculated the daily median depth \pm IQR for each shark, and plotted each shark's bathythermograph and depth trend together to visualise the relationship between each shark's depth and the water column thermal structure, particularly the mixed layer, over time. I calculated the Pearson correlation between the median daily depth of the sharks and the daily estimates of mixed layer depth to quantify the strength of the relationship.

4.3.5.3 Seasonal variations in depth and temperature

To calculate summary statistics for all tag data pooled together, I standardised the histograms for all tags to common depth and temperature bins so that the proportion of time spent in each depth or temperature bin could be averaged across tags. This was necessary since the programmed histogram depth (Supplementary Table 4.1) and temperature (Supplementary Table 4.2) bin boundaries differed between tags. All data were re-binned using the histogram bin boundaries for Tag 1, with maximum depth and temperature values set to 1000 m and 34°C, respectively (Supplementary Tables 4.1 and 4.2). I used linear interpolation to allocate time spent within the original bins to the new standardised histogram bin boundaries. Having standardised the histogram data, I pooled the data across tags by day and calendar month, and calculated overall median depth and temperature for each day. I then compared trends in the sharks' median daily depth and ambient temperature, by calendar month, with median MLD and SST, respectively, using box plots.

4.3.5.4 Diel and lunar variations in depth and temperature

For the five tags with data recorded at 6-hour or shorter intervals, I aggregated histogram data by diel period (TOD), classified as *day* if data were recorded between approximately 6am to 6pm local time, otherwise *night*. Summary depth and temperature statistics were calculated using the same bin interpolation methodology as above. Lunar phase (new, waxing, full, waning) was assigned to each date in the data using the function `lunar.phase()` in the R package *lunar* (Lazaridis 2014). Median depth was calculated for each shark in each day/night period for each day. To test for the effect of time of day and lunar phase on shark median depth I first calculated the difference between semi-diel median depth, in each half-day period, and the 30-day rolling daily median depth, to remove seasonal effects. Analysis of variance was then used to test for significant effects of time of day and lunar phase, and the interaction between them, on seasonally-adjusted median depth. Tukey's test of Honestly Significant Difference was used to test for significant effects of the interaction between time of day and lunar phase. I calculated the mean percentage of time sharks spent below depth thresholds (75, 100, 150 m) and temperature thresholds (25, 22, 18°C), overall and by diel period, by interpolating within the depth and temperature bins of the histogram data.

4.3.5.5 Modelling of median depth against environmental factors

I modelled the median daily depth of each shark against environmental factors for all seven tags using generalised linear mixed-effects modelling (Bolker et al. 2009) implemented in the function `lme()` in the R package *nlme* (Pinheiro et al. 2018). The dataset for all seven tags included 770 daily

depth records. Mixed layer depth (in metres), sea surface temperature (SST, in °C), lunar phase (new, waxing, full, waning) and shark total length (in centimetres) were tested as candidate fixed predictor variables, with tag ID (identifying individual sharks) included as a random effect. The significance of the random intercept ($1|TagID$) was tested using the methodology of Zuur et al. (Zuur et al. 2009) which compares the AIC and likelihood ratio scores of a generalised least squares model without the random effect with a mixed model including the random effect term.

Model building was performed using forward selection, starting from a null model with random effect only and adding and combining predictors sequentially, following the method employed by Kock et al. (2013). The first stage tested all predictors individually. The explanatory power of each model was evaluated using the Akaike information criterion (AIC), Bayesian information criterion (BIC) and likelihood ratio tests (`anova()` function in R) to determine whether additional variables added during model selection increased the model's goodness of fit (Zuur et al. 2009). Subsequent stages repeated this process, adding each of the remaining predictors individually to the best model from the previous round. Both explanatory power (lower AIC) and model parsimony (lower BIC) were considered in choosing the final model. I plotted model residuals against fitted values to check for trends or heteroscedasticity in the distribution of residuals. Partial residual plots for each fixed predictor variable were generated using the function `visreg()` in the package *visreg* (Breheny & Burchett 2017). I calculated pseudo- R^2 values (Schielzeth & Nakagawa 2013) to estimate the variance explained by the fixed predictors only (marginal variance) and both the fixed and random effects (conditional variance) using the function `r.squaredGLMM()` in the package *MuMin* (multi-model inference, Bartoń 2018).

The mixed-effects model selection process was repeated for five tags with 481 days of finer-scale temporal data. Median depth was calculated separately for day (0600 to 1800) and night (1800 to 0600) periods for each shark and day in the dataset, creating a set of 962 semi-diel depth records. Environmental variables were summarised at the same temporal resolution. Model building and testing was carried out as above, with TOD (day or night) tested as an additional fixed predictor, together with the interaction between time of day and lunar phase.

4.3.5.6 Dive profiles relative to dive depth, duration and ambient conditions

The depth-time series from the recovered PAT (Tag 7, ID 391401800) contained 180 days of continuous depth records at 15 second intervals, allowing analysis of individual dives performed by that shark. For this analysis, a dive was considered to start when the shark moved below 100 m and

end when it returned to this depth. The threshold for the start of dives was set at 100 m, since that was the maximum depth of *in situ* estimates of the mixed layer depth (see Results). Although shallow dives to depths between 100 m and 200 m were observed, analysis focussed on mesopelagic dives below 200 m because visual examination of depth-time plots identified a distinctive and abrupt rate transition in the ascent portion of many of these dives that warranted further investigation.

4.3.5.7 Characterising dive ascent profiles

A custom window function was used to algorithmically identify discontinuities (hereafter breakpoints) in the ascent trajectory of each dive. A breakpoint was defined as an instantaneous reduction in ascent rate of at least 50%, before and after which the ascent rate had been relatively constant for at least one minute. The window function was initialised at the start of each dive's ascent (i.e. after the deepest point) and then moved through the remaining depth-time series in increments of 15 s (i.e. one time step in the tag data). The depth, date and time of qualifying points in the dive profiles were recorded. A full description of the function's operation and the associated R code are included in the Supplementary Material. To compare all dive profiles, I standardised the time axis of each dive profile by defining the breakpoint of each depth-time series as $t = 0$ and calculated the average depth at each relative time step for all dive profiles.

4.3.5.8 Estimating water column temperature and dissolved oxygen profiles

Temperature data for each dive, at 10 m intervals, were obtained directly from the tag data. Climatological DO values for the study area were downloaded from the NOAA World Ocean Atlas (WOA, <https://www.nodc.noaa.gov/cgi-bin/OC5/woa13/woa13oxnu.pl>, monthly means, 1 degree latitude/longitude resolution). The WOA data provide average vertical DO profiles at 5m to 50 m resolution. The dataset's vertical resolution decreases with depth: 25m resolution from 100 m to 500 m, 50 m resolution from 500 m to 1500 m. To generate DO profiles for each dive, I first interpolated vertically within each WOA record to get DO values at 10 m intervals. I then interpolated horizontally and temporally between locations and dates in the WOA DO data to estimate values for the locations and dates of the shark's individual dives. Approximate dive location was assumed from the tag's geolocation estimates. Spatial interpolation between dive locations and the locations in the WOA dataset was performed with the R package *akima*, using a cubic-spline interpolation based on the method of Akima et al. (1978). I assumed that the monthly averages in

the WOA data corresponded to the 15th day of each month, and I then used a linear interpolation to estimate DO values on the date of each dive.

Using the water column DO profiles, I calculated the depth for each dive at which DO levels dropped below 2.5 ml l⁻¹, which I assumed as a threshold for respiratory stress in a species like the silvertip shark. A DO level below 2.5 ml l⁻¹ was assumed based on DO thresholds for behavioural change, corresponding to respiratory stress, reported in the literature for active ram-breathing shark species, including mako sharks (*Isurus oxyrinchus*, Vetter et al. 2008), and bonnethead (*Sphyrna tiburo*) and blacknose sharks (*Carcharhinus acronotus*, Carlson & Parsons 2001). I separately estimated the depth of the upper bound of the local oxygen minimum zone (OMZ) by analysing the gradient of the DO-depth curve at each dive location, assuming that DO declines relatively steeply from the surface to the start of the OMZ but stabilises at that depth (Sewell & Fage 1948).

4.3.5.9 Modelling dive profiles against environmental conditions

I tested the relative importance of DO relative to temperature, dive duration and dive depth as factors influencing diving behaviour using Pearson correlation coefficients. The function `cor.test()` in R was used to calculate correlation coefficients between the depth of the breakpoint in ascent rate for each dive and the depth of the local OMZ, the depth of the 2.5 ml l⁻¹ DO isopleth, the amount of time the shark spent below 100 m (i.e. below the mixed layer), the amount of time the shark spent in waters cooler than 18°C, the maximum depth of the dive, and the depth of 18°C isotherm. 18°C was chosen as the temperature threshold for these analyses since silvertip sharks ordinarily spend the majority of their time in waters warmer than this temperature (see Results), suggesting that it marks an approximate lower bound of their normal thermal niche. I separately investigated whether the depth at which changes in ascent rate from dives occurred was correlated with rates of increase in DO levels rather than absolute values. Rapidly rising DO levels would, hypothetically, signal that the shark had exited the OMZ. For each dive, I calculated the mean instantaneous ascent rate in metres per second and the corresponding vertical rate of change in DO concentration for each time step, in ml per litre per metre of ascent. I pooled these data for all dives and calculated the mean vertical ascent rate change \pm CI for four discrete levels of the rate of change in DO concentration, < -0.01 ml l⁻¹ m⁻¹, -0.01 to $+0.01$ ml l⁻¹ m⁻¹, $+0.01$ to $+0.03$ ml l⁻¹ m⁻¹, and $> +0.03$ ml l⁻¹ m⁻¹.

4.4 Results

4.4.1 Overview of tag deployments

Seven silvertip sharks between 145 cm and 185 cm total length (mean = 158.4 ± 10.0 CI) were tagged with pop-up satellite archival tags (PATs) between 12 February 2013 and 27 March 2014 (Table 4.1). A total of 770 daily data records were obtained from the seven tags (mean = 126 ± 20 days, range = 101 to 180 days, Table 4.1). Two satellite tags released at their pre-programmed time (120 and 180 days after deployment); the remaining five tags released prematurely between 101 and 127 days after deployment (49-71% of the programmed time, Table 4.1). The maximum depth (\pm measurement error) recorded on these tags ranged from 328 ± 4 m to 792 ± 4 m (Table 4.1).

4.4.2 Horizontal movements of the sharks based on geolocation estimates

The geolocation-based position estimates indicate that it is unlikely that any of the tagged sharks left the BIOT MPA and suggest that sharks spent most of their time close to the BIOT reef system (Figure 4.1c). However, estimated daily shark movements were small relative to the geolocation state-space model errors, meaning that the 95% confidence intervals of most daily position estimates overlapped and the state-space model could not resolve individual movement steps for the sharks (Figure 4.1c).

To better quantify geolocation error, geolocation estimates were compared with location estimates generated from acoustic tag detections for one double-tagged shark (Tag 6, ID 391401600). As the location of the acoustic receivers was known, the positions derived from acoustic telemetry were assumed to be the true location of the shark on a given day. The maximum difference between the daily geolocation-based position estimates and the true daily positions derived from acoustic telemetry was 0.2 degrees longitude and 0.25 degrees latitude, or ~ 20 km and ~ 25 km, respectively. Geolocation-based longitude estimates oscillated east and west around the shark's actual position (Supplementary Figure 4.1a), with no clear linear trend over time, whereas geolocation-based latitude estimates showed a consistent northerly drift (Supplementary Figure 4.1b). The combination of these differences led to the geolocation-based position estimate being up to 35 km from the shark's acoustic telemetry-derived location. Most such displacements were beyond the shark's likely range of movement within the time intervals between geolocation and acoustic telemetry position fixes (Supplementary Figure 4.2).

4.4.3 Variation in the median depth and ambient water temperature occupied by silvertip sharks

Daily median depth for all tagged sharks ranged from 4.0 to 77.2 m (mean 36.5 ± 0.84 m). The median daily depth for each tagged shark matched the contours of the relatively warm surface mixed layer (Figure 4.2a-g), with sharks spending 50% of their time in the lower part of the mixed layer (Figure 4.2a-g). The Pearson correlation score between shark median daily depths and the mixed layer depth, pooled for all tags, was 0.77 (Figure 4.2h), and the relationship between shark median depth and mixed layer depth appeared consistent across tags and years (Figure 4.3a). Daily mixed layer depth ranged from 18 m to 98 m. Mixed layer depth was shallowest in May (median 38 m, 95% range 24 – 51 m) and deepest in August (median 82 m, 95% range 68 – 90 m, Figure 4.3a).

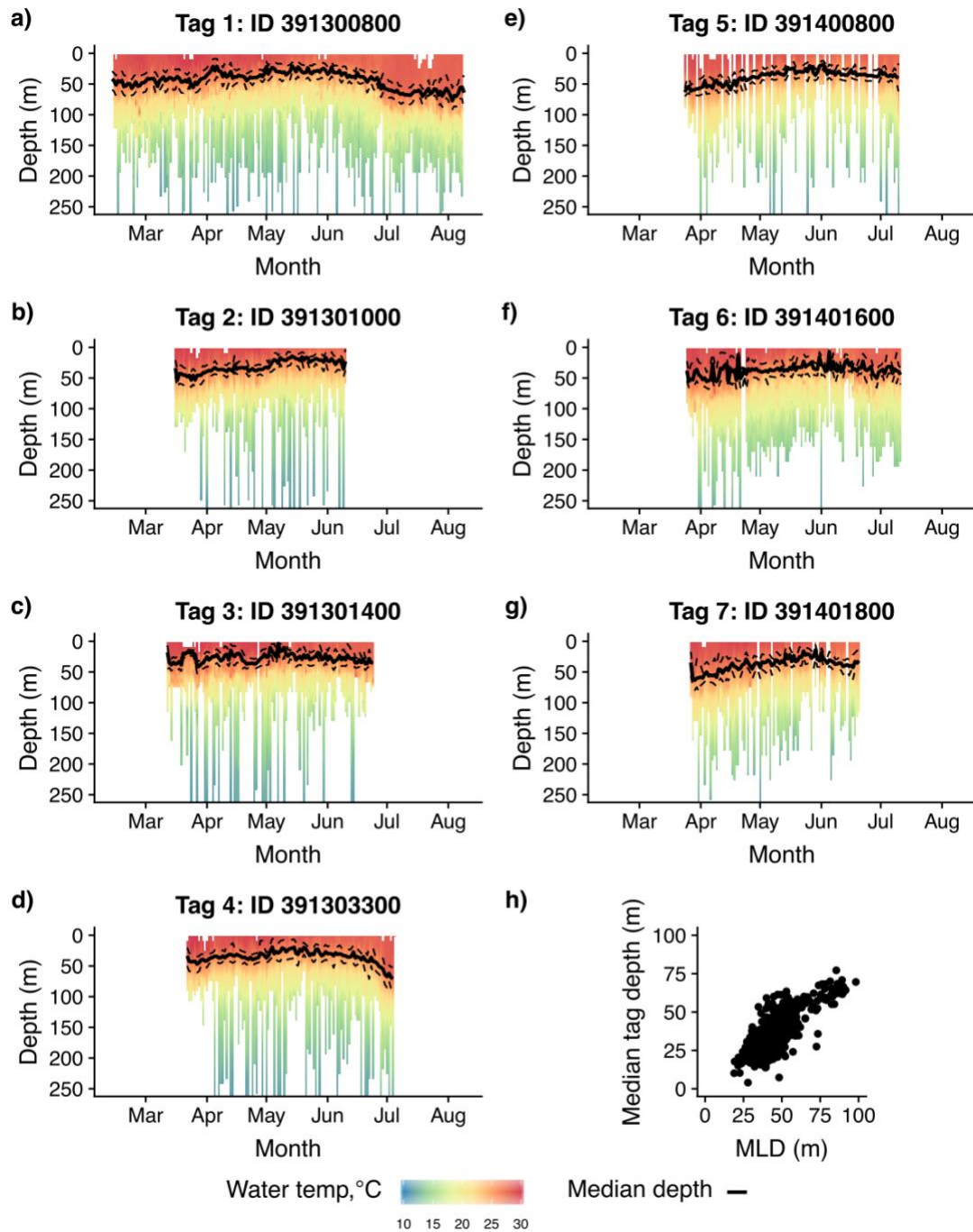


Figure 4.2: Bathythermographs (a-g) based on daily depth and temperature records for seven silvertip sharks tagged in 2013 (a-d) and 2014 (e-g). Depth range has been truncated to show greater detail. Solid line indicates median daily depth for each shark; dashed lines show upper and lower quartiles of daily depth distribution. Colour indicates ambient water temperature recorded by tags. Panel h) shows overall relationship between median daily depth and mixed layer depth (MLD), pooled for all sharks (Pearson's correlation = 0.77).

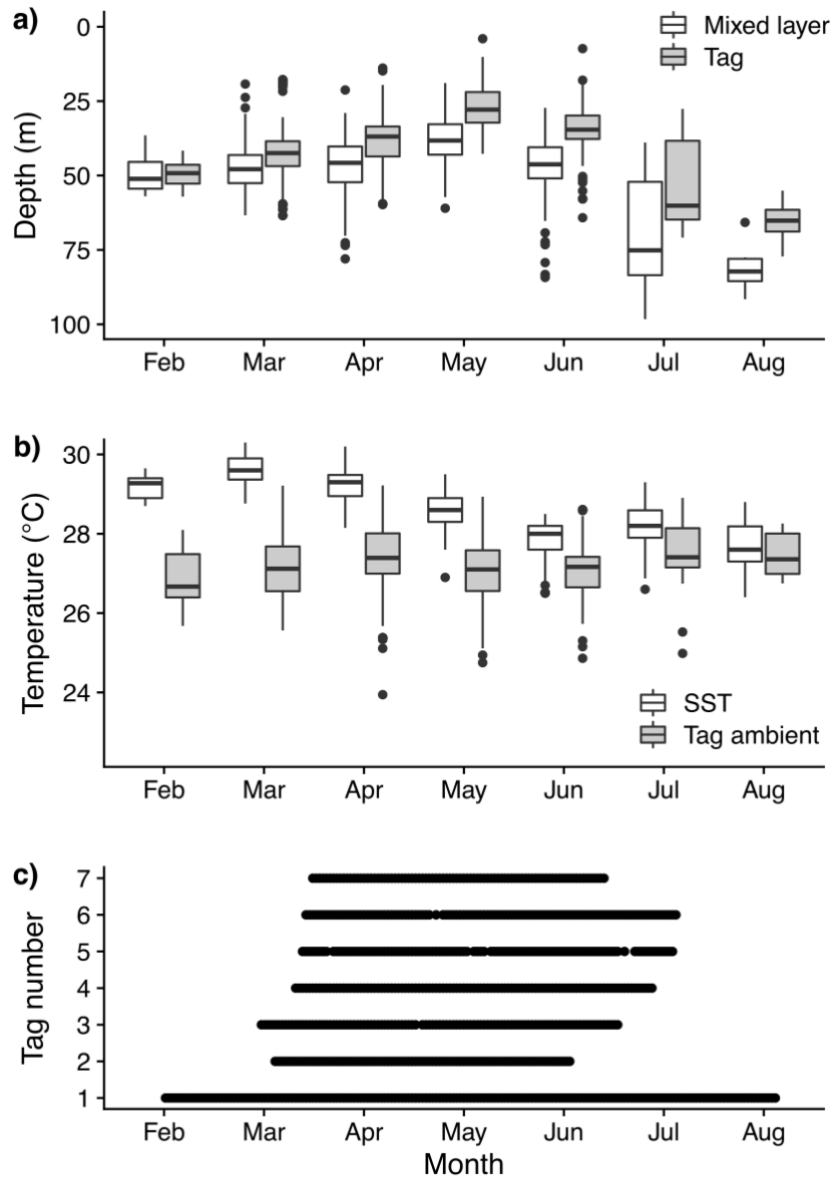


Figure 4.3: Boxplots by month of a) daily mix layer depth and daily median tag depth (grey fill) and b) daily mean sea surface temperature (SST) and daily median tag ambient temperature (grey fill), pooled across tags ($n = 7$) and years. Heavy horizontal line is monthly median; box indicates IQR; whiskers = 95% range; outliers plotted individually. Panel c) shows distribution of data records over time for each tag, with time series aligned by calendar month.

In contrast to the significant monthly variation in the sharks' median depth (Figure 4.3a; ANOVA $F_{[6,764]} = 11.2, p < 0.001$), the daily median water temperature occupied by sharks varied comparatively little. Daily median temperature averaged $27.2 \pm 0.1^\circ\text{C}$ overall (range 26.8 to 27.6°C, Figure 4.3b). Local SST, in contrast, varied by up to 3°C during the deployment periods (Figure 4.3b).

The median depth occupied by the sharks varied on shorter timescales between day and night and between lunar phases at night time (Figure 4.4). Analysis of variance followed by Tukey’s test of Honestly Significant Difference found significant effects of time of day, with sharks significantly deeper during daylight than at night during all moon phases, and there was a significant in between time of day and lunar phase, with sharks deeper on nights of the full moon compared with the new moon (Figure 4.4).

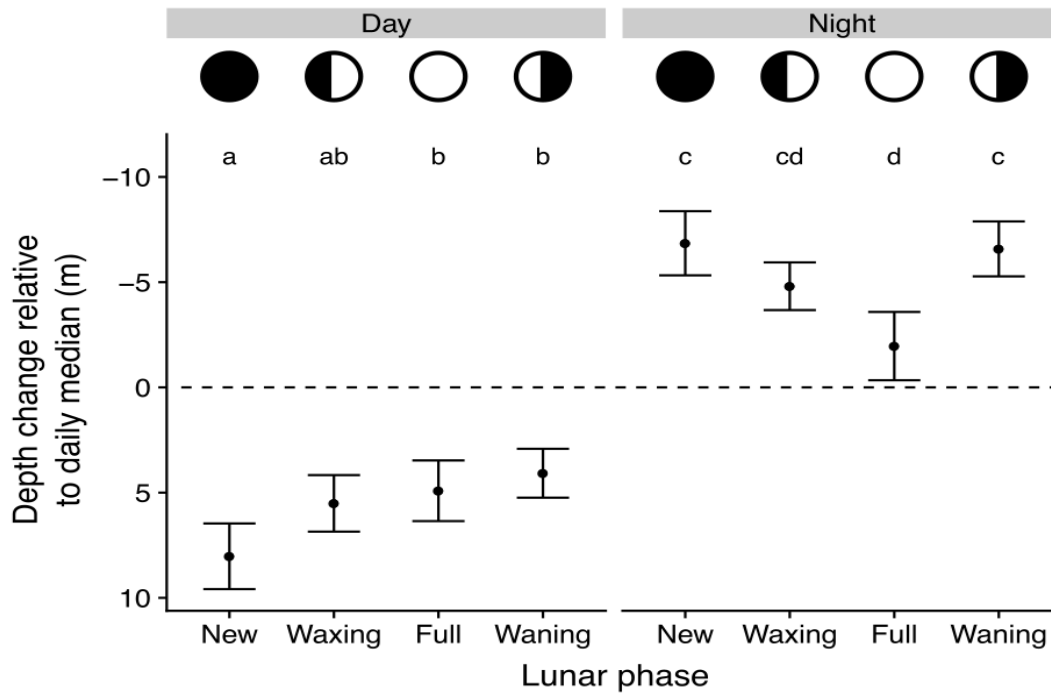


Figure 4.4: Change in the median depth occupied by silvertip sharks with time of day (day or night) and lunar phase, adjusted for seasonal variation. Error bars indicate 95% confidence interval of mean values for all sharks. Changes in median depths are standardised relative to each sharks’ 30 day rolling median depth. Lowercase letters above plot indicate results of Tukey’s test for Honestly Significant Difference for an analysis of variance test of depth change against time of day, lunar phase and their interaction. Factor combinations labelled with the same letter are not significantly different.

4.4.4 Time below depth and temperature thresholds

The sharks in the study spent an average of $5.1 \pm 0.5\%$ of their monitored time below 75 m, $1.5 \pm 0.1\%$ below 100 m and only and $0.3 \pm 0.1\%$ of their time (<5 minutes per day) below 150 m. Time spent below 100 m was significantly higher during day time, consistent with day/night patterns in median depth, but sharks spent more time below 150 m during the night (Table 4.2). Sharks spent 14% of their time in waters between 22 °C and 25 °C, i.e. up to 5 °C cooler than their median ambient temperature, but only 1% of their time (~ 14 minutes per day) in water cooler than 18°C (Table 4.2).

Table 4.2: Summary statistics for time spent below depth and temperature thresholds by tagged silvertip sharks. Mean proportion \pm 95% CI reported for total time, and for day and night time separately. T-test results for day/night comparisons shown in last column.

Threshold	Share of time spent by sharks below threshold depth or water temperatures (\pm 95% CI)			T-test results	
	Daily average	Day time 06:00-18:00	Night time 18:00 – 06:00	T	p-value
Depth					
75m	5.1 \pm 0.5%	9.1 \pm 0.9%	4.1 \pm 0.6%	-6.64	< 0.001
100m	1.5 \pm 0.1%	1.8 \pm 0.3%	1.1 \pm 0.1%	-3.56	< 0.001
150m	0.3 \pm 0.1%	0.3 \pm 0.1%	0.4 \pm 0.1%	3.01	0.002
Temperature					
25°C	20.4 \pm 0.8%	33.0 \pm 1.7%	14.5 \pm 0.9%	18.89	0.001
22°C	6.4 \pm 0.5%	11.3 \pm 1.0%	4.1 \pm 0.4%	13.35	0.001
18°C	1.1 \pm 0.1%	1.2 \pm 0.2%	0.9 \pm 0.1%	2.52	0.012

4.4.5 Modelling of shark median depth against environmental variables

The model which best predicted median daily depth for all tags included mixed layer depth, SST and lunar phase (AIC = 4848.8, BIC = 4885.6, logLik = -2416.414, Supplementary Table 4.3). The model's marginal R^2 was 0.61 and the conditional R^2 was 0.67, indicating that most of the variation was explained by the fixed predictors. The model predicted that shark median depth would be 71% of the mixed layer depth and 4.1m deeper for every 1°C increase in sea surface temperature. Standardised coefficients showed that variation in mixed layer depth had the largest fixed effect, three times greater than SST. While there was a statistically significant effect of lunar phase the effect size was very small, with difference in depth of less than 2 m between phases (Table 4.3, Supplementary Figure 4.3).

Table 4.3: Fixed effects of a generalised linear mixed model predicting the median daily depth of silvertip sharks in BIOT. Fixed effect predictors were mixed layer depth (MLD: metres), sea surface temperature (SST: °C) and lunar phase (new, waxing, full, waning). Each predictor's estimated coefficient and standard error (SE), standardised effect size (beta) and significance test result are shown. P-values less than 0.05 indicated in bold.

Predictor variable	Coefficient	SE	beta	T value	p-value
(Intercept)	-115.76	10.63	-0.02	-10.89	0.000
MLD	0.71	0.02	0.74	32.99	0.000
SST	4.13	0.36	0.24	11.32	0.000
Lunar phase (waxing)	1.38	0.67	0.05	2.06	0.039
Lunar phase (full)	0.72	0.69	0.03	1.04	0.300
Lunar phase (waning)	-0.99	0.69	-0.04	-1.44	0.149

Expanding the depth model to include time of day (day or night) as an additional factor found a model with mixed layer depth, time of day, lunar phase and SST to have the greatest explanatory power (AIC = 6721.5, BIC = 6779.6, logLik = -3348.7; Supplementary Table 4.4). The model's marginal R^2 was 0.59 and conditional R^2 was 0.62, indicating that the fixed predictors accounted for the majority of the explained variation in shark depth, with only a small random effect from individual sharks. In the semi-diel model, mixed layer depth and time of day had the largest effects, followed by SST (Table 4.4). The model predicted that shark depth would be 71% of mixed layer depth and 4.0 m per 1°C increase in SST (Table 4.4) similar to those predictors' effects in the model of daily depth (Table 4.3). Shark depth was predicted to be 14.8 m deeper during daylight and 6.1 m deeper on nights with a full moon, relative to nights of the new moon (Table 4.4, Supplementary Figure 4.4).

Table 4.4: Fixed effects of a generalised linear mixed model predicting the median daily depth of silvertip sharks in BIOT. Fixed effect predictors were mixed layer depth (MLD: m), sea surface temperature (SST: °C), time of day (TOD: day, night), lunar phase (new, waxing, full, waning) and the interaction between TOD and Moon. Each predictor's estimated coefficient and standard error (SE), standardised effect size (beta) and significance test result are shown. P-values less than 0.05 indicated in bold.

Predictor variable	Coefficient	SE	beta	T test value	p-value
(Intercept)	-105.27	12.58	-0.05	-8.37	0.000
MLD	0.71	0.02	0.64	29.91	0.000
SST	4.01	0.43	0.19	9.34	0.000
TOD (night)	-14.87	1.08	-0.38	-13.81	0.000
Lunar phase (waxing)	-0.19	1.08	0.06	-0.18	0.859
Lunar phase (full)	-1.68	1.13	0.07	-1.49	0.137
Lunar phase (waning)	-3.43	1.13	-0.04	-3.03	0.003
TOD (night) Lunar phase (waxing)	4.39	1.52	0.07	2.88	0.004
TOD (night) Lunar phase (full)	7.78	1.59	0.11	4.90	0.000
TOD (night) Lunar phase (waning)	3.95	1.59	0.06	2.48	0.013

4.4.6 Diving behaviour

The tag recovered with the full archival time series data set (Tag 1, ID 391300800, Table 4.1) contained records of 61 dives below 200 m, averaging one every three days. Dives were typically short in duration, averaging 5.3 ± 0.7 minutes, with a steady descent to 'target' depth and a rapid ascent from depth (Supplementary Figure 4.5b). On returning from dives below 200 m the vertical ascent rate decreased sharply, normally between 200 m and 100 m depth, giving ascents a 'dog-leg'

profile (Supplementary Figure 4.5a,b). Mean vertical ascent rates before and after this breakpoint in the ascent were $0.59 \pm 0.05 \text{ ms}^{-1}$ and $0.12 \pm 0.01 \text{ ms}^{-1}$, respectively, a mean reduction of 80% ($t = 19.351$, $p < 0.001$). The change in ascent rate occurred at an average depth of $121.3 \pm 7.2 \text{ m}$ (IQR 103.5 – 138.0 m), corresponding to the upper boundary of the oxygen minimum zone, above which the dissolved oxygen concentration began to rise rapidly (Figure 4.5, Supplementary Figure 4.5c,d). The shark's vertical ascent rate slowed as DO concentration began to increase at $> 0.03 \text{ ml l}^{-1}$ per metre of ascent, i.e. when the shark had reached increasingly oxygen-rich depths (Supplementary Figure 4.6). The correlations between the depth of the breakpoint in the ascent rate and the depths of the upper boundary of the OMZ and the 2.5 ml l^{-1} DO isopleth on individual dives were 0.35 ($t = 2.887$, $p = 0.005$) and 0.32 ($t = 2.625$, $p = 0.01$), respectively, both stronger than the correlations between breakpoint depth and other environmental or dive parameters, such as maximum dive depth or the shark's exposure to low temperatures (Supplementary Table 4.5).

4.5 Discussion

The current study demonstrates the utility of satellite tags in describing and modelling the drivers of fine scale vertical movements of silvertip sharks around an oceanic atoll reef system. Silvertip sharks in BIOT exhibit predictable vertical space use with respect to environmental drivers, consistently occupying the lower third of the surface mixed layer as it varied seasonally. Depth use was also predictable at shorter time scales, deeper during daylight and on nights of the full moon, with sharks apparently responding to changes in surface illumination. They also occupied a narrowly defined thermal niche and appeared to modify their diving behaviour in response to dissolved oxygen (DO) levels in the water column. Predictable space use has implications for their vulnerability to immediate threats from fisheries, whereas evidence of physiological temperature and DO thresholds might also inform their longer-term vulnerability to oceanographic changes under climate change. Reef-associated sharks have not typically been focal species for studies using satellite archival tags, since their fidelity to fixed sites makes acoustic telemetry a more cost-effective option (Whoriskey & Hindell 2016, but see Bond et al. 2015, Andrzejaczek et al. 2020, Bradley et al. 2019). My study suggests that satellite archival tags, with their capacity to gather continuous and higher resolution depth and ambient temperature data, can reveal valuable additional insights into the spatial ecology of reef-associated species.

4.5.1 Temperature and light drive as predictors of vertical space use in silvertip sharks

Most of the variation in silvertip sharks' daily median depth could be predicted by the depth of the mixed layer and the sea surface temperature, suggesting that thermoregulation might be a key driver of their overall vertical space use. While the seven sharks monitored in this study varied their daily median depth over the study period by over 50 m, they maintained a consistent median ambient temperature of around 27°C, suggesting that changes in the animals' core depth were driven by them seeking optimum thermal conditions. The median water temperature occupied by silvertip sharks in BIOT is similar to the 26.3°C average recorded by Bond et al. (2015) for an individual silvertip shark in Fiji. Both sample sizes were small, but the similarity suggests consistency in silvertip sharks' thermal niche across locations, which might be tied to basic physiological constraints. Andrzejaczek et al. (2020) obtained similar results to mine from PAT deployments on reef mantas (*Manta alfredi*) in BIOT, finding that reef mantas showed high fidelity to the 25-50 m depth strata within the mixed layer with a median temperature of 27.3 °C. Mean depths for the silvertip sharks in this study and the reef mantas studied by Andrzejaczek et al. (2020) were 36 m and 35 m respectively, suggesting that the two species may occupy similar physiological niches.

Short term vertical movements by silvertip sharks were predicted by time of day in combination with lunar phases, suggesting that silvertip sharks follow a similar light-based diel vertical migration to that seen in many pelagic species such as blue (Campana et al. 2011) and bigeye thresher sharks (*Alopias superciliosus*, Coelho et al. 2015). Vertical movements synchronised with diel and lunar cycles have also been observed for grey reef sharks in Palau (Vianna et al. 2013) and silvertip sharks on the GBR (Espinoza et al. 2015a). Espinoza et al. (2015a) hypothesised a 'hunt warm, rest cool' explanation, with silvertip sharks on the GBR resting in deep, cooler channels between reefs during the day, before hunting on reefs at night. While thermoregulation may also be the driver of short-term vertical movements by silvertip sharks in the BIOT, the fact that their vertical space use apparently varies with surface illumination suggests that the movement of vertically migrating prey may be the proximal driver of these predators' oscillating vertical space use in BIOT. Diet and stable isotope-based studies suggest that silvertip sharks exploit a high percentage of pelagic prey resources (Cortés 1999, Curnick et al. 2019). In the BIOT, where the outer reefs of atolls abut deep pelagic waters, light-driven diel vertical migration of mesopelagic squid and fishes may bring prey into the surface waters adjacent to the reefs at night, drawing predators like silvertip sharks. Andrzejaczek et al. (2020) also found that reef mantas exhibited a similar pattern of diel vertical migration near reefs in BIOT to that observed for silvertip sharks in my study. In that study, they

hypothesised that reef mantas were exploiting mesopelagic zooplankton in offshore surface waters at night (Andrzejaczek et al. 2020). Along with their similar thermal niches, this suggests that, despite very different diets and morphologies, these two reef-associated species respond to very similar environmental cues in BIOT waters and have similar physiological niches with respect to water temperature. Temperature and light levels may be fundamental drivers of large ectothermic predators around reefs, driving similar patterns in space use across disparate taxa.

4.5.2 Diving behaviour and dissolved oxygen levels

While silvertip sharks spent the majority of their time in the top 100 m of the water column, dives of up to almost 800 m were recorded, consistent with maximum dive depths reported for this species (Compagno 1984). Without additional data, the purpose of these dives cannot be determined, but possible explanations proposed in other studies of shark diving behaviour include predator avoidance, thermoregulation and foraging (Howey et al. 2016). Predator avoidance is a possible explanation, given the presence in the BIOT of large shark species like mako (Forrest 2019) and hammerhead sharks (Tickler et al. 2017) that may prey on smaller sharks, but silvertip sharks might be more likely to take refuge on the reef rather than dive to extreme depths. Similarly, thermoregulation would not seem to require dives to 800 m when cooler water lies just beneath the relatively shallow mixed layer. Foraging seems, therefore, a more plausible explanation for the dives. Periodic deep dives have been suggested as opportunistic attempts to encounter mesopelagic prey for other species including oceanic white tip (Howey et al. 2016), blue (Braun et al. 2019) and basking sharks (Queiroz et al. 2017), and may serve a similar purpose for silvertip sharks, which are known to exploit pelagic prey in the BIOT (Curnick et al. 2019). If silvertip sharks forage at depth, they may contribute to coupling deep and shallow ecosystems in the BIOT, as has been suggested to occur horizontally between pelagic and reef ecosystems as a consequence of reef shark foraging behaviour around Palmyra Atoll in the Pacific Ocean (McCauley et al. 2012, Williams et al. 2018).

A preliminary investigation of diving behaviour also found a possible influence of dissolved oxygen availability on the vertical space use of silvertip sharks. Dissolved oxygen concentration is thought to influence the vertical space use and diving behaviour of several marine predators including billfish and tunas (Prince & Goodyear 2006, Prince et al. 2010, Carlisle et al. 2016, Pohlot & Ehrhardt 2017) and mako sharks (Vetter et al. 2008, Abascal et al. 2011). Mesopelagic dives by silvertip sharks were characterised by a rapid and constant rate of descent followed by a period of assumed foraging and then a distinct 'dog-leg' ascent, with a 50-80% reduction in vertical ascent rate occurring at a fairly

consistent depth. A similar pattern was observed in dives by oceanic whitetip sharks in the Bahamas (Howey et al. 2016), which exhibited a 'transition point ascent' from dives with a vertical rate reduction of 0.53 ± 0.31 m/s, or approximately 66% of the rate before the transition. Howey et al. (2016) hypothesised that the behaviour might be driven by the sharks moving out of the OMZ after mesopelagic dives but the evidence for this was equivocal in their case, which they attributed in part to a lack of *in situ* oxygen measurements. In BIOT, this behaviour does appear to coincide with the upper bound of the local OMZ, below which DO levels are consistently below 2.5 ml l^{-1} . This level has been shown to produce signs of respiratory stress in other species of active ram-breathing sharks (Carlson & Parsons 2001). If this oxygen-limitation hypothesis is correct, an explanation for the dive profiles is that the rapid portion of the silvertip shark's ascent from dives within the OMZ is designed to minimise continued exposure to low dissolved oxygen levels and/or increase ram breathing efficiency, while the sudden deceleration reduces energy expenditure once better-oxygenated waters are reached. Bottom topography and temperature changes might also influence the profile of dives. However, topography might be expected to affect both descent and ascent profiles, and the dog-leg pattern was observed on ascents only. Although thermal stress cannot be discounted as a driver of ascent rate, heat loss during such short dives seems less likely to be a limiting factor. *In situ* measurement of oxygen, using new DO sensor tags (Coffey & Holland 2015), would help explore this question further, especially if combined with accelerometry to provide information on the shark's swimming activity under different conditions.

4.5.3 Vertical space use, management and conservation

The predictable vertical space use of silvertip sharks in response to environmental drivers may increase their vulnerability to anthropogenic threats, in particular fishing, but may also be used to tailor enforcement activities to periods of greatest risk. Species' horizontal space use is often considered when evaluating their exposure to threats like fisheries (Queiroz et al. 2019) and the efficacy of MPAs (Dwyer et al. 2020). However, vertical space use may also have important management as well as ecological implications. Based on my results, the silvertip shark's vertical niche in BIOT overlaps with the relatively shallow (30-100 m depth) longlines set by local fishing fleets (Aneesh et al. 2016, Hewapathirana & Gunawardane 2017), particularly those from Sri Lanka and India which are known to illegally fish in BIOT (Martin et al. 2013, Tickler et al. 2019). Predictable variations in their vertical space use may further increase their vulnerability by allowing fishers to target them based on simple environmental cues. Vianna et al. (2013) hypothesised a similar problem for grey reef sharks in Palau, which also showed predictable depth changes correlated with

diel and lunar cycles. Andrzejczek et al. (2020) also noted that reef mantas in BIOT occupied a predictable depth range which might increase their vulnerability to fishing gears. These results suggest that reef-associated elasmobranch predators sharing similar sets of environmental constraints and drivers may share a heightened vulnerability to fishing, but may also share benefits from protection tailored to their spatial ecology.

A preference for relatively cool waters and an apparent intolerance to low-DO conditions may have longer-term implications for silvertip sharks, particularly in remote locations like the BIOT with limited connectivity to other reef systems. Climate change is leading to warming oceans (Cheung et al. 2016), expanding OMZs (Gilly et al. 2013), and an overall reduction in DO in the ocean (Breitburg et al. 2018). Changes in oxygen availability in a warming ocean are expected to impact gill-breathing animals globally (Pauly & Cheung 2017), leading to a poleward shift in species' ranges (Cheung et al. 2009, Sunday et al. 2011, Robinson et al. 2015). Behavioural thermoregulation, i.e. moving to deeper, cooler water (Dulvy et al. 2008), may allow mobile species like silvertip sharks to adapt to warming surface waters in the short term, as they already appear to do on a seasonal basis. However, continued warming of the ocean's surface, estimated at 0.11°C per decade globally and 0.15°C per decade in the Indian Ocean (Roxy et al. 2020), may interact synergistically with changes in oxygen availability to constrain available vertical habitat for silvertip sharks. Shoaling OMZs may push silvertip sharks towards the surface (Stramma et al. 2012, Gilly et al. 2013) while warming surface waters compress their thermal habitat from above. As well as placing physiological strain on silvertip sharks, this may also increase their vulnerability to fishing by making their vertical space use more constrained and predictable. Much concern has focussed on the impact that climate change is forecast to have on fish stocks (e.g. Cheung et al. 2016). The results of this study suggest that important non-target species like reef sharks may also be affected in term of both physiological fitness and increasing restrictions to their horizontal and vertical movements. While reducing direct anthropological pressures on reef sharks and their habitats through well enforced MPAs is needed to maintain biodiversity and enhance species' resilience to environmental change (Dulvy 2006, Edgar et al. 2014, Davies et al. 2017), tackling the root causes of the warming will obviously be necessary to avert longer term impacts.

4.5.4 Limitations of the study

The first limitation to recognise is the small sample size of sharks in this study, meaning caution is required in extrapolating from these results to conclusions about silvertip sharks in general.

However, while only seven tags were analysed, there was a high degree of consistency in the relationship between depth and water column structures between sharks, and only a low proportion of variance was explained by the random effect of individual tags in mixed-effects modelling of depth. Results with respect to the sharks' depth and temperature range, and their vertical movements between day and night, are also consistent with the findings from a Fiji-based study by Bond et al. (2015), although that study tagged only one silvertip shark. The sharks tagged in this study did not include any individuals smaller than 145 cm total length, in part a deliberate choice to deploy PATs on larger sharks that would better cope with any additional drag. Consequently, the results may not be applicable to all size classes of silvertip sharks. Larger sample sizes and stratified sampling by size in future studies, in BIOT and elsewhere, are needed to improve the robustness of this study's conclusions.

This study also monitored sharks for no more than six months, and since all tags were deployed at the same time of year, my data only cover the half year from April (late Austral summer) to the following September (Austral spring). This misses the October to January period which was historically the peak fishing season for pelagic fisheries targeting tunas in the BIOT and is thought to correspond to offshore productivity peaks and yellow fin tuna spawning (Dunn & Curnick 2019, Curnick et al. 2020). Stable isotope data indicate that silvertip sharks may obtain a greater share of resources from pelagic prey during this period, and so both horizontal and vertical movements might be expected to change (Curnick et al. 2019). Setting longer release times on tags would help fill this gap, although this would come at the cost of data resolution due to tag storage and transmission limitations (Fisher et al. 2017). Tags could also be deployed with six-month release times in September to cover the missing months, but weather conditions in BIOT can be unfavourable to vessel-based research at that time of year as strong south-easterly winds and swell prevail (N. Sandes, pers. comm.).

A third limitation is the inability of the tags to resolve the fine scale horizontal movements of the tagged sharks. Pairing horizontal and vertical movements would give greater insight to the drivers behind the observed movement patterns, for example, allowing inference as to whether animals were moving offshore during dives or hugging the walls of the atoll. BIOT's location near the equator means there are only small variation in day length with incremental changes in latitude, which increased estimation errors for light-based geolocation (Hill & Braun 2001). This compounds the difficulty of tracking short movements of reef-associated sharks, and is the reason they are normally

monitored with acoustic telemetry (Whoriskey & Hindell 2016). However, data from a double-tagged shark, carrying both satellite and acoustic tags, suggest that the geolocation errors were both smaller than estimated by the state-space model, and might be further reduced by processing light-based estimates together with position data from acoustic telemetry. The error margin estimated by geolocation was of the order of one degree of latitude and longitude, or approximately 110 km at BIOT's latitude. Comparing geolocation estimates with acoustic detections suggested that the maximum error distance was approximately 35 km. Latitude estimates from geolocation showed a northerly 'drift', while errors in geolocated longitude were randomly distributed around the actual longitude determined from acoustic detections. State-space models used to refine geolocation estimates typically use auxiliary data such as bathymetry and sea surface temperature to obtain better accuracy (Teo et al. 2004). The comparison of acoustic and satellite tag position data suggests that even sporadic position 'fixes' from acoustic telemetry-derived positions might be useful in correcting drift in geolocation models, making intermediate position estimates more reliable and increasing the utility of satellite tags for reef-associated species.

4.6 Conclusion

Human fishing impacts on reef sharks are of ongoing concern, even in nominally protected areas (Bradley et al. 2019, Tickler et al. 2019), and the relatively restricted and predictable vertical niche of species like silvertip sharks may enhance their vulnerability. Their vertical range at night is focussed on the surface waters around reefs in BIOT, which may make them particularly vulnerable to illegal fishing at night when detection and enforcement are more difficult. Arrest and inspection reports submitted to the Indian Ocean Tuna Commission by the BIOT authorities include a number of accounts of vessels being encountered at dawn with their fishing gear already deployed (e.g., IOTC Secretariat 2015), and it may be that night-time fishing is already the norm for those fishing illegally in BIOT and elsewhere. Combining vertical spatial ecology with data on horizontal space use allows managers of both fisheries and protected areas to predict the times and locations of greatest vulnerability to fishing for particular species, to better prioritise enforcement efforts, and to potentially regulate fishing activity to avoid bycatch of species of concern, as has been attempted with gillnet depths to avoid cetacean bycatch (Kiszka et al. 2018). In addition to helping predict the spatial overlap of species like silvertip sharks with fishing activities, archival tags, fitted with a growing suite of environmental sensors (Coffey & Holland 2015), can also allow us to model the responses of sharks and other taxa as the ocean warms and temperature and oxygen availability

change both horizontally and vertically (Cheung et al. 2009, Gilly et al. 2013). Refining our understanding of the physiological constraints of taxa, their vulnerability to ocean warming and deoxygenation, and the likely shifts in their horizontal and vertical ranges will be vital to managing the future ocean.

4.7 References

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4.8 Supplementary material

4.8.1 Supplementary tables

Supplementary Table 4.1: Depth bin boundaries, in metres, for depth histograms transmitted by tags

Tag	ID	Bin1	Bin2	Bin3	Bin4	Bin5	Bin6	Bin7	Bin8	Bin9	Bin10	Bin11	Bin12
1	391300800	5	10	25	50	75	100	150	200	250	300	500	>500
2	391301000	5	10	25	50	75	100	150	200	250	300	500	>500
3	391301400	5	10	25	50	75	100	150	200	250	300	500	>500
4	391303300	5	10	25	50	75	100	150	200	250	300	500	>500
5	391400800	5	10	25	50	75	100	125	150	200	250	300	2000
6	391401600	5	10	25	50	75	100	125	150	200	250	300	2000
7	391401800	5	10	25	50	75	100	125	150	200	250	300	2000

Supplementary Table 4.2: Upper bin boundaries for temperature histograms transmitted by tags (in degrees centigrade)

Tag	TOPID	Bin1	Bin2	Bin3	Bin4	Bin5	Bin6	Bin7	Bin8	Bin9	Bin10	Bin11	Bin12
1	391300800	5	10	14	18	20	22	24	26	28	30	32	>32
2	391301000	5	10	14	18	20	22	24	26	28	30	32	>32
3	391301400	5	10	14	18	20	22	24	26	28	30	32	>32
4	391303300	5	10	14	18	20	22	24	26	28	30	32	>32
5	391400800	18	20	22	23	24	25	26	27	28	29	30	45
6	391401600	18	20	22	23	24	25	26	27	28	29	30	45
7	391401800	18	20	22	23	24	25	26	27	28	29	30	45

Supplementary Table 4.3: Testing generalised linear mixed models to predict the median daily depth of silvertip sharks in BIOT. Variables considered were mixed layer depth (MLD: metres), sea surface temperature (SST: °C), lunar phase (new, waxing, full, waning) and shark total length (in centimetres). Tag ID was treated as a random factor. Model variants and their AIC and BIC scores shown for candidate one, two and three variable models in forward model selection. Likelihood ratio test results shown for comparisons between the best models at each selection stage.

#	Model variant tested	AIC	BIC	Likelihood ratio test	Likelihood ratio and p-value	Marginal R ²
1	Intercept only	5544.5	5558.3	-		0.00
Stage 1: Single variable						
2	MLD	4971.5	4989.9	2 vs. 1	575.0; p < 0.001	0.57
3	Moon	5548.8	5576.4	-		0.00
4	SST	5511.6	5530.0	-		0.04
5	Total length	5545.5	5563.9	-		0.03
Stage 2: Two variables						
6	MLD + SST	4856.0	4879.0	6 vs. 2	117.4; p < 0.001	0.60
7	MLD + Moon	4964.5	4996.6	-		0.57
8	MLD + Total length	4972.3	4995.3	-		0.58
Stage 3: Three variables						
9	MLD + SST + Moon	4848.8	4885.6	9 vs. 6	13.2; p = 0.004	0.61
10	MLD + SST + Total length	4857.6	4885.2	-		0.62
Stage 4: Interactions						
11	SST + MLD*Moon	4846.0	4896.5	11 vs. 9	8.8; p = 0.032	0.59
12	MLD + Moon*SST	4850.0	4900.6	-		0.56
13	MLD*Moon*SST	4849.7	4932.4	-		0.62

Forward model selection used AIC and BIC to determine the variables which best explained the variability in the depth data. At each stage, Likelihood ratio tests were used to assess whether variables added to the best model significantly improved its explanatory power.

Supplementary Table 4.4: Testing generalised linear mixed models to predict the median semi-diel (i.e. day/night) depth, in metres, of silvertip sharks in BIOT. Variables considered were mixed layer depth (MLD: metres), sea surface temperature (SST: °C), lunar phase (new, waxing, full, waning), time of day (TOD: day, night) and shark total length (in centimetres). Tag ID was treated as a random factor. Model variants and their AIC and BIC scores shown for candidate one, two and three variable models in forward model selection. Likelihood ratio test results shown for comparisons between the best models at each selection stage. Best overall model indicated in bold.

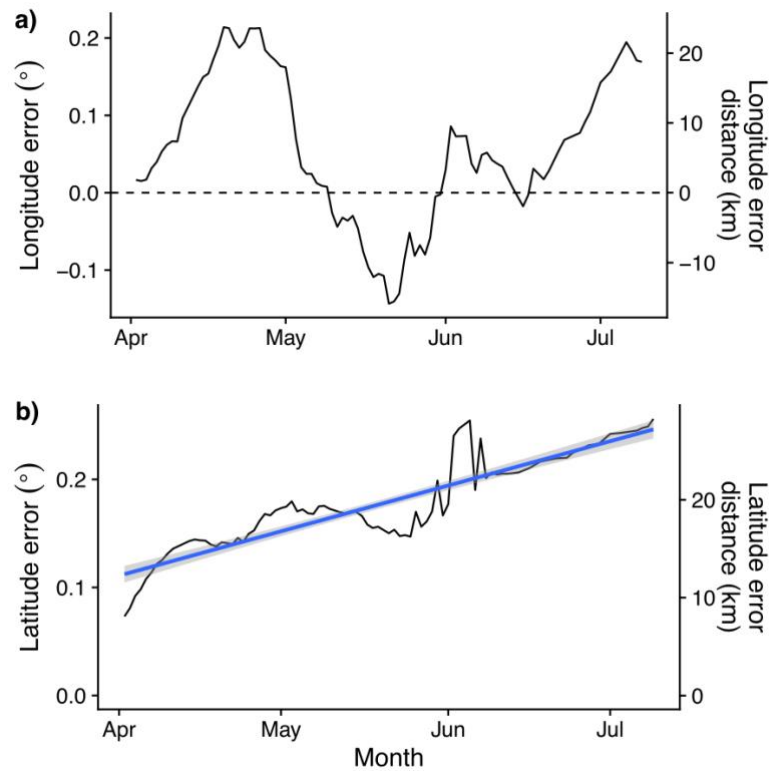
#	Model variant tested	AIC	BIC	Likelihood ratio test	Likelihood ratio and p-value	Marginal R ²
1	Intercept only	7543.0	7557.5	-		0.00
<i>Stage 1: Single variable</i>						
2	MLD	7124.0	7143.4	2 vs. 1	420.9, p < 0.001	0.39
3	TOD	7371.3	7390.6	-		0.15
4	Moon	7543.6	7572.6	-		0.01
5	SST	7530.5	7549.9	-		0.01
6	Total length	7543.9	7563.3	-		0.03
<i>Stage 2: Two variables</i>						
7	MLD + TOD	6838.5	6862.7	6 vs. 2	287.6; p < 0.001	0.54
8	MLD + Moon	7111.9	7145.8	-		0.40
9	MLD + SST	7068.8	7093.1	-		0.42
10	MLD + Total length	7123.4	7147.6	-		0.42
<i>Stage 3: Three variables</i>						
11	MLD + TOD + Moon	6819.9	6858.7	-		0.56
12	MLD + TOD + SST	6760.5	6789.6	12 vs. 7	55.4; p < 0.001	0.57
13	MLD + TOD + Total length	6838.0	6867.0	-		0.57
<i>Stage 3: Four variables</i>						
14	MLD + TOD + SST + Moon	6739.8	6783.4	14 vs. 12	26.6; p < 0.001	0.58
15	MLD + TOD + SST + Total length	6761.4	6795.3	-		0.59
<i>Stage 4: Interaction</i>						
16	MLD + TOD*Moon + SST	6721.5	6779.6	16 vs. 14	24.3; p < 0.001	0.62

Forward model selection used AIC and BIC to determine the variables which best explained the variability in the depth data. At each stage, Likelihood ratio tests were used to assess whether variables added to the best model significantly improved its explanatory power.

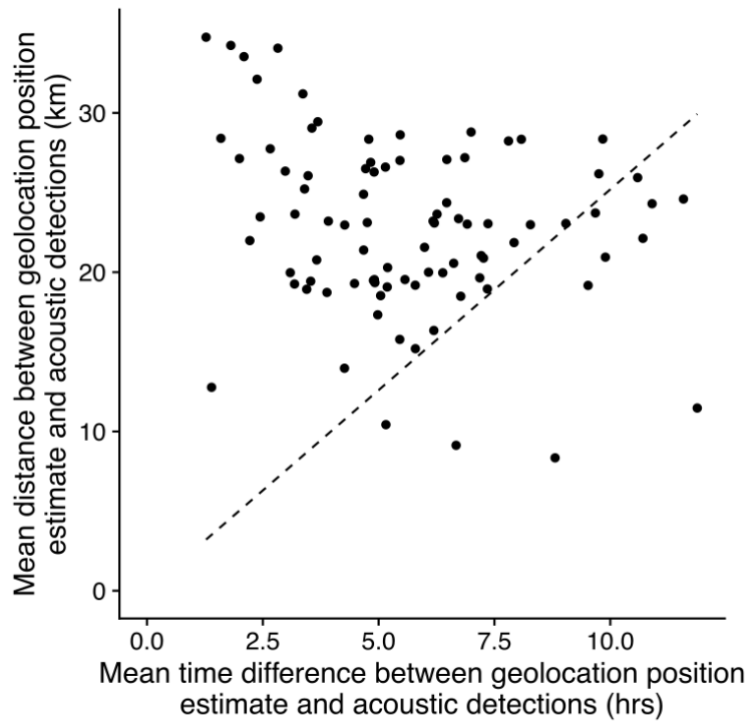
Supplementary Table 4.5: Correlation between characteristics of the ascent profiles for a 185 cm silvertip shark returning from mesopelagic dives below 200 m. Pearson's correlation coefficients were calculated between the depth of the breakpoint (i.e. >50% reduction) in the shark's vertical ascent rate, characteristics of the dive (dive depth and time spent below depth and temperature thresholds) and water column properties (temperature and dissolved oxygen profile).

	Breakpoint depth (m)	Max. dive depth (m)	Time below 150 m (minutes)	Time below 18°C (minutes)	18°C isotherm depth (m)	OMZ depth (m)
Maximum dive depth (m)	0.23	-				
Time below 150 m (minutes)	0.04	0.33	-			
Time below 18°C (minutes)	0.14	0.23	0.83	-		
18°C isotherm depth (m)	0.29	0.03	-0.03	-0.18	-	
OMZ depth (m)	0.35	0.09	0.08	-0.06	0.53	-
2.5 ml l ⁻¹ DO isopleth depth (m)	0.32	-0.04	0.03	-0.04	0.55	0.81

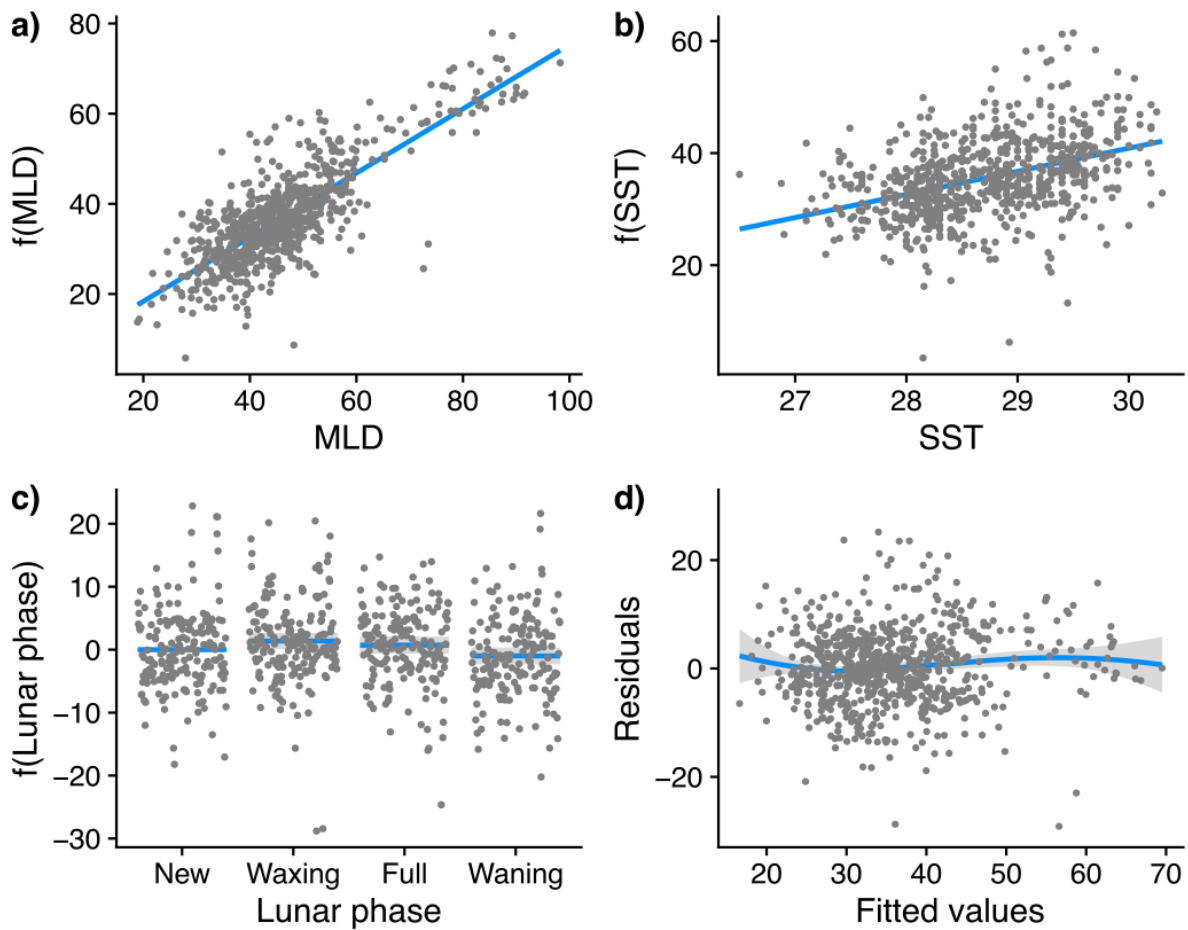
4.8.2 Supplementary figures



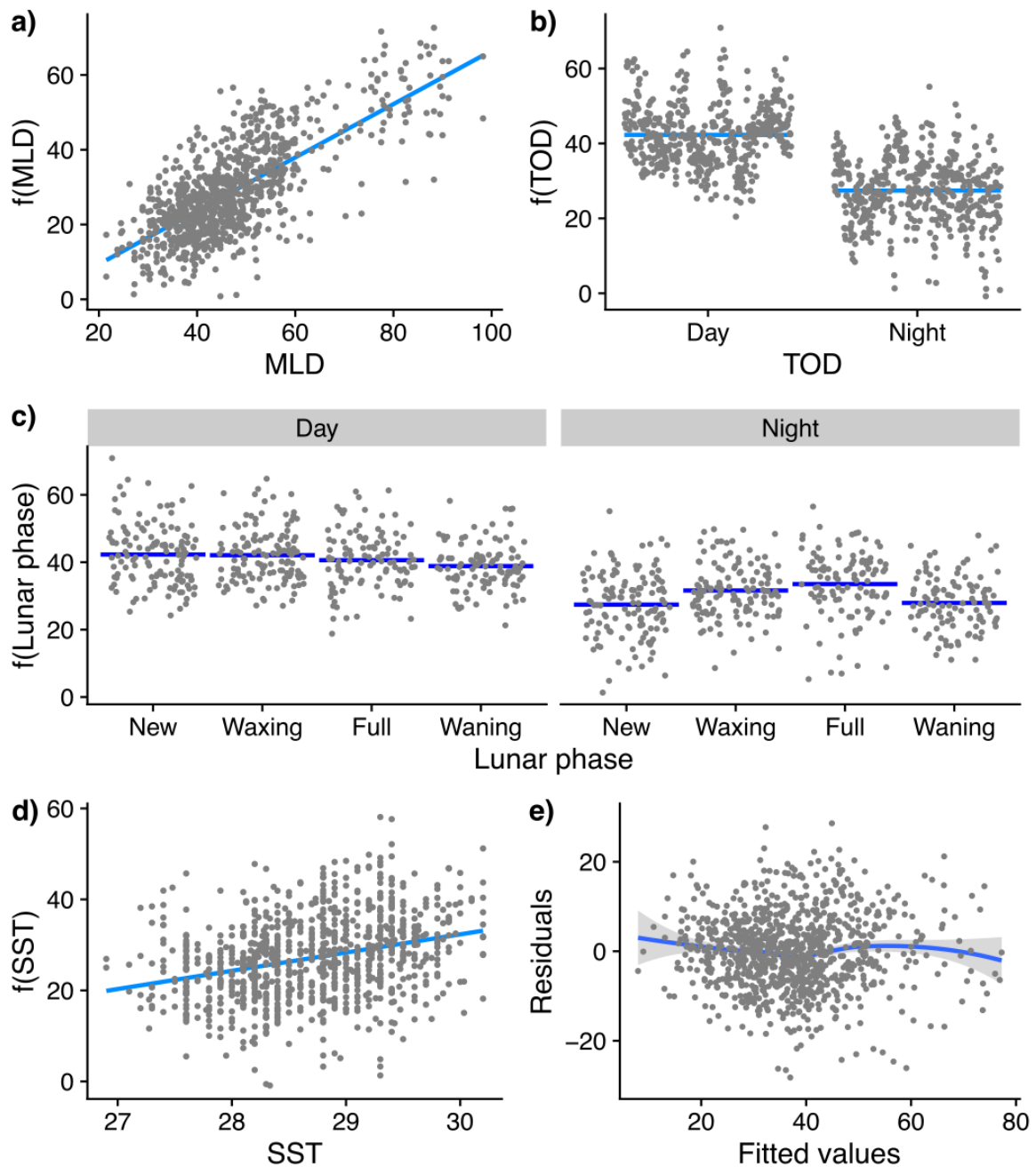
Supplementary Figure 4.1: Difference between PAT-tag geolocation estimates and acoustic tag detection locations for a silvertip shark (ID 391401600) tagged with both tags in 2014. Y-axes show difference (i.e. error), in degrees of a) longitude and b) latitude, between each day's geolocation-based position estimate and the average of the same day's acoustic detection locations, assuming that the acoustic tag-derived positions are the true position of the shark. Secondary y-axes show the position error in kilometres at the BIOT's latitude. Blue trend line and grey ribbon in (b) indicate the slope ($\pm 95\%$ CI) of the relationship between latitude error and time (intercept = 0.11 ± 0.004 degrees/ 12.1 ± 0.4 km, slope = 0.04 ± 0.002 degrees/ 4.9 ± 0.3 km per month, model $R^2 = 0.80$, $p < 0.001$)



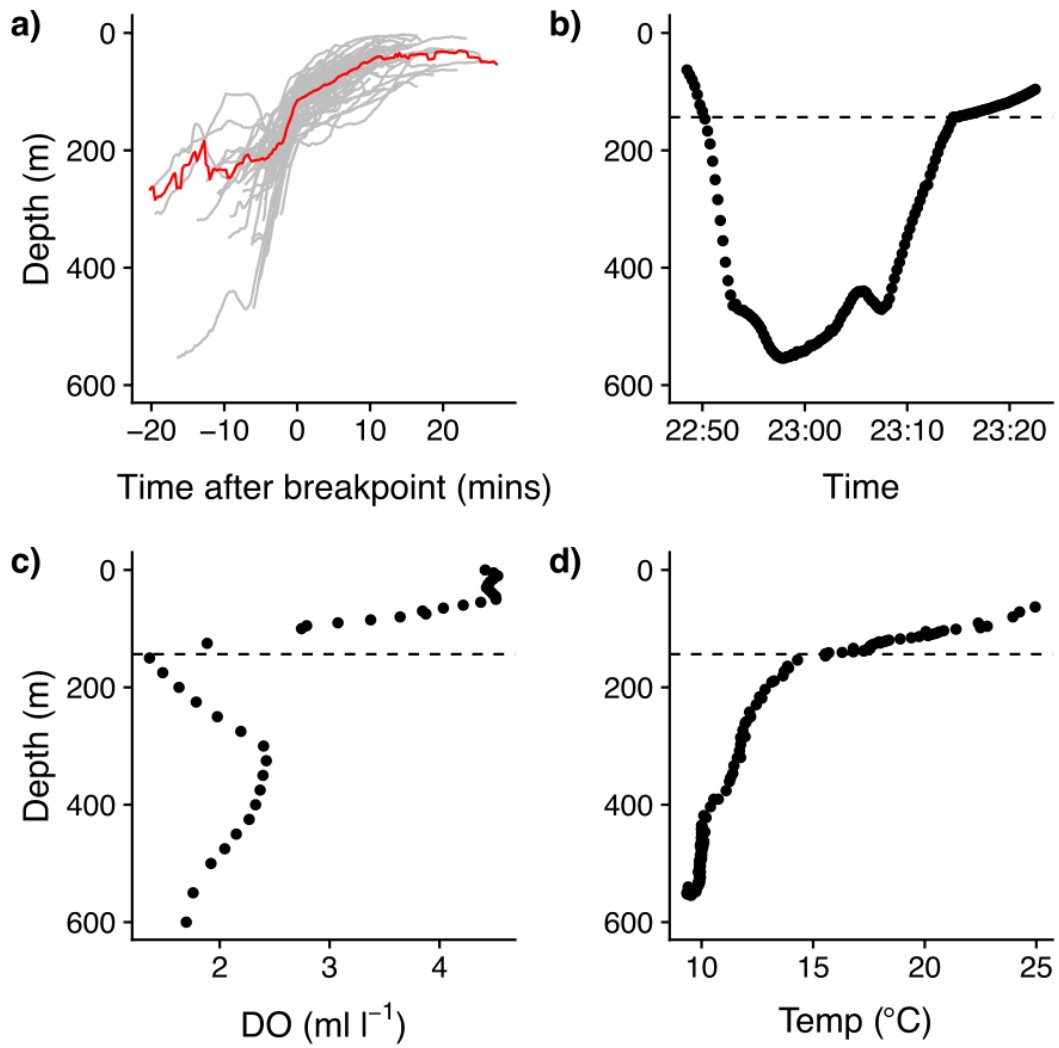
Supplementary Figure 4.2: Distance between the daily geolocation position estimate and the mean daily acoustic telemetry derived position, in kilometres, compared with the mean time difference, in hours, between the two position estimates. The dashed diagonal line indicates the distance that could have been covered in a given time by a shark swimming at 0.7 ms^{-1} , the mean swim speed for silvertip sharks reported by Ryan et al (2015). Points above the dashed line are instances when the differences between geolocation position and acoustic tag position cannot be accounted for by shark movement, indicating geolocation error.



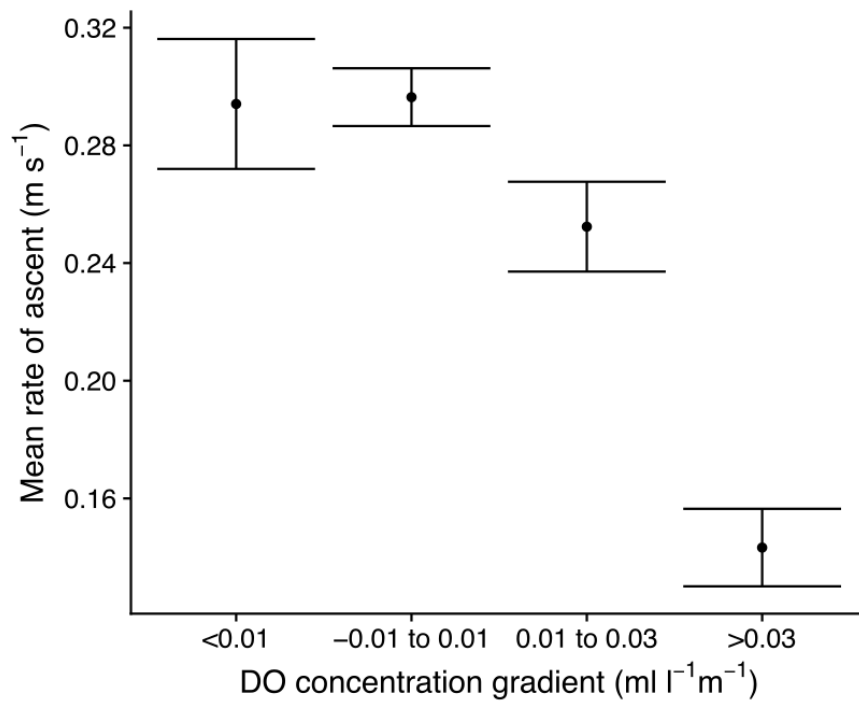
Supplementary Figure 4.3: Partial residual plots for fixed effects in a generalised linear mixed model predicting the median daily depth of five silvertip sharks in BIOT. Fixed effect predictors were mixed layer depth (MLD: m), sea surface temperature (SST: $^{\circ}C$), lunar phase (new, waxing, full, waning) and the interaction between time of day and lunar phase. Partial effects shown for a) MLD, b) TOD, c) the interaction between TOD and lunar phase, and d) SST. Panel e) shows standardised model residuals against fitted values.



Supplementary Figure 4.4: Partial residual plots for fixed effects in a generalised linear mixed model predicting the median daily depth of five silvertip sharks in BIOT. Fixed effect predictors were mixed layer depth (MLD: m), sea surface temperature (SST: °C), time of day (TOD: day, night), lunar phase (new, waxing, full, waning) and the interaction between time of day and lunar phase. Partial effects shown for a) MLD, b) TOD, c) the interaction between TOD and lunar phase, and d) SST. Panel e) shows standardised model residuals against fitted values.



Supplementary Figure 4.5: Exploratory plots of ascent profiles of dives by shark ID 391300800. a) Combined plots of ascent profiles of dives >200m, on a standardised time scale where $t = 0$ corresponds to the inflection point in the shark's vertical ascent speed in each dive; the red line shows the mean depth profile of all dives; b) an example dive profile from a single dive, showing the breakpoint in the ascent phase, indicated with the dashed line; c) dissolved oxygen (DO) and d) temperature profiles for the same dive. Dashed lines in c) and d) indicates depth of breakpoint marked in panel b).



Supplementary Figure 4.6: Relationship between the shark's mean vertical ascent rate on returning from dives, in metres per second (\pm CI, indicated by error bars), and the dissolved oxygen (DO) concentration gradient (increase in DO concentration in millilitres per litre per metre of vertical ascent).

4.8.3 Supplementary methods

4.8.3.1 Description of custom window function used to analyse dive ascent profiles

At each time step in the depth-time series, the function evaluated the average rate of change of depth with time within a defined window either side of the point being evaluated. The window width was initialised at two minutes (i.e. eight 15 s time steps) either side of the time step being evaluated, and the average ascent rate in the sections before and after was calculated. The minimum reduction in ascent rate required to qualify as a breakpoint was initialised to 80%, and reduced in 10% increments to a minimum of 50% if a qualifying point in the ascent trajectory could not be found. If no qualifying point was found, the window width either side of the test point was reduced from two minutes to one minute in steps of 15 s, and the process was repeated for each change in window width. If no qualifying point was found the algorithm moved to the next dive in the timeseries. When a breakpoint was found in a dive, the time, depth, temperature and instantaneous ascent rate change at this point were passed as the function's result.

4.8.3.2 R code to identify dives in archival tag data

```
#####  
#####
```

```
# Identifies all dives below 150m. Dive starts and ends when shark crossed 100m isobath.  
# Takes a dataframe of archival tag data (Time, Depth, Temp) as its input
```

```
find_dives = function(tag.data) {
```

```
  # Initialise an empty list to store data for individual dives
```

```
  dives = list()
```

```
  # Initialise variables for algorithm and parameters to define dives
```

```
  start = 1; end = 1 # Initial indices of dive start and end
```

```
  dmax.index = 1 # Initial index of first maximum
```

```
  i = 1 # Index of dives
```

```
  d.thresh = 150 # Minimum max dive depth to qualify as a dive
```

```
  d.thresh.upper = 100 # Depth at which a dive is deemed to start
```

```
  # Find local maximum and minimum depth points
```

```
  # Define deep maxima as change of direction (down to up) below 150m.
```

```
  # introduce small depth correction (1 cm) to consecutive identical depth measurements to  
  eliminate flat spots in depth trend for ease of finding maxima/minima
```

```
  series$Depth2 = c(series$Depth[1], sapply(2:length(series$Depth), function(i)
```

```
  ifelse(series$Depth[i] == series$Depth[i-1], series$Depth[i] + 0.01, series$Depth[i])))
```

```
  maxima = intersect(which(diff(sign(diff(series$Depth2)))== -2)+1, which(series$Depth > d.thresh))
```

```

# Define shallow minima as change of direction (up to down) above 100m.

minima = intersect(which(diff(sign(diff(series$Depth2)))==2)+1, which(series$Depth <
d.thresh.upper))

while(dmax.index <= max(maxima)) { # Look at all maxima below dive threshold (150m)

dmax.index = min(intersect(maxima, end:nrow(series))) # find next maxima not already evaluated

# define a window around each depth maxima defining the point when the shark left and returned
to the 0-100 m layer

start = max(intersect(minima, 1:dmax.index)) # find previous minima

end = min(intersect(minima, dmax.index:nrow(series))) # find subsequent minima

dives[[i]] = series[start:end, c("POSIXct.time.LCL", "Depth", "Temp")]

i = i+1
}

}

```


4.8.3.3 Custom function to identify breakpoints in dives

```
#####  
  
# Function to identify local discontinuities in ascent rate (breakpoints) in the ascent portion of  
dives.  
# Takes a list of dive profiles from archival tag data: Required fields are Time (POSIXct.time),  
Depth (numeric) and Temp (numeric).  
  
# In the case presented in Chapter 4 the Depth and Temperature data were recorded at 15  
second intervals  
  
find_breakpoints = function(dives){  
  
  # Initialise packages and variables  
  
  require(ecp)  
  
  thresh.start = 0.2 # start looking for breakpoints where ascent rate after breakpoint is <=20%  
ascent rate before breakpoint  
  thresh.max = 0.5 # ascent rate after breakpoint can be no more than half ascent rate before  
breakpoint  
  window.start = 8 # Initialise width of window (number of time steps) in which I look for a rate  
change 2 mins or 8 time steps  
  window.min = 4 # Stop looking when window width is reduced to 1 min or 4 time steps  
  
  # Dataframe to store results  
  
  results = data.frame(dive = 1:length(dives), # index of dive in the list of dives  
    breakpoint.index = NA, # rownumber of breakpoint in the dive data  
    breakpoint.time = NA, # rownumber of breakpoint in the dive data  
    breakpoint.depth = NA, # rownumber of breakpoint in the dive data  
    breakpoint.temp = NA, # rownumber of breakpoint in the dive data
```

```

    rate.delta = NA, # rate of ascent change at breakpoint
    win.val = NA, # window width used
    thresh.val = NA # threshold rate change used
)

min.gap = 5 # breakpoint must be this many metres shallower than max depth
min.asc.rate = 5 # metres ascent per time step (15s) to qualify as ascending = 0.3m/s

# Examine each dive the in the list

for (i in dives){

temp = dives[[i]]

if(max(temp$Depth)<200) next # Only consider dives 200m or deeper

# Initialise vectors to store exploratory results

breakpoints = numeric() # stores a vector of candidate breakpoints
rate.delta = numeric() # local change in ascent rate at breakpoint
thresh.val = numeric() # threshold value for ascent rate change used
win.val = numeric() # window width used

thresh = thresh.start # initialise threshold to lowest value

# search for breakpoint within rate change and window constraints until a breakpoint is found or
the search constraints are exceeded

while(length(rate.chg) == 0 & thresh <= thresh.max) {

window = window.start # initialise window to maximum value

while(length(rate.chg) == 0 & window >= window.min){

```

```

# I track the index of the time step for the dive (k)
# Only look for inflections after the deepest point of the dive
for (k in max(which(temp$Depth == max(temp$Depth))):length(temp$Depth)-window){ # set
search range between last time at max depth and the end of the dive time series

# Check that the breakpoint is happening during an ascent phase and is above 200m (i.e. not
oscillations at depth) and below the thermocline (Temp <22 deg C)
if(mean(diff(temp$Depth[(k-window):k]))<0 & mean(diff(temp$Depth[k:(k+window)]))<0 &
temp$Depth[k]<200 & temp$Temp[k] < 22) {

# Check that the ascent rate difference before and after the breakpoint is less than the
threshold criteria (range 20% to 50% of pre-breakpoint rate)
if((mean(diff(temp$Depth[k:(k+window)]))/mean(diff(temp$Depth[(k-window):k]))<=thresh &
abs(mean(diff(temp$Depth[(k-window):k]))) > min.asc.rate) {

# add constraint that all time steps must have same sign (i.e. are part of a continuous ascent
not an ascend/descend sequence)

# check that the shark does not dive again

if((temp$Depth[k]+min.gap) > max(temp$Depth[(k+1):length(temp$Depth)])) {

# add the time step to the vector of inflection points
breakpoint.index = c(breakpoint.index, k)

# store the parameters of the breakpoint
rate.delta = c(rate.delta, mean(diff(temp$Depth[k:(k+window)]))/mean(diff(temp$Depth[(k-
window):k])))
thresh.val = c(thresh.val, thresh)
win.val = c(win.val, window)
}
}
}

```

```

    }
  }
  # If no qualifying breakpoint found, make the window shorter and try again
  window = window - 1
}

# If no breakpoint found with the initial rate threshold increase the rate change threshold and try
again
thresh = thresh + 0.05
}

if(length(rate.chg) == 0) next # skip to next dive if no breakpoint was found

# In multiple candidate breakpoints are identifies, use the breakpoint with the greatest ascent rate
reduction

j = breakpoints[rate.delta == min(rate.delta)][1]

results[i, ]$breakpoint.index = j
results[i, ]$breakpoint.time = temp[j,]$Time
results[i, ]$breakpoint.depth = temp[j,]$Depth
results[i, ]$breakpoint.temp = temp[j,]$Temp
results[i, ]$rate.delta = rate.delta[rate.delta == min(rate.delta)][1]
results[i, ]$thresh.val = thresh.val[rate.delta == min(rate.delta)][1]
results[i, ]$win.val = win.val[rate.delta == min(rate.delta)][1]

}

return(results)

}

```

Chapter 5: Potential detection of illegal fishing by passive acoustic telemetry

5.1 Abstract

Acoustic tagging is typically used to gather data on the spatial ecology of diverse marine taxa, informing questions about spatio-temporal attributes such as residency and home range, but detection data may also reveal unanticipated insights. Many species demonstrate predictable site-fidelity, and so a sudden cessation of detections for multiple individuals may be evidence of an atypical event. During 2013 and 2014, we acoustically tagged 47 grey reef sharks (*Carcharhinus amblyrhynchos*) and 48 silvertip sharks (*Carcharhinus albimarginatus*) near reefs in the British Indian Ocean Territory (BIOT) Marine Protected Area (MPA). From March 2013 to November 2014 inclusive, tags were 'lost', i.e. permanently ceased to be detected within the monitoring area, at an average rate of 2.6 ± 1.0 tags per month. Between 1st and 10th December 2014, detection data suggest the near-simultaneous loss of 15 of the remaining 43 active tagged sharks, a monthly loss rate over five times higher than during the previous 21 months. Between 4th and 14th December of 2014 the BIOT patrol vessel encountered 17 vessels engaged in suspected illegal fishing in the northern BIOT MPA; such sightings averaged one per month during the previous 8 months. Two of these vessels were arrested with a total of 359 sharks on board, of which grey reef and silvertip sharks constituted 47% by number. The unusual and coincident peaks in tag loss and vessel sightings, and the catch composition of the arrested vessels, suggests illegal fishing as a plausible explanation for the unusual pattern in our detection data. A Cox proportional hazards model found that the presence of fishing vessels increased the risk of tag loss by a factor of 6.0 (95% CI: 2.6 – 14.0, $p < 0.001$). Based on the number of vessels sighted and the average number of sharks on vessels arrested in BIOT during 2014, we conservatively estimate that over 2,000 sharks may have been removed during the suspected fishing event. Based on average catch compositions, over 1,000 would have been grey reef and silvertip sharks. Assuming a closed population mark-recapture model, over one third of the locally resident reef sharks may have been removed from the monitoring area. The data suggest that even sporadic fishing events may have a marked impact on local reef shark populations, but also demonstrate the potential of electronic tagging a tool for detecting illegal or otherwise unreported fishing activity.

5.2 Introduction

Acoustic telemetry, and electronic tagging in general, is an increasingly popular method of gathering data on the spatial ecology of diverse marine taxa (Carey et al. 1982, Freitas et al. 2009, Campbell et al. 2010, Vianna et al. 2013, Burnett et al. 2014). Acoustic tags produce data when tagged animals are in range of a receiving unit that records the tag's unique code plus a time stamp, as well as sensor data, such as depth (Freitas et al. 2009, Vianna et al. 2013), temperature (Carey et al. 1982, Campbell et al. 2010) and acceleration (Burnett et al. 2014), if available (Kessel et al. 2014). Data are typically interpreted in terms of residency patterns within a network of receiver elements, with gaps in detection assumed to be absences from the area. Gaps in detection may occur for multiple reasons, which may be classified as true and false absences. True absences occur when an animal (or, more accurately, a tag) leaves the monitored area (determined by the number and location of receivers, and their detection range). This may occur for multiple reasons, including mortality/predation (Rechisky & Welch 2010, Halfyard et al. 2017), migration (Papastamatiou et al. 2013, Espinoza et al. 2015b, Chapple et al. 2016) and tag shedding or expulsion (Sandstrom et al. 2013, Jepsen et al. 2015). False absences occur when an animal is present within the area being monitored but remains undetected. This typically occurs due to decreases in receiver detection efficiency with environmental conditions, tag or battery failure, interference with tag signals arising from biogenic noise or other tags, or a tag simply failing to transmit while the animal is in range of the receiver due to the length of the programmed transmission interval (Heupel et al. 2006).

Acoustic telemetry is frequently employed to study reef shark movements and behaviour due to the potentially important role they play in reef ecosystem connectivity and health and the growing emphasis on conserving coral reef ecosystems world-wide (McCauley et al. 2012, Vianna et al. 2014, Espinoza et al. 2015c, Speed et al. 2016). Reef sharks generally exhibit high degrees of fidelity to tagging sites or reefs, and remain within the range of detection arrays for long periods (Barnett et al. 2012, Chin et al. 2013, Heupel & Simpfendorfer 2014). While reef sharks have been shown to make regular journeys between adjacent reefs in coastal waters (Espinoza et al. 2015a), these occurred over distances of 10-30 km, in water shallower than 100 m. Conversely long distance movements across deep waters off the continental shelf appear rare, although data from both acoustic and satellite archival tags indicate that pelagic movements by reef sharks do occur (Barnett et al. 2012, White et al. 2017). These behavioural characteristics suggest that the simultaneous

cessation of detections from a group of tagged animals may indicate a significant atypical event, such as a mass change in behaviour or mortality.

The growing demand for marine protein and ongoing demand for shark fins have increasingly made reef sharks the target of commercial as well as traditional subsistence fisheries (Dent & Clarke 2015, Kizhakudan et al. 2015). Consequently, reef-based fishing for these species by both legal and illegal fishing operations is widespread and is thought to have driven sharp declines in abundance in affected areas (Meekan et al. 2006, Clua & Vignaud 2016). Marine protected areas and shark sanctuaries have been declared around the world to attempt to relieve the fishing pressure on sharks, but deterring illegal fishing remains challenging given the paucity of alternatives for many fishers, the incentive provided by the relatively lucrative fin trade, and the logistics of enforcement (Carr et al. 2013, Vianna et al. 2016). Where shark populations are monitored using acoustic telemetry it is therefore possible that fishing may lead to the permanent removal of a tag from the monitoring area (hereafter 'tag loss'), even when the study site is officially closed to fishing. Predatory fishes such as sharks are typically targeted using longlines consisting of thousands of baited hooks, and so fishing impacts might manifest in acoustic data sets as sudden decreases in the number of tags being detected within the array, as animals are actively removed from the system.

I present a case study from an on-going acoustic monitoring project in the British Indian Ocean Territory (BIOT) Marine Protected Area (MPA). I examine patterns in the temporal clustering of tag loss events (i.e. the last date of detection for tags within the study) alongside data on reported sightings or arrests of suspected illegal fishing vessels, to see if there is a threshold of tag loss that might be considered unusual, and whether this correlates with fishing or natural drivers such as weather. Catch data from fishing vessels arrested in BIOT at the time are used to generate estimates of the potential impact on the local shark population by such fishing events.

5.3 Methods

5.3.1 Data collection

Data were collected as part of an on-going acoustic telemetry project in the BIOT MPA (Figure 5.1). The project commenced in February 2013 with the deployment of an array of 30 acoustic receivers (Vemco Ltd. Halifax, Canada), and was expanded in April 2014 to 48 receiver elements (Figure 5.1). The principal species monitored are determined by availability when shark fishing in the region and to date have been primarily grey reef (*Carcharhinus amblyrhynchos*) and silvertip sharks

(*Carcharhinus albimarginatus*). 66 sharks were tagged in February and March 2013 (38 grey reef and 28 silvertip sharks) and a further 29 in March 2014 (9 grey reef and 20 silvertip sharks). Grey reef sharks ranged in total length from 75 to 140 cm, and silvertip sharks from 83 to 180 cm. Sharks in the first year were primarily tagged externally using a dart and leader system; from April 2014 all sharks were tagged internally. Receivers were serviced and detection data downloaded annually at the same time of year (March – May), and were last downloaded in March 2018. Animal handling procedures were approved by the Stanford University Administrative Panel on Laboratory Animal Care under permit APLAC-10765, held by Hopkins Marine Station's Block Laboratory.

5.3.2 Data analysis

Tag IDs in the detection data were matched to metadata for tagged animals (species, sex, length), and time series of the daily detections of each tag were visualised in an abacus plot. Potential lost tags were identified as any that were detected post tagging but which ceased to be detected before April 2015 (i.e. have remained undetected for at least three years). I calculated mean daily and monthly loss rates and 95% confidence intervals for the first and second years of the project, up until the suspected fishing event in December 2014 (March 2013 – March 2014 and April 2014 – December 2015 respectively) and also for the total period from February 2013 to December 2014.

Data on illegal fishing activity were obtained from reports made by the UK representatives to the Indian Ocean Tuna Commission (IOTC Secretariat 2015). Dates, locations and catch details, where available, were extracted for all vessels sighted by the BIOT Patrol Vessel Pacific Marlin during 2014. The distribution of vessel sightings and tag losses per month from April to December 2014 were plotted and visually compared. The mean catches (total and by species) and confidence intervals were calculated from the catches found on all vessels arrested in 2014. The mean catch per vessel was multiplied by the total number of vessels sighted in December 2014 to infer the potential total shark catch for the suspected illegal fishing event. Assuming a closed population and tagged animals were no different than their untagged conspecifics (except for the presence of a tag), we used a simple Lincoln-Peterson index (Lincoln 1930) to broadly estimate the potential share of the local shark population removed by the fishing event.

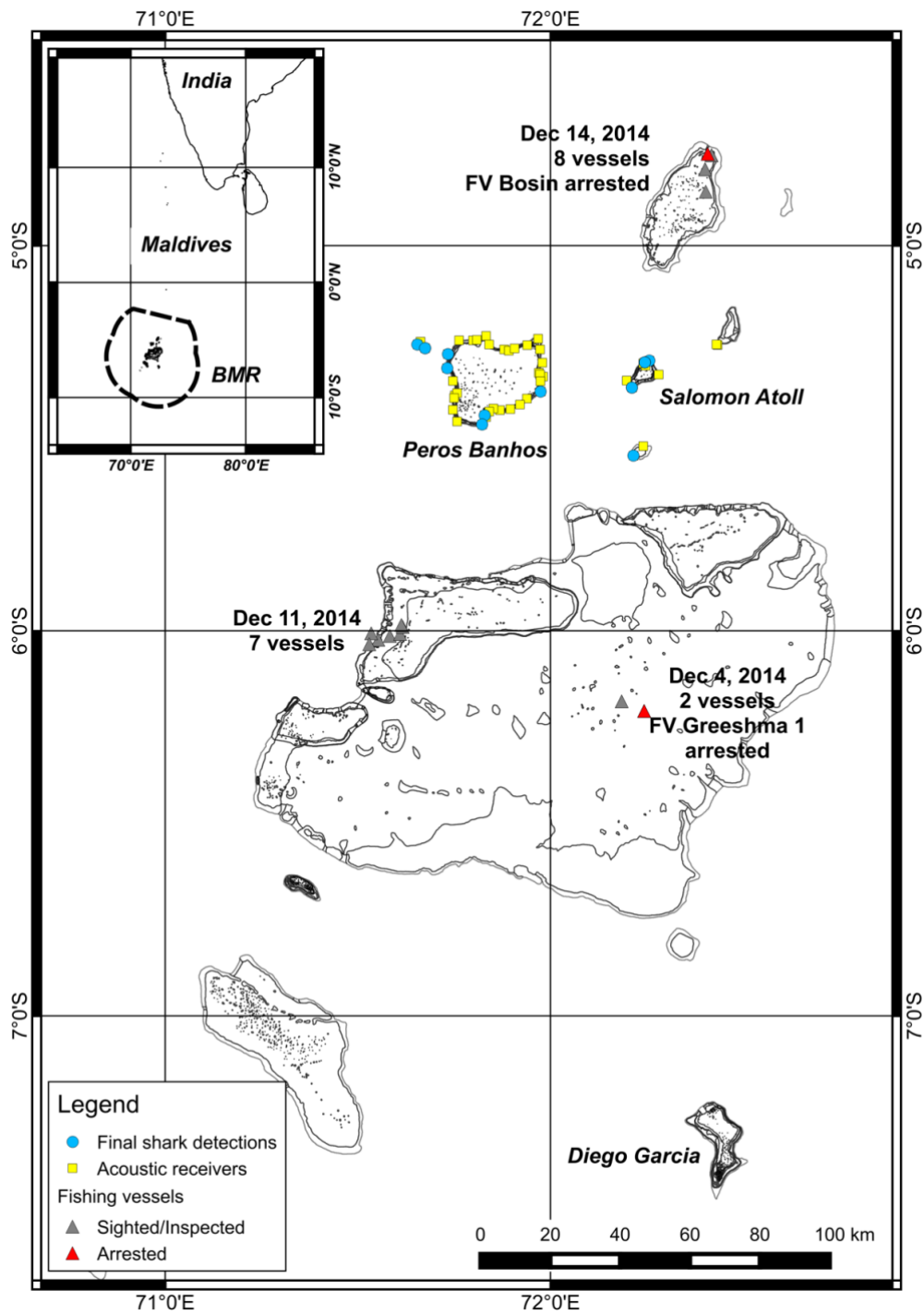


Figure 5.1: Map of the BIOT MPA showing location of receiver array (yellow squares), dates and locations of encounters with illegal fishing vessels (triangles), and the last detection locations of 15 sharks in December 2014 (blue circles). Inset shows boundary of the BIOT MPA (dashed line) and its location in the Indian Ocean.

I used a Cox proportional hazards analysis to examine the influence of species and the presence of fishing vessels on the survivorship of individual sharks. Survival time was taken as the time from tagging to last detection, and sharks whose last detection data fell within three years of the end of the data time series were censored. Thus 'mortality' was coded as 1 for all sharks which had not been observed for 3 or more years as at March 2018, and 0 otherwise. Fishing vessel presence was 1 if at least one fishing vessel had been sighted or arrested up to 2 days after a shark's last detection data, and 0 otherwise. Kaplan-Meier curves were plotted separately for survival models with species (grey reef shark – GRS or silvertip shark – STS) and fishing presence as covariates. A Cox proportional hazard model was used to calculate hazard rates for both species and fishing vessel in a combined model.

Weather conditions (wind speed and wave height) at the time of the fishing event were obtained from the European Centre for Medium-Range Weather Forecasts ERA-Interim reanalysed data set (<https://www.ecmwf.int/en/forecasts/datasets/archive-datasets/reanalysis-datasets/era-interim>). Data were extracted for the period June 2014 to June 2015 for the northern part of BIOT (-6.5 to -4.5 °S; 71.5 to 72.5 °E) and averaged for each date. Data on the average port cost of marine diesel oil in US dollars per metric tonne were downloaded from the industry website Bunker Index (http://www.bunkerindex.com/prices/bixfree.php?priceindex_id=4). Prices were converted to US dollars per litre assuming an average density of 0.890 kgm⁻³ (<https://www.exxonmobil.com/english-GQ/Commercial-Fuel/pds/GLXXExxonMobil-Marine-Distillate-Fuel>). Trends in both meteorological and fuel price data were smoothed using a seven-day rolling mean and plotted against time.

5.4 Results

The number of sharks being detected within the receiver array declined over time, following each tagging field trip. This loss rate averaged 4.1 ± 1.4 tags per month during 2013, but reduced to 1.3 ± 0.9 tags per month during 2014 (Figure 5.2). The combined average loss rate for this period was 2.6 ± 1.0 tags per month (SD = 2.3 tags per month). Reduced loss/failure rates were likely a result of initial tags being placed externally, followed by surgical implantation of tags after 2013. Following the April 2014 tagging trip, 43 animals (15 grey reef sharks and 28 silvertip sharks) were considered active within the study area (Figure 5.2). Detection activity varied among individual sharks with mean detection rate ranging from 1.5 to 30 days per month but showed no obvious temporal patterns (Figure 5.3).

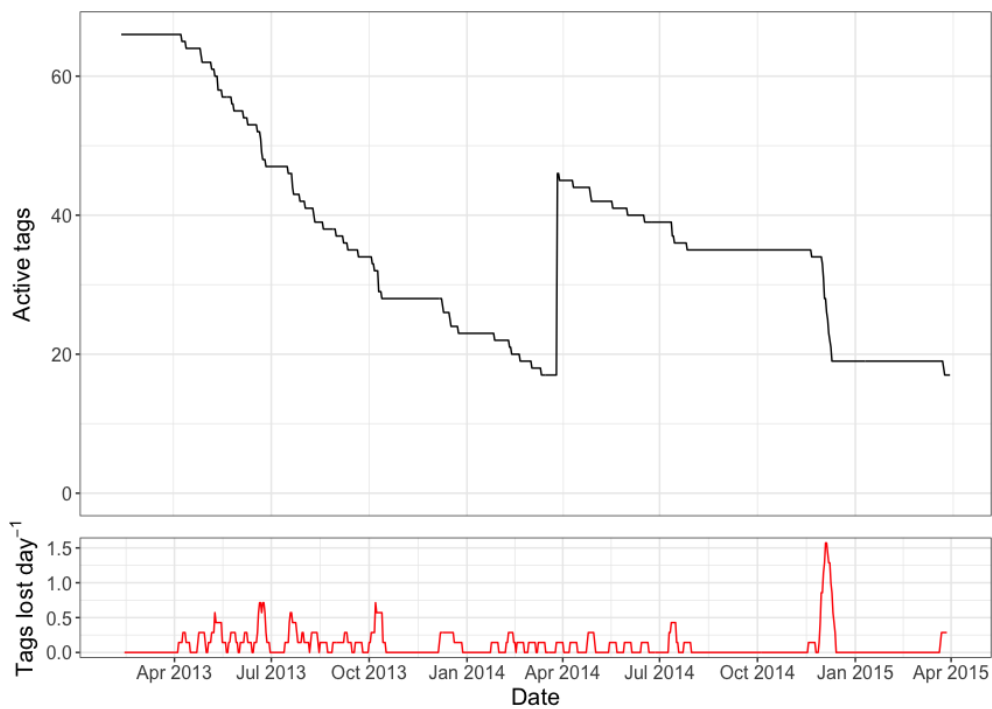


Figure 5.2: Trend in active reef shark tags by the acoustic monitoring network in the BIOT MPA over two years, March 2013 – March 2015.

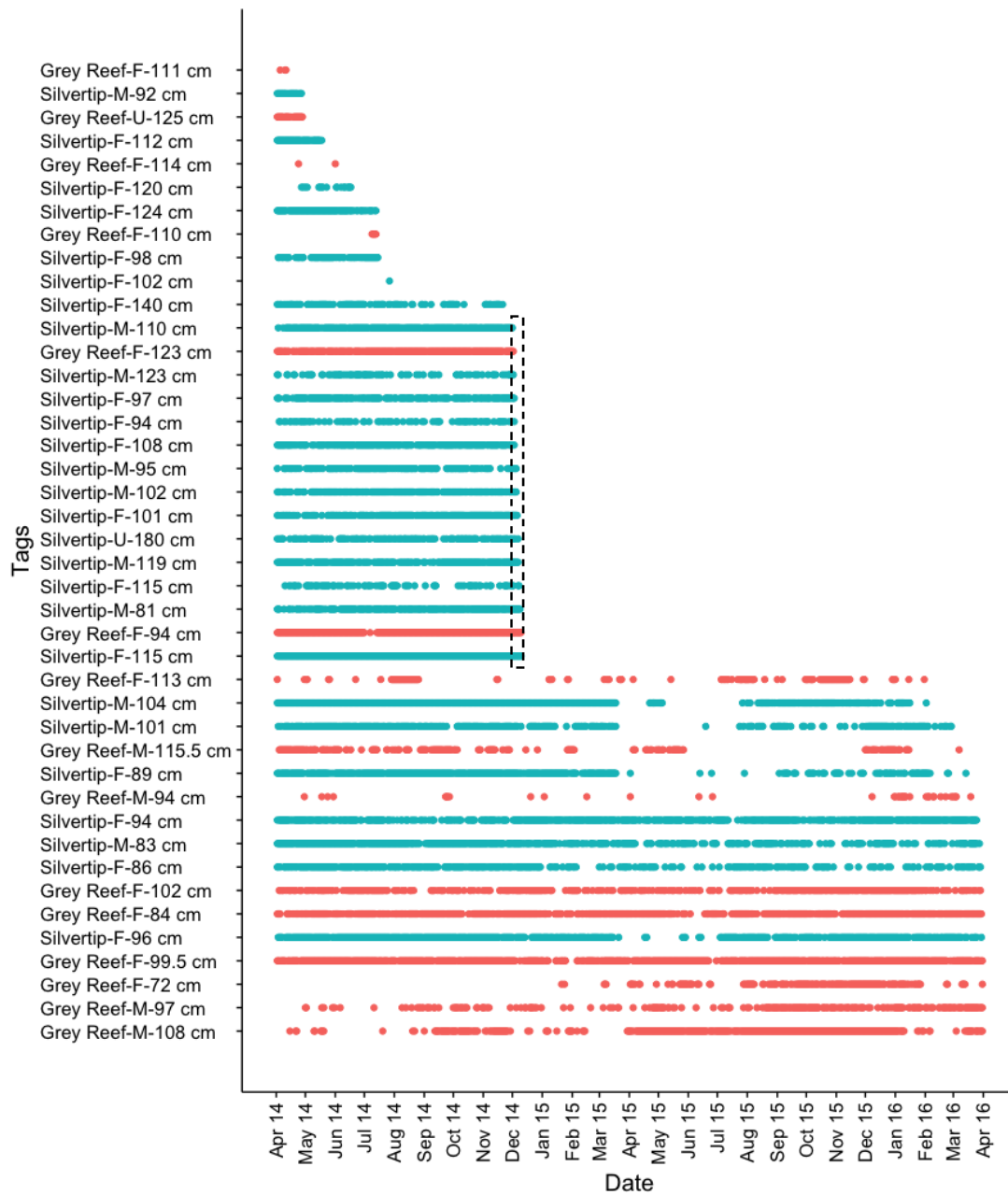


Figure 5.3: Abacus plot of daily tag activity between April 2014 and April 2016, for grey reef (red) and silvertip sharks (green). Dotted region shows timing of suspected illegal fishing event. Tags are ordered by date of most recent detection (note that data from April 2016 onwards have not yet been retrieved from the field). Tag labels are in the format 'Species-Sex-Fork Length'.

From December 1 to December 10 2014, 15 previously active sharks (2 grey reef sharks and 13 silvertip sharks) ceased to be detected and had not been redetected as of March 2018 (Figure 5.2, Figure 5.3). Fork lengths were 94 and 123 cm for the two grey reef sharks and ranged from 81-180 cm for silvertip sharks. There were 8 females and 6 males among the 14 animals for which sex data were recorded (Table 5.1, Supplementary Table 5.1). These animals had all been detected consistently since tagging, with a mean interval between consecutive detections of 2.1 ± 0.1 hours and a maximum absence of 37.5 days (900 hours; Figure 5.3). The remaining tags showed no change in detection activity during and after the December 1-10 period (Figure 5.3), and detection of sharks continued at the locations assumed to have been affected by fishing (Supplementary Figure 5.1).

Table 5.1: Demographic data on sharks lost in December 2014

Species	Sex				Fork length (cm)			
	#	M	F	U	Mean	CI	Min	Max
Grey Reef	2		2		106.0	19.8	94	123
Silvertip	13	6	6	1	114.4	7.0	81	180

The BIOT Patrol Vessel (BPV) reported encountering a total of 17 suspected illegal fishing vessels on the 4th, 11th and 14th of December 2014 (2, 7 and 8 vessels per day, respectively) in locations surrounding the monitored area (IOTC Secretariat 2015)⁹. The majority of the Indian-flagged vessels were encountered in the known anchorage in the northwest corner of Blenheim Reef (Figure 5.1). The BPV had reported sighting an average of 1 vessel per month in the previous eight months (Figure 5.4). Comparing monthly tag losses and vessel sightings from March to December 2014 revealed similar patterns, with the peak level of fishing vessel sightings in December corresponding with the highest loss in tag detections (Figure 5.4). Cox proportional hazards analysis found that the hazard ratio for tag loss associated with fishing events was 6.0 (95% CI: 2.6-14.0, $p < 0.001$, Figure 5.5, Table 5.2). Kaplan-Meier curves suggest presence of fishing reduced tag survival time by over 50% (zero probability of survival by 631 days, Supplementary Figure 5.2). The fishing event coincided with a period of calm weather in northern part of BIOT, with mean wind speeds of 4.5 ms^{-1} (8.7 kts) and wave heights of 1.3 m during the first half of December (Supplementary Figure 5.3).

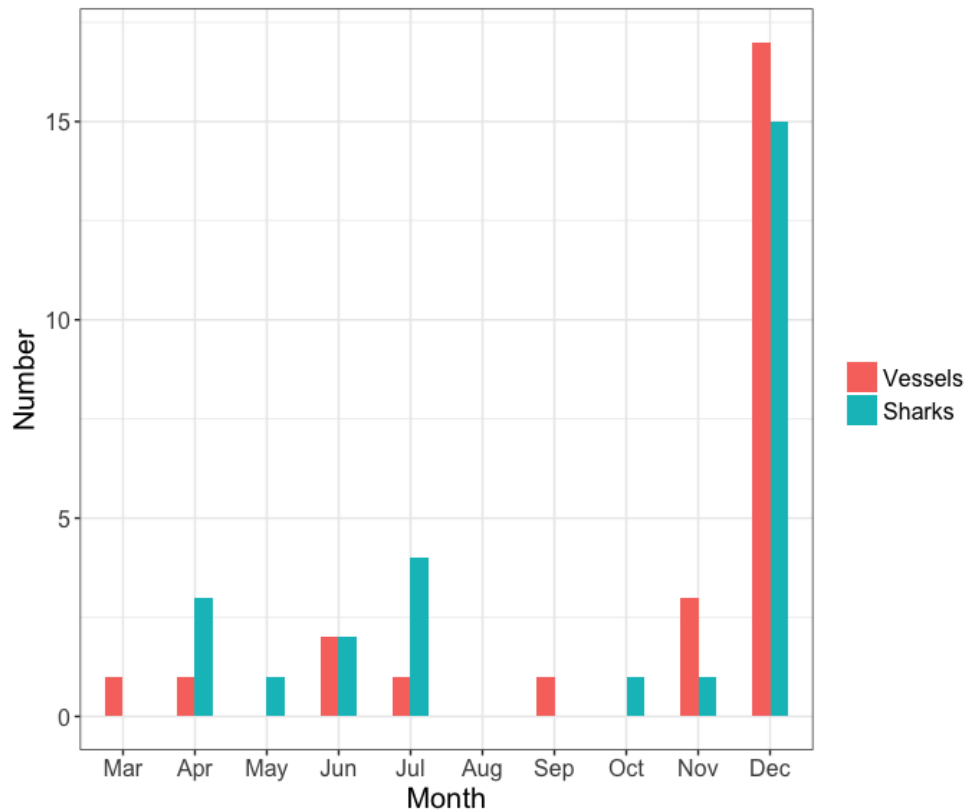


Figure 5.4: Number of illegal fishing vessel sightings and number of tags ceasing to be detected in the BIOT MPA by month, March to December 2014.

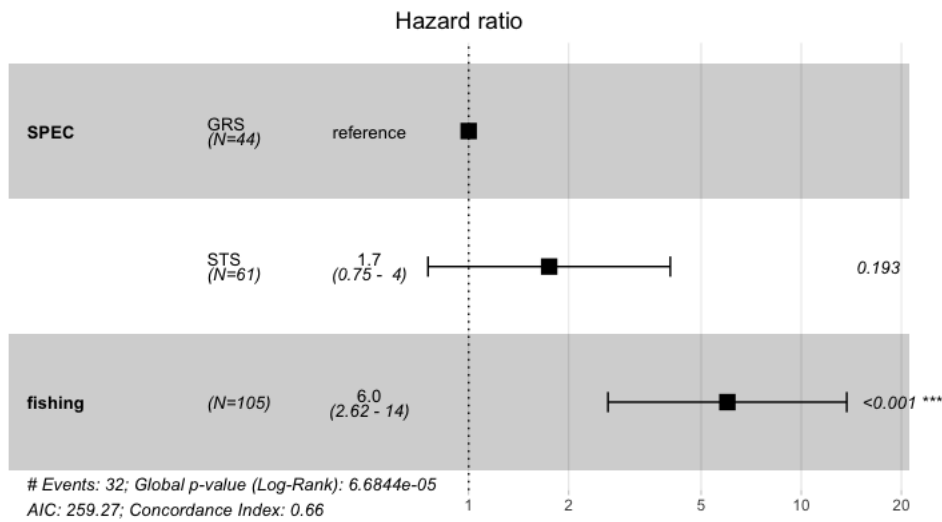


Figure 5.5: Forest plot of Cox proportional hazard model for tag loss, with shark species and presence of fishing at time of last detection as covariates. Error bars show 95% confidence interval of hazard ratio. Hazard ratios greater than 1 indicate increased risk of tag loss.

Table 5.2: Parameters of the Cox proportional hazard model of the effects of shark species and fishing vessel presence on tag loss (shark survival time)

term	Coefficient	SE	Hazard ratio (HR: e^{coef})	Z score	p-value	HR CI lower	HR CI upper
species:STS	0.56	0.43	1.8	1.30	0.193	0.76	4.0
fishing	1.79	0.42	6.0	4.25	<0.001	2.62	13.7

Of the 17 vessels detected in December 2014, two vessels were detained with an average of 180 sharks each on board (Table 5.3). One vessel had 308 sharks on board, including 98 silvertip and 60 grey reef sharks; the other had 51 sharks on board, including 28 silvertip and 4 grey reef sharks (IOTC Secretariat 2015). Catch data from reports for all arrests made in the BIOT MPA during 2014 gave a lower mean catch size of 135 ± 57 sharks per vessel, of which 9.8% were grey reef sharks and 37.6% were silvertip sharks (IOTC Secretariat 2015, Supplementary Table 5.2). If we assume these numbers are representative of a typical fishing catch within BIOT, then extrapolating from the observed data, the 17 vessels sighted in December 2014 could have collectively yielded a potential total catch of >2000 sharks of which >200 would have been grey reef sharks and nearly 900 would have been silvertip sharks. Based on the assumption that these fishing vessels removed 15 of 43 tagged sharks considered to remain at large at the time, an abundance index, assuming equal catchability and a closed system, would imply that nearly one-third of the local shark population was removed.

Table 5.3: Species and numbers of sharks found on board fishing vessels (FV) in December 2014

Shark species	Vessel name (Arrest Date)		Mean catch	
	FV Greeshma (4/12/14)	FV Bosin (14/12/14)	Number	Percent
Silvertip	98	28	63	35%
Grey reef	60	4	32	18%
White tip reef		13	7	4%
Black tip reef	54	6	30	17%
Blacktip	50		25	14%
Other shark	28		14	8%
Tiger	10		5	3%
Bull	6		3	2%
Scalloped Hammerhead	1		1	0%
Oceanic White Tip	1		1	0%
Total	308	51	180	100%

5.5 Discussion

Acoustic telemetry provides data about tagged animals within a detection area that is determined empirically within a location but usually is less than 500 m in total reception (Kessel et al. 2014). Thus, acoustic tagging does not produce information about animals outside the detection range of receivers, and so, in most cases, nothing can be known for certain about why tagged animals ceased being detected. However, reef sharks have been observed to exhibit high degrees of site fidelity, remaining at home reefs or within groups of adjacent reefs for months at a time with few, brief absences (Barnett et al. 2010, Field et al. 2010, Espinoza et al. 2015a). Residency is thought to be higher to reefs that are geographically isolated, as in the case of BIOT, although limited instances of connectivity between groups of reefs separated by distances of tens, rather than hundreds, of kilometres have been shown on the GBR, Hawaii and Palmyra (Espinoza et al. 2015a, Filous et al. 2017, White et al. 2017). Where animals have been observed to exhibit mass movements there has typically been a clear driver – a change in environmental conditions (Heupel et al. 2003), reproduction (Espinoza et al. 2015b), migratory stage or the arrival of a predator at the study site (Pyle et al. 1999) – and animals were often detected subsequent to the event.

In this study we describe a sudden drop in activity amongst the acoustically tagged sharks in a study site and hypothesize that a sudden increase in the rate of tag loss may represent a ‘fishing signature’ that corresponds to the illegal fishing activity in the area at the same time. This is supported by the concordance between levels of tag loss and apparent fishing activity throughout the rest of the 2014 monitoring period, and survival analysis which found that the presence of fishing vessels was associated with shorter survival times and a six-fold higher risk of ‘mortality’ based on Kaplan-Meier curves and Cox proportional hazard modelling respectively. Given the difficulty in detecting illegal fishing in a remote area the size of the BIOT MPA, it is possible that the sightings data do not accurately reflect true levels of fishing activity. However, assuming consistent patrolling effort in each month, levels of sightings/arrests are assumed to be proportional to fishing effort; Price et al (2008) assumed that sightings represented 10% of total incursions by illegal fishing vessels. Acoustic tagging may therefore be able to provide data from which to deduce enforcement efficiency by recording undetected IUU events. Tag loss during the month of our assumed fishing event was over 3 standard deviations above the average for the preceding 21 months of monitoring, suggesting an extreme event. Once a baseline for ‘natural’ tag loss from an acoustic array is established, monthly spikes in tag loss might be used to infer an undetected fishing incursion.

Alternative explanations for the observed loss of tags must be considered, including mass movements linked to age and sex, predation, and equipment failure. However, given the scale of the tag loss, credible alternatives to the hypothesis of removal by fishing seem unlikely. Female grey reef sharks on the Great Barrier Reef have been observed to leave home reef sites at certain times of year, which is assumed to correspond to parturition among pregnant individuals (Espinoza et al. 2015b). Similarly, site fidelity has been shown to vary ontogenetically with younger individuals less site-attached than larger, older sharks of the same species (Espinoza et al. 2015b). However, our data show a simultaneous change in behaviour of a group of animals of mixed species, sex and sizes from multiple sites across the monitored reefs (Figure 5.3, Figure 5.4, Supplementary Table 5.2). A second potential driver could be local or atoll-wide environmental conditions driving a mass exodus of sharks. However, detection patterns among the remaining tagged animals were unchanged through the period in question (Figure 5.3). Smaller reef sharks are known to be preyed on by larger species such as hammerheads (Cortés 1999, Mourier et al. 2013), and predation of silvertip sharks in BIOT is suspected based on archival tag data (unpublished data). Natural predation cannot therefore be discounted as being responsible for at least some of the 'lost' tags. However, we consider it unlikely to account for such a concentration of incidents. Finally, it is possible that the loss of tags reflected equipment failure, either of tags or receivers, but again this is unlikely. The tags had been operating for between 19% and 34% of their nominal battery life, were from different production batches, and had been performing consistently well since deployment (Figure 5.1, Supplementary Table 5.2). The receiver network was clearly working properly as the remaining tags continued to be detected. The pattern of indiscriminate loss of sharks of mixed species, sex and age from multiple sites over a short period could however be explained by fishing activity by a group of vessels moving through the atolls during that period. This hypothesis is also supported by the fact that silvertip sharks formed the majority of both the sharks observed in vessel catches and of the tags that had disappeared. We note that our sharks also fall well within the size distribution of animals taken by illegal fishing vessels in previous years (Martin et al. 2013), confirming that these vessel target size classes overlapping our tagged cohort. Finally, a tag deployed during the most recent tagging field work in BIOT, in April 2018, was returned from a fishing market in Sri Lanka (B Block, pers. comm.) confirming the interaction between illegal fisheries and animals in our tagging program.

Illegal fisheries targeting sharks have been implicated in the reductions of reef shark numbers in the BIOT MPA during the 1980 and 1990s, prior to the start formal protection, as reported by Graham

et al. (2010). Illegal vessel sightings began to be reported in 1996 but are assumed to have been occurring prior to the start of fisheries patrols (Ferretti et al. 2018). Although legal fisheries were licensed to fish in BIOT until the MPA was created in 2010, these were assumed to have minimal impact on reef sharks (Ferretti et al. 2018). Illegal vessels targeting shark have continued to be reported by the BIOT MPA authorities since the MPA's creation, and anecdotal evidence from vessel sightings and discarded long lines on reefs during scientific expeditions suggest that the problem is on-going. The pattern of vessel sightings reported by the BIOT patrol vessel suggests that fishing activity is sporadic with occasional pulses of activity, perhaps in response to market demand, fuel prices or weather conditions. The December 2014 vessel sightings corresponded with a drop in mean wind speed and wave height in the local area, presumably creating favourable conditions for fishing (Supplementary Figure 5.3). Calm weather and surface conditions may also have favoured the vessels transiting into and out of BIOT from their home ports in India and Sri Lanka. Late 2014 also saw a 25% fall in the price of marine diesel oil relative to the middle of the year (<http://www.bunkerindex.com>, Supplementary Figure 5.3) which would have lowered the costs of a relatively long transit to the BIOT fishing grounds. There may be other underlying macroeconomic and political drivers affecting levels of illegal fishing in BIOT. The majority of the vessels sighted in December 2014 came from Tamil Nadu in south western India, where since 2013 the government has been offering increasing subsidies to convert trawlers to tuna longliners, in order to reduce fishing pressure and conflict in waters shared with neighbouring Sri Lanka (http://www.fisheries.tn.gov.in/pdf/Tuna_guidelinesGO.pdf). Starting at 25%, this subsidy has now been increased to 70% of the vessel conversion cost, with the government aiming to convert 2,000 trawlers to deep sea longlining (<https://www.thehindu.com/todays-paper/tp-national/tp-tamilnadu/deep-sea-fishing-project-receives-good-response/article19537620.ece>). If successful, and unless properly policed, this policy may lead to an increased number of vessels targeting the BIOT MPA.

The high proportion of reef-associated sharks found in the seized catches of illegal fishing vessels, suggest that illegal fishing activities specifically target these species rather than taking them as bycatch. This is corroborated by the observation that the size of 15 individuals described here fell within the size range observed in catches of reef sharks taken by illegal fishing vessels in previous years (Martin et al. 2013, Supplementary Figure 5.4). While the exact number of sharks removed during such incursions cannot be known, the mean catches of the nine illegal fishing vessels detained in BIOT during 2014 contained an average of 137 sharks per vessel, suggesting that over

2000 animals may have been removed by the 17 vessels observed during December 2014. This per-vessel estimate is lower than the mean catches of the two Indian flagged vessels arrested at the time (180 sharks per vessel), so our estimate of per-vessel catch might be considered conservative. We may also have underestimated the total number of vessels involved in the fishing event, given an estimated detection efficiency by the patrol vessel of only 10% (Price et al. 2008). Regardless of the true total, the sharks removed likely represent a significant proportion of the local population. Assuming the tagged sharks are representative of the local un-tagged animals a simple closed population mark-recapture model would suggest that as much as one third of the reef sharks could have been removed from the monitored reefs in vicinity of our tagging sites during December 2014. However, since the location and total effort of the fishing activities is unknown, this estimate may represent a very localised impact. Ferretti et al. (2018) reconstructed grey reef and silvertips shark population trajectories using a Bayesian approach, and concluded that silvertip sharks were at very low abundance relative to both historical numbers and current grey reef shark abundance (Ferretti et al. 2018). The illegal fishing data analysed here certainly indicates that silvertip removals may be higher than those of grey reef sharks, but whether this should be interpreted as meaning silvertips are at lower abundance, or is an artefact of fishing technique or depth, would require additional investigation. However, the note of alarm for silvertip sharks sounded by Ferretti et al.'s analysis appears to be justified if current levels of removal are sustained.

5.6 Conclusion

Given the relatively low fecundity of most reef sharks (Smith et al. 1998, Hisano et al. 2011), large illegal fishing events, such as described above and suspected to have occurred in December 2014, may have a lasting negative impact on overall reef shark abundance, impacting the effectiveness of MPAs and with implications for ecosystem health. Our data show that fishing can also cause significant losses to acoustic monitoring projects in terms of both potential data and equipment, given that a tag's useful life can be up to ten years without animal mortality. However, our data suggest that further developments in electronic tagging may offer a means to police and deter illegal fishing in protected areas, by remotely detecting fishing events as they happen, as well as perhaps allowing mortality of species of conservation interest in legal fisheries to be better quantified. Satellite-linked receivers, such as the Vemco VR4 Global, are an existing tool that might be used to remotely monitor presence/absence of tagged animals in real time. Additionally, technologies such as FastLoc-GPS might be adapted to transmit the locations of sharks as they are removed from the

water, using a similar approach to that used with Smart Position and Temperature (SPOT) tags. Bradley et al. (2019) reported a similar case of apparent illegal fishing of tagged sharks in the Marshall Islands Shark Sanctuary. In their case, grey reef sharks had been fitted with satellite archival tags, which began transmitting when the animals were removed from the water, and appear to have tracked the vessels involved to ports in the Philippines and Guam. This shows the potential of tag technologies to provide real-time data on illegal fishing, although a much cheaper tag would be needed for this approach to be cost effective. Along with satellite monitoring of vessel activity (Kroodsma et al. 2018, Bradley et al. 2019), such remote fishing detection techniques could be used in large remote marine protected areas to complement other enforcement methods, and to better focus resources. By improving detection efficiency by enforcement assets, electronic tagging and complementary technologies to offers a means to reduce the currently high cost of effectively enforcing large marine protected areas (McCrea-Strub et al. 2011) helping them to achieve their conservation goals.

5.7 References

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5.8 Supplementary materials

5.8.1 Supplementary tables

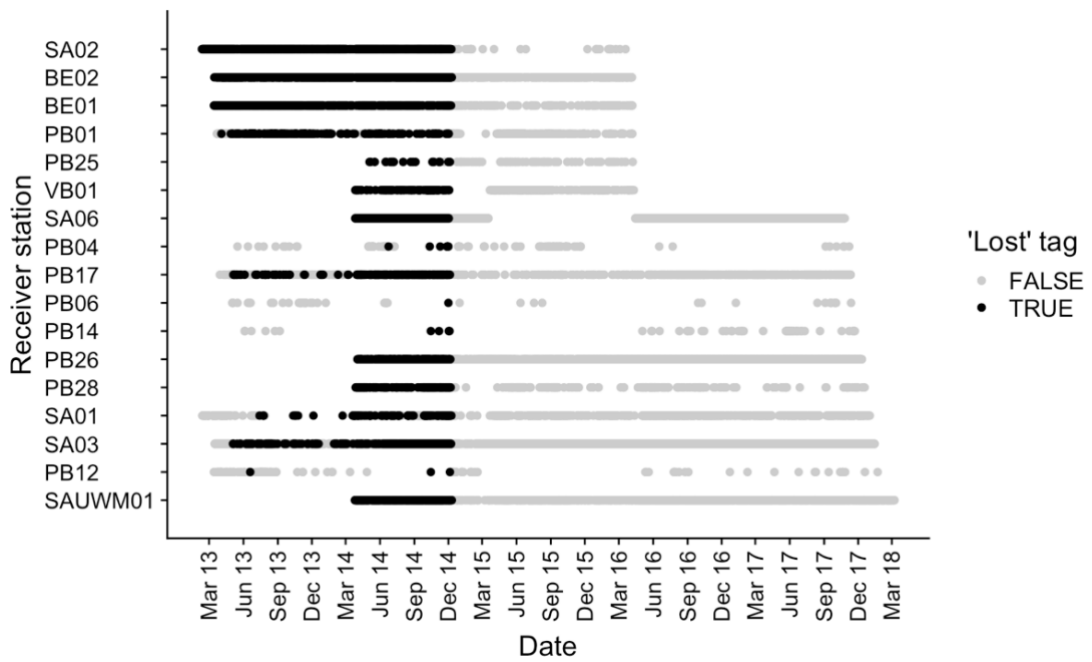
Supplementary Table 5.1: Details of 15 acoustic tags assumed to be removed by fishing in December 2014

Tag attributes							Shark attributes				
Tag ID	Purchased	Code space	Type	Nominal delay (s)	Estimated life (days)	Deployed	Expected expiry	% life used	Species	Sex	Total length (cm)
27590	13/12/12	A69-9001	V16-4x	120	2000	5/2/13	29/7/18	34%	Silvertip	U	180
27611	13/12/12	A69-9001	V16-4x	120	2000	9/2/13	2/8/18	33%	Silvertip	F	115
27603	13/12/12	A69-9001	V16-4x	120	2000	12/3/13	2/9/18	32%	Silvertip	M	119
27584	13/12/12	A69-9001	V16-4x	120	2000	17/3/13	7/9/18	32%	Silvertip	F	108
13576	12/6/12	A69-9002	V16P-4x	180	3000	22/3/13	8/6/21	21%	Grey reef	F	100
34177	11/6/12	A69-1303	V16-4x	120	2000	22/3/13	12/9/18	31%	Silvertip	M	115
52975	11/6/12	A69-1303	V16-4x	120	2000	22/3/13	12/9/18	31%	Silvertip	M	123
25536	19/2/14	A69-1601	V16-4H	60	854	22/3/14	23/7/16	31%	Silvertip	M	128
25544	19/2/14	A69-1601	V16-4H	60	854	24/3/14	25/7/16	31%	Silvertip	M	134
25552	19/2/14	A69-9002	V16TP-6H	60	1314	25/3/14	29/10/17	20%	Grey reef	F	140
12950	19/2/14	A69-9002	V16TP-6H	60	1314	25/3/14	29/10/17	20%	Silvertip	F	119
25542	19/2/14	A69-1601	V16-4H	60	854	25/3/14	26/7/16	30%	Silvertip	F	115
12958	19/2/14	A69-9002	V16TP-6H	60	1314	27/3/14	31/10/17	20%	Silvertip	F	114
12952	19/2/14	A69-9002	V16TP-6H	60	1314	29/3/14	2/11/17	19%	Silvertip	M	97
12968	19/2/14	A69-9002	V16TP-6H	60	1314	29/3/14	2/11/17	19%	Silvertip	M	115

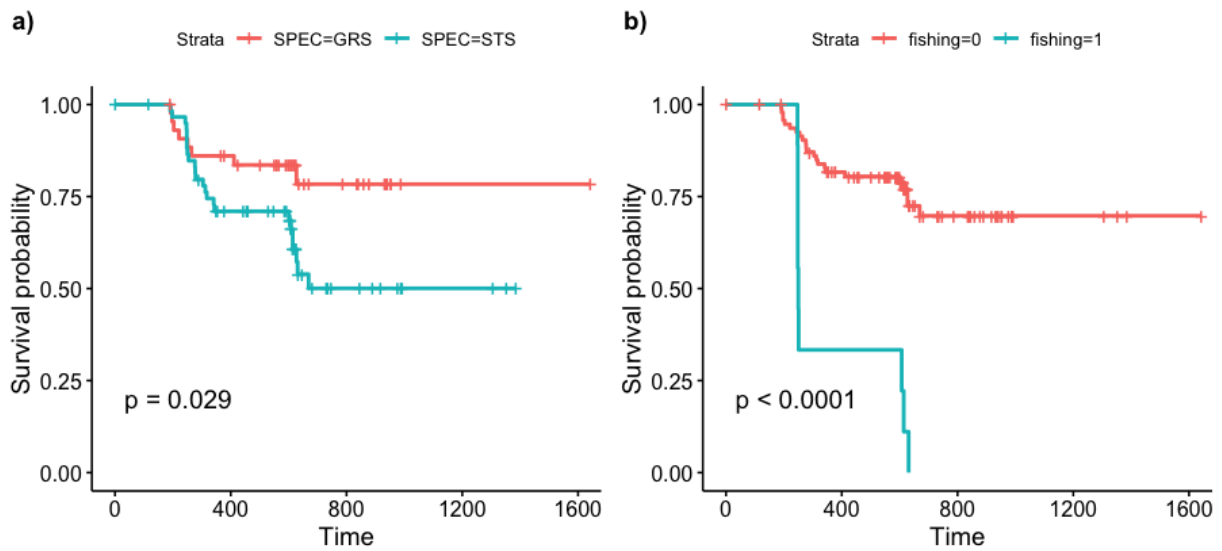
Supplementary Table 5.2: Details of catches from nine fishing vessels detained in the BIOT during 2014

	Arrest details										Mean	Catch share
	Date	18/03/14	18/04/14	21/06/14	21/06/14	06/11/14	06/11/14	01/12/14	04/12/14	14/12/14		
Vessel name	Sulara 2	Imasha 2	Stef Ania Duwa	Thiwanka 5	Kavidya Duwa	Otto 2	FV Jane	FV Greeshma 1	FV Bosin			
Grey reef	24	-	16	-	14	1	-	60	4	13.2	9.8%	
Silvertip	106	28	51	16	50	44	34	98	28	50.6	37.6%	
Black tip reef	-	-	47	14	1	12	-	54	6	14.9	11.1%	
White tip reef	55	-	-	9	48	18	-	-	13	15.9	11.8%	
Tiger	16	-	-	4	13	15	3	10	-	6.8	5.0%	
Sandbar	3	-	-	-	6	-	37	-	-	5.1	3.8%	
Hammerhead	9	-	-	2	1	1	4	1	-	2.0	1.5%	
Bull	5	-	-	-	12	5	12	6	-	4.4	3.3%	
Blacktip	-	-	-	-	-	-	3	50	-	5.9	4.4%	
Oceanic white tip	19	-	-	-	-	1	4	1	-	2.8	2.1%	
Spinner	-	-	-	-	-	-	6	-	-	0.7	0.5%	
Mako	-	-	-	-	5	-	-	-	-	0.6	0.4%	
Silky	-	-	-	-	3	-	-	-	-	0.3	0.2%	
Unidentified shark	-	45	-	-	1	3	26	28	-	11.4	8.5%	
Total	237	73	114	45	154	100	129	308	51	134.6		

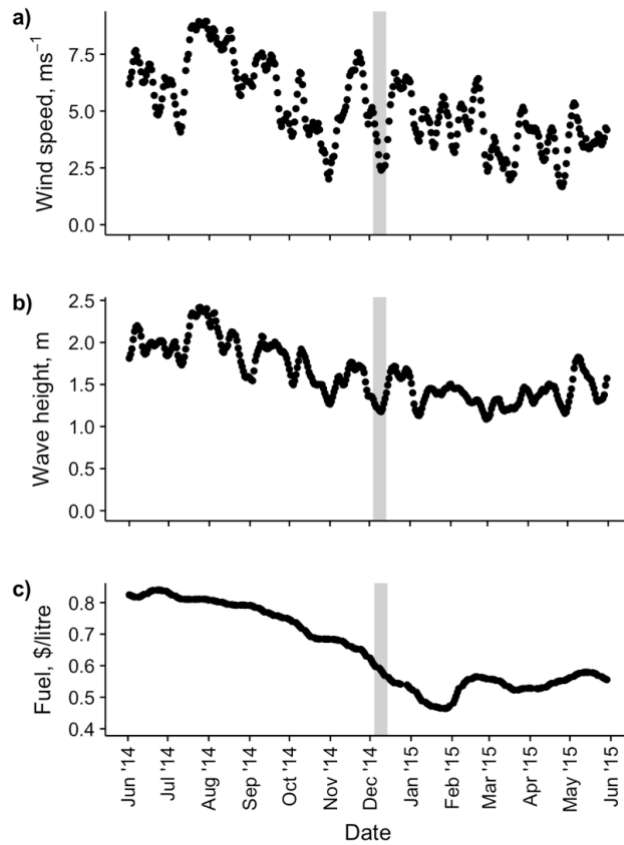
5.8.2 Supplementary figures



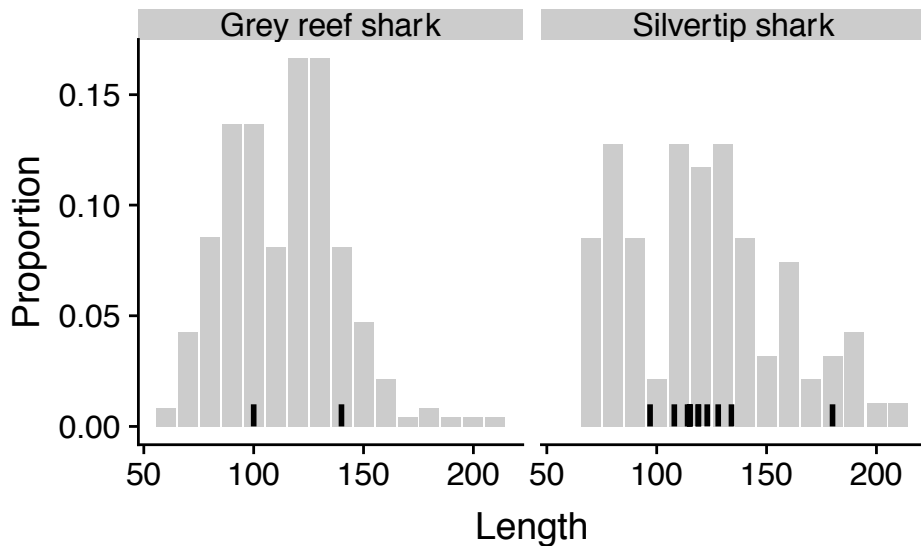
Supplementary Figure 5.1: Detection activity of 'lost' (black) and other (grey) tags at locations presumed affected by fishing activity in December 2014.



Supplementary Figure 5.2: Kaplan-Meier curves for time to tag loss for grey reef and silvertip sharks by a) species and b) fishing vessel presence



Supplementary Figure 5.3: Seven-day rolling average values of a) Wind speed and b) wave height for the BIOT EEZ area, and c) Marine Diesel Oil price, from June 2014 to June 2015. Period of the suspected illegal fishing event in December 2014 indicated with a grey bar.



Supplementary Figure 5.4: Length distributions (TL) for grey reef sharks and silvertip sharks observed on illegal fishing vessels in BIOT from 2007-2013. Black whiskers indicate lengths of animals considered lost (fished) during the December 2014 IUU fishing incident.

Chapter 6: General discussion

The industrialisation of the ocean has multiplied and deepened humanity's impact on marine ecosystems (McCauley et al. 2015). Resource extraction, particularly fishing, coastal development, and chemical and noise pollution are now major forces shaping marine ecosystems, along with increased warming, deoxygenation and acidification of the ocean due to greenhouse gas emissions (Jackson et al. 2001, McCauley et al. 2015). Beginning in the 1950s, the Anthropocene's 'great acceleration' (Steffen et al. 2007) has been marked by widespread degradation of coastal and marine habitats, including a 50% decline in live coral reefs (Bruno & Selig 2007, Hughes et al. 2017), and the destruction of an estimated 35% of mangrove forests (Polidoro et al. 2010) and 30% of seagrass beds (Waycott et al. 2009). Habitats from the coast to the deepest marine trenches are simultaneously being polluted with plastic debris (Jambeck et al. 2015, Jamieson et al. 2019). Systematic overexploitation of fish populations has caused marine defaunation and trophic downgrading (Pauly et al. 1998, McCauley et al. 2015) and altered benthic habitats (Thrush & Dayton 2002, Clark et al. 2019). Populations of large predatory fishes and sharks have declined by up to 90% (Ferretti et al. 2010, Collette et al. 2011), total marine catch has been declining since the mid-1990s (Pauly & Zeller 2016) despite ongoing increases in subsidised fishing effort (Rousseau et al. 2019), and even deep seamount habitats thousands of metres below the surface have been serially depleted of fish (Victorero et al. 2018). Such damage impairs the vital ecosystem services provided by the oceans, particularly food-security and climate regulation (Srinivasan et al. 2010, Salinas et al. 2020). As marine biodiversity continues to decline at an alarming rate (IPBES 2019), measures to avoid, mitigate and repair ecosystem damage are key to sustaining the quality of human life on Earth (Griggs et al. 2013, Johnson et al. 2017).

Restoring and maintaining healthy marine ecosystems requires the integration of ecological, social, economic and technical knowledge (Friedman et al. 2020). My thesis focussed on a small part of this challenge by investigating the spatial ecology of sharks around a group of oceanic coral reefs in the British Indian Ocean Territory (BIOT) in the context of questions about their ecosystem role (Heupel et al. 2019), vulnerability to fishing (Meekan et al. 2006, Graham et al. 2010, MacNeil et al. 2020) and other anthropogenic threats (Cheung et al. 2009), and the requirements and efficacy of spatial protection (Dwyer et al. 2020). My focal species, grey reef (*Carcharhinus amblyrhynchos*) and silvertip sharks (*Carcharhinus albimarginatus*), have been shown to have overlapping but distinct diets and horizontal space use (Espinoza et al. 2015b, Curnick et al. 2019), which potentially

translates into different ecosystem roles and levels of exposure to fishing (Meekan et al. 2006). There is also evidence that they occupy different depth ranges, with silvertip sharks found to be more abundant on deeper features (Tickler et al. 2017), suggesting differences in their three-dimensional space use and habitat associations. Historical data from the BIOT suggests that both species have been impacted by illegal fishing (Martin et al. 2013), leading to population declines (Graham et al. 2010). Finally, marine species in tropical regions are expected to exhibit poleward range shifts in response to warming oceans (Cheung et al. 2009, Sunday et al. 2015), with reduced oxygen availability acting as an additional constraint (Breitburg et al. 2018).

6.1 Thesis overview

Chapter Two begins by examining trends in the increase and spatial expansion of shark catches between 1950 and 2014, using reconstructed catch data from the *Sea Around Us*. Reconstructed shark catches more than doubled but the area fished for sharks increased seven-fold, suggesting declining catch per unit effort. Concerningly, there was an associated lack of reliable and informative catch data, a prerequisite of scientific monitoring and management. Potentially only half of the likely total shark catches are captured in official statistics, and almost two-thirds of those are not identified to species. The spatial analysis of catch data showed that the BIOT is located within a global hotspot of shark fishing in the tropical Indian Ocean, with coastal nations to the north of BIOT, including India and Sri Lanka, among the world's leading shark fishing countries. This highlights the importance of effective protections for reef sharks in the region and the value of the BIOT Marine Protected Area (MPA).

In Chapter Three, I used acoustic tagging technology to quantify differences in the space use, home ranges, and visitation patterns of grey reef and silvertip sharks within the BIOT's reef systems. Grey reef sharks showed higher attendance at reef sites, particularly at night, and smaller activity spaces, consistent with studies on the Great Barrier Reef where they have also been monitored alongside silvertip sharks (Espinoza et al. 2015b). Silvertip sharks moved greater distances within the reef system and appeared to spend more time away from reefs, consistent with studies of diet (Curnick et al. 2019) and spatial ecology (Barnett et al. 2012, Espinoza et al. 2015b) in BIOT and elsewhere. There was also some evidence of intraspecific variation with BIOT, with larger individuals of both species detected less at night, suggesting ontogenetic changes in behaviour and foraging. Additionally, silvertip sharks on deeper seamounts appeared to exhibit higher and more consistent attendance than conspecifics at shallow sites. While differences in receiver coverage and tag

detection between shallow and deep sites cannot be ruled out as an explanation for the latter pattern, local aggregations of sharks in response to enhanced productivity at the seamount (Hosegood et al. 2019) may partly explain the higher density of tag detections observed. Such intra-specific variation in spatial ecology in response to prey availability has also been observed with reef sharks in French Polynesia in response to fish spawning aggregations (Rhodes et al. 2019). My results provide additional evidence for resource partitioning and functional differences within the reef shark guild and the importance of preserving shark diversity on coral reefs (Roff et al. 2016), as well as suggesting context-dependent plasticity in space use by reef sharks.

Chapter Four examined the vertical space use of silvertip sharks, using archival tags to gather high-resolution depth and temperature data. Although based on a limited sample, the data provide evidence that silvertip sharks connect epi- and mesopelagic food webs between the surface and 800 m depth. Temporal variation in the vertical movements of silvertip sharks monitored also correlated with diel and lunar cycles associated with the vertical migration of pelagic prey. In common with other large active ectothermic predators (Howey-Jordan et al. 2013, Banez 2019), the core vertical space use of silvertip sharks appears to be constrained by temperature and dissolved oxygen (DO) levels. Short-term variations in vertical space use may help predict both silvertip sharks' susceptibility to different fishing gears. Modelling short-term vertical space use against water temperature and DO may also help define the physiological niche of the silvertip shark with respect to these parameters.

In my final data chapter, I presented a case study resulting from the intersection of illegal fishing activity with our shark tagging project in the BIOT. In this 'natural experiment' (*sensu* Barley & Meeuwig 2016), illegal fishing was associated with a halving of the time at liberty for individual sharks, implying early mortality. Analysis of the catch composition of the vessels involved suggested that over 2,000 sharks were removed in a single incident in December 2014, almost half of which were silvertip and grey reef sharks. The results show the importance of effective protection if MPAs are to maintain or rebuild reef shark populations, but also the potential of animal-borne tags to potentially complement satellite and other technologies in enhancing the policing of MPAs (Kroodsma et al. 2018, Toonen & Bush 2018, Belhabib et al. 2020).

6.2 Emerging themes

My thesis has approached the challenge of better understanding reef sharks and the threats they face by using data spanning a wide range of spatial and temporal scales, from a 65-year dataset on the global distribution of shark fishing to minute-by-minute depth and temperature measurements for individual sharks. Considered together, several themes emerge from the individual analyses: (1) the importance of understanding space use and the spatial dimensions of threats in shark conservation; (2) the challenge of promoting the coexistence of fisheries and sharks; (3) the role and requirements of effective spatial protection; and (4) the potential for technology as a tool to both better understand and better protect sharks.

6.2.1 Movement matters in understanding and protecting marine predators

Hussey et al. (2015) called telemetry a “panoramic window into the underwater world”. Studying how sharks use the three-dimensional space around them increases our understanding of their ecosystem roles (McCauley et al. 2012), vulnerability to threats (Queiroz et al. 2019), and their response to environmental change (Hazen et al. 2019). It can also help us understand how to better monitor them (Nykänen et al. 2018) and how they might best be protected (Dwyer et al. 2020).

Combined, my findings on the horizontal and vertical spatial ecologies of grey reef and silvertip sharks (Chapters Three and Four) support earlier work positing distinct ecosystem roles and resource portioning within the reef shark guild, with silvertip sharks the larger and more mobile reef-associated species, compared with their smaller cousins (Heupel et al. 2014, 2019, Roff et al. 2016). However, while some authors have also suggested functional redundancy exists between reef sharks and large piscivorous teleosts (e.g., Frisch et al. 2016), my results support the view that sharks play unique and important ecosystem roles on reefs, relative to bony fishes and each other (McCauley et al. 2012, Ruppert et al. 2013, Williams et al. 2018, Barley et al. 2020). Grey reef and silvertip sharks in the BIOT both have home ranges of the order of tens of square kilometres, much larger than teleost predators such as coral trout (*Plectropomus leopardus*, Zeller 1997) or giant trevally (*Caranx ignobilis*, Meyer et al. 2007). Larger activity spaces, in the context of the ‘ecology of fear’ hypothesis (Zanette & Clinchy 2019), predict that individual reef sharks will influence competitor and prey species over a proportionally larger area. Similarly, longer and deeper ranges of horizontal and vertical movement, respectively, imply that reef sharks mediate greater degrees of ecosystem connectivity via mechanisms such as nutrient transfer (Williams et al. 2018). Horizontal nutrient subsidies by predators are believed to be important in enhancing coral reef

health in oligotrophic waters (Williams et al. 2018, Graham et al. 2018), whereas vertical nutrient transfer may play an important role in supporting primary production and carbon sequestration at the ocean's surface (Buesseler et al. 2020).

In the context of the wider literature on reef shark spatial ecology, my findings suggest that the movement and space use patterns of reef sharks, and therefore their ecological role, might be context-specific within study locations, varying with local competition, habitat and topography. Whereas I found that silvertip sharks were detected less frequently around reefs at night, Espinoza et al. (2015a) found that silvertip sharks spent more time near reefs at night but apparently dispersed to deeper water off-reef during the day. This may relate to differences in reef morphology and surroundings. The reefs studied by Espinoza et al. (2015a) on the GBR are set in relatively shallow shelf waters and surrounded by sandy channels ~50 m deep. Higher night time detections of silvertip sharks on the GBR may therefore relate to the concentration of available prey resources on reefs. In the BIOT, most reefs are immediately adjacent to the deep open ocean, which may give silvertip sharks more direct access to pelagic prey resources migrating to the surface at night. Combining data on the horizontal and vertical movements of silvertip sharks (Chapters Three and Four) suggests depth changes between day and night are similar on the GBR and in BIOT, possibly driven by thermoregulation (Sims et al. 2006, Espinoza et al. 2015a), but the direction of movement, onto or off the reef, differs. There also appears to be evidence of location-specific differences in spatial ecology for grey reef sharks. Stable isotope data from Palmyra indicates that, in the apparent absence of silvertip sharks, grey reef sharks occupy a semi-pelagic niche (McCauley et al. 2012), with tagging data showing wide-ranging movements in offshore waters (White et al. 2017). Grey reef sharks monitored alongside silvertip sharks in the BIOT and on the GBR (Espinoza et al. 2015b) show smaller movement ranges and less dietary evidence of offshore foraging (Curnick et al. 2019). This may reflect an expanded spatial and ecological niche for grey reef sharks in Palmyra, which is constrained by competition from a larger species in the BIOT and GBR. There also appears to be some evidence of context-dependent space use within species, with silvertip sharks apparently showing higher residency and more limited dispersal around deeper seamounts within the BIOT MPA, notwithstanding the caveats discussed in Chapter 4. Commonality across studies does exist, however, with, for example, the consistently larger activity spaces and movement ranges reported for silvertip sharks (Espinoza et al. 2015b). However, given the relatively limited number of studies to date, there appears to be a need to investigate reef shark spatial ecology across a wider range of sites and habitats to determine what is universally true and what is context-dependent.

As well as informing our understating of species' ecology and ecosystem role, horizontal and vertical space use may also increase our understanding of their vulnerability to anthropogenic threats. In the BIOT case study, silvertip sharks appear to both range more widely, potentially into epipelagic waters away from reefs, and vary their depth predictably in response to diel and lunar variation in light levels and seasonal variations in water temperature. These factors may make them easier to target with the shallow longlines commonly employed by fishing vessels in the region, which typically set lines overnight when the sharks would be nearest to the surface (Aneesh et al. 2016, Hewapathirana & Gunawardane 2017). A higher vulnerability of silvertip sharks to fishing, as a consequence of their space use, is consistent with the higher fishing mortality of tagged silvertip sharks documented in Chapter Five and the higher catches of silvertip sharks observed on illegal fishing vessels in the MPA (IOTC Secretariat 2015). Understanding fisheries risk factors related to different species' spatial ecologies allows for tailored approaches to spatial protection and enforcement (Jacoby et al. 2020). It may also provide a basis for management to identify at-risk 'litmus' species with which to detect fishing pressure on the wider reef shark assemblage.

Modelling vertical movements against water column properties, particularly temperature and dissolved oxygen, may also be used to quantify reef sharks' physiological limits and predict their longer-term response to overall warming and deoxygenation of the ocean. Ocean warming is already driving horizontal range shifts in other marine taxa (Cheung et al. 2012, Pinsky et al. 2020), and may also affect the depth of available habitat (Gilly et al. 2013). If the environmental niches of silvertip sharks and related species are constrained by their basic physiology, as seems plausible, a poleward shift in thermal habitat availability may place populations at isolated reef systems like the BIOT at increased risk of local extirpation. Vertical compression of physiologically suitable habitat, on the other hand, might constrain a species' access to mesopelagic prey and/or increase their vulnerability to fishing by confining them to a narrower depth range.

6.2.2 Sustainable shark fisheries are a challenge

Fisheries data are incomplete in terms of both catch volumes and taxonomic resolution (Pauly & Zeller 2016), but an earlier regional analysis suggests that the problem is particularly acute for sharks (Cashion et al. 2019). In Chapter Two, I found that this trend is evident globally, with higher levels of underreporting, particularly due to bycatch and discarding issues, and poorer taxonomic resolution for the global shark catch, relative to fisheries in general. This is worrying in the context of the rapid increase in shark catches, and their concentration in regions like the tropical Indian

Ocean where management capacity is generally low (Pitcher et al. 2009). Sustainably managed shark fisheries are already the exception, rather than the rule, and weak data collection undermines the goal of expanding scientific management of shark populations (Simpfendorfer & Dulvy 2017).

Species-level catch reporting also appears biased towards oceanic species, particularly blue shark (*Prionace glauca*), even though the majority of sharks are caught in tropical coastal areas and reef shark declines have been widely observed (Nevill et al. 2007, Ward-Paige et al. 2010, Graham et al. 2010, Nadon et al. 2012, Juhel et al. 2018, MacNeil et al. 2020). This implies under-reporting or misidentification of reef sharks in official fisheries statistics, a hypothesis supported by the evidence, presented in Chapter Five, that grey reef and silvertip sharks are actively targeted in BIOT by illegal fishing vessels from neighbouring coastal states. This is just one example of a likely source of under-reporting of reef shark catches and highlights the uncertainty around reef shark catch estimates for the region. It also underscores the challenge of sustainably managing sharks in fisheries with large fleets and limited flag state control. This challenge is exacerbated by the frequent classification of sharks as bycatch, and the attendant reduction in management focus, when their value and abundance in catches typically makes them a, if not the, target of the fishery (Oliver et al. 2015). This affects not only fisheries in developing countries but also the industrialised fleets of European Union and Asian countries, as well as the United States (Molony 2005, Mejuto et al. 2009), and creates important loopholes in the management of sharks (Fowler 2016).

Evidence of historic declines in reef shark abundance, and regional (MacNeil et al. 2020) and local (Meekan et al. 2006, Juhel et al. 2018) extirpations all point to an urgent need to improve management of these species. Improvements in the collection and reporting of data on shark catches are clearly needed. The data that do exist, and which are made publicly available through the catch reconstruction work of the *Sea Around Us*, can be leveraged using data-limited assessment methods (Froese et al. 2017, 2018). However, the major information gaps remaining in the reconstructed shark catch data analysed in Chapter Two suggest that management of sharks that cannot currently be addressed solely by the computing, setting and enforcing of catch limits within fisheries. Complementary precautionary measures, such as marine protected areas (Carr & Raimondi 1999), may also be required to ensure that management decisions are robust to incomplete data and limited enforcement capacity (Edgar et al. 2019).

6.2.3 *The role of marine protected areas*

Marine protected areas are widely recognised as critical to restoring and maintaining marine habitats, biodiversity and biomass, including of predators like sharks (Speed et al. 2018, Martín et al. 2020), against a background of increasing anthropogenic threats (Lester et al. 2009, Edgar et al. 2014, Sala & Giakoumi 2018). To be effective, MPAs must take account of the space use of species of conservation interest (Bonfil 1999, White et al. 2017), and the information derived from studying species' spatial ecologies can therefore be a vital component in their design (Chapman et al. 2005, Lea et al. 2016, Dwyer et al. 2020).

While very large MPAs like the BIOT likely provide full protection to reef sharks, at least in terms of their movement range (Chapter 3; Carlisle et al. 2019, in Appendix III), most MPAs are smaller and located in coastal areas where trade-offs with other stakeholders are required (UNEP-WCMC 2018, Mizrahi et al. 2019). Here, using spatial ecology to tailor the design of individual reserves, potentially networking them together based on movement corridors, may allow the maximum benefits to sharks with the minimum of loss to other marine resource users (Martín et al. 2020). The vertical space use of sharks (Chapter 4) and their depth preferences may also help identify cryptic habitats that are important to incorporate into MPA design, such as deeper structures for silvertips sharks. The opportunity exists to use this knowledge, in combination with data on the spatial distribution of threats like fishing, to move towards the existing global goals for MPA coverage – 10% by 2020 and 30% by 2030 (Zhao et al. 2020) – in a way that strategically targets locations of genuine ecological importance and vulnerability. This would seem preferable to the continued expansion of MPAs into 'residual' areas where fishing pressure, and the benefits of removing it, are already low (Devillers et al. 2015, 2020). Informed spatial planning also needs to be paired with strong enforcement if MPAs are to be effective in compensating for fisheries' impact on sharks outside their boundaries (Rife et al. 2013). As Chapter Five demonstrated, partial protection leaves sharks and other high-value target species exposed to smash-and-grab fishing incursions which may quickly decimate local populations. This mechanism may be also behind the stark differences seen in shark abundances between 'no-take' and 'no-entry' areas on the Great Barrier Reef (GBR; Robbins et al. 2006, Frisch & Rizzari 2019). On the GBR legal access to no-take areas for non-extractive users appears to provide cover for illegal fishing activity (Frisch & Rizzari 2019), suggesting that, beyond banning extractive activities, full protection for sharks may also require largely excluding all human activity from an MPA. Even this may not completely relieve anthropogenic pressures, with even an old established no entry reserve in New Caledonia holding lower shark biomass than more remote

marine wilderness area (D'agata et al. 2016). However, given the challenges of maintaining shark populations in the presence of persistent illegal fishing, no-entry areas may simplify enforcement by making the illegal activity more obvious, and may also be more amenable to the use of lower-cost enforcement methods such as remote sensing (Kachelriess et al. 2014, Belhabib et al. 2020). Finally, while the focus of my thesis was on reef-associated sharks, my analysis of global trends and spatial patterns in shark fisheries suggested a rapid increase in shark catches in High Seas areas. Spatial ecology has been used to identify areas of overlap between sharks and pelagic fisheries (Queiroz et al. 2019) and suggests a role for MPAs focussed on sharks and other important predators in areas beyond national jurisdiction (Gjerde et al. 2016).

6.2.4 Technology as a tool to understand and protect sharks

Technology has allowed humans to become a uniquely powerful predator and the biggest threat to the rest of the world's large animals (Ripple et al. 2019). But the tools that have made us effective hunters can also make us better stewards. Satellites allow fishing captains to locate schools with pinpoint precision, but have also allowed us to track sharks, whales and turtles across the ocean and to understand, and perhaps mitigate, current and future threats (Block et al. 2011, Queiroz et al. 2019).

The insights into the three-dimensional space use of grey reef and silvertip sharks, presented in Chapters Three and Four, were derived using years of high-resolution movement data and *in-situ* environmental measurements from animal-borne tags. The cost of setting up and maintaining an acoustic array is not trivial, particularly when the research involves significant vessel and travel costs as well as the cost of the actual equipment. However, in a remote area like the BIOT, the acoustic array has provided years of continuous monitoring without the need for a permanent scientific presence. Satellite tags, though currently limited in their battery life and data storage and transmission, are rapidly evolving and the latest incarnations offer customisable sensor payloads, and, theoretically at least, vastly improved data storage and transmission (<https://www.desertstar.com/page/seatag-mod>). Accelerometers (Andrzejczek et al. 2020), dissolved oxygen monitors (Coffey & Holland 2015) and cameras (Jewell et al. 2019) can potentially augment the location, depth and temperature data collected 'as standard' and provide a more sophisticated understanding of a species' ecology, vulnerabilities and conservation needs. Integrating tagging data with other monitoring technologies (discussed in the "Future directions" section, below) will further increase their utility.

An unexpected finding of this study was that animal-borne tags might also be a tool for fisheries managers, by providing evidence of illegal fishing activity. Although the tag detection patterns reported in Chapter Five may fall short of being a ‘smoking gun’ linking individual vessels to illegal activity, they implicate the shark fishing fleets of India and Sri Lanka in ongoing poaching of sharks in BIOT. A limit of the technology was the lack of real-time data – we found the signature of an illegal fishing event in the detection data months after the incident. Since those findings were published, another study has reported detecting shark fishing in the Marshall Islands shark sanctuary using satellite archival tags, which provided real-time tracks of the vessels involved as they transported the animals to ports in the Philippines and Guam (Bradley et al. 2019). Tags may, in the future, be adapted to provide not just ecological but enforcement data.

6.3 Addressing study limitations

A key limitation in interpreting the raw telemetry results from this study, and an area for future work for the BIOT acoustic telemetry project, is the absence of representative detection efficiency data from across the entire acoustic array. The probability of a tag being detected by an acoustic receiver may vary with location or time of day (Melnychuk 2012) which can influence the interpretation of the data (Payne et al. 2010). A common technique to account for this is to deploy control tags with known transmission characteristics so that ‘true’ detection probability and its temporal drivers at key locations can be inferred. In the BIOT case, control tags were deployed at only a few locations within the shallow atoll reef section of the array and none were used on the seamount sites. Therefore, the higher overall attendance and higher night time detections observed for silvertip sharks on the seamounts may be artefacts of enhanced detection probability, rather than intra-specific variation in behaviour, as I suggest. Overall detection probability from deep, surface-oriented acoustic receivers might be expected to be higher than for shallow units, based on their field of view. However, this does not explain why silvertip sharks, which move shallower at night, are detected *less* and not *more* on the shallow receivers at night when they should be moving higher into the field of view of the receivers. This suggests that lower night time detections reflect behaviour, not detection bias. Secondly, higher attendance of silvertip sharks at the seamounts, as suggested by observed detection patterns, is consistent with both direct observations of relative shark abundance across BIOT using BRUVS (Tickler et al. 2017), which found the highest density of silvertip sharks on the seamounts, as well as echosounder and oceanographic surveys of the seamounts (Fasolo 2013, Hosegood et al. 2019) which show fish biomass to be concentrated over

the seamount flanks. Seamounts are known to enhance and concentrate pelagic biomass (Morato et al. 2010) and, indeed, may be critical refugia for marine predators (Letessier et al. 2019).

A second limitation is the inability of satellite archival tags to adequately resolved small horizontal movements at low latitude locations like the BIOT (Hill & Braun 2001). This restricted my analyses to the depth and temperature data recorded by those tags and meant I lacked independent position data to corroborate hypotheses about the movements of sharks when out of range of the receivers. Deep dives by silvertip sharks suggest that they do indeed move off the reef into deep water, but without more precise position data this cannot be confirmed. Use of Smart Position and Temperature (SPOT) tags, which relay live positions when a tagged animal is at the surface, might help resolve this question. This technique was used successfully by White et al. (2017) to track offshore movements by grey reef sharks at Palmyra Atoll. However, silvertip sharks likely spend less time at the surface, given their depth-use profile, and therefore this may not be an appropriate approach. An alternative would be to deploy more of the deep acoustically-released (AR) receivers in offshore areas to 'log' offshore movements by tagged animals. This would be contingent on finding offshore locations that were within the operating depth range of the AR receivers (<500 m).

Lastly, despite the work done by the *Sea Around Us* in reconstructing the global fisheries catches of the past seven decades, large gaps in the catch data on sharks remain. The data compiled by the *Sea Around Us* on shark catches is very likely correct in terms of the magnitude of increase in shark catches and the main locations, coastal states and fishing entities involved. However, a lack of taxonomic resolution within the identified shark catch, and the large volume of the global catch still recorded as "marine fishes not elsewhere included" means that uncertainties remain regarding both the total volume of the shark catch and the catches of individual species. In particular, coastal species caught in artisanal fisheries may be particularly under-represented due to challenges facing both species identification and data collection in those fisheries. DNA-based identification of sharks in fishing markets suggests that coastal shark species may represent a higher share of the global catch than is recorded in official data (Van Houtan et al. 2020), a finding consistent with spatial and temporal declines in coastal and reef sharks (Graham et al. 2010, Nadon et al. 2012, Dwyer et al. 2020). Ongoing work by the groups like *the Sea Around Us* to recover and consolidate fisheries data must be complemented by improved and expanded data collection to address these uncertainties.

6.4 Future research directions

6.4.1 High resolution in situ data collection by reef sharks

While archival tags are typically used on wide-ranging species such as pelagic sharks and tunas (Block et al. 2011), the results presented in Chapter Four suggest that they may also be of value in describing the fine-scale vertical space use of more site-resident species. While cost is clearly an issue, relative to lower-cost acoustic tags, the high-resolution depth and temperature data collected by archival tags may allow important questions regarding reef shark ecology and their ecosystem roles to be better resolved (Heupel et al. 2019). Understanding how reef-associated species respond to water column structures, including temperature gradients and oxygen profiles (Coffey & Holland 2015), and how this differs between them may help us predict their responses to future environmental changes (Sunday et al. 2015).

To mitigate satellite tags' relative inability to resolve fine-scale horizontal movements of species like reef-associated sharks, satellite and acoustic tags might be paired to take advantage of their relative strengths in continuous data collection and location precision, respectively. In Chapter Four, I used data from a double-tagged individual to estimate the position error generated by light-based geolocation of a silvertip shark. A refinement of this approach would be to integrate acoustic telemetry-derived positions into the state-space model used for light-based geolocation, anchoring the resulting track to these points and correcting the model's drift. This has previously been done for pelagic sharks double-tagged with GPS and geolocation tags (Winship et al. 2011). Acoustic tags would provide a relatively cheaper 'ground-truthing' option for reef-associated or coastal species with smaller and more predictable activity spaces. This approach obviously assumes that the double-tagged animals are moving within the coverage of an acoustic array, and issues of animal ethics will also need to be considered as double-tagging will place additional strain on individual sharks (Cooke et al. 2013).

6.4.2 Integrating spatial ecology with other survey methodologies

Variations in spatial ecology between and within individual species impact both their interactions with the rest of the marine ecosystem and the likelihood that we will encounter them during survey activities (Nykänen et al. 2018). Nykänen et al. (2018) showed that aerial counts of blue sharks could be corrected for their availability at the surface using models of diving behaviour and vertical space use derived from telemetry data. Similarly, a growing body of information on the horizontal and vertical space use of reef sharks could be integrated with data from point-in-time-and-space surveys

of relative abundances, such as BRUVS surveys, to help interpret results or to mathematically correct for assumed availability bias. For example, BRUVS-based assessments of reef shark abundance in BIOT found grey reef sharks to be the most abundant species at shallow reef sites (< 30 m depth), but silvertip sharks were more abundant on a deep seamount (~70-80 m depth) opportunistically surveyed during the same project (Tickler et al. 2017). Given that the vertical movement of silvertip sharks indicates that they occupy depths of 50-60 m during daylight but are far shallower at night, daytime surveys around reef crests might fail to detect them, even when abundant. Telemetry might be used to both design and/or correct static abundance surveys to provide a more accurate picture of the distribution and relative abundance of reef shark species.

6.4.3 Learning from shark conservation to anticipate future ocean challenges.

The exploitation of the mesopelagic realm and deep ocean is yet to begin in earnest, but the fishing and mining industries looking towards the potential abundance of protein, “nutraceuticals” and metal-bearing minerals they contain (Miller et al. 2018, Hidalgo & Browman 2019). A window exists to use both techniques and insights from research in the surface waters to ensure that expansion into hitherto unexploited depths does not repeat past mistakes. Human impacts have already begun to be seen in these largely unexplored parts of the ocean, with microplastics from the surface appearing in even the deepest parts of the abyss (Jamieson et al. 2019). Understanding the ecologies of species living at these depths will help identify vulnerabilities and understand ecologically-important linkages before we break them. Documenting the current diversity and abundance of life in the deep, and then ensuring total transparency around any extractive activities that do take place, including comprehensive and accurate recording and reporting of catch data, will allow us to track our impact in real-time. Finally, given that even the best management regimes can be blind-sided by unpredictable nature, any future expansion of fisheries or mining demands a precautionary approach centred on setting large and representative areas aside from all forms of extraction. Expanded data collection, including from animal telemetry, will be needed to inform the development of high- and deep- seas protection regimes, including the area-based measures being considered as part of the United Nations negotiations on biodiversity conservation in areas beyond national jurisdiction (Humphries & Harden-Davies 2020).

6.5 Closing thoughts

A recurring theme of the modern era has been one of letting the resource extraction genie out of the bottle, then belatedly attempting to reinsert the cork (Roberts 2010). Ever since in 1883 Thomas

Huxley pronounced the seas to be 'inexhaustible', fishing has leveraged the technology of the age to rapidly reshape first coastal ecosystems and then the High Seas (Roberts 2010, Tickler et al. 2018), while conservation efforts have trailed in its wake (McCauley et al. 2015). On continental shelves and in the upper levels of much of the open ocean, the job is now to save what is left and promote the recovery of that which is still salvageable. In some cases, we are already in triage mode, with species like the vaquita (*Phocoena sinus*) headed towards extinction (Jaramillo-Legorreta et al. 2019).

Modern research tools not only let us study animals without killing them, as was the norm for much of the 19th and 20th centuries (Burnett 2012), but also allow us to look into their lives in unprecedented detail. Coupled with the hindsight gleaned from our past mistakes, this gives us motivation and opportunity to repair some of the damage and pre-empt problems we might be on the cusp of creating. Integrating transparent data on the impacts we inflict on the oceans with a fine-scale understanding of the movements of marine animals, their needs and their vulnerabilities can allow us to tread more lightly in the 21st century. In the coming decades, rising human population and consumption may further strain our relationship with the natural world. We need to recognise that the other creatures with which we share the planet, and on whom we depend, need their space too.

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Appendices

Appendix 1: Far from home: Distance patterns of global fishing fleets.

ENVIRONMENTAL STUDIES

Far from home: Distance patterns of global fishing fleets

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Postwar growth of industrial fisheries catch to its peak in 1996 was driven by increasing fleet capacity and geographical expansion. An investigation of the latter, using spatially allocated reconstructed catch data to quantify “mean distance to fishing grounds,” found global trends to be dominated by the expansion histories of a small number of distant-water fishing countries. While most countries fished largely in local waters, Taiwan, South Korea, Spain, and China rapidly increased their mean distance to fishing grounds by 2000 to 4000 km between 1950 and 2014. Others, including Japan and the former USSR, expanded in the postwar decades but then retrenched from the mid-1970s, as access to other countries’ waters became increasingly restricted with the advent of exclusive economic zones formalized in the 1982 United Nations Convention on the Law of the Sea. Since 1950, heavily subsidized fleets have increased the total fished area from 60% to more than 90% of the world’s oceans, doubling the average distance traveled from home ports but catching only one-third of the historical amount per kilometer traveled. Catch per unit area has declined by 22% since the mid-1990s, as fleets approach the limits of geographical expansion. Allowing these trends to continue threatens the bioeconomic sustainability of fisheries globally.

INTRODUCTION

Distant-water fishing, that is, fishing in areas far removed from a country’s domestic waters, existed well before the 19th century industrialization with, for example, Europeans fishing for Atlantic cod (*Gadus morhua*) off Newfoundland from the early 16th century (1) and Indonesians first fishing for *trepan* (sea cucumber) in northern Australia in the late 17th century (2). However, the practice accelerated with the deployment of the first steam trawlers around the British Isles in the 1880s (3). The increased fishing capacity of engine-powered trawlers led to greatly improved catches, but their introduction was soon followed by signs of depletion in coastal fish stocks and conflict with smaller inshore fishers (4). Vessels capable of moving further offshore did so, targeting less heavily exploited fishing grounds and beginning a process of progressive spatial expansion, first into the open North Sea, then south to the coasts of Spain and Portugal, and north into the North Atlantic waters around Iceland (4). The latter move ultimately led to a series of Cod Wars between 1958 and 1976, which culminated in the expulsion of British fishers from Icelandic waters (5). The industrial fleets of other developed countries followed similar patterns of expansion, interrupted only by wars and other crises (6, 7). Increasing competition between domestic and foreign fishing vessels for national fisheries resources was one of the motivations behind the series of international negotiations in the 1970s and 1980s, leading to the adoption of the United Nations Convention on the Law of the Sea (UNCLOS) in 1982 (8). Key to UNCLOS was its permission for maritime countries to declare 200-nautical mile exclusive economic zones (EEZs), within which they have exclusive responsibility and control over resource exploitation, management, and conservation. Although UNCLOS did not come into force until 1995, countries began asserting their sovereign rights to fisheries resources in unilaterally declared EEZs or exclusive fisheries zones after the early rounds of UNCLOS III discussions began in 1973, and

EEZ declarations accelerated in the 1980s. The expansion of sovereign claims to fisheries marked the beginning of the end of unrestricted and uncontrolled open-access fishing for distant-water fleets (9). However, this formalization of resource ownership and control affected the activities of the distant-water fishing fleets of major industrialized countries only briefly, as countries quickly moved to negotiate extensive access agreements for their fishing vessels, particularly in the waters of developing countries (10–12).

While a long history of expansion is well documented (3, 6), the second half of the 20th century saw an unprecedented increase in catching power, as industrial fisheries reaped a peace dividend from wartime technologies such as LORAN [long-range navigation; a precursor to Global Positioning System (GPS)], radar, and sonar (13–15). The postwar period also marked the start, in 1950, of detailed record collection at the global scale by the Food and Agriculture Organization (FAO) of the United Nations (16). However, while a huge and laudable undertaking, the FAO data ultimately derive from the annual reports of flag states, which have differed greatly in quality and scope of the data submitted, both between countries and years. These data are characterized by poor spatial resolution.

The Sea Around Us addresses several shortcomings in the data reported by FAO on behalf of flag states by reconstructing unreported catches using complementary data sources and in-country expertise to extend and harmonize official reported data. This catch data reconstruction process also allows Sea Around Us data to separate wider-ranging industrial from relatively local artisanal, subsistence, and recreational fisheries (17–19). Furthermore, the sector-specific reconstructed catches have been spatially allocated to a half-degree latitude-longitude resolution spatial grid system, using both biological probability distributions for each taxon in the catch data sets and detailed information on EEZ fishing access agreements and available spatial catch information (20). These high-resolution spatial and temporal reconstructed catch data have allowed the geographical expansion of industrial fisheries over time to be quantified and visualized. Here, we have examined, for the first time, the trends since 1950 in the mean distances traveled to fish by the industrial fleets of the 20 largest fishing countries, collectively accounting for 80% of global industrial catches, and the trend in total industrial catch relative to the growth in the total area fished.

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RESULTS

Analysis of the mean distance traveled by the industrial fleets of the world's 20 largest fishing countries between their home countries and the locations where catches were taken illustrates three distinct patterns: rapid and largely continuous expansion (Fig. 1A), early expansion followed by stabilization or retrenchment (Fig. 1B), and limited or no expansion (Fig. 1C). The fishing fleets of Taiwan, South Korea, Spain, and China have continuously expanded their mean distance to fishing grounds by at least 2000 km since the 1950s, with the first three of these now fishing, on average, more than 3000 km from their home ports (Fig. 1A). These are globally operating distant-water fleets and flag states, accounting for nearly 20% of the global industrial catch over the last decade (Fig. 1A). Spain was already fishing, on average, nearly 1500 km from home at the start of global data records in 1950 (Fig. 1A), largely driven by the country's long history of fishing for Atlantic cod off the Canadian east coast. Five countries or former countries that currently account for about 27% of global industrial catches showed expansion during the early postwar decades but appear to have curtailed or consolidated their distant-water operations since then (Fig. 1B). This includes the former USSR, which had a large distant-water fleet during the 1950s and 1960s, operating, on average, more than 2000 km from home. In scale and early timing of expansion, the former USSR is only exceeded by Spain, South Korea, and Japan (Fig. 1, A and B). However, while Spain and South Korea have continued a fairly monotonic expansion, the countries of the former USSR began to retrench in the 1970s. Japan, after rapid postwar industrial expansion, also consolidated its fishing effort within the Indo-Pacific region starting in the 1970s (Fig. 1B). The remaining 11 of the 20 largest fishing countries, accounting for 33% of global industrial catches, have shown little or no expansionist efforts over the last 65 years (Fig. 1C). Norway has begun to fish relatively further afield in recent years, likely driven by the rapid growth in contribution of its Antarctic krill (*Euphausia superba*) fishery from <1% of the national total catch in 2006 to 7% in 2014 (www.searoundus.org). For the top 20 fishing countries, catches caught on the high seas

or in the EEZs of other countries grew by more than 600% between 1950 and 2014, increasing their contribution to global catches from 16 to 23% over this period (www.searoundus.org). Catches by distant-water or "foreign" vessels have therefore grown faster than catches by countries within their own waters, illustrating the increasing importance of distant-water fishing among the countries that supply most of the world's wild-caught seafood.

Driven strongly by the trends in fishing distance among the 20 largest fishing countries, the net effect since 1950 is a global doubling of the mean distance fished from port (fig. S1). However, this net expansion has been associated with a strong decline in the catch obtained per kilometer traveled over the 65-year time period. Catches declined from more than 25 metric tons per 1000 km traveled in the early 1950s to approximately 7 metric tons per 1000 km traveled by 2014 (Fig. 2). The global industrial fishing catch increased fivefold between 1950 and its peak of 100 million metric tons in 1996 but has declined steadily by around 18% over the two decades since (Fig. 3A). In contrast, the percentage of total ice-free ocean area used for industrial fishing increased rapidly from 60 to 90% during the 1950s and 1960s, plateaued through the mid-1990s, and has expanded by less than 5% in the last two decades (Fig. 3B). The combination of these two patterns suggests that industrial catch per unit area of ocean fished expanded through peak catch in 1996 but has since declined by 22% (Fig. 3C).

A comparison of the spatial distribution of industrial catches between the 1950s and the 2000s illustrates and confirms the predominance of continental shelf waters as the source of most fish (Fig. 4, A and B). Expansions were most pronounced along the coasts and archipelagic waters of Southeast Asia, Africa, South America, and the South Asian subcontinent (Fig. 4, A and B). However, offshore and high seas waters have also become increasingly exploited in the past 65 years, with essentially no waters other than those at extreme high latitudes presently unfished to some degree (Fig. 4B).

DISCUSSION

The trends in the spatial expansion of industrial fisheries and their overall catch together indicate that we may be approaching the physical limits of expansion in capture fisheries (Figs. 3B and 4). Similar concerns have been raised by work showing the rapidly growing proportion of marine primary productivity being redirected to human consumption (6).

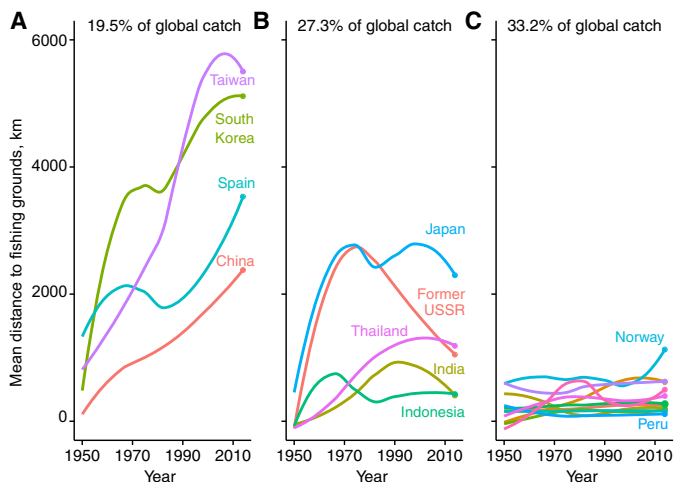


Fig. 1. Trends in the distance traveled to fish from 1950 to 2014. Mean distance to fishing grounds for the world's 20 largest industrial fishing countries (by tonnage) grouped by expansion history: (A) rapid and continuous expansion, (B) expansion followed by retrenchment, and (C) limited expansion. Percentage of global catch over the past decade is shown at the top of each panel. Countries not labeled in (C) are Argentina, Chile, Iceland, Malaysia, Mexico, Morocco, Philippines, and United States.

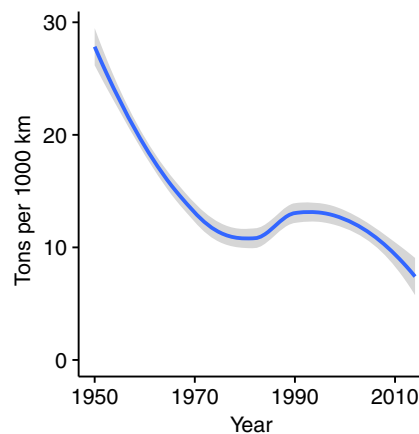


Fig. 2. Trend in mean global industrial catch per 1000 km traveled from 1950 to 2014. Gray band indicates $\pm 95\%$ confidence interval of LOWESS smoothed time series.

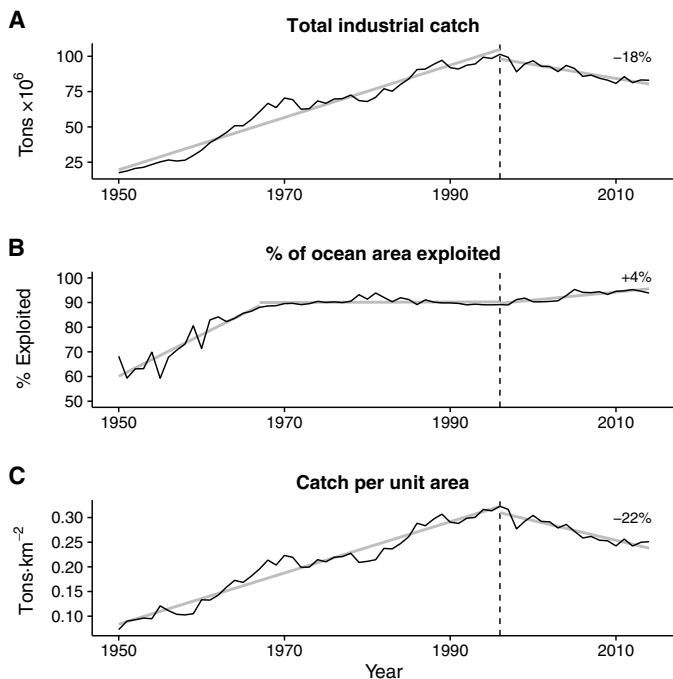


Fig. 3. Trends in total catch and area fished by global industrial fisheries, 1950–2014. (A) Global industrial fisheries catch (8), (B) percentage of ice-free ocean area exploited, and (C) industrial catch per unit ocean area. Dashed line indicates year of peak global catch in 1996, with percentage growth/decline since 1996 labeled on each time series.

The trends in catch and effort data presented here suggest that the continuous increase in global catches to peak catch in 1996 (17) resulted from a combination of intensifying fishing effort and geographical expansion, which together masked underlying declines in the stocks being targeted (21). Between 1950 and 1970, the fraction of the global ocean exploited by fisheries grew by half and catches increased strongly. We suggest that this continued expansion and the concurrent intensification of fishing effort sequentially depleted new areas of the ocean such that catches peaked in 1996 when the rate at which new stocks were discovered could no longer keep up with the declines in existing stocks (17, 18, 22). This mechanism of serial discovery and depletion of fishing grounds is exemplified by the correlation between time series of fishing pressure and ecosystem regime change in large marine ecosystems (23) and the “boom and bust” trends documented in deep sea trawl fisheries over the last 65 years (24). By our measure, total industrial catch per unit ocean area has declined by 22% since 1996, despite spatial expansion having continued, albeit slowly. Further expansion into the remaining accessible areas of the polar seas, even if it were ecologically justifiable, seems unlikely to reverse this trend (Figs. 3B and 4).

Distance trends observed here imply that most of the fishing countries concentrate their effort in relatively local waters, with Peru, for example, largely focusing on its domestic fishery for Peruvian anchoveta (*Engraulis ringens*) (25). In addition, several former distant-water fishing fleets either have retrenched to domestic or regional waters near home countries or have been reduced or abolished (Fig. 1, B and C). For example, the countries of the former USSR fished extensively in the waters of the southwest Atlantic and the EEZs of Argentina, Uruguay, and Brazil before the collapse of the Soviet Union with its state support of distant-water fisheries. They have since reduced their distant-water activities to concentrate on northeast Atlantic, European, and western

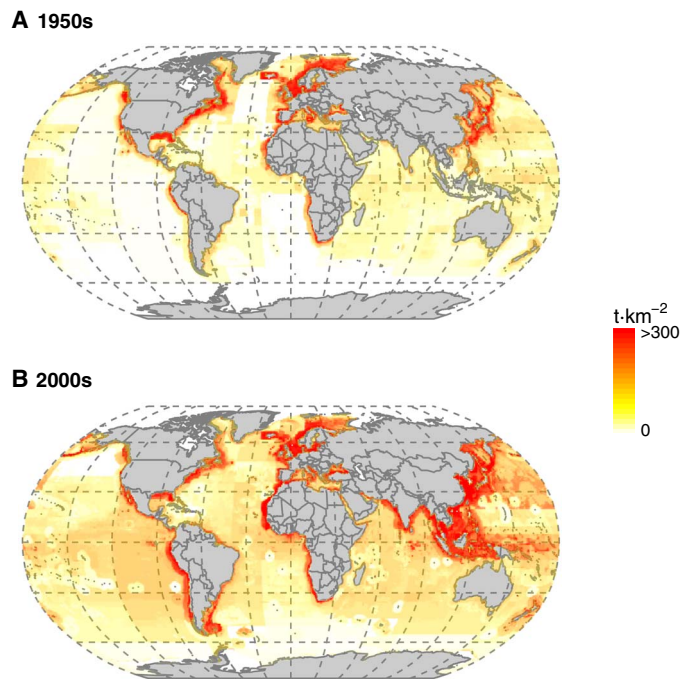


Fig. 4. Spatial mapping of the distribution and intensity of industrial fishing catch. Mean industrial fisheries catch in metric tons per square kilometer by catch location during the (A) 1950s and (B) 2000s.

Pacific waters closer to domestic ports (23). Japan, after rapid postwar expansion aimed at improving domestic food supply, began consolidating its distant-water fishing effort from the mid-1970s, as access to many of its traditional fishing grounds became increasingly restricted with the emergence of the EEZ regime and increasing competition from low-cost fishing countries. Rising domestic labor costs and growing wealth also shifted Japanese food supply policy toward imports, paving the way for fleet reductions and spatial retrenchments that have helped remaining Japanese distant-water fishing to be relatively profitable (26, 27). For the few countries seemingly locked into the expansionist strategy, such as China and South Korea, distant-water fleets have become the mainstay of their industrial fisheries, with catches from outside their EEZs contributing 39 and 45%, respectively, of national total catches (www.searoundus.org). However, returns from this activity, in terms of catch per unit distance traveled, appear to have declined sharply, likely a combined result of declining fish stocks and the greater distances required to access them (Fig. 2). Long-haul distant-water fishing also incurs significantly higher fuel and crew costs (28) due to the long travel times to fishing grounds [for example, (29)]. To keep vessels fishing, fuel costs may be partly offset by generous government subsidies (30–32), and there is a good correlation between the distance a country fishes from home and the level of subsidies paid for fuel, vessel, and fleet support. In the case of Taiwan, these payments amount to more than 80% of the landed value of the industrial fishing catch (fig. S2). The relationship between subsidies and fishing distance suggests that expansion has been driven, in large part, by national policies that actively promote distant-water fishing through the provision of fuel and vessel subsidies. A recent analysis of the economics of high seas fishing found that profits from these activities for the major distant-water fishing countries would be greatly reduced, or even disappear completely, if fleets were not subsidized (33). While governments continue to subsidize fleet expansion,

the labor costs of these operations can typically only be reduced by cutting back on crew numbers, pay, or working conditions, which may be contributing to the growing tally of human rights and labor abuses that have been recorded on fishing vessels (28, 34). Illegal fishing and the use of flags of convenience can also serve to reduce the cost component for vessels suffering diminishing returns (35).

Continuing distant-water fishing activities are also increasingly viable only due to the growing number of refrigerated transshipment and resupply vessels (or “reefers”) that allow individual fishing vessels to remain at sea for extended periods and avoid the fuel expenditure and lengthy breaks in fishing required to return to port or their home countries (34, 36). However, by transshipping and aggregating catches, and thus allowing fishing vessels to avoid port visits, reefers may also facilitate the “laundering” of illegally caught fish and permit other crimes at sea to remain undetected (37, 38). Transshipment also denies developing countries that host distant-water fleets (for example, in West Africa) the revenue from port activities and the processing and exporting of seafood associated with foreign fleets (36).

Our findings on the spatial expansion of industrial fishing are consistent with previous estimates by the Sea Around Us using only the FAO reported landings data (6). The spatial allocation of reconstructed fisheries data reported here assumes that fish are caught wherever a species’ spatial distribution overlaps the operating sphere of a fishery targeting it, in proportion to its habitat preference–driven probability distribution (20). Therefore, this approach likely constitutes an upper bound to the current spatial coverage of fisheries, with some locations at the fringes of a taxon’s distributional range likely not commercially viable for fisheries. For comparison, a recent analysis of vessel automatic identification system (AIS) data by Global Fishing Watch (GFW) and partners estimated that up to 73% of the oceans was fished in 2016, based on identifying gear-specific vessel movements assumed to indicate fishing activity and after taking into account spatial variations in AIS satellite coverage (34). Given that not all vessels carry or consistently use AIS transponders, for example, turning them off to preserve commercial secrecy around fishing grounds or during illicit activities, it is likely that the GFW figure is a lower-bound estimate of the area currently in use by industrial fisheries. Our analysis is able to provide historical context to the more precise but incomplete and temporally limited AIS data, showing how different countries have risen and fallen as distant-water fishing powers. The GFW study found that China, Spain, Taiwan, Japan, and South Korea dominate global industrial fishing effort; our results confirm that these five are also the world’s most important distant-water fishing countries in terms of distance traveled (34). Collaborative research efforts combining AIS data and catch reconstructions will further refine our understanding of the spatial distribution of catch and effort in these fisheries.

Global catch per unit of effort has halved since FAO records began in 1950, despite a steady improvement in fishing power and technology (39). Our analysis corroborates this evidence of diminishing returns, showing that, while fisheries have extended their reach into all but the polar extremes of the global oceans, catch per unit area and per kilometer traveled have declined continuously for over two decades. Considered alongside the well-documented increase in the number of overfished stocks (21), these trends warrant an urgent reduction in fishing effort if declines in fisheries productivity are to be halted and reversed. Reducing the high levels of fuel and capacity-enhancing subsidies paid by fishing countries, in particular by the very small number of countries that fish the furthest from home (Fig. 1, A and B), would be a powerful first step in addressing our global overfishing problem and

returning an element of economic rationality to commercial fisheries (33). Reducing the subsidies that enable unprofitable fishing on the high seas would also reduce income inequality among maritime countries (40). Fish are a vital component of global food and economic security, and further degrading the productive capacity of the oceans puts both at risk for hundreds of millions, if not billions, of people and increases the risk of fisheries conflict (41). As with other spheres of human endeavor, recognizing that there are physical limits to growth on a finite planet is vital to humanity’s long-term well-being. The oceans, once thought boundless and inexhaustible, may at last now also be proving a barrier to our quest for endless growth.

MATERIALS AND METHODS

The data were extracted from the global reconstructed fisheries catch database of the Sea Around Us (18). All Sea Around Us data and associated documentation and descriptions are freely accessible and downloadable at www.seaaroundus.org. Data can also be accessed through an R package via the Sea Around Us GitHub site at <https://github.com/seaaroundus/>. These data consist of more than 270 country-level catch reconstructions that currently cover 1950–2014 and that account for all fishing sectors (industrial, artisanal, subsistence, and recreational) as well as landed and discarded catches (42). These reconstructed data include best estimates of all unreported catches by year, fishing sector, and taxon for each country, following the established and well-documented catch reconstruction methodology (20, 43). It should also be noted that the baseline data for the Sea Around Us catch reconstructions are the data reported by member states to the FAO. Hence, all catches are assigned to a flag state (country) rather than that of the country of beneficial ownership. Thus, catch by vessels flagged to Togo but owned by a South Korean company, for example, will be assigned to Togo in both the original FAO data and the Sea Around Us reconstructed catch data. Had we been able to assign flag of convenience and open registry catches to beneficial owners, the average fishing distance of countries with significant numbers of foreign flagged vessels, such as Taiwan, Spain, and South Korea, would likely increase because, in many cases, those catches are treated as “local” catches of the flag state in our analysis rather than distant-water fishing by the beneficial owner country.

These reconstructed catch data sets were mapped onto a grid of $1/2^\circ \times 1/2^\circ$ latitude and longitude cells overlaid over the global oceans to generate data for more than 150,000 oceanic grid cells. Allocations of catch data to individual cells take into account spatial variation in species’ abundance, as well as political and historical accessibility of EEZ waters by the fleets of each fishing country (20). For the current analyses, only industrial sector data were used, as these represent the catches of fleets, including distant-water fleets, that fish domestically and internationally, that is, also outside of national EEZ waters. The nonindustrial catches from the small-scale artisanal, subsistence, and recreational sectors are excluded here as they are assumed to be spatially restricted to the inshore fishing areas within each home country’s EEZ (20). Larger “artisanal” operators capable of operating further out to sea would be included as “industrial” vessels under the Sea Around Us classification [for example, the large semi-industrial pirogue fleets of Senegal that fish throughout many West African countries (44)]. Filtering for industrial fishing only, >62 million cell/fishing entity/catch/year allocation records were extracted from the Sea Around Us database, together with grid cell metadata (latitude and longitude of cell centroid and total water area). These data formed the basis for all spatial analyses. Catch locations were deemed to be spatially represented by the cell centroids.

Distances to fishing grounds were calculated from each relevant cell centroid to the nearest major port of each fishing country. Port locations were obtained from the World Ports Index (WPI) (https://msi.nga.mil/MSISiteContent/StaticFiles/NAV_PUBS/WPI/WPI_Shapefile.zip). For a small number of island fishing countries without port listings in the WPI, the geographical center of their landmass was used instead of port locations. Geographical centers for the relevant island entities were downloaded from the Center for International Development at Harvard University (<https://sites.hks.harvard.edu/cid/ciddata/geographydata.htm>).

The catch-weighted average distance between the major ports of each fishing country and fishing grounds (cells with catch taken by each country in question) was calculated for each fishing country and year as follows (fig. S3):

1) Catches were summed within each $1/2^\circ \times 1/2^\circ$ grid cell (Catch in cell). The great circle distance from each grid cell centroid to the fishing country's nearest domestic port (Distance to cell) was then calculated using the function `distGeo()` in the R package `geosphere`.

2) The catch-weighted mean distance traveled to fish, for each country and year (1950–2014), was calculated as the weighted mean of all catch distances as follows

$$\frac{\sum_{i=1}^{180,000} (\text{Distance to cell}_i \times \text{Catch in cell}_i)}{\text{Total catch}}$$

The purpose of the calculation was to generate a measure that captured relative changes over time in geographic reach of the fisheries of the major fishing countries, and the distance measure derived here is therefore a simplification of the actual distances traveled by industrial fishing vessels. In particular, the great circle distance used here is the shortest straight-line distance between a country's major ports and the location of allocated fishing catches. This calculated distance thus ignored realities affecting actual vessel travel distances, including landmasses, shipping routes, and other navigational complexities. In addition, distances moved within a given $1/2^\circ$ cell to achieve the catch within that cell (that is, smaller-scale “searching” and fishing operation patterns) were not included here. We also omitted factors that would likely reduce an individual vessel's actual distance to fish, such as temporary or seasonal “home-porting” in ports outside a vessel's flag country, or the use of support vessels for catch transshipment and refueling at sea.

The mean distance traveled to fish was visualized for the 20 largest fishing countries, as ranked by total catch. The fishing countries of the former USSR (Estonia, Georgia, Latvia, Lithuania, Russia, and Ukraine) were treated as a single fishing entity to capture the expansion history of the Soviet Union, given its significant role in postwar industrial fisheries. Distance trends for each country were plotted as smoothed time series using locally weighted regression (LOWESS) (45) with a span coefficient of 0.75, implemented in the `stat_smooth()` function in the R package `ggplot2`. Plots were grouped according to three distance trends over the 65-year time period: steady and rapid increase, initial increase followed by stagnation or decline, or little or no increase.

The mean fishing distance for the global industrial fleet in each year was calculated as the catch-weighted mean of all individual country fishing distances, as calculated above. A smoothed time series ($\pm 95\%$ confidence interval) was plotted as per the method above. Tons of fish caught per 1000 km traveled were calculated by year for all countries' industrial fisheries by dividing the global industrial catch by the total distance traveled to fish by all countries, with individual country's fishing distances calculated using the methodology described above.

Total industrial catch and total area fished were calculated by summing total catch and total cell area with industrial catch by year for the entire data set. Only the water area of each cell was used, where cells crossed coastlines. The trend in total area fished was presented as a percentage of the total ice-free ocean area. This was taken to be the total ocean area, 361.9 million km^2 , minus the combined mean summer minimum ice coverage for the Arctic and Southern Oceans of 9.6 million km^2 (<https://nsidc.org/cryosphere/seaice/index.html>). Total ice-free ocean area available to fish was therefore estimated to be 352.3 million km^2 . Industrial catch per unit area (metric tons per square kilometer) was calculated as the total industrial catch divided by the total area fished in each year. The data were plotted as line charts overlaid with broken stick regression lines showing points of inflection in the trend lines, notably the point of peak fish in 1996.

The global geographical distribution of industrial catch was mapped for the first and last decades of the time series (1950–1959 and 2005–2014) by averaging total industrial catch in each cell for each 10-year period and plotting the resulting values as a spatially defined raster superimposed on the world map. Since the distribution of cell catch values was highly skewed, catch per unit area in each cell was color-coded using a logarithmic scale, to give greater visual resolution among the smaller values.

To examine the relationship between fishing distance and government subsidies, mean distance to fish was plotted against harmful (fuel and capacity-enhancing) subsidies as a percent of landings. Subsidies were taken from Sumaila *et al.* (31). The relationship was tested using linear regression, and the line of best fit ($\pm 95\%$ confidence interval) was added to the scatterplot. All analyses were performed using the R Statistical Language and packages in RStudio.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/4/8/eaar3279/DC1>

Fig. S1. Mean distance traveled to fishing grounds by the world's industrial fisheries.

Fig. S2. Mean distance traveled to fishing grounds versus harmful subsidies.

Fig. S3. Schematic of methodology used for great circle distance calculations.

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Acknowledgments: We appreciate the detailed and constructive reviews we received, which greatly improved the text. **Funding:** The authors acknowledge the support of the Sea Around Us and the Sea Around Us–Indian Ocean. All Sea Around Us activities are supported by the Oak Foundation, the Marisla Foundation, Oceana, the MAVA Foundation, the David and Lucile Packard Foundation, and the Paul M. Angell Family Foundation. **Author contributions:** D.P., D.Z., and J.J.M. conceived the analysis. D.T. analyzed the data, with support from M.-L.P., and produced the figures. D.P., D.Z., and D.T. wrote the manuscript, with reviews and edits by M.-L.P. and J.J.M. **Competing interests:** D.Z. is a member of the scientific advisory board of Denver (USA)-based NGO Secure Fisheries but receives no compensation or funding in this capacity. The other authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Data used in the analyses reported above are available upon request from the Sea Around Us (www.seaaroundus.org). Additional data related to this paper may be requested from the authors.

Submitted 26 October 2017

Accepted 10 July 2018

Published 1 August 2018

10.1126/sciadv.aar3279

Citation: D. Tickler, J. J. Meeuwig, M.-L. Palomares, D. Pauly, D. Zeller, Far from home: Distance patterns of global fishing fleets. *Sci. Adv.* **4**, eaar3279 (2018).


Appendix 2: Modern slavery and the race to fish.

ARTICLE

DOI: 10.1038/s41467-018-07118-9

OPEN

Modern slavery and the race to fish

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Marine fisheries are in crisis, requiring twice the fishing effort of the 1950s to catch the same quantity of fish, and with many fleets operating beyond economic or ecological sustainability. A possible consequence of diminishing returns in this race to fish is serious labour abuses, including modern slavery, which exploit vulnerable workers to reduce costs. Here, we use the Global Slavery Index (GSI), a national-level indicator, as a proxy for modern slavery and labour abuses in fisheries. GSI estimates and fisheries governance are correlated at the national level among the major fishing countries. Furthermore, countries having documented labour abuses at sea share key features, including higher levels of subsidised distant-water fishing and poor catch reporting. Further research into modern slavery in the fisheries sector is needed to better understand how the issue relates to overfishing and fisheries policy, as well as measures to reduce risk in these labour markets.

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Since the mid-1990s, global marine fisheries catches have steadily decreased¹ while fishing effort has continued to increase, leading to intense competition, declining catch-per-unit-of-effort and fisheries profitability, and the over-exploitation of many stocks^{1–4}. The consequent race to fish has been exacerbated by harmful government subsidies that enable fishing effort to persist beyond bio-economic limits⁵. The underlying pattern of decline has been masked in the officially reported data by inconsistent data reporting from some areas of the world^{1,6,7} and by a presentist bias⁸ that assumes improved catch reporting equals increased catches⁹. The resultant overly optimistic trend in government data has fostered suboptimal policies, in particular the allocation of resources to harmful capacity-enhancing subsidies rather than enforcement or stock rebuilding^{1,6,7}. Failure to manage fisheries sustainably has serious implications for human welfare, as fish (here meaning finfish and invertebrates) provide billions of people with protein and vital nutrients¹⁰, as well as employment and livelihoods for hundreds of millions of people¹¹.

Falling productivity and financial returns in commercial fisheries can pressure vessels to cut operating costs, at the extreme by fishing illegally, circumventing licensing costs and catch limits¹², and by reducing expenditure on crew pay, safety and living conditions. Estimates of fishing labour costs suggest that they comprise 30–50% of total fishing costs^{4,13}. The large contribution of labour to fishing costs suggests that, in addition to government subsidies received for fuel, vessel operators can capture a significant additional subsidy by aggressively reducing expenditure on crew, for example, by non-compliance with labour and safety standards or by withholding pay.

The push to reduce operating expenses to maintain profitability has occurred in the context of rising living standards and employment expectations in industrialised fishing countries, leading to domestic crew shortages and higher wage demands^{14,15}. Concurrently, the political marginalisation of coastal, small-scale fisheries throughout the developing world¹⁶, exacerbated by population growth, has contributed to a surplus of domestic and migrant labour in developing countries^{17–19}. This has polarised labour supply and demand between developed/emerging and developing economies, forcing people in the latter group to engage in any work available, including as fishing crew in an industry highly motivated to cut costs and that often operates out of reach of enforcement agencies^{14,20}.

Given the nature of working at sea, labour conditions of fishing crews are difficult to monitor. Supported by reefers and supply ships, fishing vessels can remain at sea for months during which time the crew may be unable to disembark²¹, with living and working conditions on such vessels generally beyond the oversight of regulators¹⁵. Given jurisdictional complexities, it is also often unclear in which country a crew member can seek redress in cases of abuse²². While flag-state responsibility matters, the growing use of flags of convenience further weakens the capacity to enforce regulations^{23,24}. These factors facilitate the use of exploitative employment practices to reduce labour costs at the expense of worker pay, safety and freedom²⁵.

The isolation of workers at sea makes the extent of labour issues in fisheries difficult to quantify. In recent years, however, high profile media investigations have identified a number of cases of extreme labour abuses in fisheries, some involving hundreds of fishing crew. Investigations of the Thai, Taiwanese and South Korean fishing industries identified cases of human trafficking, forced confinement, physical abuse and even murder^{26–30}. These incidents have not been confined just to the high seas or the waters of weaker jurisdictions. Some of the cases involving South Korean vessels took place while under charter in New Zealand waters^{31–33}. There have also been allegations of human

trafficking and debt bondage of African and Asian crew on domestic vessels in British and Irish fisheries^{34–36} and trafficking and confinement among South East Asian fishers employed in US fisheries in Hawaii³⁷. The US State Department lists 40 countries as source, destination or transit countries for human trafficking in fisheries³⁸, and vessels exploiting fishing crew have been encountered in the waters of Indonesia, Papua New Guinea, Russia and South Africa, as well as New Zealand^{25,39–41}. Labour rights abuses in fisheries appear widespread and serious, in many cases meeting the definition of modern slavery.

Modern slavery is defined, for the purposes of measurement, by the International Labour Organisation and the Walk Free Foundation (WFF) as “any situation of exploitation that a person cannot refuse or leave because of threats, violence, coercion, deception, and/or abuse of power”. This includes “forced labour, debt bondage, forced marriage, slavery and slavery-like practices and human trafficking”⁴². As the United Nations Office on Drugs and Crime notes, “the common denominator of these crimes is that they are all forms of exploitation in which one person is under the control of another”⁴³. At present, at least 40 million people are estimated to be trapped in modern slavery in textile, agriculture, construction and fisheries sectors, as well as in the sex industry and in forced marriage⁴². Modern slavery exists at the extreme end of a spectrum of exploitative and abusive labour practices, many of which remain legal in the jurisdiction in which they occur and/or are entered into voluntarily by workers^{14,20,25,44}. Commentators rightly argue that a narrow focus on slavery, without broader attention to the needs, ambitions and vulnerability of workers, risks inadequate or even counter-productive responses^{25,44}. However, unlike other labour issues, slavery is universally illegal, with prohibitions enshrined in global agreements including the 1926 Slavery Convention and the United Nations Convention on the Law of the Sea. It can therefore, in principal, be addressed using existing legal frameworks and instruments, and measures that identify and tackle slavery may have a positive impact on other less explicit forms of labour abuse. Importantly for the purpose of identifying global patterns, the above definition of modern slavery has allowed country-level estimates of the prevalence of modern slavery to be made by the Global Slavery Index (GSI)⁴⁵. While not directly quantifying slavery at sea, the GSI data provide a proxy for analysing the relationship between the prevalence of slavery-like practices in a country and fisheries’ characteristics at the global level, which may help identify drivers and policy priorities.

In addition to the structural elements in industrial fisheries that may incentivise and enable modern slavery and labour rights abuses, the global seafood trade is another critical dimension of the issue. Seafood is the world’s most widely traded food commodity⁴⁶, involving complex supply chains, with the chain of custody often passing through several intermediaries and countries before reaching the consumer. Traceability issues often arise before the fish even enter the supply chain, with the widely used practice of transshipment at sea allowing catches of multiple fishing vessels to be combined before landing, making the tracing of fish back to individual vessels currently impossible⁴⁷. A lack of consistent, accurate and transparent data from the point of capture to its final destination means that seafood caught illegally or unethically can effectively be laundered by combining it with legally caught fish in subsequent processing steps. The large consumer markets of the global north, including the USA and Europe, import large volumes of seafood to supplement domestic supply. Given that, for example, up to 32% of wild-caught fish imported into the US is estimated to have been caught illegally⁴⁸, it seems likely that fish caught under conditions of modern slavery can also enter the domestic supply chains of countries otherwise considered low risk for labour issues in fishing.

Kittinger et al.⁴⁹ called for the research community to more explicitly recognise and address the social dimensions of the ecological crises in the oceans. Modern slavery at sea is such an issue, but there is currently a paucity of quantitative research. The global data on country-level slavery from the GSI⁴⁵ and comprehensive data on fisheries and seafood trade from the *Sea Around Us*^{1,50} and the United Nations' COMTRADE database provide a base for a preliminary investigation. Here we (1) examine the empirical relationship between the GSI's country-wide prevalence of modern slavery (in all aspects of a country's economy) and fisheries' governance and financial performance; (2) separately identify factors common to those countries with reported labour issues specific to fisheries; and (3) model potential consumer exposure to modern slavery-derived seafood products by quantifying the flows of fish from high (GSI-based) slavery risk environments to relatively lower slavery risk markets.

Results

Analyses. Our analyses were performed in three separate stages. The first used linear models to test the overall relationship between the national prevalence of modern slavery, across all aspects of a country's economy, and industrial fisheries attributes among the major fishing countries of the world. Country-level estimates of the overall prevalence of modern slavery (of all types and across all economic aspects of a country) were taken from the GSI⁴⁵, and fisheries catch and economic data were obtained from the *Sea Around Us*^{1,50}. Here national-level GSI data covering all socio-economic aspects of a country were used as a proxy for likely fisheries-specific estimates of slavery prevalence, which are currently lacking for fisheries at the global level. The second stage used a multivariate clustering approach to identify additional fisheries and economic factors shared by countries with specifically identified slavery issues in fisheries, as reported in the literature and media; this second analysis did not use GSI data. The goal was to develop a qualitative risk model based on the fisheries and socio-economic factors associated with reported incidents of slavery that can frame further research efforts. The third analysis used United Nations' COMTRADE data and the GSI slavery prevalence measure to model the impact of the global trade in seafood on the presence of potentially slave-caught or processed seafood in consumer markets in the United States and Europe, regions where the risk of slave-produced seafood in domestic fisheries is otherwise considered low.

Country-level slavery and fisheries metrics. Linear regression modelling focused on the 20 highest-volume fishing countries, collectively landing over 80% of global industrial fisheries catch. Exploratory analysis found the best explanatory variables to be percentage of unreported catch and landed value of catch (Supplementary Table 1). The mapping of unreported catch (Fig. 1a), mean landed value of the catch (Fig. 1b), and the overall prevalence of modern slavery at the country level (Fig. 1c) for the world's major fishing countries suggest regional hot-spots of forced labour or modern slavery in Asia, Sub-Saharan Africa and parts of South America. Generally, these are areas with relatively high levels of unreported catch, predominantly low value fisheries and a relatively high overall prevalence of modern slavery at a national level. The country-wide prevalence of modern slavery in a given country is positively correlated with higher levels of unreported catch ($R^2 = 0.24$, $p = 0.017$, Fig. 1d) and negatively correlated with the landed value per tonne of fish being caught ($R^2 = 0.26$, $p = 0.013$, Fig. 1e). The multiple linear regression model using both variables explained 46% of the variance in the overall prevalence of country-wide modern slavery among countries ($p < 0.01$, Fig. 1f). Thus a high level of unreported catch,

representing poor management or enforcement oversight of fisheries, and a low unit-value catch, indicating poorer profitability, all other things being equal, correlate with a higher prevalence of modern slavery in the general economy of that country (Fig. 1f). While correlation is not causation, these results suggest a link between the presence of slavery and the overall performance of a country's fisheries. The analysis suggests broad underlying trends, yet also identifies outliers whose fisheries performance and country-level modern slavery prevalence do not fit the overall trend. While caution is needed when making inferences about specific economic sector-level labour abuses from the country-level GSI, the present analysis provides a basis for further, detailed sector-specific investigation.

Risk factors associated with known labour abuses at sea.

Having identified in the first analysis a broad correlation between the prevalence of modern slavery at the country level and two key fisheries attributes (unreported catch and mean landed value) for the top 20 fishing countries, we performed a separate principal component analysis (PCA) for the same 20 countries. The PCA grouped countries across six variables describing their economic status and fisheries performance/policy: unreported catch (% Unreported), percentage of catch caught outside their own exclusive economic zone (EEZ) (% Catch outside EEZ), per person Gross Domestic Product (GDP per capita; www.imf.org), level of harmful subsidies as a percentage of landed value (% Subsidy), mean landed value per fisher (Value per fisher), and mean distance of catch (Distance). No GSI data were used for this analysis. PCA summarises information contained in a group of n predictor variables as n principal components that capture the main dimensions of variation among the groups being measured, in this case the top 20 fishing countries. The first two components of the PCA explained 74% of the variation between countries. The first principal component axis (PC1) explained 44% of variance between countries and was correlated most strongly with '% Subsidy', '% Catch outside EEZ' and 'Distance'. The second principal component axis (PC2) explained a further 30% of variance and was correlated positively with '% Unreported' and negatively with 'GDP per capita' and 'Value per fisher' (Fig. 2). Overall, the individual explanatory variables made similar contributions to the model (Supplementary Figure 1). Clustering countries based on their score (i.e. location) on the first two PCA dimensions divided them into three distinct groups (Fig. 2). The first cluster comprised seven countries (red in Fig. 2), most of which have been reported for or suspected in serious labour abuses on fishing vessels^{15,32,39,40,51,52}. Countries with documented incidents of serious labour abuses in fisheries are therefore characterised by high levels of unreported catch ('% Unreported'), a high proportion of catch taken outside their own EEZs ('% Catch outside EEZ') at a greater distance from home waters ('Distance') and higher than average levels of harmful subsidies ('% Subsidy'). It appears that distance from home waters, non-EEZ fishing and poor fisheries oversight ('% Unreported') may substitute as potential risk factors for modern slavery in fisheries. However, owing to a lack of fisheries specific data on modern slavery by country, such conclusions must be drawn with caution and require further investigation.

The second group of countries (orange in Fig. 2) included mainly South American and Asian fishing countries with largely domestic fisheries or fisheries that use the waters of immediate neighbours. These countries were characterised not only by low levels of fishing outside their own or immediate neighbours' EEZs ('% Catch outside EEZ') and low levels of harmful subsidies ('% Subsidy') but also relatively low GDP per capita ('GDP per capita') and low value fisheries ('Value per fisher'). Future

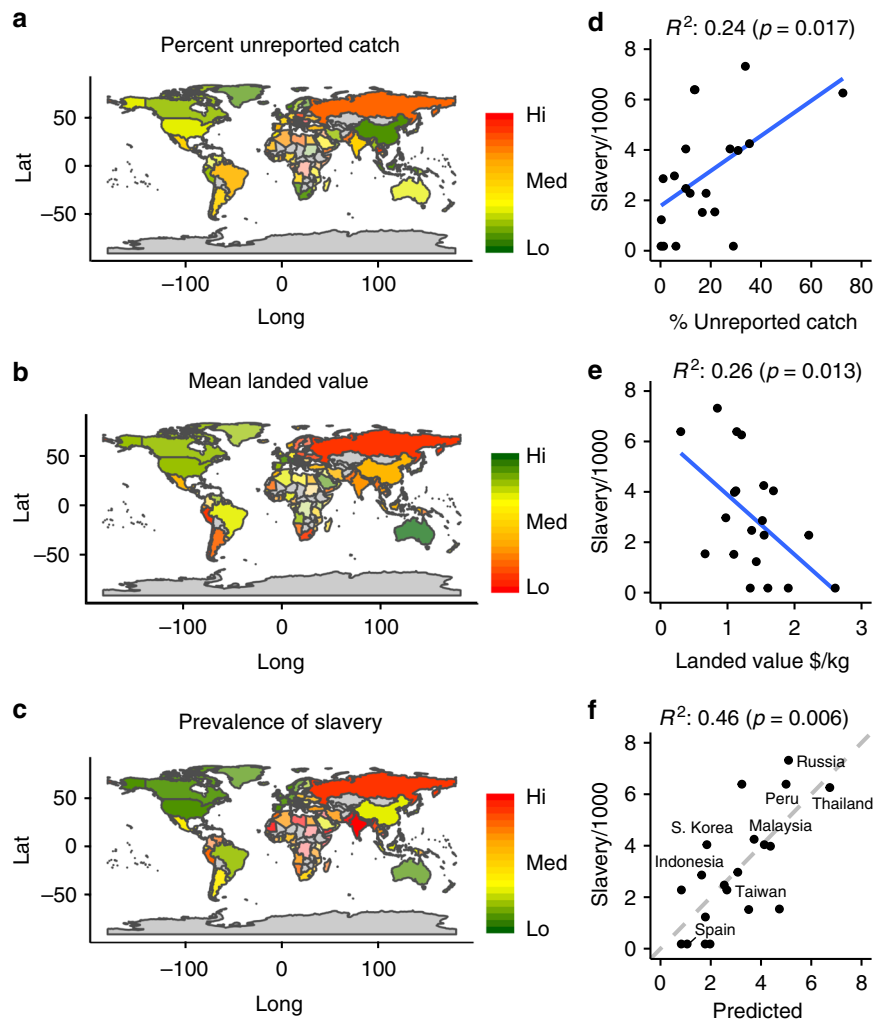


Fig. 1 Global patterns in country-level slavery and fisheries catch and value. Maps show **a** percentage of unreported catch, **b** mean landed catch value per kg, and **c** national prevalence of slavery, colour-coded by country. Scatterplots show relationship between country-level slavery prevalence and individual fisheries variables for the 20 largest fishing countries: **d** prevalence of slavery per thousand people (Slavery/1000) vs unreported catch (% Unreported catch), **e** prevalence of slavery vs mean landed value (Landed value \$/kg), and **f** observed against predicted values for a combined model, with selected European, Asian and South American countries labelled. Regression model R^2 values and F -test p values are labelled on scatterplots

research may show how these countries and these fisheries parameters relate to potential labour abuses or modern slavery in fisheries. The third group (green in Fig. 2) consisted of countries generally deemed low slavery risk (the USA and three European fishing countries) that were associated with low levels of unreported catch ('% Unreported'), high GDP per person ('GDP per capita') and high landed value per fisher ('Value per fisher').

Global trade and slave-produced seafood. Finally, we assessed seafood trade data in relation to modern slavery risk to understand the extent to which fish being caught and processed by high slavery-risk countries is potentially consumed in markets that have a low risk of slavery in their own domestic supply chain. Globally, an average of >33 million tonnes of seafood were traded annually between 2005 and 2014, based on harmonised UN COMTRADE data (<http://www.cepii.fr>). Seafood supply in the top developed countries includes significant proportions of imported wild-caught fish: in the United States, around 45% of domestically consumed seafood is imported wild-caught fish

(<http://www.nmfs.noaa.gov>), while in the EU this is 50%⁵³. Total imports are even higher when aquaculture products are considered. Consequently, the seafood available to consumers in these otherwise low slavery-risk countries can end up being a mix of domestic products from local fisheries, predominately in national waters, and products imported from a wide variety of other countries, including from countries with a higher risk of country-wide slavery.

The United States is highly dependent on imported seafood to meet domestic demand and accounts for roughly 14% of global seafood imports. It has a national slavery prevalence of 1.8 victims per 10,000 persons in the population (0.018%)⁴⁵. Expressed in term of kilograms of potential slavery-risk seafood per tonne, this equates to a slavery risk of 0.2 kg per tonne of domestically produced seafood, assuming the national prevalence of slavery is applied to all sectors of the seafood industry. Based on the average volumes of seafood imported from other countries, in particular from Asia-Pacific countries, seafood imported into the US has an average potential slavery risk of 3.1 kg per tonne, 17 times higher than the risk of seafood sourced from domestic fisheries (Fig. 3a). After accounting for the mix of domestic and imported seafood in

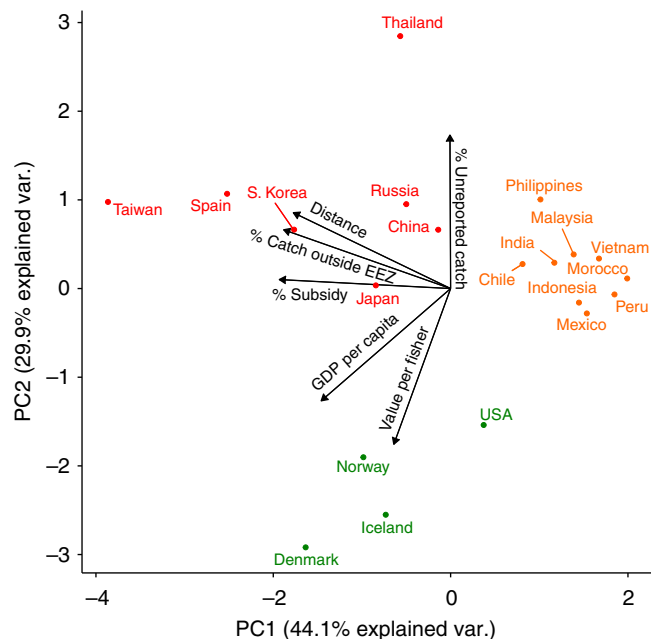


Fig. 2 Biplot of principal components analysis (PCA) for the top 20 industrial fishing countries. Countries are represented based on their aggregate scores across three economic and three fishing activity measures. Arrows indicate direction of increasing value for each variable. Colour-coding indicates cluster membership determined by *k*-means clustering of countries based on their scores on the main PCA dimensions (PC1 and PC2)

US domestic supply, the potential slavery risk of seafood supply within the United States increases 8.5 times due to its dependence on imports (Fig. 3a).

Similarly, the low slavery-risk countries of Europe also account for 14% of global seafood imports. Based on the GSI assessment, these countries (i.e., Denmark, France, Germany, Ireland, Netherlands, Norway, Spain, Sweden and United Kingdom) have an average national slavery prevalence of 2.8 victims per 10,000 persons (0.028%) across their combined populations. Considering the slavery prevalence of the countries from where seafood is imported into this block, the potential slavery risk of imported seafood is 3.8 kg per tonne, 13 times higher than that for their domestically sourced seafood (0.3 kg per tonne). Thus the mix of imported and domestically sourced seafood increases consumer exposure to potentially slavery-derived products is 8.6 times (Fig. 3b), similar to the modelled effect in the United States.

Discussion

Sustainable fisheries underpin both environmental and socio-economic development goals for the oceans⁵⁴, but until recently much of the research has focused on environmental and economic impacts, with less focus on human rights^{4,29}. While links between modern slavery and environmental destruction in illegal mining and deforestation are now well recognised⁵⁵, the connections between environmental challenges and human rights in fisheries have been less systematically documented. However, labour issues in fisheries have received increased attention in recent years^{14,15,25,56}, leading to emerging responses from governments and trading partners (e.g. Thailand-EU), non-governmental organisations (NGOs, e.g. Fair Trade), and major industry-research partnerships such as the Seafood Business for Ocean Stewardship initiative (SeaBOS^{57,58}). An understanding of potential slavery at sea at the global level can place these isolated cases and responses in a broader policy context.

The present analyses have focussed on using comprehensive and publicly available global data sets to examine empirical links between country-level slavery prevalence and industrial fisheries and the role of the global trade in seafood in moving seafood products from potentially high slavery-risk producer to low-risk consumer countries. Treating the national, non-fisheries-specific prevalence of modern slavery measured by the GSI⁴⁵ as a proxy for the as-yet unmeasured slavery risk across fishing industry sectors, we found a correlation between the prevalence of modern slavery within a country and proxies for poor fisheries accountability (i.e., high levels of unreported catch) and low profitability (i.e., low landed value of the catch) in the industrial fisheries of the major fishing countries. It should be emphasised that the GSI is not currently designed to differentiate sector-specific slavery risks, such as for fisheries. Indeed, localised fisheries-specific surveys conducted by NGOs suggest that the national, country-level GSI measure used here may in fact underestimate modern slavery practices in some industrialised fishing fleets. For example, interviews with migrant fishers in Thailand found that 17% of respondents had experienced conditions of modern slavery⁵⁹, compared with the GSI's estimate of <1% of workers nationally across all sectors. Conversely, for countries where land-based slavery practices dominate (for example, mining or agriculture), the GSI's estimate may imply a higher risk for fisheries than may be the case. With this caveat, there remains a broadly linear relationship between national, country-wide levels of slavery prevalence and poor fisheries performance, based on the global data currently available.

To explore risk factors linking the smaller subset of known incidents of slavery at sea, a separate multivariate analysis was then used to identify fisheries and economic attributes shared by those countries with documented fisheries-specific labour abuses. Cluster analysis indicated that countries with documented labour abuses in sections of their fishing industry share several key features: high levels of harmful capacity-enhancing subsidies, likely leading to excess fishing capacity, increased competition and reduced per-vessel profitability; low catch value per individual fisher, suggesting downward pressure on wages; high levels of undocumented fishing activity, implying poor monitoring and enforcement of vessel operations at sea; and a reliance on fishing far from home in the waters of other countries where regulatory violations may be more likely to go undetected by domestic agencies. Additional evidence of the role of distant-water fisheries in slavery at sea appears in reports detailing specific cases of labour abuse in fisheries, with many victims never even visiting their employer's country (i.e. the vessel's flag or beneficial ownership state), instead transiting through maritime hubs or countries closer to fishing grounds^{15,51}. The nature of distant-water fishing operations, where transhipment of catch and crew at sea are commonplace and observer coverage is typically low, appears to facilitate illegal behaviour⁴⁷. The last factor in our multivariate model, GDP per capita, may reflect the importance of economic disparity between labour demand and labour supply countries in driving labour migration, with documented incidents of slavery occurring in countries with relatively high per capita wealth compared to the country of origin of the victims⁵⁹. For example, Thailand's GDP per capita is over three and four times that of Myanmar and Cambodia, respectively, i.e. countries from which it sources the majority of its foreign fishing labour (www.imf.org)⁶⁰. In drawing these conclusions from our analyses, we recognise that fisheries within a single country will differ widely on both social and environmental performance metrics, as the coexistence of Fair Trade-certified tuna fisheries (www.FairTradeUSA.org) and fishing slaves trapped on islands in Indonesia²⁶ demonstrates. Nevertheless, while such distinctions must be factored into domestic policy, a model of the common drivers of potential

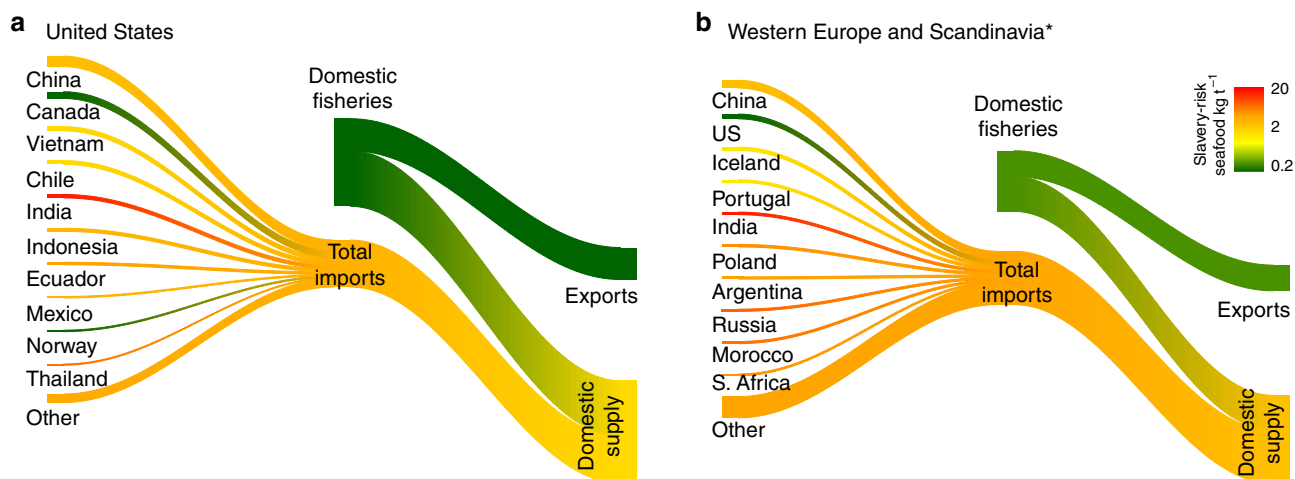


Fig. 3 River plots showing the impact of seafood imports on the modern slavery risk of domestically consumed seafood. Slavery risk is expressed in kilograms of seafood from slavery-risk countries per tonne consumed. Slavery risk scores based on the Global Slavery Index; trade flows from CEPII's BACI database of harmonised UN COMTRADE data. Plots show seafood imports for **a** the United States and **b** Western Europe and Scandinavia (includes Denmark, France, Germany, Ireland, Netherlands, Norway, Spain, Sweden, and United Kingdom). Colour of trade flow components indicates the intensity of slavery risk

slavery at sea across fishing countries can provide a framework to prioritise research and policy development at the international level. While exploratory in nature, our findings suggest that the well-recognised subsidy-fuelled race to fish, a lack of adequate monitoring, control and surveillance of industrial fishing activities and the influence of economic disparity on labour markets has made this sector a fertile ground for modern slavery and other violations^{24,61,62}.

The volume, diversity and global scale of the international trade in seafood⁴⁶ means that seafood produced by countries with poor records in both modern slavery and fisheries governance may find its way into the domestic markets of better regulated countries. Potentially slave-caught or processed seafood can reach consumers directly, as wild-caught product, and indirectly via fishmeal used in livestock and aquaculture feed. Fishmeal supplied by reduction fisheries targeting pelagic fishes, together with millions of tonnes of unmarketable trash fish caught as bycatch, eventually end up on consumer plates as farmed salmon, tuna or prawns or even pork, chicken, eggs or beef^{63,64}. Many wealthy seafood producing countries, including the United States and European countries, export much of the fish produced by their own fisheries and meet net domestic demand with imports of cheaper seafood products from areas such as Southeast Asia, Africa and Russia^{65,66}. Our analysis of UN trade data suggested that this could result in a greater than eight-fold increase in the exposure of their consumers to potentially slave-caught or produced seafood. To date, however, cases linking specific products to labour abuses have been isolated, and further work on traceability as well as fisheries slavery is required to confirm this hypothesis. For comparison, work done to model the flow of illegally caught seafood into the major consumer markets of the US and Japan (together almost 30% of global seafood imports) found that illegally caught products likely constituted 20–32% and 24–36%, respectively, of each country's wild seafood imports^{48,67}. It seems plausible that the current lack of supply chain transparency and product traceability that allows the products of illegal and unreported fishing to enter supply chains also facilitates the international movement of slave-caught and processed seafood.

The issues raised by our modelling of slavery, fisheries and seafood trade suggest four broad areas of policy engagement: (1) regulation and enforcement, specifically universal minimum

standards for crew pay and conditions, such as those specified in the International Labour Organisation's Work in Fishing Convention (C-188), and improved monitoring and enforcement of currently weak jurisdictions, including the high seas, to reduce the scope for unsustainable and unethical fishing practices⁶⁸; (2) supply chain transparency, specifically by adopting supply chain legislation, such as the UK's Modern Slavery Act (Modern Slavery Act 2015, s 54), which can bolster industry-led efforts such as SeaBOS to leverage businesses' market position to tackle sustainability and ethical issues⁵⁸. Policing supply chains can be supported by technologies, such as Blockchain ledgers and smart seafood labelling, which improve the security and lower the cost of reliable supply chain data⁶⁹; (3) industry restructuring, specifically by reducing harmful subsidies that currently overcapitalise fishing capacity^{5,70}, and redirecting subsidies towards enforcement and the rebuilding of sustainably managed small-scale fisheries capable of providing more and better livelihoods^{11,71}; and (4) improving equity between stakeholders in fisheries, specifically by restricting high seas fishing, which is currently dominated by higher-income countries⁷². Complete closure of the high seas to fishing has been modelled to reduce income inequality among fishing countries by 50%, by ensuring more equitable access to valuable migratory fish stocks⁷³.

These issues have also emerged as key topics in the broader discussions of sustainability in global fisheries as they affect our current ability to effectively manage fisheries for the collective benefit of humanity. This apparent overlap offers an opportunity to leverage regional and international initiatives to benefit both ecological sustainability and social/ethical goals. As research around labour issues in fisheries crystallises, there is great potential for marine scientists and social scientists to collaborate in developing policy frameworks that jointly tackle sustainability and human rights issues. The rapid expansion of industrialised fishing over the past 60+ years has negatively impacted the ability of marine ecosystems to sustainably supply humanity with seafood. The concurrent failure by government decision makers, policy developers and fisheries managers in many regions to adapt to the changes in industrial fisheries has rendered much of the high seas, as well as the waters of developing countries in fisheries-rich areas such as West Africa, open to abuse of both fisheries regulations and international labour standards, allowing illegal fishing and, potentially, labour abuses to flourish^{15,24,73,74}.

Modern slavery and fisheries' performance appear linked at the international level, with a correlation between increased prevalence of country-level modern slavery and higher levels of unreported catches and lower mean value of the catch of industrial fisheries for the 20 countries who supply the bulk of the world's wild-caught seafood. Further research and improved data are urgently needed, as the GSI can presently only report on the risk of slavery at the whole-country level. Given the current lack of reliable data on the prevalence of fishery-specific slavery and labour abuses, the country-level GSI is the most appropriate substitute metric currently available. Based on the limited information available on specific instances of slavery at sea, the over-subsidised and often poorly governed, distant-water fishing fleets of higher-income countries may be at particular risk of labour abuses and modern slavery. Our preliminary trade model, using peer-to-peer trade in seafood products, indicates that products of fisheries from slavery-prone regions/countries may be consumed in developed countries in significant quantities, potentially making seafood consumers in developed countries unwitting participants in modern slavery.

Much additional work is required to quantify the prevalence of labour abuses and modern slavery in seafood capture, aquaculture, processing and in the seafood supply chain. Generating comprehensive and accurate estimates of the prevalence of modern slavery in the fishing industry and seafood supply chain will not be easy, as fishing vessels rank among the world's most inaccessible workplaces. However, like the challenge of enforcing environmentally more benign fishing practices, it is an obstacle that must be overcome.

Methods

Data sources. Data on global fish catches by fishing country were obtained from the *Sea Around Us* reconstructed global catch database¹. The methods used for catch data reconstructions and the spatial allocation of global catches are well established⁷⁵ and individual country reconstructions are summarised in Pauly and Zeller⁵⁰, with detailed technical descriptions accessible via www.seaaroundus.org for each country. Using the *Sea Around Us* reconstructed catch data, we calculated the annual mean (\pm SE) reported and unreported industrial landings (in tonnes, excluding discarded catch) for the decade between 2005 and 2014 for the top 20 industrial fishing countries representing 80% of global landings. Thus here the term catch is used to represent landed catch (i.e. landings) and excludes discarded catch⁷⁶. In line with international data reporting mechanisms, all catches are supposed to be reported by the flag-state of the fishing vessel (i.e., the flag flown by the fishing vessel) and not the country of residence of the beneficial owner. The fishing activity modelled in our analysis is therefore that of the flag-state reporting the catch on behalf of its flagged fleets. Clearly, flag-hopping, i.e. the tendency by some distant-water fleets to regularly and often rapidly re-register to different flags, makes data reporting for distant-water fleets challenging, and better resolution of this issue needs to be a subject of further investigation.

Data on fisheries employment in the industrial sector used here were taken from Teh and Sumaila¹¹, excluding small-scale fisheries. Estimates of fisheries subsidies by category (beneficial, harmful and ambiguous) and type (fuel, vessel buyback, etc.) were obtained from the *Sea Around Us*⁵. Estimates of GDP per capita, in purchasing power parity-adjusted US dollars, were obtained from the International Monetary Foundation's IMF DataMapper site (<https://www.imf.org/external/datamapper/PPP/PPPC@WEO/OEMDC/ADVEC/WEOORLD>). The catch weighted mean distance of fishing activity from home for each fishing country was calculated using the $\frac{1}{2} \times \frac{1}{2}$ degree cell-allocated catch data of the *Sea Around Us*⁷⁵. *Sea Around Us* catch data are spatially allocated by intersecting biological probability distributions for each taxon in the catch data with a global fishing access database detailing in which country's EEZ foreign fleets are permitted or have been observed to fish⁷⁵. Distance from home for each catch cell was calculated as the great circle distance between the centroid of each catch cell and the closest domestic port of the fishing country, with port locations taken from the World Ports Index. The catch weighted mean distance was the weighted average of all such cell-port distances, weighted by the catch for that country in each spatial cell, using the methodology employed in Tickler et al.⁷⁷.

Data on the scale of modern slavery were taken from the GSI database⁴⁵, which reports estimates of vulnerability to and prevalence of slavery for 167 countries. Modern slavery was defined as 'situations of exploitation that a person cannot refuse or leave because of threats, violence, coercion, abuse of power or deception'⁴⁵. Slavery vulnerability scores in the GSI were generated based on a detailed model of country-level measures of governance and civil protections⁴⁵. Prevalence, defined as the percentage of the population trapped in modern slavery,

was estimated from data collected on behalf of the WFF as part of the Gallup World Poll (www.gallup.com) through face-to-face interviews with >42,000 respondents in 25 countries between 2014 and 2016. Estimates for unsurveyed countries were extrapolated from the subset of surveyed countries using a model based on the relationship between prevalence and vulnerability⁴⁵. Slavery prevalence was presented in this study as individuals per 1000 population rather than a percentage for ease of comprehension and represents country-wide slavery prevalence across all economic sectors and not fishing-sector-specific slavery. A detailed description of the methods used for measuring modern slavery is provided in the 2016 GSI⁴⁵ and the references therein.

Global trade flows for seafood commodities, estimated as imports and exports of individual seafood commodities in tonnes of seafood product (not wet weight) by country, were taken from the BACI harmonised trade database provided by the Centre d'Etudes Prospectives et d'Informations Internationales (CEPII) in France (www.cepii.fr). The BACI database uses data from the UN's COMTRADE database, processed so as to resolve inconsistencies between commodity-level import and export volumes and values between countries. BACI data categorised by commodity using the 2012 harmonised system six-digit codes were used, wherein the group of commodities beginning with 03---- represents both wild-caught and farmed seafood products; it was not possible to distinguish between farmed and wild-caught products. The BACI estimates of trade flows were averaged for 2011–2014.

GSI and fisheries performance measures. The relationship between country-wide slavery prevalence and candidate fisheries measures (percentage of unreported landings, landed value of catch per kg and tonnes landed per fisher) was tested using multiple linear regression, with competing models compared using sample size corrected Akaike's Information Criteria (AIC) scores (AICc). Model data were taken from the top 20 industrial fishing countries, representing 80% of global catch. Given the high prevalence of land-based modern slavery in India⁴⁵, our approach was to treat India as an outlier for the linear regression analysis. This decision was made based on additional information available for India, for which GSI data were collected at the state level, indicating that modern slavery levels in land-locked states heavily influenced the whole-country estimate. The best model, judged by AICc, used percentage of unreported landings and landed value of catch per kg as predictor variables (Supplementary Table 1). The relationships between country-wide slavery prevalence and percentage of unreported catch and between country-wide slavery prevalence and the mean landed value of catch were visualised in individual scatterplots. Model fit for the final model was visualised by plotting observed against predicted values.

Sensitivity analysis was performed on the final multiple regression model to test the effect of uncertainty in the fisheries and slavery estimates on the model outcome. Fisheries parameters were modelled for each country as being normally distributed with the mean and standard deviation calculated from the 2005–2014 *Sea Around Us* data. Country-wide slavery data were modelled as normally distributed with a mean equal to the reported value and standard deviation equal to the 95% confidence interval divided by 1.96. A Monte Carlo simulation of 10,000 model runs of the multiple linear regression model was used to build a distribution of R^2 values based on likely values for model inputs. Histograms of the output for three alternatives were plotted: varying all variables, varying only fisheries variables and varying only slavery variables (Supplementary Figure 2). The median R^2 value for models varying all variables was 0.29, vs 0.46 for the model using mean fisheries values and the GSI-reported country-wide slavery values, which is reported in the results.

To visualise global geographic patterns in both country-wide slavery and fisheries performance, fishing countries' mean values for the predictor and response variables used in the final model (percentage of unreported catch, landed value of catch per kg, and slavery prevalence at the national level) were mapped. Countries were classified by the three measures, with red representing poor performance (high unreported catch, low mean landed value, high country-wide slavery prevalence) and green the opposite. The classification of prevalence of modern slavery, as reported in the GSI, are country-wide data and not specific to the fisheries sector.

Modelling risk factors associated with slavery at sea. PCA followed by k -means clustering was performed on the top 20 fishing countries based on 6 measures hypothesised to predict the occurrence of modern slavery in fisheries: unreported catch ('% Unreported'), mean landed value per fisher ('Value per fisher'), percentage of catch caught outside their own EEZ ('Catch outside EEZ'), GDP per capita (www.imf.org), level of harmful subsidies as a percentage of landed value ('% Subsidy'⁷⁵) and mean distance of catch ('Distance') calculated from cell-level catch data of the *Sea Around Us*^{1,75}. The objective of the analysis was to identify the shared characteristics of groups of major fishing countries based on their involvement in known cases of modern slavery in fisheries, to explain outliers in the linear model and to identify other at-risk fisheries that were not highlighted by the linear analysis. Scores on the first two principle components of the PCA, capturing the most important components of variation in the predictor data set, were used to group the countries using a k -means clustering algorithm (i.e. grouping countries into k groups based on their similarity across the composite measures). The optimum number of clusters (k) for this step was determined analytically using the

NbClust() function in R, which finds the number of clusters that minimises the total within-cluster variance (i.e. makes the group members as alike as possible). The first two components of the PCA were visualised as a biplot, with the cluster members colour-coded (red, orange, green) based on their score on the first two PCA components.

Slavery and global seafood trade. The impact of imports of seafood into a country or region on the country-wide slavery prevalence (risk) associated with its domestic seafood supply was modelled using commodity-level country-to-country trade flows in the BACI harmonised UN COMTRADE data. The BACI data allow individual commodity flows between countries to be identified, so that flows of seafood carrying different slavery risks, based on country of production, can be precisely estimated. No distinction could be made between seafood caught by a country and exported, or imported, processed and re-exported, since that level of information is not supplied. However, this was not a significant issue since national cross-sectoral country-wide slavery prevalence was being used to score seafood exported from a country. Therefore, it was implicitly assumed that all seafood exported by a given country, whether caught by domestic fleets or processed from imports, carried the same risk of potentially involving slavery. The slavery prevalence of seafood imports into a particular country or group of countries was then calculated as average of the GSI country-wide slavery prevalence scores of the countries supplying that seafood, weighted by tonnes of seafood products imported from each country. Although the GSI slavery prevalence is not specific to the capture fisheries sector, traded fisheries products necessarily involve labour across multiple sectors beyond fisheries, and so a cross-sectoral estimate of the prevalence of slavery gives a reasonable estimate of the slavery risk of products originating in or being re-exported from a particular country. Domestic supply in turn was the average of the slavery prevalence of imports and domestic production, weighted by import tonnage and domestic production net of exports. Internal trade within a bloc of importing countries was considered part of domestic supply, rather than exports. Seafood trade and consumption flows were visualised using a Sankey plot (also known as a river plot) where the width of connections between nodes is proportional to tonnes traded or produced. River plots were produced in this way for the United States (14% of global imports) and the low slavery risk seafood-importing countries of Western Europe (Denmark, France, Germany, Ireland, Netherlands, Norway, Spain, Sweden and United Kingdom; 14% of global imports).

All statistical analyses were performed using the R statistical language and packages in R Studio.

Data availability

All relevant data are available on request from the authors. All *Sea Around Us* data are freely available via www.seaaroundus.org and can also be accessed via the R package *seaaroundus* (see <https://github.com/seaaroundus/>). Teh & Sumaila's fisheries employment estimates are available at https://onlinelibrary.wiley.com/action/downloadSupplement?https://doi.org/10.1111/j.1467-2979.2011.00450.x&file=faf450_sm_Table.S1.doc. Country-level estimates of the prevalence of modern slavery were taken from the Global Slavery Index (<https://www.walkfreefoundation.org/>). Global trade flows for seafood commodities are provided by the Centre d'Etudes Prospectives et d'Informations Internationales (CEPII) (<http://www.cepii.fr>). The economic data used can be obtained from the International Monetary Foundation's DataMapper site (<https://www.imf.org/external/datamapper>).

Received: 5 October 2017 Accepted: 26 September 2018

Published online: 07 November 2018

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Acknowledgements

D.T., J.J.M., D.P., U.R.S. and D.Z. acknowledge the support of the *Sea Around Us*, the Fisheries Economics Research Unit and the *Sea Around Us* – Indian Ocean. All *Sea Around Us* activities are supported by the Marisla Foundation, the Paul M. Angell Family Foundation, the Oak Foundation, the MAVA Foundation, the David and Lucile Packard Foundation and Oceana. K.B. F.D., E.G., J.J.L., B.O. and D.T. acknowledge the support of the Walk Free Foundation.

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J.J.M., J.A.H.F., F.D., D.P., D.T. and D.Z. were involved in the conception of the project and bringing together the Walk Free Foundation and *Sea Around Us* databases. D.T. performed all data analyses and figure preparation, supported by E.G., J.J.L. and B.O. who collated and prepared the data sources and performed supporting analyses. D.T., J.J.M., F.D. and D.Z. drafted the manuscript, with substantial editorial input from K.B., J.A.H.F., E.G., B.O., D.P. and U.R.S.

Additional information

Supplementary Information accompanies this paper at <https://doi.org/10.1038/s41467-018-07118-9>.

Competing interests: The authors declare no competing interests.

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Appendix 3: Estimating space use of mobile fishes in a large marine protected area with methodological considerations in acoustic array design.



Estimating Space Use of Mobile Fishes in a Large Marine Protected Area With Methodological Considerations in Acoustic Array Design

OPEN ACCESS

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Specialty section:

This article was submitted to
Marine Megafauna,
a section of the journal
Frontiers in Marine Science

Received: 22 February 2019

Accepted: 30 April 2019

Published: 22 May 2019

Citation:

Carlisle AB, Tickler D, Dale JJ,
Ferretti F, Curnick DJ, Chapple TK,
Schallert RJ, Castleton M and
Block BA (2019) Estimating Space
Use of Mobile Fishes in a Large
Marine Protected Area With
Methodological Considerations
in Acoustic Array Design.
Front. Mar. Sci. 6:256.
doi: 10.3389/fmars.2019.00256

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Marine protected areas (MPAs) have become an increasingly important tool to protect and conserve marine resources. However, there remains much debate about how effective MPAs are, especially in terms of their ability to protect mobile marine species such as teleost and chondrichthyan fishes. We used satellite and acoustic tags to assess the ability of a large oceanic MPA, the British Indian Ocean Territory MPA (BIOT MPA), to protect seven species of pelagic and reef-associated teleost and chondrichthyan fishes. We satellite-tagged 26 animals from six species (Blue Marlin, Reef Mantas, Sailfish, Silky Sharks, Silvertip Sharks, and Yellowfin Tuna), producing 2,735 days of movement data. We also acoustically tagged 121 sharks from two species (Grey Reef and Silvertip Sharks), which were monitored for up to 40 months across a large acoustic receiver array spanning the MPA. We found that the activity spaces of all satellite-tagged animals, including pelagic species, were much smaller than the area of the BIOT MPA, even taking into account errors associated with position estimates. Estimates of space use of acoustically tagged sharks, based on dynamic Brownian Bridge Movement Models (dBBMM), were also much smaller than the size of the MPA. However, we found important limitations when using dBBMM and demonstrate its sensitivity to both study duration and array design. We found that Grey Reef Sharks should be monitored for at least 1 year and Silvertip Sharks for 2 years before their activity space can be effectively estimated. We also demonstrate the potentially important role that intraspecific variability in spatial ecology may play in influencing the ability of MPAs to effectively protect populations of mobile species. Overall, our results suggest that, with effective enforcement, MPAs on the scale of the BIOT MPA potentially offer protection

to a variety of pelagic and reef species with a range of spatial ecologies. We suggest that animals need to be tagged across seasons, years, and ontogenetic stages, in order to fully characterize their spatial ecology, which is fundamental to developing and implementing effective MPAs to conserve the full life history of target species.

Keywords: spatial ecology, marine protected areas, coral reef, acoustic tag, satellite telemetry, conservation

INTRODUCTION

The need to effectively manage marine resources and ecosystems in the face of increasing human exploitation and climate change is one of the pressing conservation issues of our time. Marine protected areas (MPAs), areas where extractive activities are restricted or prohibited, have become an important tool to help resource managers conserve and protect marine ecosystems and resources. While the ability of MPAs to protect marine species will depend on many factors, including the location of the MPAs, the spatial ecology of species of interest, and the level of enforcement, MPAs have the potential to provide protection to many marine taxa, including mobile species such as sharks (Edgar et al., 2014; Ward-Paige, 2017; White et al., 2017; Speed et al., 2018). Due to their known and perceived conservation benefits, the number of MPAs has increased dramatically over the past five decades (Worm, 2017). The total area protected is accelerating even more rapidly, in particular due to an emphasis in recent years on the creation of very large MPAs, which typically encompass hundreds of thousands of square kilometers of remote, oceanic habitat, often enclosing entire reef or island systems (e.g., Phoenix Islands Protected Area, Pacific Remote Islands Marine National Monument, Rapa Nui Marine Park, and Pitcairn Islands Marine Reserve) (Letessier et al., 2017).

However, despite their increasing implementation, much remains unclear about how to best design MPAs to achieve specified goals, particularly that of protecting mobile marine taxa of management and conservation interest, which includes many teleost and chondrichthyan fishes (Sibert et al., 2012; Kaplan et al., 2014; Boerder et al., 2017). The movement patterns of mobile fishes can be complex and highly variable within and across species, with some transient species wandering over large areas (Meyer et al., 2009; O'Toole et al., 2011; Ferreira et al., 2015), while others exhibit various migration strategies (Block et al., 2011; Jaine et al., 2014) or ontogenetic shifts in habitat or space use (Dahlgren and Eggleston, 2000; Carlisle et al., 2015). Movement dynamics are a key consideration when planning spatial protection for these species. At the extremes, transient or highly migratory species (e.g., pelagic fishes and sharks) may not be amenable to full protection by even the largest MPA, whereas highly resident species (e.g., small reef fish) can be protected by MPAs at the scale of single reefs (Mumby et al., 2006; Mee et al., 2017), if there is appropriate enforcement of the MPA. Nevertheless, even for highly mobile species, appropriately designed MPAs have the capacity to protect key habitats that fulfill important ecological or life history needs for a species, such as reproduction or foraging (Runge et al., 2014; Hays et al., 2019).

While it is critical to fully describe the spatial ecology of taxa of conservation and management interest in order

to design effective MPAs, accurately quantifying the activity space of mobile teleost and chondrichthyan fishes remains challenging due to technological and logistical issues associated with accurately characterizing the movements and distributions of marine fishes. The use of electronic tags is one of the most common approaches to study their movements and spatial ecology (Arnold and Dewar, 2001; Block et al., 2011; Hussey et al., 2015). While advances in electronic tag technologies over the last several decades have greatly improved our understanding of the spatial ecology of fishes, each design has different limitations in terms of its capacity to describe the movements of fishes. Importantly, these technologies often have substantial error associated with positional estimates, though this varies across tag technologies (Teo et al., 2004; Kessel et al., 2014). This is particularly true in the case tags that use light-based geolocation to reconstruct tracks of tagged animals. This approach can have errors in latitude and longitude in excess of several degrees (Teo et al., 2004; Winship et al., 2012), which, depending upon the scale of the error and the size of the MPA, can bias inferences regarding the degree of protection provided by an MPA. On the other extreme, acoustic monitoring approaches can provide fine scale estimates of space use, but only provide information when tagged animals are within range of an acoustic receiver. One method to estimate space use from acoustic data is the use of Brownian Bridge models, which generate probability distributions for animal locations between successive detections based on conditional random walks between locations (Horne et al., 2007). This approach is increasingly being used to estimate patterns of space use from acoustic receiver arrays (Pagès et al., 2013; Becker et al., 2016; Acolas et al., 2017; Oh et al., 2017), though it is known to be sensitive to irregular detection records or large temporal gaps in detections (Horne et al., 2007; Pagès et al., 2013), which are common in acoustic tag data. One approach to mitigate these limitations is to use a combination of tagging technologies to evaluate the degree of protection conferred on mobile taxa by existing MPAs (Weng et al., 2005; Meyer et al., 2010; Carlisle et al., 2011; Papastamatiou et al., 2015; Drymon and Wells, 2017).

The British Indian Ocean Territory MPA (BIOT MPA) is one of the largest no-take MPAs in the world. Established in 2010, the BIOT MPA contains the islands and atolls of the Chagos Archipelago and extends out to the 200 nautical mile (nm) exclusive economic zone (EEZ), bringing the total MPA area to ~640,000 km² (Figure 1). The only resident human population in the BIOT MPA is based on Diego Garcia, in the south east of the MPA, where approximately 3,000 individuals support a joint United Kingdom–United States military base. Its remote location and low population density means that the MPA is relatively free from local anthropogenic effects (Sheppard et al., 2012)

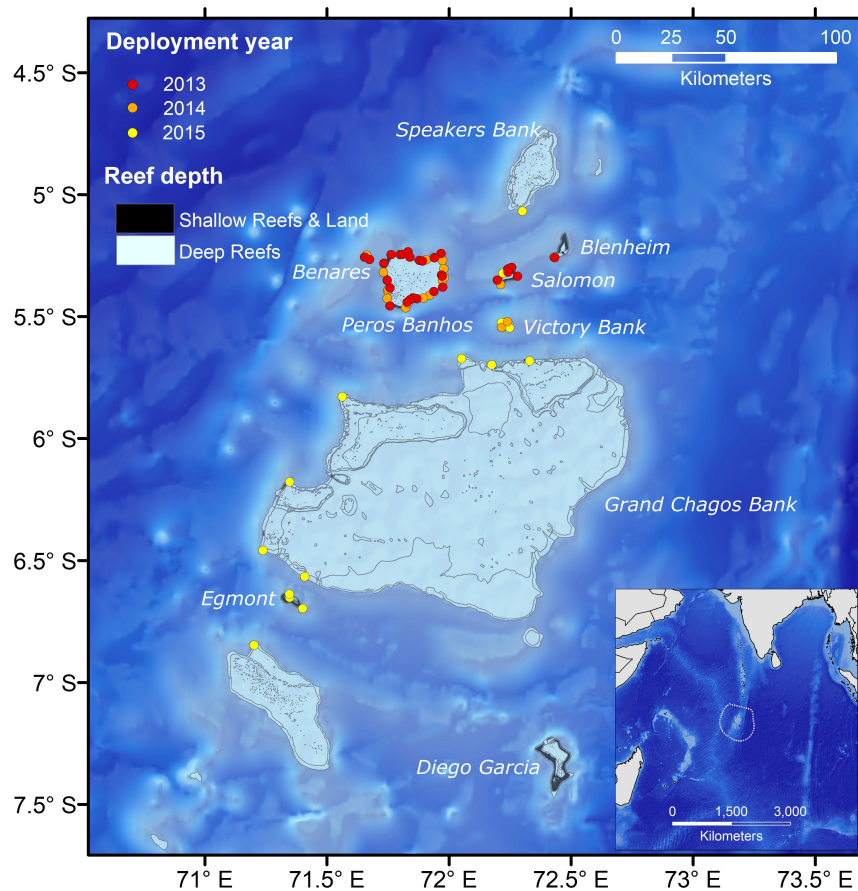


FIGURE 1 | Acoustic array in the BIOT MPA showing year of deployment for acoustic receivers. The inset shows the location of the BIOT MPA with the extent of the MPA being shown by the dotted line. Shallow reefs are $< \sim 20$ m, deep reefs are ~ 100 to 20 m in depth. Gray lines show contours of major submerged features. Note that there is little land in the archipelago.

and therefore boasts a relatively high reef fish biomass (Graham et al., 2013) and abundance of top predators (Graham and McClanahan, 2013). However, the MPA has been targeted by illegal, unreported and unregulated fishing (IUU) (IOTC-2015-WPEB11-48), predominantly by vessels from India and Sri Lanka fishing for sharks (Graham et al., 2010), a problem that continues to be a significant management concern (Ferretti et al., 2018; Tickler et al., 2019).

Since 2013, a research program has been working to better understand the ecology of the MPA, sponsored by the Bertarelli Programme in Marine Science¹ and supported by the United Kingdom Foreign and Commonwealth Office and British Indian Ocean Territory Administration. As part of this program, a variety of species of sharks and predatory fishes have been tagged with satellite and acoustic tags. These tags have not only provided information on the species' fine-scale spatial and temporal ecology, but also allowed us to investigate the ability of the BIOT MPA to effectively protect a range of pelagic and reef-associated teleost and chondrichthyan fishes. In this paper we estimate the activity space of seven mobile reef

and pelagic species in the BIOT MPA using a combination of electronic tag technologies, and present a preliminary assessment of the potential effectiveness of this MPA for their protection. We also describe several factors that influence the ability of electronic tags to fully describe the spatial ecology of mobile marine species, including choice of electronic tagging technology, study duration and, in the case of acoustic tagging, the design of the acoustic receiver array.

MATERIALS AND METHODS

Between 2013 and 2016, seven species of teleost and chondrichthyan fishes were tagged in the BIOT MPA with pop-up archival transmitting satellite tags (MiniPAT models 247A and 348A, Wildlife Computers, Redmond, WA United States), acoustic tags (VR16 coded tags, 69 kHz, transmission interval 30–90 s, Vemco, Halifax, Nova Scotia, Canada), or both. Pelagic species were tagged opportunistically and included Blue Marlin (*Makaira nigricans*), Sailfish (*Istiophorus platypterus*), Silky Sharks (*Carcharhinus falciformis*), and Yellowfin Tuna (*Thunnus albacares*). Reef species included Grey Reef Sharks

¹<https://marinescience.fondation-bertarelli.org/>

(*Carcharhinus amblyrhynchos*), Reef Mantas (*Manta alfredi*), and Silvertip Sharks (*Carcharhinus albimarginatus*). All sharks were caught from small boats using hand lines with barbless circle hooks. Billfish and tunas were caught on lures, with billfish tagged in the water alongside the boat. Reef Mantas were all tagged in the water by free divers. Except for larger sharks (>~1.5 m) which were kept in the water, all other animals were brought onto the boat and restrained, a seawater hose inserted into their mouth to irrigate the gills, and a wet cloth placed over their eyes. Once restrained, the animals were measured, tagged, and had tissue samples collected for genetic and stable isotope analyses.

Externally attached satellite tags were leadered with ~15 cm of 180 kg monofilament (Moimoi, Kobe, Japan), covered with a layer of Spectra and shrink wrap, and attached to a titanium dart. External tags were embedded in the dorsal musculature below the dorsal fin in sharks and fishes and off the midline of the posterior disc in Reef Mantas. For sharks, acoustic tags were implanted intraperitoneally through a small incision (~2–3 cm) just off the midline of their abdomen. Total handling time was generally less than 5 min. All procedures were approved by the Stanford University Administrative Panel on Laboratory Animal Care (APLAC) under permit APLAC-10765.

Satellite Tag Analysis

MiniPATs recorded temperature, depth, and light data for the duration of the tag deployments and detached after a user defined period of time and transmitted summaries of archived data sets to orbiting Argos receivers. Light data from MiniPATs were processed using the manufacturer's software (Wildlife Computers DAP Processor 3.0) and geolocations estimated following Teo et al. (2004). A Bayesian state space model (SSM) was used to generate the most probable track while quantifying the uncertainty associated with each daily position (Block et al., 2011; Winship et al., 2012). We saved the full posterior distribution of daily location estimates (20,000 estimates of position for each day) from the SSM for all tags for use in further analysis.

We used the Geospatial Modeling Environment version 0.7.3.0 (Beyer, 2012) to estimate 50% (core activity space) and 95% (total activity space) kernel utilization distributions (KUDs) for satellite tag tracks. To incorporate SSM model error into analysis of space use, we calculated KUDs for both the SSM track and the full posterior distribution of estimated positions used to generate the most probable SSM track (hereafter PD positions) (**Supplementary Figure S1**). The KUDs for the SSM tracks represent the least conservative (smallest) estimate of space use of the tagged animals, while the PD KUDs take into account SSM model error and represent the most conservative (largest) estimate of space use. For each tag we also calculated the proportion of the full dataset of PD positions that were inside the boundary of the BIOT MPA.

We analyzed the SSM tracks to investigate how long animals spent in areas of a given scale using residence time analysis (Barraquand and Benhamou, 2008), which is an extension of first passage time analysis (Johnson et al., 1992). Residence time analysis estimates the time an animal spends within a circle of a given radius centered on a given location, including travel time to and from that location. The animal is not considered to have left

the circle until it has spent more than a user defined maximum time threshold outside the circle, which we set to 1 day. We used that threshold because it would provide the most conservative (lowest) estimate of time spent in an area of a given radius, and would reduce the risk of overestimating duration of residency. Residence time analysis was implemented in R (version 3.4) using the package 'adehabitat' version 1.8.18 (Calenge, 2006).

Acoustic Receiver Array

An array of acoustic receivers, primarily comprised of VR2W receivers (Vemco Inc., Nova Scotia, Canada), was deployed around the BIOT MPA starting in 2013 and then expanded during 2014 and 2015 (**Figure 1**). VR2W acoustic receivers were attached to a subsurface mooring consisting of an anchor, three meters of polypropylene line, and a float. Due to permitting and diving regulations, receivers were predominantly placed on the fore reefs of the atolls between 15 and 20 m depth. The northern atolls (Benares Shoal, Peros Banhos, Salomon, Victory Bank) had the highest density of receivers as they were the geographic focus of the study, which over time expanded to cover a broader area of the archipelago. In 2013, 20 VR2W receivers were deployed around Peros Banhos, five at Salomon Atoll and three at Benares Shoals and Blenheim Reef. In subsequent years the array in the northern atolls was further expanded while the broader array was also extended to other areas of the archipelago. In 2014 and 2015, 36 additional VR2W units were added (22 in 2014; 14 in 2015) to include Victory Bank, Great Chagos Bank, Egmont Island, and Speakers Bank. Two VR4 Global units were also deployed in 2013 and four VR4 Underwater Monitors in 2014. Receivers were downloaded and serviced annually.

Acoustic Tag Analysis

Monthly KUDs were estimated for the acoustic tag data using a dynamic Brownian Bridge Movement Model (dBBMM) (Kranstauber et al., 2012) implemented in R statistical software version 3.3.1 using the package 'move' (Kranstauber et al., 2013). The dBBMM is an extension of the Brownian Bridge Movement Model (BBMM) which approximates the movement between consecutive data points using a conditional random walk, taking into account the distance and elapsed time between consecutive data points (Horne et al., 2007). A key parameter of this framework estimated from the data is the variance of Brownian motion (σ^2_m), which defines the animal's mobility along a path. Whereas the BBMM uses a constant σ^2_m along the entire movement path, the dBBMM allows the σ^2_m to vary along the path based on estimates within a sliding window providing a more precise estimate of the KUD by incorporating behavioral changes in the estimate of σ^2_m (Kranstauber et al., 2012). For each month of an animal's detection data, a 95% KUD was estimated using the dBBMM. Individual monthly polygons, starting with the first month of data, were incrementally overlaid and a union operation performed in order to investigate how the cumulative space (i.e., total area of the union at each time step) use increased over time.

The cumulative space use of individual animals over time changed following a sigmoid curve. We modeled this process to estimate total space use for each species and understand how monitoring time affects estimates of space use. We applied

non-linear mixed effect models to the monthly dBBMM KUD estimates. The non-linear model was a sigmoid model with three parameters

$$y(x) = \frac{\phi_1}{1 + e^{[(\phi_2 - x)/\phi_3]}}$$

where ϕ_1 is the asymptote, ϕ_2 is x at $\phi_1/2$ and ϕ_3 is a scale parameter. Initially, we tested a random effect (shark ID) for the three parameters. The analysis suggested that the inter-individual variation of ϕ_2 and ϕ_3 was marginal, and significant only on ϕ_1 , especially for Silvertip Sharks. Therefore, we eventually left the random effect only on $\phi_{1j[i]}$

$$\phi_{1j} \sim N(\mu_{\phi_3}, \sigma_{\phi_3}^2)$$

For $j = 1, \dots, J$, where J are individual sharks. Additionally, we tested whether the individual variation on the curve asymptote could be explained by changes in the size of the array, expressed by the minimum convex polygon (MCP) of the array receiver locations at any time in the study period (see section “Acoustic Receiver Array”), but the effect was not significant (**Supplementary Tables S1, S2**), so array size did not influence estimated patterns of space use. Before fitting the models we removed the individuals with less than five months of observations ($n = 33$ Grey Reefs and 21 Silvertips) and sharks with activity spaces greater than 800 km² (two Grey Reefs) as these emerged as outliers compared to all other individuals in the dataset. This left 26 Grey Reefs and 33 Silvertips for further analyses.

We used the duration of gaps in acoustic detection to estimate whether a shark could have left the BIOT MPA assuming a straight-line movement from location of the last detection before the gap toward the MPA boundary and then back to the location of the first detection after the gap. The distance from the center of the MPA to the boundary was ~450 km. Time intervals between consecutive detection events were combined with mean cruising swim speeds of both species (Ryan et al., 2015) to calculate the maximum distance an individual could have traveled. This was compared with the minimum round-trip distance from the starting point to the nearest part of the MPA boundary to the finish point. Where the computed swim distance exceeded the boundary round trip distance, it was determined that the shark theoretically could have left the MPA. The number and total time for all such events was summed by individual and species and compared with total monitoring period and total number of movement events.

Array Design Modeling

The ability of acoustic monitoring to describe the distribution of an acoustically tagged animal will be determined by how the spatial ecology of the animal overlaps with the acoustic array, hence array design fundamentally constrains the types of observations and questions that acoustic monitoring can be used to address (Clements et al., 2005; Heupel et al., 2006). Optimally, something is known about the spatial ecology of the species of interest which can guide the array design. However, often there is no *a priori* information on the patterns of space use of a

species of interest to guide array design, as obtaining that type of information is often a goal of these types of studies. Furthermore, once the data are collected from an acoustic receiver array, rarely are there any sensitivity analyses conducted to understand how array design might have influenced the results.

To investigate the effect of array design on different analyses of acoustic tag data (residency indices, gaps in detection, and dBBMM estimates), we investigated two aspects of receiver placement: receiver location (i.e., array size relative to tagging location), and array density (i.e., distance between adjacent receivers), by subsampling our existing dataset. For these analyses we used data from the densest part of the BIOT array in the northern atolls and banks at Peros Banhos, Benares Shoal, Salomon Atoll, and Victory Bank. Detection data for 2014 and 2015 were used, but only data from array elements present in the 2014 season were retained since all array elements deployed in 2014 were used over both years, providing a consistent baseline for our analyses. Shark tags with fewer than 30 days of detections were excluded ($n = 39$).

To investigate the effect of receiver distance relative to shark tagging location, a matrix of distances between shark tagging locations and receivers was produced using the function `dist()` in the package ‘*vegan*’. We used a Euclidean distance measure calculated on the matrix of individual shark tagging and receiver locations, and the mean residency index (days detected per total days monitored) of each shark at receivers 5, 10, 15, 20... 70 km from their tagging location was calculated, as well as a weighted average per species. The number of individual sharks of each species detected at increasing distances from their tagging location was also calculated. The probability of detecting a shark at different radii from tagging location was then modeled using a generalized linear model with a logit link function, with ‘successes’ being the number of tags of a species detected at a given distance and ‘failures’ the number of undetected tags based on the total tags for that species. An interaction between species, as a factor, and tagging location-receiver distance was used to test the hypothesis that Silvertip Sharks range further, on average, than Grey Reef Sharks.

To model the effect of array density on detection metrics (residency indices, gaps in detection), we filtered the detection data based on subsets of the existing receiver array. Subsets of receivers from the northern array were selected based on a minimum threshold distance between adjacent receivers, which was varied from 0 to a maximum of 20 km. At spacing greater than 20 km between receivers, the simulated arrays had too few elements to produce data that could be usefully analyzed. To generate the sub-arrays, a matrix of array distances was calculated using the function `dist()` in the package ‘*vegan*’ with a Euclidean distance measure as above. For each threshold distance, a random starting node in the array was chosen and the distance to the remaining receivers tested iteratively. On each iteration an additional receiver was added only if it was at least the threshold distance from all receivers previously selected. This process was repeated until no further receivers could be added to the subsampled array. The subsampling was repeated 1,000 times for each distance step, with duplicate sub-arrays discarded. This process generated a group of receiver sub-arrays that was

comprised only of receivers that were above a given threshold distance from each other. The raw detection data were filtered based on the subsampled arrays and the observed residency index and mean time interval between pairs of consecutive detections was calculated for each individual shark. Median and IQR of these metrics were then calculated for each array spacing.

We investigated the potential effect of array density on observed activity space using data from a Silvertip with a high overall residency, long monitoring period, and relatively high mobility (visiting 18 receivers). Sub-setting this shark's detection data for smaller/less dense arrays provides a reasonable indication of the effect of reduced receiver coverage on estimates of activity space. For each distance step, ten subsets of the array were randomly generated and used the distance based method described above, subject to the additional condition that they contained at least two of the receivers visited by the shark (the dBMM model requires at least two different locations in the data to make a UD estimate). The 95% KUD using the dBMM implementation described above was calculated for each iteration, and the mean and CI for each distance step plotted against array spacing.

We also evaluated the potential effect that the size of the array, in terms of receiver coverage relative to tagging location, had on dBMM 95% KUD estimates. We used data from nine Silvertip Sharks with relatively high residency (>33% of days) and which were detected at 8 or more receivers, in order to have enough data to model, and sequentially added data from receivers in order of their distance from a shark's tagging location. For each array iteration, we estimated the 95% KUD using dBMM as described above. Although we attempted the same analysis with Grey Reef Sharks, their high level of residency to often a single receiver made the analysis uninformative, and hence we analyzed data for Silvertip Sharks only.

RESULTS

Satellite Tagging

Twenty-six MiniPATs were deployed on six species in the BIOT MPA (Blue Marlin, Reef Mantas, Sailfish, Silky Shark, Silvertip Shark, and Yellowfin Tuna) between 2013 and 2016. (**Figure 2** and **Table 1**). Tags transmitted time series and summarized data sets of temperature, depth, and light to the Argos system. However, here we only report on patterns of horizontal space use in tagged animals. Deployment lengths ranged from 7 to 269 days (median 104.5, 23–180 days interquartile range, IQR).

Activity Space From Satellite Tags

Overall, activity spaces (50 and 95% KUDs) of the SSM tracks of tagged animals were much smaller than those estimated from the PD positions, and all KUDs were all much smaller than the area of the BIOT MPA (**Table 1**). All but one of the tagged animals remained within the BIOT MPA for the duration of the tag deployments (up to 269 days), even taking into account model error (**Figure 2** and **Table 1**). The median of all 95% KUDs of PD positions, the most conservative (largest) estimate of activity space, was 8.1% (6.6–11.3% IQR) the size of the MPA, whereas

for the 50% KUDs of PD positions it was 1.9% (1.6–2.2% IQR) (**Table 1**). A Silky Shark (6913001) was the only animal observed leaving the BIOT MPA. Over the course of the 86 days track, it remained in the vicinity of the archipelago for ~2 months before making a directed easterly movement to about 83°E, where it remained for several weeks. This shark had the largest activity space of any tagged animal, with a 95% KUD of the SSM track being 199,706 km² (~32% size of the BIOT MPA) and the 95% KUD of the PD positions being 433,086 km² (~69% size of the BIOT MPA). The other Silky Shark, which remained within the BIOT MPA around the archipelago for 269 days, used a much smaller area with 95% KUDs that were ~20–30% the size of its conspecific.

Based on the SSM tracks, Silvertip Sharks generally had larger activity spaces, about three times larger, than Reef Mantas. They also had much more variability in KUD estimates than Reef Mantas, which had narrower interquartile ranges for both 50 and 95% KUDs. Two Silvertip Sharks (3913008 and 3913010) had the longest tracks of the reef-associated species (**Table 1**). These two animals appeared to move across much of the archipelago, while the others all generally remained around the northern atolls, where they were tagged (**Figure 2** and **Table 1**). However, the tag attached to Silvertip Shark 3913008, which had the longest track and largest KUD, detached several km from the original tagging location. Reef Manta 5216006 was the only reef species that appeared to make an extended (~2 months, ~100 km offshore) pelagic excursion away from the archipelago though it returned to its tagging location (Egmont) prior to its tag detaching. Even considering uncertainty around the SSM tracks, based on distance between tagging location and pop-up location, Silvertip Sharks and Reef Mantas were moving between atolls, islands, and other features of the archipelago which are generally separated by distances < 20–40 km. This is supported by data from a Silvertip Shark that was double tagged with both acoustic and satellite tags. The animal was detected frequently on the receivers while the satellite tag was attached, allowing the mean daily position obtained by acoustic detections to be compared directly with the estimated SSM positions. The difference between daily SSM positions and the mean daily location derived from acoustic detections differed by less than 0.25 degrees of longitude or latitude, approximately 25 km at the latitude of the BIOT MPA (**Supplementary Figure S2**). This provides some evidence that our SSM positions were relatively accurate, and also suggests that the double tagged shark was moving within a relatively tight radius of the reefs, even when not detected by receivers.

Residence time analysis suggested that reef-associated species and some pelagic species exhibit a high degree of residency in areas much smaller than the size of the BIOT MPA (**Figure 3**), which is consistent with activity space estimates for pelagic and reef species. Reef Mantas exhibited the highest degree of residency, spending extended periods of time in areas with radii 5–25% that of the MPA. Silvertip Sharks were generally less resident (spent less time) in areas of a given radius relative to Reef Mantas, exhibiting wider ranging, more directed movements. Sailfish were the most residential pelagic fish, spending extended periods of time in areas much smaller than the BIOT MPA.

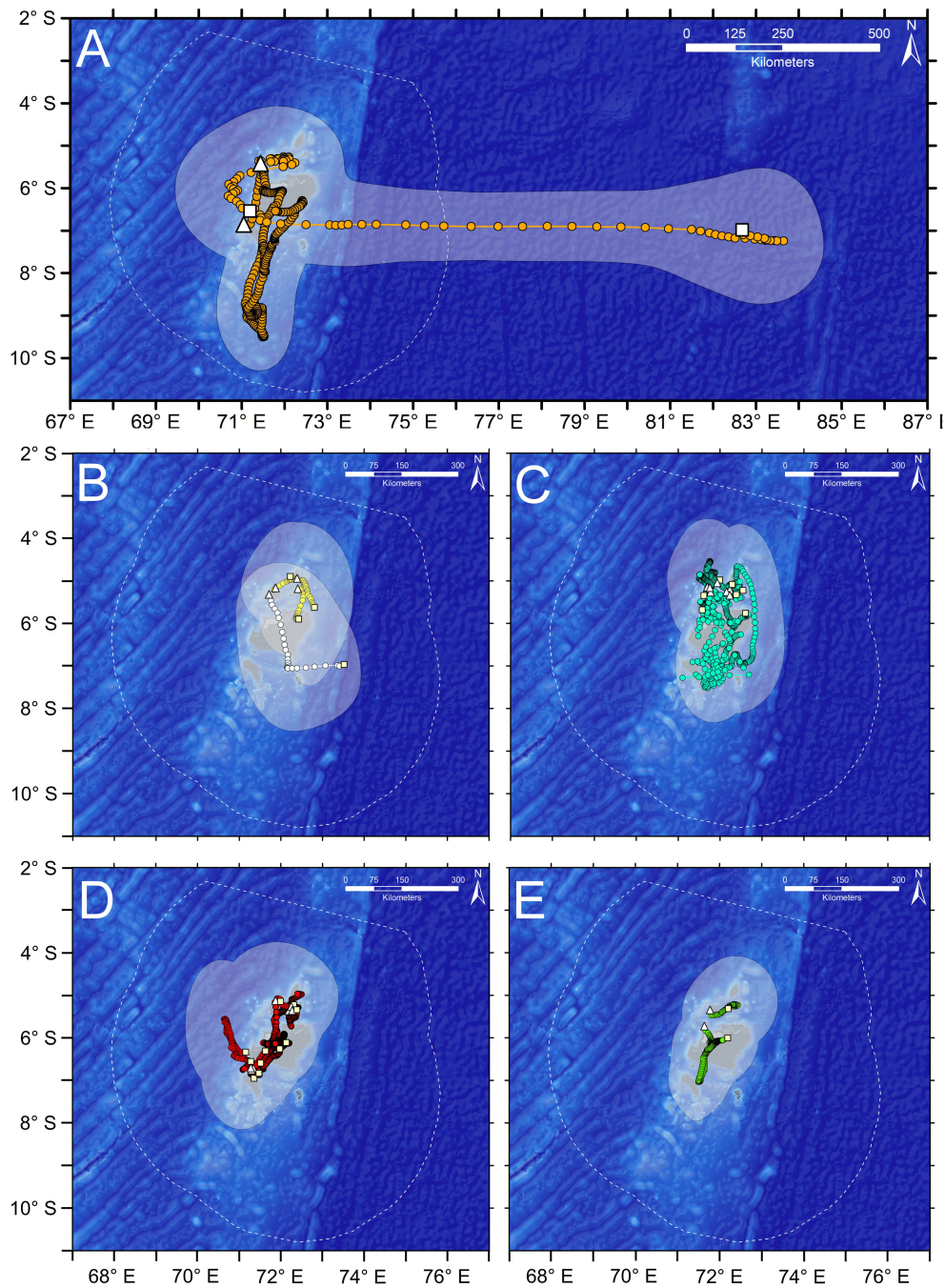


FIGURE 2 | State space model tracks, and 95% KUD (shaded polygon) of full posterior distribution of estimated positions from SSM model for satellite-tagged pelagic fishes and elasmobranchs in BIOT MPA. Tagging location is indicated with the white triangle, pop-up position with white square. Boundary of the BIOT MPA is shown with the dotted white line. **(A)** Silky Sharks (SKY, $n = 2$), **(B)** Blue Marlin (BLM, white, $n = 1$) and Yellowfin Tuna (YFT, yellow, $n = 3$), **(C)** Silvertip Sharks (STP, $n = 7$), **(D)** Reef Mantas (MAN, $n = 11$), and **(E)** Sailfish (SAI, $n = 2$).

Yellowfin Tuna and Blue Marlin exhibited directed movements and were less resident although animals were only tracked for very short periods of time (<26 days). The two Silky Sharks showed completely different patterns, with one spending ~200 days in an area with a radius ~80% the size of the MPA and the other being the only animal to be observed leaving the BIOT

MPA, having very low residency across all spatial scales. While caution should be used when interpreting these results as they are based on modeled tracks, we believe that the relative differences in residency patterns are generally valid, as even modeled tracks are able to distinguish between directed movements and more residential behaviors.

TABLE 1 | Activity space of fishes and elasmobranchs tagged with satellite tags (miniPATs) in BIOT MPA.

Sp.	ID	Date	Size (cm)	Sex	Track length (km)	Pop-off distance (km)	Track duration (days)	Prog. duration (days)	Tr. 50% KUD (km ²)	Tr. 95% KUD (km ²)	PD. 50% KUD (km ²)	PD. 95% KUD (km ²)	Tr. 50% % MPA	Tr. 95% KUD % MPA	PD. 50% KUD % MPA	PD. 95% KUD % MPA
YFT	1113005	3/15/2013	100	U	75	73	12	180	224	890	12,583	55,476	0.04	0.14	2.00	8.81
YFT	1113006	3/15/2013	99	U	112	58	26	180	200	1,023	12,912	76,711	0.03	0.16	2.05	12.18
YFT	1113007	3/15/2013	108	U	177	40	14	180	339	1,739	10,331	41,680	0.05	0.28	1.64	6.62
BLM	5516002	4/16/2016	U	U	409	303	23	180	6,750	28,773	26,686	114,012	2.29	0.42	4.24	18.11
SKY	6913001	2/12/2013	194	U	2350	1152	86	180	49,669	199,706	77,930	433,086	7.89	31.71	12.38	68.78
SKY	6913002	3/21/2013	195	F	1488	43	269	270	11,248	38,641	34,532	120,256	1.79	6.14	5.48	19.10
SAI	7013007	3/19/2013	225	U	414	44	184	180	643	3,121	10,232	52,838	0.10	0.50	1.62	8.39
SAI	7016001	3/24/2016	220	U	126	41	50	180	141	667	11,551	51,361	0.02	0.11	1.83	8.16
STP	3913008	2/12/2013	155	U	3113	4	180	180	9,037	35,191	13,058	62,386	1.44	5.59	2.07	9.91
STP	3913010	3/16/2013	134	M	567	111	105	270	6,648	24,884	23,438	94,191	1.06	3.95	3.72	14.96
STP	3913014	3/12/2013	134	U	291	87	116	180	733	2,879	12,728	50,632	0.12	0.46	2.02	8.04
STP	3913033	3/22/2013	124	U	267	4	104	180	761	2,864	12,711	52,600	0.12	0.45	2.02	8.35
STP	3914008	3/24/2014	161	F	178	298	121	120	178	734	7,706	28,647	0.03	0.12	1.22	4.55
STP	3914016	3/25/2014	133	F	196	59	108	180	183	691	9,213	36,759	0.03	0.11	1.46	5.84
STP	3914018	3/27/2014	150	F	204	58	101	180	686	3,287	12,528	49,465	0.11	0.52	1.99	7.86
MAN	5213001	2/13/2013	290	U	549	15	180	180	1,090	4,761	9,964	41,618	0.17	0.76	1.58	6.61
MAN	5214001	3/30/2014	250*	U	45	28	7	180	11	53	10,552	47,721	0.00	0.01	1.68	7.58
MAN	5214002	3/30/2014	250*	U	88	89	7	120	105	398	10,372	45,698	0.02	0.06	1.65	7.26
MAN	5215003	3/25/2015	250*	U	171	76	157	180	74	440	7,910	30,329	0.01	0.07	1.26	4.82
MAN	5215014	3/29/2015	250*	U	103	4	14	180	323	1,097	14,149	74,177	0.05	0.17	2.25	11.78
MAN	5216006	3/29/2016	250*	F	369	28	89	240	1,090	3,807	18,285	77,110	0.17	0.60	2.90	12.25
MAN	5216007	3/29/2016	250*	U	103	50	17	180	23	152	11,751	53,965	0.00	0.02	1.87	8.57
MAN	5216008	3/29/2016	250*	U	249	22	149	180	306	955	9,088	34,985	0.05	0.15	1.44	5.56
MAN	5216017	4/14/2016	250*	F	466	4	254	270	1,597	5,738	13,747	49,719	0.25	0.91	2.18	7.90
MAN	5216018	4/15/2016	250*	U	262	6	180	180	281	1,140	9,099	35,830	0.04	0.18	1.44	5.69
MAN	5216025	2/16/2016	250*	F	145	92	182	180	16	170	7,458	27,951	0.00	0.03	1.18	4.44

Size is TL for sharks, DW for mantas, and CFL for teleosts. Area of each tag's 50% (core activity space) and 95% (total activity space) kernel utilization distributions (KUDs) are shown for modeled SSM tracks (Tr) as well as for full posterior distribution (PD.) of estimated positions from SSM model. KUD % MPA columns show the (%) of the different KUDs relative to the area of the BIOT MPA (~630,000 km²). YFT, Yellowfin Tuna; BLM, Blue Marlin; SKY, Silky Shark; SAI, Sailfish; STP, Silvertip Shark; MAN, Reef Manta. * Estimated DW.

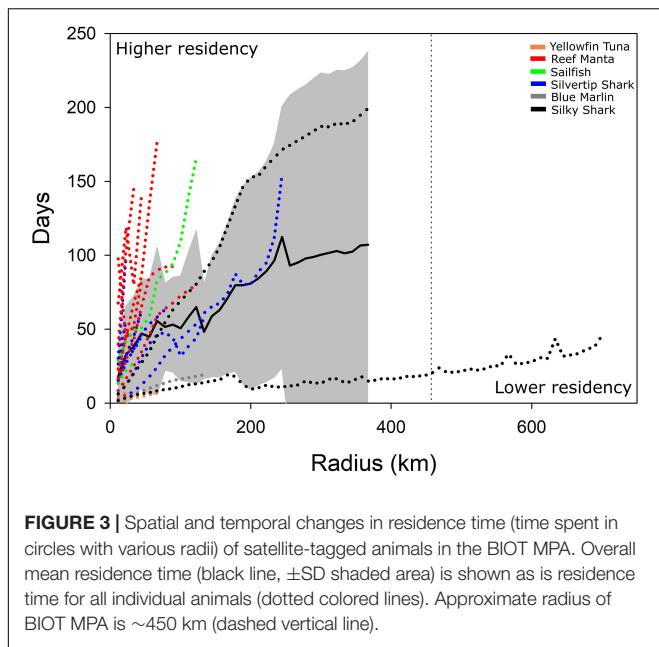


FIGURE 3 | Spatial and temporal changes in residence time (time spent in circles with various radii) of satellite-tagged animals in the BIOT MPA. Overall mean residence time (black line, \pm SD shaded area) is shown as is residence time for all individual animals (dotted colored lines). Approximate radius of BIOT MPA is \sim 450 km (dashed vertical line).

Acoustic Tagging

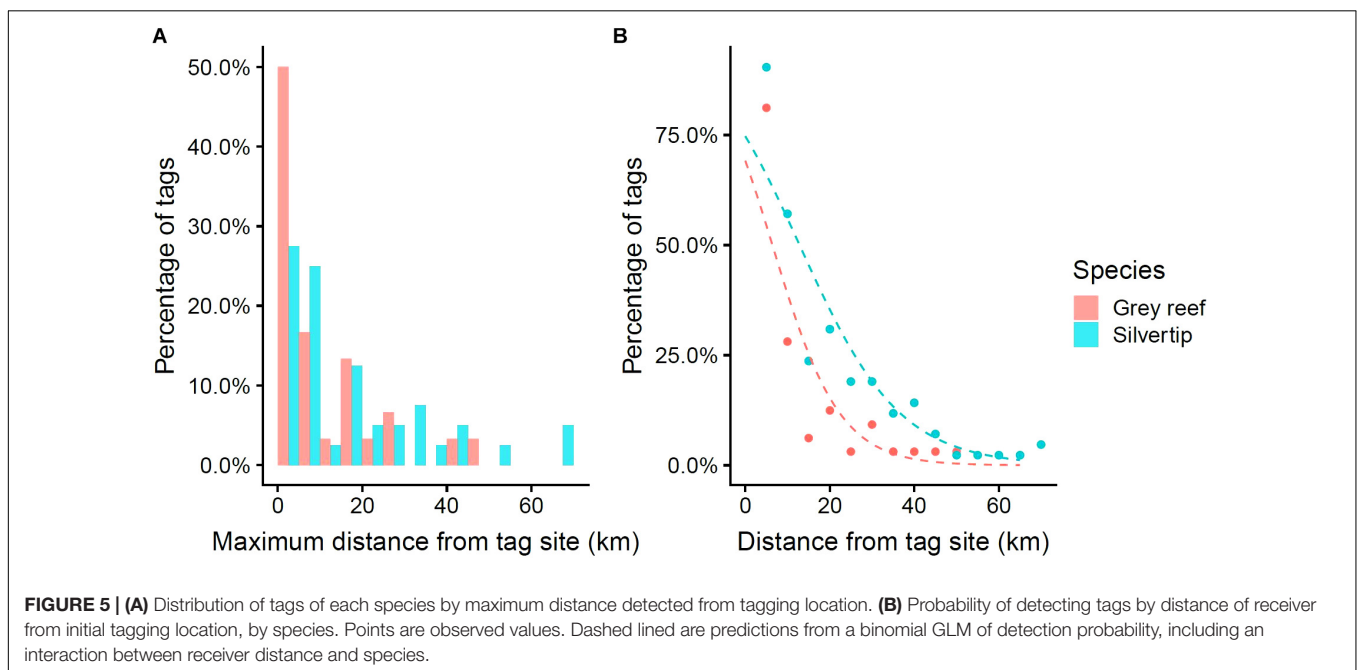
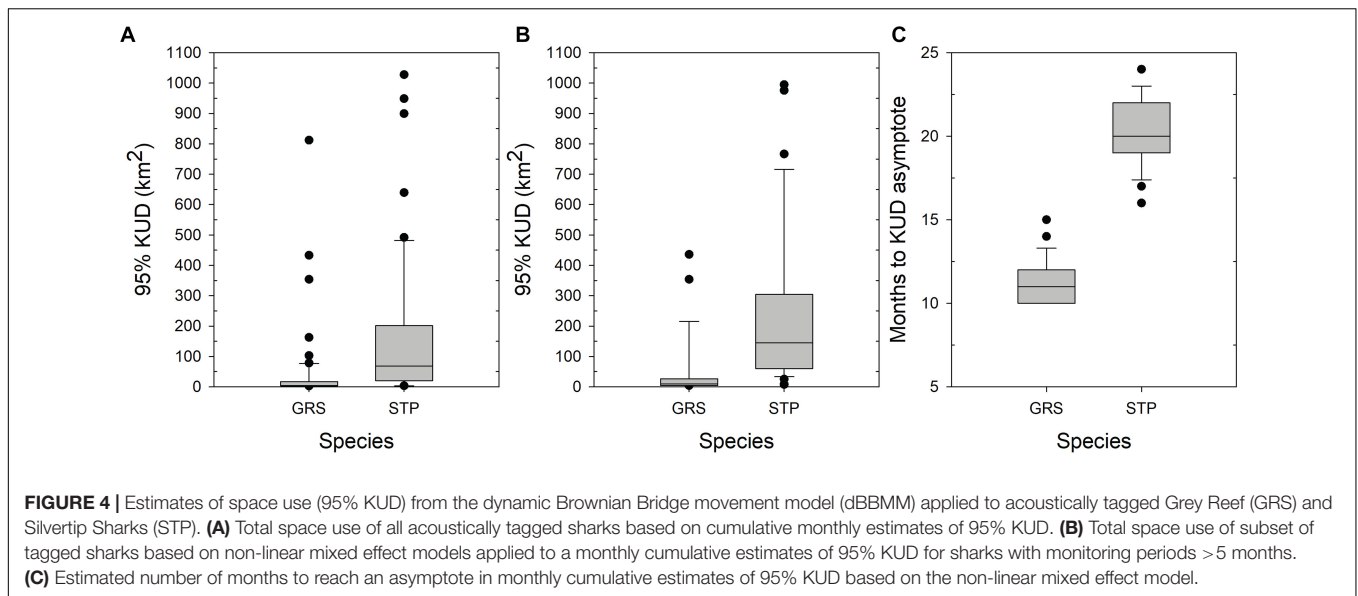
A total of 121 Grey Reef and Silvertip Sharks were acoustically tagged and monitored from February 2013 to March 2016 (Table 2). Our tagging of Grey Reef Sharks was biased toward females but had an even mix of mature and immature animals (Last and Stevens, 2009), whereas Silvertips had a relatively equal representation between the sexes but were primarily immature animals (Last and Stevens, 2009). Cumulative 95% KUDs were estimated for 61 Grey Reef Sharks (mean TL 112.7 cm \pm 17.4 SD) and 60 Silvertip Sharks (mean TL 121.9 cm \pm 22.4 SD). Animals tagged in 2013 were monitored for up to a maximum of 40 months (Grey Reef: maximum 1,197 days, Silvertip: 1,122 days), while animals tagged later in the study had shorter monitoring periods.

Dynamic Brownian Bridge Movement Model estimates of space use based on cumulative monthly 95% KUD estimates for the full data sets of Grey Reef and Silvertip Sharks were roughly half the size of those of the subsets of animals used in the non-linear mixed effects model, reflecting shorter tracks with more restricted movements across the array (Table 2 and Figure 4). Based on the cumulative dBBMM, Grey Reef Sharks used in the model ($n = 26$) had a median space use of 8.3 km² (3.7–38.1 IQR, mean 50.4 km² \pm 107.2 SD), whereas for all Grey Reef Sharks ($n = 61$) it was 4.5 km² (2.8–17.3 IQR, mean 41.4 km² \pm 124.4 SD). On average the tagged Grey Reef Sharks reached this level of space use after approximately 11 months (median, 10.0–12.0 IQR) (Figure 4). Silvertip Sharks used in the model ($n = 33$) had a median cumulative 95% KUD of 134.4 km² (74.4–333.2 IQR, mean 278.6 km² \pm 331.7 SD), while for all tagged Silvertips ($n = 60$) it was 68.8 km² (20.3–201.4 IQR, mean 170.1 km² \pm 274.6 SD), which was reached after approximately 20 months (19.0–22.0 IQR) (Figure 4). For the subset of sharks used in the non-linear mixed effects model, the estimated space use from the model was consistent with

TABLE 2 | Metadata and median and interquartile range (IQR) 95% KUD estimates for acoustically tagged Grey Reef (GRS) and Silvertip (STP) Sharks based on the dynamic Brownian Bridge movement model (dBBMM).

Species	n	Sex (F/M/U)	TL (cm)			Monitoring time (days)			# Detections			BB 95% KUD (km ²)			Mod. 95% KUD (km ²)			Months to asymptote		
			Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR
GRS (Model)	26	16/7/4	111.5	104.8–125.0	408.0	348.8–746.0	7828.5	4127.5–12124.0	8.3	3.7–38.1	10.0	4.3–26.9	11.0	10.0–12.0	na	na	na	na	na	na
GRS (All)	61	41/17/3	110.0	103.5–124.5	255.0	92.5–426.0	1042.0	190.0–6822.0	4.5	3.7–17.3	na	na	na	na	na	na	na	na	na	na
STP (Model)	33	14/16/3	119.0	108.5–131.5	492.0	315.5–710.5	1587.0	718.0–5386.5	134.4	74.4–333.2	144.7	60.4–304.5	20.0	19.0–22.0	na	na	na	na	na	na
STP (All)	60	29/25/6	117.0	107.2–130.2	347.5	220.2–626.0	726.0	419.8–2129.5	68.8	20.3–201.4	na	na	na	na	na	na	na	na	na	na

95% KUD shows space use estimates based on the dBBMM, whereas Mod. 95% KUD shows estimated space use based on a non-linear mixed effect models applied to the cumulative monthly dBBMM KUD estimates for individual sharks. Note that a subset of data were used in the model (tracks > 5 months). The non-linear mixed effect model also estimated time it takes to reach an asymptote in cumulative monthly dBBMM estimates (Months to asymptote). For animals used in the mixed effect model, we present the modeled KUD estimates as well as the dBBMM estimate for the entire dataset for those individual sharks.

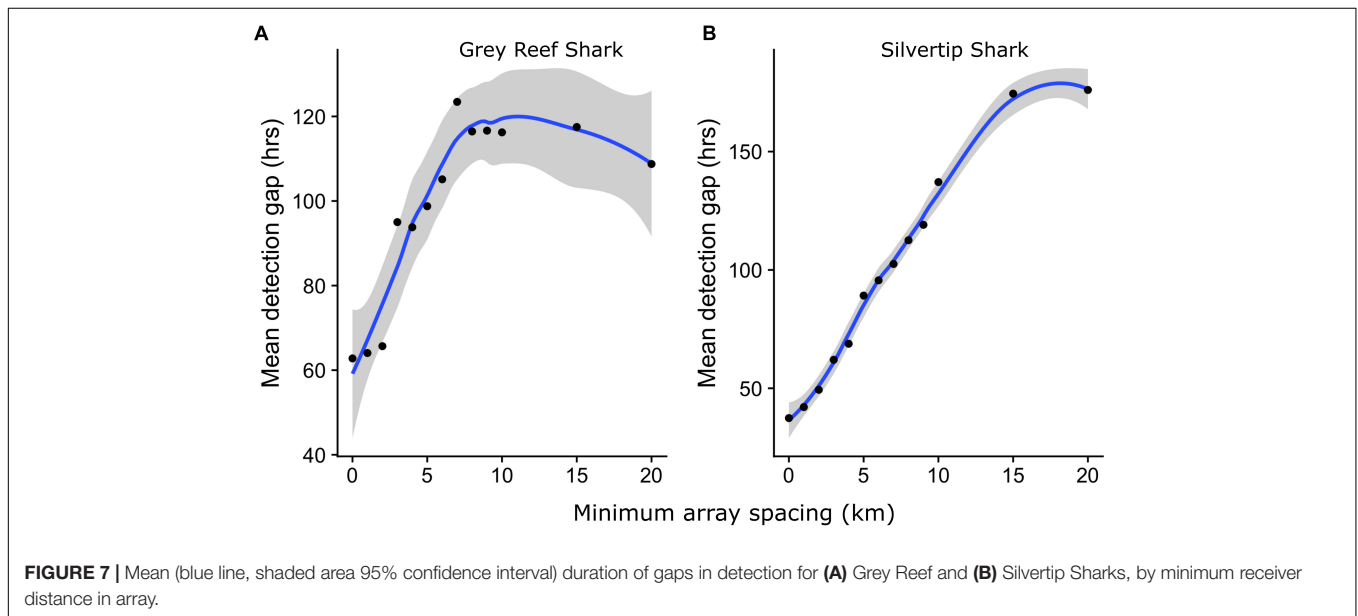
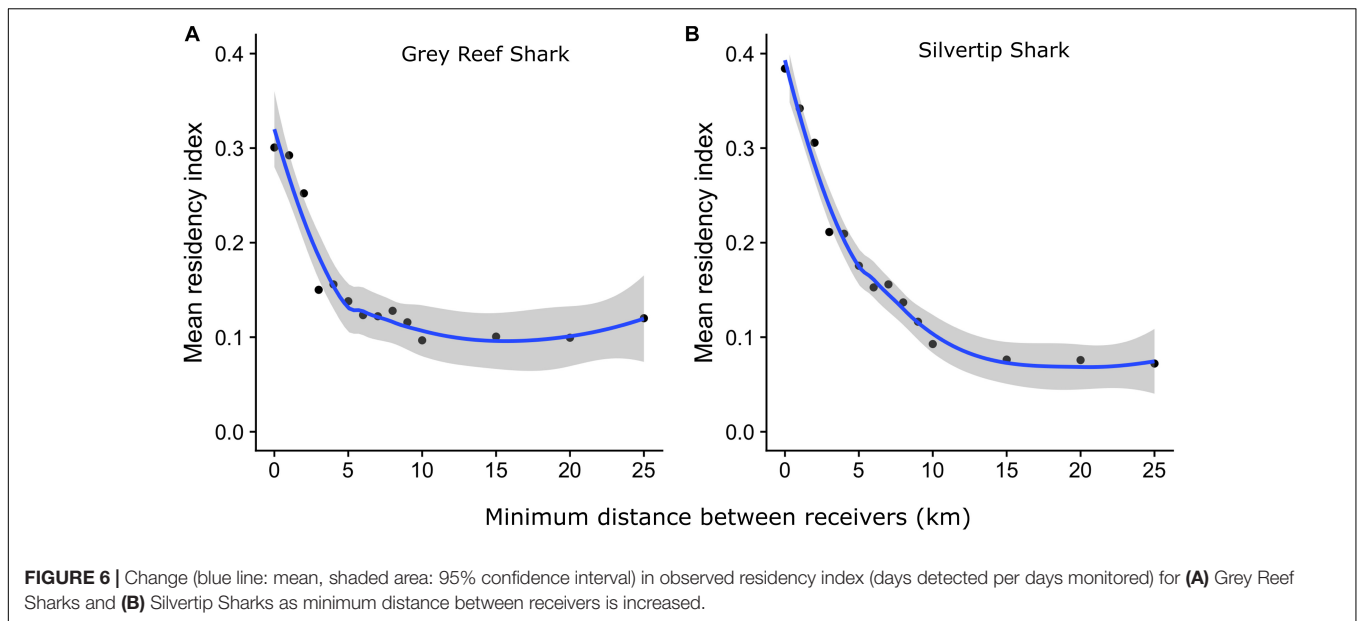


estimates from the cumulative dBBM for all tagged sharks (Table 2). Both species exhibited a high degree of intraspecific variability in space use.

Based on the duration of the gaps in detection and average swimming speed of both species, 52% of the acoustically tagged Grey Reef Sharks and 78% of the Silvertip Sharks could have left the BIOT MPA during gaps in detection (Supplementary Table S4). Of the sharks that potentially left the MPA, on average they had 2–3 gaps of sufficient duration (>7–8 days) to allow them to have potentially crossed the MPA boundary and returned. This does not indicate that sharks actually left the BIOT MPA, just that they theoretically could have under the least conservative scenario (swimming straight to the MPA boundary).

Array Spacing Simulations

Grey reef and Silvertip Sharks both showed a steep decline in detection probability with distance from their tagging site, with the effect more pronounced for Grey Reef Sharks. The maximum distance recorded in a Grey Reef Shark was 45 km, but over half of the animals were never detected more than 5 km from their tagging site. Silvertips on the other hand roamed further afield, with 70% traveling more than 5 km from their tagging site, visiting an average of 6.5 sites each versus 3.3 for Grey Reefs ($t = 3.316, p < 0.001$), and moving up to 70 km from their original location (Figure 5). The odds of detecting a Grey Reef Shark 5 km from its tagging site was three times that of detecting it at 10 km. The probability of Silvertip Shark detection declined more

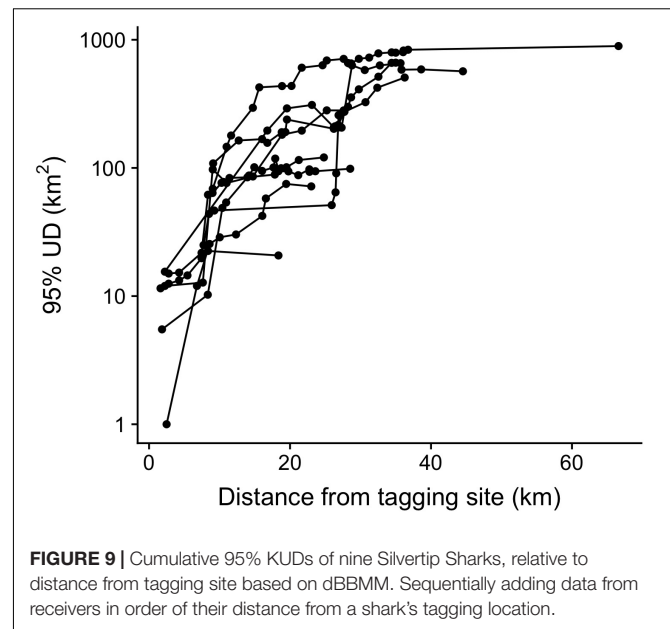
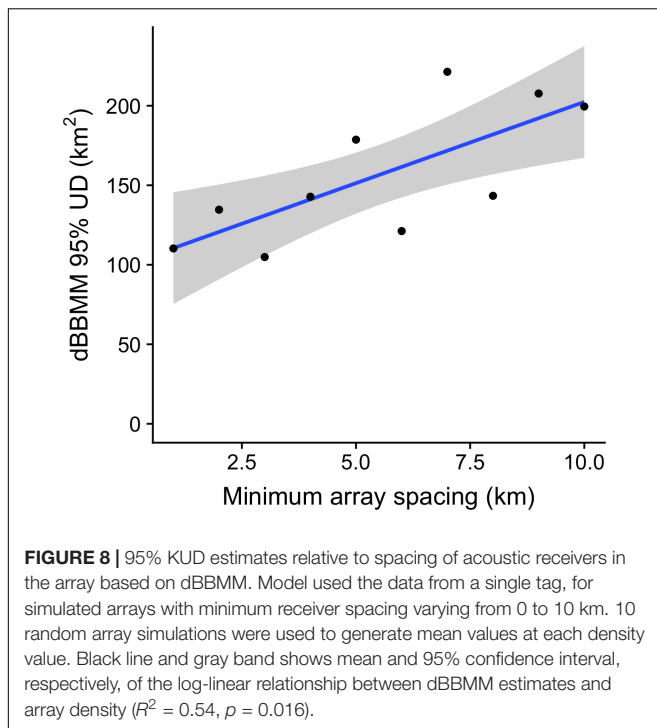


slowly with distance, with detection at 5 km only 1.5 times that at 10 km (**Figure 5**). A binomial generalized linear model (GLM) found a significant interaction between species and tagging-site-to-receiver distance, with the probability of detection remaining consistently higher for Silvertips with increasing distance (**Supplementary Table S3**). The probability of detecting individuals of both species declined with distance away from the tagging site, but detection probability declined more gradually for Silvertips (**Figure 5** and **Supplementary Table S3**).

When we modeled the effect of decreasing array density by subsampling the receiver array based on minimum distance thresholds, the residency index of both species declined with increasing separation of the receivers (**Figure 6**). Consistent with the species-specific relationships between detection probability and tagging-site-to-receiver distance reported above, Grey Reef

Sharks showed a greater sensitivity to array spacing than Silvertips, although observed residency and tag detection declined to similar levels for both once receiver spacing exceeded 10–15 km and this plateau was reached earlier in Grey Reef Sharks than Silvertips.

The mean duration of gaps in detection increased with increasing receiver separation for both species (**Figure 7**). The mean duration of gaps in detection increased sharply for Grey Reef Sharks as the spacing between receivers increased, plateauing at around 120 h in arrays with 10 km receiver spacing. The mean detection gap for Silvertips increased more slowly and plateaued once receiver spacing exceeded 15 km. Since acoustic telemetry provides presence-only data, such gaps represent blind spots in our monitoring of animals. Dynamic Brownian Bridge Movement Models attempt to fill in these gaps



by assuming that animals follow a conditional random walk (a random walk between known starting and ending positions) between subsequent detections. However, the randomness of a movement increases with detection gap length, all other things being equal, as the animal has more time to wander and so certainty over where it might go decreases. We tested the effect of reduced receiver coverage on the activity space estimates generated by a dBBMM, by generating KUD estimates for detections within different sub-arrays for a single shark with high baseline residency and broad use of the receiver network. 95% KUD estimates increased with receiver separation (Figure 8), consistent with the increase in detection gap length (Figure 7) and reduction in number of total detections (Supplementary Figure S3).

Finally, we looked at the role of receiver coverage, relative to tagging location, in influencing KUD estimates derived by dBBMM. KUD estimates for a subset of Silvertip Sharks increased as receivers were added to the area around their tagging site, up to a distance of approximately 30 km whereupon data from additional receivers made little difference to KUD estimates (Figure 9). This is consistent with the overall pattern of Silvertip Sharks which showed that the majority of animals were only ever detected within 30 km of their tagging site (Figure 4A).

DISCUSSION

Electronic tagging of pelagic and reef species in the BIOT MPA suggests that the MPA is large enough to provide significant spatial protection to marine species with diverse spatial ecologies, and that even some highly mobile pelagic species may spend extended periods within its borders. This result was

consistent across all approaches, and did not change even when incorporating the error associated with different tag technologies. Hence, with effective enforcement, MPAs on the scale of the BIOT MPA potentially offer considerable protection to a range of pelagic and reef species. However, intraspecific variability in movement dynamics suggests that, in particular for pelagic species, only a portion of a given population may be sufficiently resident within an MPA to benefit from protection, with the most mobile individuals, or life history stages, remaining vulnerable to fishing outside of the MPA boundaries, regardless of the size of the MPA. However, our ability to fully characterize the full space use of animals in the BIOT MPA is hindered by limitations that are typical of electronic tagging studies, including low sample size, limited deployment duration, acoustic receiver coverage, and a limited ability to tag both sexes across ontogenetic stages and seasons.

While sample size and deployment duration were limited for all pelagic animals in this remote archipelago, tagging data provided evidence that even some highly mobile pelagic species may derive some protection from the BIOT MPA. A Silky Shark was the only animal observed outside the boundaries of the BIOT MPA, even accounting for significant error in estimated positions, and the areas used by all other tagged pelagic animals, based on all metrics, were much smaller than the size the BIOT MPA. Some pelagic species spent extended periods of time within the BIOT MPA as well. For example, Sailfish spent the duration of their tag deployments within the BIOT MPA (up to 180 days), consistent with other studies showing that they are more abundant around islands, reefs, and other neritic habitats, relative to other pelagic species (Nakamura, 1985). This suggests a higher degree of residency around neritic habitats, and that this species should be more amenable to protection by large MPAs that enclose such features.

Satellite tagging demonstrated that MPAs on the scale of the BIOT MPA are large enough to provide protection to mobile reef

species (Silvertips and Reef Mantas). All tagged Silvertips and Reef Mantas spent the duration of their satellite tag deployments within the boundary of the BIOT MPA, had high residency estimates for areas much smaller than the MPA, and had activity spaces smaller than pelagic species and much smaller than the area of the BIOT MPA. While a pelagic Silky Shark was observed leaving the MPA, a Reef Manta was the only satellite-tagged reef-associated species to exhibit a potential pelagic excursion away from the archipelago. It is unclear whether or not this apparent movement was a result of SSM error, however, the estimated location error (~ 60 km) during the offshore movement was less than the minimum distance to land at its furthest point (~ 100 km), suggesting the offshore movement was real. However, the manta returned to the tagging location (Egmont Atoll) prior to the tag popping up, suggesting that if it did move offshore then it had some degree of fidelity to that site.

Intraspecific Variability in Space Use

Our results demonstrate that intraspecific variability in spatial ecology can impact the ability of MPAs to protect both pelagic and reef species. While there are populations or sub-populations of teleosts and elasmobranchs that show high fidelity to oceanic archipelagos, particularly isolated ones such as the BIOT MPA (Cowen et al., 2000; Planes et al., 2009), even reef-associated species such as reef sharks often display some degree of large scale dispersal or movements (Whitney et al., 2012; Chin et al., 2013; White et al., 2017). These large scale movements outside the MPAs boundary can expose them to fishing, which often is focused around MPA boundaries to take advantage of 'spillover' effects (Kellner et al., 2007; Boerder et al., 2017). Both satellite and acoustic tags demonstrated that intraspecific variability in space use will affect the ability of large MPAs, like the BIOT MPA, to protect all individuals of a species. For example, the two Silky Sharks tagged in this study displayed completely different patterns of residency within the MPA, despite being a similar size (~ 2 m): one spent the entire 270-day deployment within the BIOT MPA, while the other one was the only tagged animal to be observed leaving the MPA (Figures 2, 3). Even amongst reef-associated species, individual activity spaces could vary by orders of magnitude. The high degree of intraspecific variability in activity space for Silvertip Sharks based on acoustic and satellite tag data suggests vulnerability to fishing outside MPAs, especially for MPAs of smaller scale, may vary significantly within a population. Reef Mantas, due to their smaller activity spaces and lower intra-specific variability (Table 1), may be more amenable to protection at smaller spatial scales compared to Silvertip Sharks.

Importance of Study Duration

For reef-associated species, or pelagic species that exhibit some degree of association with atolls, reefs, or other bathymetric features, acoustic tags and arrays can provide insight into their space use. One major benefit of acoustic tags is that tag batteries can last > 10 years, meaning that data from monitored animals can provide insight into changes in activity space across years and ontogenetic stages. This approach would offer a more complete understanding of the activity space of these

species, as well as provide the opportunity to estimate their full activity space, or home range. Using cumulative dBBMM KUDs we were able to show that estimates of activity space are sensitive to study duration, and that the time required for space use estimates to reach an asymptote is species dependent, and variable across individuals. Grey Reef Sharks required at least 11 months of acoustic monitoring before KUD estimates approached an asymptote. For Silvertips this period was 20 months, reflecting their higher mobility and lower residency to individual reefs. However, the sample size, skewed sex ratio for Grey Reef Sharks, skewed size distribution in Silvertip Sharks, and current study duration limited our ability to evaluate longer term changes related to ontogeny and sex. Continued monitoring should start to reveal ontogenetic changes in activity space, and begin to outline the actual full home range of individual animals, loosely defined as "the area traversed by the individual in its normal activities of food gathering, mating and caring for young" (Burt, 1943). These results show the necessity of maintaining acoustic monitoring infrastructure over extended periods if reliable estimate of species' activity spaces are to be achieved.

Effect of Array Design

To provide insight into how receiver spacing influences the ability of our acoustic receiver array to characterize the space use of species with different spatial ecologies, we modeled the hypothetical impact of different array designs by varying the minimum distance between receiver elements in subsets of the real array, treating our actual array and full dataset as the baseline. Movement and residency metrics calculated on the resulting detection data subsets from arrays of different receiver densities were compared with baseline results, by species, and showed clear inter-specific differences in the impact of array design choices, which were related to differences in species spatial ecology. Consistent with the activity space analysis discussed above, Grey Reef Sharks generally showed higher site fidelity and dispersed shorter distances from their tagging sites, with over half the individuals never detected more than 5 km from their original location. While these limited movements are consistent with prior studies of Grey Reef Sharks (Bond et al., 2012; Vianna et al., 2013; Espinoza et al., 2015), our study was biased toward females, which have been reported to exhibit a higher degree of site fidelity than males (Espinoza et al., 2015), suggesting that we may be underestimating space use for the Grey Reef Shark population in the BIOT MPA. Silvertips were further ranging, with 70% traveling more than 5 km from their tagging site and sharks being detected up to 70 km from their original tagging location.

Residency indices were sensitive to reductions in array density (increased spacing between receivers). Residency indices declined to 30% of baseline values once spacing exceeded 5 km for Grey Reef Sharks and 10 km for Silvertips, suggesting that residency estimates for both species are biased downward in sparse receiver arrays. The shape of the curves suggests that our baseline metrics, and acoustic receiver array, may also underestimate true residency since both increase sharply as receiver spacing is reduced and reached a maximum of between 0.3 and 0.4 for both species.

The length of gaps between detections also increases with the distance between receivers, an intuitive finding that has the potential to bias space estimates obtained using Brownian Bridge based methods that seek to overcome the “presence only” nature of acoustic telemetry data. This is potentially important, for during extended gaps with no detection, we are unable to evaluate whether an animal could have left the MPA boundaries or was simply outside the detection range of the receivers. However, our results suggest that overall our tagged animals had relatively few gaps long enough (>7–8 days) for them to leave the MPA under the least conservative scenarios (straight line movement to MPA boundaries and back). Importantly, satellite tag data indicated that no Silvertips left the MPA, so extended gaps in the acoustic detection record for this species (and Grey Reef Sharks as well) likely do not indicate that sharks left the MPA. Thus, the MPA can potentially provide significant conservation value for mobile reef and pelagic fishes. However, the efficacy of any MPA is also largely dependent on effective enforcement (Edgar et al., 2014). In the case of the BIOT MPA, IUU (Ferretti et al., 2018; Tickler et al., 2019) and drifting fish aggregation devices (dFADs) (Davies et al., 2017) still pose significant management concerns within the MPA boundary.

Using dBMM to estimate space use for a single Silvertip Shark, which exhibited a high degree of residency to the array but which moved widely within the array, we found that 95% KUD estimates increased as array spacing was reduced, with estimates showing a high degree of variability between different receiver sub-arrays. Furthermore, using data from a subset of Silvertips, we demonstrate that increasing the size of the array in terms of distance from tagging location increases 95% KUD dBMM estimates. However, we found that extending the array to distances beyond ~30 km from tagging location did not have a large effect on 95% KUD estimates for Silvertip Sharks. dBMMs using acoustic telemetry data appear highly sensitive to the size, location and number of elements in the array generating the detection data, and extended and irregular gaps in detections. Hence, any inferences about space use will likely be heavily biased by the interaction between the tagging location and home range of an individual sharks and the size and density of the array. This calls into question the reliability of these techniques for estimating home range from aquatic acoustic data sets that are inherently irregular in periodicity, as opposed to the terrestrial tracking data for which they were developed (Horne et al., 2007). However, our results do indicate that relative differences between species, within a given array, can be detected. This is useful information for management, even if the absolute values of the home range estimates are likely a consequence, in part, of how the model data were collected.

Consistent with previous studies (Bond et al., 2012; Vianna et al., 2013; Espinoza et al., 2015), the movements of individual Grey Reef Sharks are much more restricted than Silvertips, hence a denser, smaller array (maximum receiver spacing 1–5 km) will provide better estimates of space use for Grey Reef Sharks than for Silvertips, which require a larger array (maximum spacing 1–10 km) to capture their wider ranging movements. Hence, in areas with similar habitat types as this study (series of coral reef atolls and submerged shoals in relatively close proximity),

having smaller, more dense receiver arrays will provide more robust estimates of space use than would ones that are less dense but geographically more expansive. Furthermore, tagging should occur near the center of the receiver array in order to optimize the efficiency of the receiver array. We suggest that tagging locations be identified prior to deployment of the array if working in larger scale atolls or reef systems or if that is not possible to attempt to tag within the center of the array. Based on our data, an array that extends further than 20 km or 30 km from the tagging location will provide little added value for Silvertips and Grey Reef Sharks, respectively, though how applicable this result is to these species in other parts of their distribution remains to be tested.

Overall, our array modeling exercise demonstrates how array design can affect common estimates of space use derived from acoustic receiver data and how this sensitivity will be driven by the underlying spatial ecology of the study species. In most acoustic tagging studies, data are analyzed and interpreted without directly assessing how the array design may be influencing the results. Our results suggest that sensitivity analyses, similar to what we have done, should be conducted to understand how array design may be influencing the results and interpretations. These types of analyses can provide valuable insight into what the data are and are not able to reliably tell you, and can provide useful insight into the spatial ecology of the species as well.

Other Methodological Considerations

Electronic tagging remains one of the best ways to understand the spatial ecology of mobile marine fishes, however, there are important limitations to this approach. Due to logistical challenges, expense of tags, and battery and tag retention limitations, it can be challenging to use electronic tags to fully characterize the space use of mobile marine taxa. Tags are generally applied to animals that can be caught and tagged, which often leads to particular size classes and ontogenetic stages being studied (Hazen et al., 2012). In order to fully characterize the home range of a species and understand the ability of MPAs to provide protection to a given population, the space use of animals of all life history stages needs to be characterized and understood. Ontogenetic shifts in habitat are ubiquitous in the natural world, including in teleosts and chondrichthyan fishes (Grubbs, 2010). As a result, the habitats used and space required by juveniles will be very different than that of adults, affecting their vulnerability to different stressors (e.g., fishing pressure). Tagging can also be limited to times or seasons when animals are available for study, or by whether field work can occur, leading to seasonal bias in tagging, which will affect our understanding of species movement dynamics and vulnerability to different sources of mortality.

Even if the full activity space of a species has been characterized, this information may not capture the full ecological requirements of a species within an MPA. Stable isotope analysis suggests that Grey Reef Sharks at Palmyra Atoll in the Pacific may receive a substantial trophic subsidy from offshore pelagic ecosystems outside of the MPA, whether through movements of the sharks or their prey (McCauley et al., 2012b; White et al., 2017). Seabirds return to colonies on islands and atolls and fertilize local ecosystems with resources from distant

pelagic habitats (McCauley et al., 2012a). Other isolated oceanic habitats, such as seamounts, also may require trophic subsidies to support populations of large, upper trophic level predators (Koslow, 1997). Hence, factors from outside the boundary of an MPA can still affect the ecosystem function and ecology of species within an MPA through cross-system trophic linkages and subsidies (Curnick et al., 2019). Hence, these potential linkages need to be characterized and understood to understand how an MPA, and the species it supports, fits into the broader regional and oceanic context.

Logistical and financial challenges associated with electronic tagging in a remote location, tag attachment, and the difficulty of finding and tagging species on short expeditions make it difficult to fully characterize seasonal, interannual, or longer term (decadal or ontogenetic) changes in animal behaviors. Hence to fully characterize the space use of these animals, and to understand how effective MPAs of various sizes will be at protecting them across their full life history, there must be significant investment in long term studies that are able to capture the full temporal and spatial dynamics of monitored populations. This is important as fully characterizing the spatial ecology of marine species, and understanding its variability, is a prerequisite for designing effective MPAs able to protect animal populations occurring within their boundaries. Yet MPAs are often designed and implemented without having access to or considering this type of information. However, by fully characterizing the spatial ecology of marine species, and understanding its variability, it should be possible to design MPAs that confer protection on a meaningful proportion of the population, thus achieving the desired conservation outcomes. This suggests that, if properly enforced, the expansion of very large oceanic MPAs that has occurred over the last decade should provide effective protection to local populations of mobile reef-associated species as well as several pelagic species that exhibit the necessary degree of site fidelity. However, our results demonstrate that to develop effective science-based conservation and management strategies that account for the spatial ecology of a mobile marine species requires sustained investment in research that uses technologies and study designs that are able to fully account for the intraspecific diversity in movement patterns across sexes and ontogeny.

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DATA AVAILABILITY

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

All procedures were approved by the Stanford University Administrative Panel on Laboratory Animal Care (APLAC) under permit APLAC-10765.

AUTHOR CONTRIBUTIONS

AC, DT, JD, FF, DC, TC, RS, MC, and BB contributed to the design and implementation of the research. AC, DT, JD, and FF collected, processed, and analyzed the data and wrote the manuscript. DC, TC, RS, MC, and BB collected data and helped to writing the manuscript.

FUNDING

Funding for this project was provided by the Bertarelli Foundation and contributed to the Bertarelli Programme in Marine Science.

ACKNOWLEDGMENTS

We would like to thank the United Kingdom Foreign and Commonwealth Office and the British Indian Ocean Territory Administration for granting us permission to undertake the research.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00256/full#supplementary-material>

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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